The dynamics of disturbed Mexican pine-oak forest: A modelling approach

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Thesis submitted in fulfilment of the requirements for Doctor of Philosophy

University of Edinburgh

2001

Abstract

Description of a case study site is combined with computer based simulation in order to develop a model of the dynamics of disturbed pine-oak forest in Southern Mexico. Contemporary ecological theory surrounding the problem of predicting forest dynamics is briefly reviewed. A conceptual framework for the study is presented based on a consideration of the forest as a whole system. Data provided by a forest inventory are subjected to spatially explicit multivariate analysis. This reveals both simple spatial patterns of species distribution and high local variability in forest structure and composition. Initial results of monitoring temporal change in permanent sample plots are analysed and an estimate of forest productivity produced. Slash and burn farming is proposed as causing the disturbance which has shaped the documented pattern. Mortality of trees caused by a recent forest fire is summarised using logistic regression models. The rate of recolonisation and the persistence of trees by resprouting following disturbance is documented, both in burned areas and areas used for temporary slash and burn agriculture. Multivariate analysis is used to reveal trends in species composition in abandoned slash and burn sites. Non parametric techniques for estimating species richness and species-area relationships are subjected to a critical analysis when applied to the problem of comparing the diversity of woody species in slash and burn sites and closed forest. The human decision making process associated with slash and burn clearance is described and modelled using Bayesian networks which synthesise indigenous knowledge of the system. A critical review of individual based forest models (IBMs) introduces the simulation approach to studying the dynamics of the disturbed forest. An IBM is programmed and paramaterised using data obtained from the site. Measurements of tree growth rings and canopy light permeability are incorporated in the model. The model is validated against the inventory data. It is then used to investigate a series of scenarios based on changes in usage patterns. The model suggests that whole system level behaviour may be predictable, although patch scale variability is high. A simplified cellular automaton interactive landscape model is derived from the IBM and used to investigate the process of the spread of pines over a disturbed landscape.

Finally an integrative conceptual model of pine-oak dynamics is presented which summarises both observations and simulation studies. The conceptual model presents the forest as a shifting mosaic of patches and suggests that a number of different, but predictable responses to disturbance may be expected. Pine-oak forest is a resilient forest type, but may have replaced a more species rich assemblage as a result of disturbance. Contemporary patterns of use may be leading to chronic degradation of the forest's productive capacity. The implications of the model for sustainable management and conservation of this forest type are discussed.

Acknowledgements

This work was supported by European Community grant ERBIC-18CT97-0146 to the project SUCRE (Sustainable use, Conservation and Restoration of Native forests) under the INCO programme for Scientific and Technological Cooperation with the Developing Countries.

Without the support provided by Adrian Newton this work would not have been possible. Thanks also go to Colin Legg who provided insightful comments regarding vegetation, statistics and modelling matters.

My greatest debt of gratitude is owed to the entire community of Santa Rita Sonora whose help and tolerance made the fieldwork possible. Invaluable assistance in the field came from Jose Luis Santiz-Gomez of Sonora who also provided accommodation and friendship.

Many colleagues and students in El Colegio de La Frontera Sur contributed their thoughts and experience. I am especially grateful to Mario González-Espinosa for his patience and support, Neptali Ramírez-Marcial for stimulating debates regarding the ecology of the local vegetation, Pedro Quintana Ascencio for help with mathematical matters and Miguel Martínez-Ico for his encyclopaedic knowledge of the flora of Chiapas and the Ecosur herbarium which allowed specimens to be quickly identified. Special thanks also go to the Edinburgh University student Johana Pulli for help with fieldwork during her visit.

Thanks go to my parents for their patience during the final stages of completing the work.

Finally, this thesis could not have been written without the inspiration of my son Michael and his mother Adriana Fortolís to whom it is dedicated.

Contents

Introduction

The montane pine-oak forests of Chiapas are a unique vegetation type. While falling within a broad classification of mixed broadleaf/needleleaf forest (WCMC 1997) that is normally associated with mid latitudes, they are essentially tropical forests with a canopy dominated by temperate genera. Their understorey contains a mixture of species of both tropical and temperate origin (Miranda 1952; Breedlove 1981). Branches and trunks support vascular epiphytes including orchids, bromeliads and epiphytic cacti. Annual fluctuations in mean temperature are lower than the diurnal range. Growth is reduced in winter months not by low temperatures and low light, but by limited water availability. The pattern of anthropogenic disturbance of Southern Mexican forests is quite unlike that found in regions where planned resource use has replaced subsistence farming. In order to draw on information generated by research in other areas tools need to be found which enable suitable comparisons to be made, while avoiding inappropriate analogies.

Pine-oak forest in the state of Chiapas: Southern Mexico

The widespread abundance of pines and oaks and their importance as timber trees has led to a wealth of literature concerning the properties and dynamic of a range of different pine, oak or pine-oak forests. While pine and hardwood stands tend to be spatially segregated at northern latitudes (Desponts and Payette 1993; Richardson 1998) mixed forests of pines and broadleaved species become increasingly frequent in warmer southern areas (Cowell 1995; Schwartz 1994; Farjon 1996).

Forest, woodland and woodland fragments with canopies consisting of an intimate mixture of pine and oak are an integral part of the landscape of the highlands of Chiapas in Southern Mexico (Miranda 1952; Breedlove 1981). The composition and structural attributes of this unique type of tropical montane (1400- 2600 m a.s.l.) vegetation have been influenced by centuries of disturbance by the indigenous Mayan population of the region (Collier 1975). In recent years tree cover has declined and become increasingly fragmented (Gonzalez-Espinosa *et al.* 1991; Gonzalez-Espinosa *et al.* 1995; De Jong *et al.* 1999; Ochoa-Gaona and Gonzalez-Espinosa 2000). Remaining forests are vulnerable to degradation and alteration in their structure and composition. Changes in species composition are linked to changes in usage patterns (Gonzalez-Espinosa *et al.* 1991, Quintana Ascencio and Gonzalez-Espinosa

1993; Ramírez-Marcial, Gonzalez-Espinosa and García-Moya. 1996). Concern has been expressed that an extensive and irreversible spread of pines within these montane forests may be taking place (Gonzalez-Espinosa *et al.* 1997). Because pine dominated forests contain fewer understorey species than oak forest (Rzedowski 1991; Gonzalez-Espinosa *et al.* 1997) the change could be threatening the rich regional floristic diversity (Gonzalez-Espinosa *et al.* 1995; Ramírez-Marcial, Gonzalez-Espinosa and García-Moya 1996).

From the perspective of the rural population of forest users, pine–oak forests have three principal roles, each of which is associated with a particular form of anthropogenic impact. They provide timber, fuelwood and ecological services. Species composition is the critical factor that determines the ability of pine-oak forest to meet the demands placed on it.

Pine timber is used locally for construction and carpentry. Sale of pine timber is one of the few available sources of income for some rural communities. The long term future of pine timber production in the highlands relies completely on the natural regeneration of existing stocks. Although regulations are in place to prevent over extraction, concern has been expressed regarding both the efficacy of current legal restrictions and the extent to which they are respected (Montoya-Gomez 1995a; Montoya-Gomez 1995b). Timber companies have traditionally paid small stumpage fees to indigenous communities in return for permission to cut pine timber. Initiatives to encourage community forestry have had little impact to date, although the experience of neighbouring states is more encouraging.

The rural population relies exclusively on fuel wood for cooking and heating (Gonzalez-Espinosa *et al.* 1995). Oaks provide dense slow burning wood and are therefore an essential resource for all subsistence farming communities. Although resinous pine wood is used for starting fires, pine burns rapidly and is not a preferred domestic fuel. Fuelwood collection has been assumed to be an important cause of deforestation, particularly of oak dominated forest (Montoya-Gomez, 1995a). Initiatives to increase efficiency of use have been promoted as means of conserving forest stocks.

The most important ecological services provided by the forest are hydrological buffering and nutrient cycling. These forest functions have been particularly important in sustaining subsistence agriculture. Slash and burn maize farming known as *milpa* has traditionally been a cyclical activity that has disturbed the forest and initiated secondary stand development (Collier 1975; Pool-Novelo 1997). Under this system trees played an essential role in restoring the productive potential of sites following temporary maize cultivation. Broad leafed species such as oaks with comparatively rapidly decaying leaves may have been particularly valuable in nutrient cycling. The increase in the human population has led to intensification of agriculture. Contemporary slash and burn is now more commonly associated with permanent deforestation, particularly when milpa is combined with grazing.

In addition to the disturbance associated with these three principal types of usage, unplanned fires and chronic stress caused by grazing must be included in the list of factors responsible for forest change. Yet despite human impact these forests have maintained a greater degree of structural and functional diversity than many comparable temperate systems (Breedlove 1973). This has occurred without documented formal management. Social and economic forces are now rapidly altering the pattern of land use. The long term consequences of novel scenarios are unknown. There is a need to develop tools that may predict the impact of this change.

The role of ecological theory and models in the study of forest dynamics

Natural forests are complex phenomena that show complex, often non-linear, dynamics over long time scales. Predicting forest change from an ecological perspective thus involves confronting a unique set of challenges. While general ecological theory provides the conceptual framework for addressing such complexity, concepts alone do not predict the behaviour of ecological phenomena (Ford 2000). Rules linking concepts such as ecosystem structure and function (Vitousek and Hooper 1993) or diversity and stability (May 1973) have been sought. However general theories that provide an operational basis for predicting the behaviour of ecological systems have remained illusive (Simberloff 1981; Peters 1991; Schrader-Frechette and McCoy 1993; Ford 2000 although see Huston 1979; Grime 1979; Huston 1994 and Hubbell in press).

A particular difficulty in the application of ecological theory to the study of forest change arose from the historical development of vegetation science. The approach of Clements (1916), which suggested a fundamental predictability from holistic principles, was influential in forming the vocabulary used to describe vegetation processes. Yet Clements' concepts were criticised from their inception as leading to over generalised statements which failed to emphasise linkages between pattern and process (Watt 1947). Detailed, species or site specific, information seems to be necessary in order to build effective predictive models representing the behaviour of complex vegetation systems (Gleason 1917; Tansley 1935;

Gleason 1939). Later commentators and reviewers continued to raise fundamental objections and present counter examples which eroded the credibility of Clements' orderly concept of predictable successional change (Drury and Nisbet 1973; Picket 1976; Connell and Slatyer 1977; Peet and Christensen 1980; McIntosh 1981). The legacy of this early debate has been a historical tendency towards semantic and conceptual confusion (McIntosh 1985). Terms such as *climax* communities fell into disuse while descriptors such as *primary* and *secondary* forest, which are associated with a linear view of succession and a particular type of disturbance, continued to be freely used, particularly in studies aimed at producing vegetation classifications. Vegetation classifications are useful tools for communication, but may provide a static view of a dynamic system. There was a need for models that could clarify and unify concepts.

To a large degree the unification needed for understanding changing forests has come about through simulation modelling and systems based approaches. When vegetation is viewed as a dynamic system, the artificial division between individualistic and holistic views can be replaced by a coherent synthesis. This recognises that apparent contradictions are rather easily resolved once clarity in defining the scale at which processes are perceived is achieved (O'Neill 1989; Allen and Starr 1982; Allen and Hookstra 1994). Contemporary approaches to modelling vegetation processes use Gleason's individualistic perspective as an operational tool for small scale prediction while using broader generalisations where appropriate at larger scales (Shugart and O'Neill 1979; Acevedo Urban and Ablan 1995; Huston 1994; Bazzaz 1996; Shugart 1998; Urban Acevedo and Garman 1999). It is now usually assumed that detailed contextual knowledge is required in order to predict changes in species composition (Grubb 1992). However, there is still a need to extract generality from case studies, to find common patterns that can be linked to repeated processes (Levin 1992; Shugart 1998). This can only be achieved when simplifications are found which reduce complexity to tractable levels at larger scales (Botkin 1993b). The search for appropriate models linking site specific data to more general principles and observations underlies the work presented in this thesis. The approach adopted has been not been to attempt to directly test competing theories regarding succession or forest change. Instead observations and simulations have been combined in the search for an operational model of the dynamics of disturbed pine-oak forest in the highlands of Chiapas. Contemporary concepts concerning linkages between scales have been used as an underlying unifying framework.

The formation of generalised statements from the study of the details of a phenomenon requires taking a systematic approach. Caswell (1976) defines a *system* as "a collection of entities which influence each others behaviour". Under this definition a subset of interacting entities taken from an otherwise intractably complex system can itself form a system. Such a system, which has been deliberately simplified in order to gain understanding, may be called a *model* (Grimm 1994). In order to build an *ecological model*, conceptual connections are maintained between a simplified system and a natural phenomenon of interest (Ford 2000). The desirability of retaining an explicit link between the real and simplified system suggests that the most appropriate use of models is often as a complement to manipulative experiments designed to test the predictions of conceptual simplifications of the real system (Krebs 1988; Krebs 1991; Underwood 1997). Unfortunately, given the temporal scale of forest change, an experimental approach is rarely practical. This leads to some well recognised operational and epistemological challenges (Ford 2000). Computer based simulations provide a means of studying conceptual models, but they should not become a substitute for empirical investigation (Hall 1988; Peters 1991). The key to effective use of computer simulation for ecological modelling may lie in ensuring that study of the model does not become separated from the study of the system on which it is based (Hall 1988; Grimm 1994; Ford 2000). Models can be assessed by their ability to make predictions, but the most useful model predictions are not untestable statements about some future system state. If predictions that are consistent with observed phenomena are derived from assumptions regarding underlying processes, progress in understanding the phenomena as a system has been made.

A systems approach to forest change

<u>The components of the system: People and trees</u>

In order to simplify a complex system it must first be analysed and its key components recognised (Caswell 1988). The contemporary human impact on terrestrial ecosystems may have artificially simplified the task of identifying the most important component of change in many forest systems. Forests would cover the landscape of Chiapas in the absence of human intervention (Rzedowski 1991). Yet less than half the land area of the highlands is now forested (De Jong *et al.* 1999). Predicting real life change in such a situation may seem to involve predicting rates of deforestation (e.g. Poore 1989). Models that predict deforestation use knowledge drawn from sociological and political studies, but often draw a comparatively small amount of input from the discipline of forest ecology. However both the questions asked and the answers provided by ecologically oriented studies of forest systems could have very direct connections with real life problems. Even when reduced to a minimal level of complexity, a system comprising people and trees is subtle and unpredictable. Deforestation is not the only possible outcome of interactions between them. Forests change through use in multiple ways. As a consequence forest users change their pattern of exploitation. The feedbacks that occur can cause unexpected spatial and temporal patterns. Models in which trees and people are interacting elements of a single system can address some of the most interesting and relevant contemporary questions. This raises particular challenges. Ecological understanding alone is insufficient to predict the behaviour of the system. Knowledge of the link between human decision making and natural forest dynamics is required.

The dynamic: Disturbance and responses to disturbance.

In exploited forests that are otherwise unmanaged, disturbance is the most noticeable form of interaction between people and trees. Sousa (1984) provides a definition of disturbance that is especially useful in the context of forest systems. A *disturbance* is "*a discrete, punctuated killing, displacement or damaging of one or more individuals that directly or indirectly creates an opportunity for new individuals to become established*". Disturbance can be an integral part of a forest system and does not necessarily cause a change in its normal functioning (although see Forman and Godron 1986 for a contrasting definition of disturbance which directly contradicts this statement).

Disturbance can be associated with a wide range of dynamic behaviour. A traditional linear view of successional change has been avoided as a conceptual base for this study. Instead ideas drawn from systems theory have been used in the interpretation of field observations and simulation results. Some terminology taken from system theory may be useful when referring to a forest's response to disturbance at a generalised level. Pimm (1991) defines *resilience* as a measure of "*how fast a variable that has been displaced from equilibrium returns to it*". Because equilibrium may be difficult to recognise, resilience will be used to refer to a variable's tendency to return to any state and may also be used when a holistic perspective of the system is adopted. When viewed at appropriate scale resilience results in fluctuations around a point of attraction. A resilient system may thus be in *dynamic equilibrium* (Huston 1994). *Stability* (Holling 1973) may only be apparent as an emergent property at a large scale. Even mature, apparently stable forest systems show dynamic rather than static equilibria when viewed from certain perspectives (Huston 1979). If little or no change in a variable or a system occurs as a result of a potential disturbance then it is *resistant*. Resistance may also be referred to as *inertia* (Westman 1978). Where a variable or a key system process suffers a gradual reduction in its value the system may be *degrading*. A disturbance, which reaches some threshold level, may *flip* the system from one equilibria or dynamic equilibria to another (Scheffer *et al.* 1995). Such a flip may also be referred to as a *collapse* if it precludes any return to a former, usually desirable, state.

Anthropogenic disturbance can undoubtedly often lead to the complete collapse of forest function. Deforestation occurs either intentionally or unintentionally as a result of human action. Many neotropical forests are declining in extent as a result of human intervention (Hecht 1993; Fearnside 1997). Mexican forests are being lost at a particularly rapid rate (Sohn, Moran and Gurri 1999; Trejo and Dirzo 2000). The contemporary deforestation rate in some municipalities of the highlands of Chiapas may be between 2 and 4% per year (Ochoa-Gaona and Gonzalez-Espinosa 2000). However deforestation is not the only possible consequence of use. The importance of both recent and historical human disturbance in shaping the structural attributes of forested land previously referred to as "*pristine*" is now widely recognised (Sprugel 1991; Attiwill 1994). High levels of disturbance inevitably lead to a change in at least a subset of forest attributes. Damage associated with disturbance may cause nutrient loss, soil compaction and erosion. Removal of timber causes mechanical damage to non-timber forest components. The numbers of large trees, snags, fallen decaying trees and the fauna and flora associated with them decline in most exploited forests (Crow 1990). Nevertheless these impacts do not necessarily reduce forest cover over longer time scales. Anthropogenic disturbance can have much more subtle effects.

Even in the absence of anthropogenic intervention, "natural" forests are typified by disturbances. These take the form of small-scale *autogenic* disturbances such as an individual tree's senescence and death or large-scale *allogenic* disturbances caused by hurricanes or fire. Because of natural resilience within forest systems, disturbances cause local fluctuations around a point of attraction. Contemporary perspectives on forest systems have stressed resistance, resilience and the dynamic nature of equilibria (Everham and Brockaw 1996; Romme *et al.* 1998; Dale *et al.*1998). Fire adapted forests and shrublands have received particular attention as examples of resilience in nature (Purdie and Slatyer 1976; Keeley and Zedler 1978; Noble and Slatyer 1980; Gill 1981; Keeley 1986; Kruger 1983; Goldammer and Jenkins 1990; Braithwaite 1996). An alternative but complementary viewpoint which places less emphasis on dynamic processes and more on the system's level of inertia has also proved useful in conceptualising disturbed systems. Egler (1954) pointed out that many communities show a degree of compositional inertia following disturbance due to seedbanks and resprouting. In these cases observed responses following disturbance are dependant on the initial floristic composition.

Change in species composition begins as a local phenomenon that takes place as opportunities for colonisation arise following disturbance. A knowledge of both individual level response to disturbance and the spatial extent and temporal periodicity of disturbance must be incorporated into the working of any model of the system designed to predict long term compositional change. If contemporary anthropogenic impact is comparable to the historical disturbance regime in intensity, spatial scale, periodicity and the variance associated with these terms, system integrity will probably be maintained in the face of biomass destruction or removal (Romme *et al.* 1998). Such disturbance may even be essential in order to maintain the current system fluctuating around its current point of attraction. Nevertheless forests, which seem to be in dynamic equilibrium when viewed at the appropriate local scale, may be changing when seen over larger temporal and spatial scales. The points of attraction around which local fluctuations now occur may well have first arisen as a consequence of unnatural levels of historical disturbance caused by human activity. Changes in the position of the point of attraction may be much more difficult to perceive than the short term dynamic.

In a move towards operationalising these abstract views of systems Connell (1978a; 1978b) shaped the concept of a dynamic equilibrium into the *intermediate disturbance hypothesis*. When applied to plant communities the hypothesis predicts that some species increase with increasing rates of disturbance while others decline. Maximum diversity occurs at intermediate levels of disturbance. The legacy of Clements descriptions of inherently predictable patterns of change has led to species favoured by disturbance being widely referred to as *early successional*, while those which decline under disturbance regimes are referred to as *late successional*. Due to widespread use these terms are unavoidable and can still form a convenient shorthand for expressing concepts. However their usage has been minimised in this work in order to avoid circularity in the arguments presented. The view which sees forests as a *shifting mosaic* of *gaps* and nongaps (Watt 1925; Watt 1947; Shugart 1984, Hubbell and Foster 1986; Whitmore 1989) has instead been used as the operational framework for modelling localised interactions, although the gaps produced by anthropogenic disturbance are often much larger than those assumed under the classic models. In addition useful underlying heuristic input has been provided by Grime's (1979) scheme of plant strategies that includes an axis based on environmental stress tolerance. Grime defines stress as "*the external constraints which limit the biomass production of all or* *part of the vegetation*". *Stress*, such as nutrient deficiencies, defoliation, fluctuating temperatures or water shortage may all have to be endured by plants as a result of anthropogenic activity. This provides an additional cause for changes in species composition. Following Grime, stress has been regarded in this study as distinct from disturbance, being a chronic process affecting plant growth and survival rather than a discrete event. Models involving stress have not been built and stress has not been investigated empirically, but the presence of stress in the system and the contribution it may play in system degradation has been recognised.

Turning the conceptual framework provided by the extremely rich body of theory surrounding dynamic equilibria, gap phase regeneration, intermediate disturbance and plant strategies into operational research requires precise testable statements regarding the system of interest. Such statements can be derived from simulation models, but models should be regarded as preliminary statements, or complex theories concerning the system of interest. They are meant to stimulate a further cycle of testing and validation through further research.

Setting bounds to the system: A case study approach

Questions concerning the dynamics of whole forest systems may have overwhelming societal relevance, but the complexity of the system could render them intractable. Nevertheless a reductionist approach to forest research has little relevance until a set of precise questions for it to address have been formulated. Broad questions can only be turned into an operational framework for research by placing narrow boundaries on the system of interest. The subsistence nature of forest exploitation in the region helps to set such bounds by reducing the extent to which external influences must be considered. A single village and its associated forest form a bounded system that becomes an appropriate unit for study.

A case study approach is useful for addressing the question of forest change for pragmatic and operational considerations. If an individualistic perspective on vegetation change is adopted, insight into system functioning can best be obtained from detailed investigation of the processes occurring within forested areas. In the case of forest change in Chiapas identifying links between pattern and process which lead to operational theories of change is not yet possible from analysis of remotely sensed information at a regional scale, except where deforestation is of interest. Access to multiple field sites was limited during the period of study due to conflicts in the region. Schrader-Frechette and McCoy (1993) have argued for the increased use of case studies as a means of studying complex ecological phenomena whose behaviour cannot be predicted by general theory. However in novel situations uncertainty can pose considerable operational challenges. Schrader-Frechette and McCoy outline five sources of uncertainty in case studies

1. *Undefined subject and target systems.*
2. *Unknowable boundary conditions.*
3. *Unknown bias in results*
4. *The variability in the nature of the underlying phenomena*
5. *Poor data*

They suggest that given these uncertainties it is often impossible to perform classical experimentation or to specify uncontroversial null hypotheses. They therefore propose a method that "*tends to be heuristic (encouraging further discovery and investigation rather than confirmation of hypothesis) and inductive (rather than deductive). The method employs multiple sources and kinds of evidence and is holistic in that it investigates a contemporary phenomenon in a real-life context.*". Extension and generalisation of the results occurs through "*internal theorising which produces valuable heuristics*".

Such an approach to a case study has been adopted by this thesis. Its weakness is that it could lead to an informal *ad hoc* approach to theory formulation. The use of simulation models was used as a means of confronting this problem and permitting the integration of a body of externally generated knowledge into the process of theorising regarding the case under consideration. Simulation models are especially useful in defining, clarifying and quantifying areas of uncertainty. In order to move from site specific knowledge to general prediction detailed quantitative knowledge must be converted into more general qualitative statements. Statistical inference plays a vital role in this process. Yet statistical inference relies on assumptions regarding the independence of multiple sampling units which are often violated when a single case study is considered. The existence of a correlation may be the only suitable hypothesis for formal testing. Yet correlations provide no support for arguments which invoke causality. Exploratory data analysis in novel areas uses weak inference. The challenges to interpretation caused by lack of independence, multiple correlation, poorly formed prior hypotheses and lack of manipulative experiments form a further theme that has been discussed in this work. An attempt has been made to incorporate this uncertainty into all the models produced.

Objectives

The study aims to test the postulate (Ford 2000) that pine-oak forests in Chiapas are becoming increasingly dominated by pines as anthropogenic impact intensifies. This is thought to occur as a result of shifts in points of attraction around which dynamic systems oscillate at a localised scale, leading to a larger scale trend. In order to provide evidence that can test this a series of questions are addressed in a site specific context:

1. What spatial and temporal patterns in forest composition and structure can be observed at the site?
2. To what extent have historic anthropogenic influences determined the structure and composition of the existing forest?
3. How does the forest respond to disturbances and which key processes are responsible for this response?
4. How does the structure and composition of the forest interact with the system of human decision-making that determines the disturbance regime?
5. What is the trajectory of current structural and compositional change?
6. How might changing patterns of use alter this trajectory?

To address these site specific questions required the development and assessment of suitable tools. An important goal of the study was to develop a framework for analysing these questions that could be used for other similar case studies in the region.

Structure of the work

The thesis has been presented in three parts:

1) In the first part a descriptive approach to the case study is adopted. Inference is drawn concerning patterns of forest change from the details of the single forest system. The linkage between the disturbance regimes and the structure and composition of the forest is considered to be a key factor in forest change. Some questions raised have clear connections with forest timber yield, but the issue of forest productivity has been approached from the perspective of its connection with compositional change. Methods, concepts and terminology have been drawn from the field of ecology, rather than forestry. Most of the study has concentrated on

the small number of key canopy forming species which form the principal structural elements of the vegetation, but change in the wider species assemblage has also been investigated and discussed especially in the context of the most dramatic form of human impact, slash and burn clearance for agriculture.

2) In the second part the human element becomes the focus of study. Forests are disturbed as a result of decisions made by forest users. The periodicity and intensity of disturbance affects forest composition, and thus these decisions must be understood if the forest is to be perceived as a working system. A novel form of modelling the decision making process is evaluated in this context.

3) In the third part it is recognised that wider inference requires a more general perspective. Two simulation models are developed. Both are ecological models, rather than forest yield models, although yield is predicted. The first is closely linked to data drawn from the case study. The second model aims to shift the focus upwards from the single study site towards more general conclusions regarding broad patterns of change in pine-oak forest.

Finally a general integrated verbal model of change in the pine-oak forests of Chiapas is proposed which draws on the preceding lines of evidence to extend the starting postulate that that disturbance of montane pine-oak forest leads to increased pine dominance.

Part 1. Describing patterns and processes in the natural system: Introduction

Understanding patterns in terms of the processes that produce them is both an essential element of scientific enquiry and the key to the development of principles for management. The subject has fascinated empiricists and theorists alike (Bolker and Pacala 1997). Without an understanding of pattern and the mechanisms that underlie pattern each system must be evaluated without any basis for extrapolation from previous experience (Levin 1992). Evaluation of patterns provides the initial clues from which inferences regarding the processes occurring in previously unstudied areas may be drawn.

Systems such as natural forests in which the dynamics of interest can be understood as the collective behaviour of aggregates of similar units have great potential for developing and utilising a mechanistic understanding of pattern formation in an applied context. Once patterns are detected and described attention can turn to the mechanisms that generate and maintain them (Cale and Yealey 1989). Therefore it is appropriate to begin an exploration of the dynamics of disturbed pine-oak woodland with a description and analysis of its spatial and structural pattern.

Pattern in natural systems often appears as multiple correlations between multiple variables. Under such circumstances few statistical hypotheses can be tested other than those which establish that pattern is non random. While statistical analysis can help to pull apart the network of interconnecting variables and partial out variability, causality can only be weakly inferred unless patterns can be predicted *a priori* from pre existing models. In this case study operational models were developed as work progressed. The exploratory nature of many of the statistical methods used in this section has therefore been emphasised.

This section comprises four chapters. The first chapter is split into three sub chapters. Chapter 1.1 provides some initial background information. Chapter 1.2 provides the context for later work with a description of forest structure using information from a forest inventory. Chapter 1.3 adds patch level detail to the description of forest structure through focusing on data from permanent sample plots. In chapter 2 the process of disturbance is addressed as the effects of fire as a disturbing factor are investigated. Chapter 3 looks at how slash and burn (*milpa*) clearance followed by regeneration might be shaping forest structure. Chapter 4 continues the theme by investigating how compositional differences between milpa and forest can be detected.

Chapter 1. Spatial and structural pattern in disturbed pine- oak woodland

1:1 Introduction to the field site: The bienes comunales of the Ejido of Santa Rita Sonora

The site, centred at 16° 33′ N 92° 05′ W, consists of 1,027 hectares of disturbed woodland. The area was selected for study because;

1. Community forest management of the site had been proposed as a means to achieve rural development goals. Lack of knowledge of the underlying ecology of the forests of the region was one of the barriers preventing the implementation of sustainable management.

2. Knowledge of forest change in this region had a particular relevance. The area has little agricultural potential and is undergoing rapid population growth. Forests are the most important natural resource for the inhabitants of one of the most marginalised rural communities in the state.

3. The site was situated within a large contiguous forested area about which little was known. The descriptive element of the study did not repeat any other previous work.

4. The site had very clearly already undergone a process of historical disturbance. Understanding the effect this disturbance had on the forest would provide considerable insight into the effect of contemporary processes.

History of the site

Before beginning a more detailed treatment of forest characteristics a brief account of the history of the field site is provided. This information has been derived in part from interviews with the oldest inhabitants of the village.

Up to the construction of a paved road in 1994 the area had been isolated and almost completely unstudied. Few botanical collections are recorded for the municipality and none from the immediate area of study. No previous ecologically oriented studies had been undertaken at the site or in any similar forest in the Tojolobal region. Only large-scale soil and topographical maps were available. Satellite images and aerial photographs show that the site is part of the largest single contiguous area of montane forest remaining in Chiapas. This had at one time been assumed to be a species rich broadleaved forest based on assumptions regarding climatic characteristics (Bubb 1991). It is now apparent that most of the extant forest has been subjected to long term anthropogenic disturbance. Although the forest supports a rich flora of understorey shrubs, herbs and epiphytes the canopy is dominated by a small number of pine and oak species.

The forest is considered to have potential for commercial exploitation. To date the complex challenges presented by social and political conditions in the region have proved a barrier to the development of community based forest management. Regional forest management initiatives stress fire control and the enforcement of conservative extraction quotas. Sylvicultural intervention to attain longer-term goals has not been attempted. Forest exploitation is strictly regulated under Mexican law, but experience in the area suggests that it is necessary to draw a distinction between normative harvesting and practices observed in the field (see Klooster 2000 for further examples of this difficulty in a Mexican context). This reality did lead to inevitable logistical challenges for fieldwork in the area[1].

The community of Santa Rita Sonora consists entirely of Tojolobal speakers, one of the three principal indigenous Mayan languages spoken in the highlands of Chiapas. Tojolobal speakers now number around 50,000 people (Lenkersdorf 1999) concentrated in an area to the north of Comitán (figure 1.1). Until the nineteen forties most of the land in the Tojolobal speaking region belonged to a few owners of Spanish decent. This period, referred to as the "*baldio*" is remembered with great bitterness by the oldest members of the community. When traditional land rights were restored, community organisations were established, although demands for greater local autonomy, particularly with regard to natural resource use, is a continuing cause of conflict in the region.

The social and political structures, which arose in the Tojolobal region following the restoration of land rights, have few clear connections with pre Hispanic traditions. The lack of a highly visible cultural identity seems to explain, in least in part, the remarkable neglect of the Tojolobal by anthropological research. Thus although work by Lenkersdorf (1999) is

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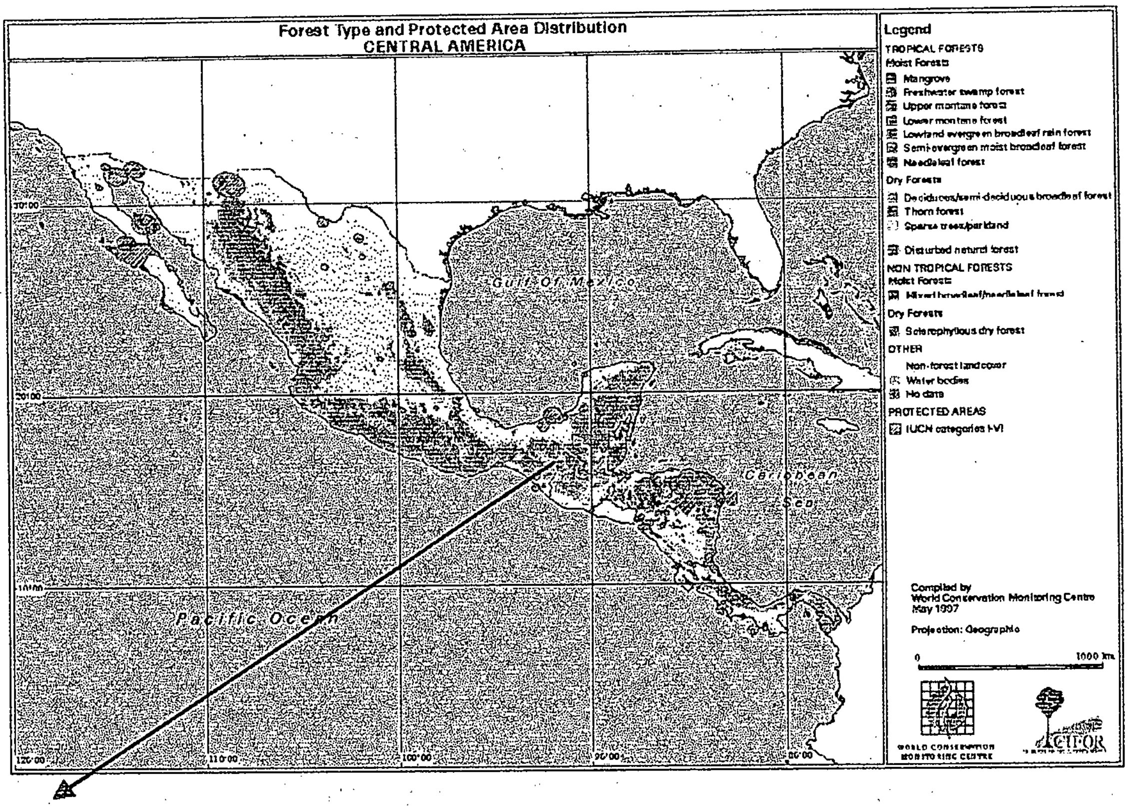
[1] The site actually used in the study was a replacement for a site which was unsuitable due to tensions arising from forest exploitation.

now revealing the hidden richness of the Tojolobal culture and language, the history of the area remains comparatively unstudied. The Tojolobal benefited from post revolutionary land reforms implemented by the government of President Lazaro Cárdenas. During this period communities received rights to land formerly in private hands and the contemporary pattern of land division in the area were established. The ejido system, a form of collective farm unique to Mexico (Dunn 2000) developed during this period and is now the focal point of the Tojolobal social and productive organisation.

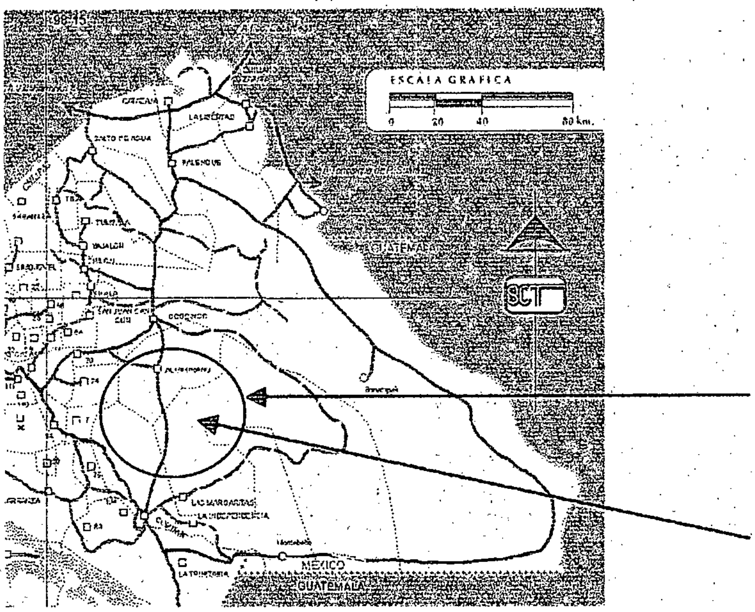
Legal documents show that the ejido of Sonora was founded on 13 October 1944. The 1,070 hectares of land, which previously formed the hacienda of Santa Rita (figure 1.2), was bought for a nominal sum by around a dozen families. Most had worked for the previous owner. Although land rights gave the community a degree of security, development has been slow. Electricity and piped drinking water first became available in Sonora in 1999. The main economic activity carried out within the community remains subsistence farming, with little surplus produced for sale. Poor maize harvests have caused considerable hardship and led to seasonal emigration from the area. Traditionally work was sought in Comitán, but many members of the community now spend several months each year in Cancún, Quintana Roo working on construction sites.

Since the founding of the ejido the population of Sonora has increased to 72 families and the original area granted to the community has been extended twice. In 1969 a further 1,107 hectares were added to the ejido. In 1987, 1,027 hectares of state owned forested land was legally recognised as belonging to the community. These *bienes comunales* (communal land) were never part of the hacienda. They have only been disturbed by indigenous patterns of subsistence land usage. This usage apparently continued during the time of the "*baldio*" when forested land was used for slash and burn farming both by workers on the hacienda, and groups of subsistence farmers who refused to work for the hacienda. These communal lands support a forest type that is typical of a wider area around Sonora. It is this forest that forms the study area referred to throughout this work.

Figure 1.1 Position of the field site in the Southern Mexican state of Chiapas. Source WCMC, Cambridge (1997)



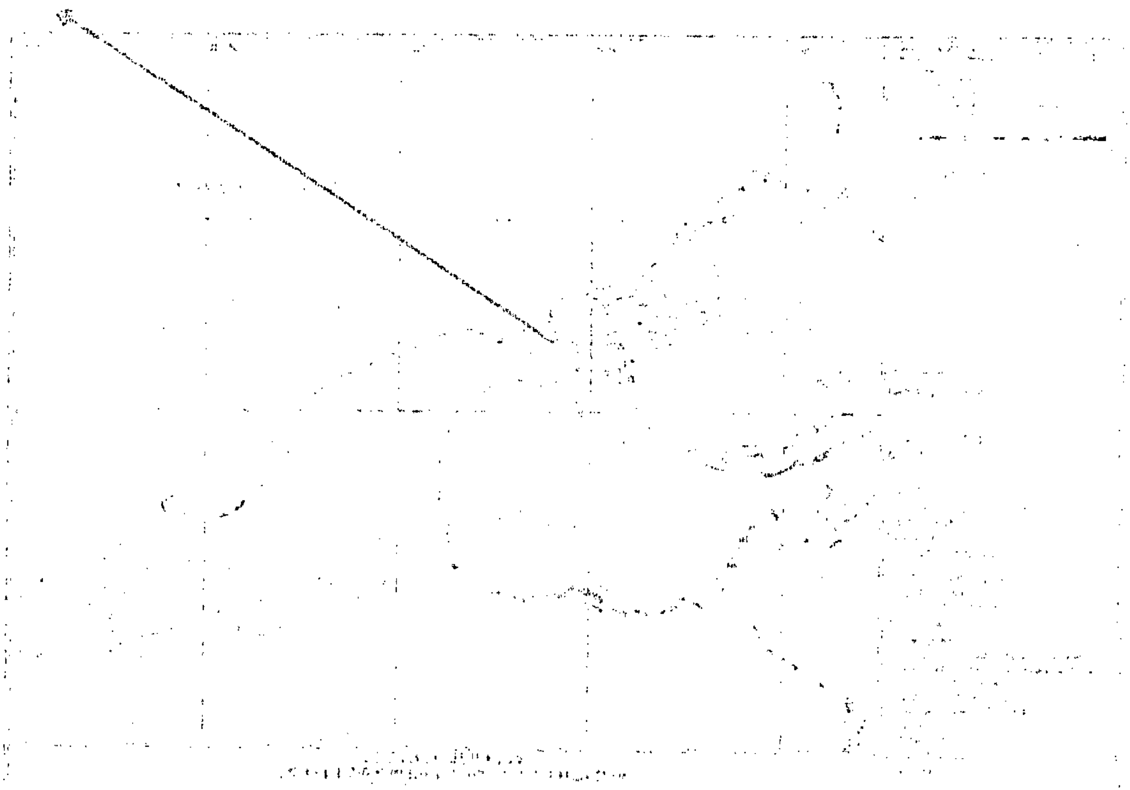
South Eastern Chiapas. To the East lies Guatemala. Note that the Tojolobal speaking area and the field site lie to the west of the protected area of the Lacandon lowland rainforest and to the South East of the more densely populated Central Highlands. Source SCT 1998.



Tojolobal speaking region

Santa Rita Sonora

Figure 1.1 Position of the field site in the Southern Mexican State of Chiapas. Source WCMC Cambridge (1997)



South Eastern Chiapas. To the East lies Guatemala. Note that the Tojolobal speaking area and the field site lie to the west of the protected area of the Lacandon lowland rainforest and to the South East of the more densely populated Central Highlands. Source SCT 1990

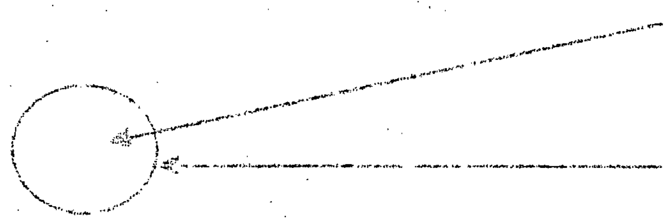


Figure 1.2. Plan of the current ejido of Santa Rita, Sonora 16° 33′N 92° 05′ W transcribed from legal documents granting land tenure.

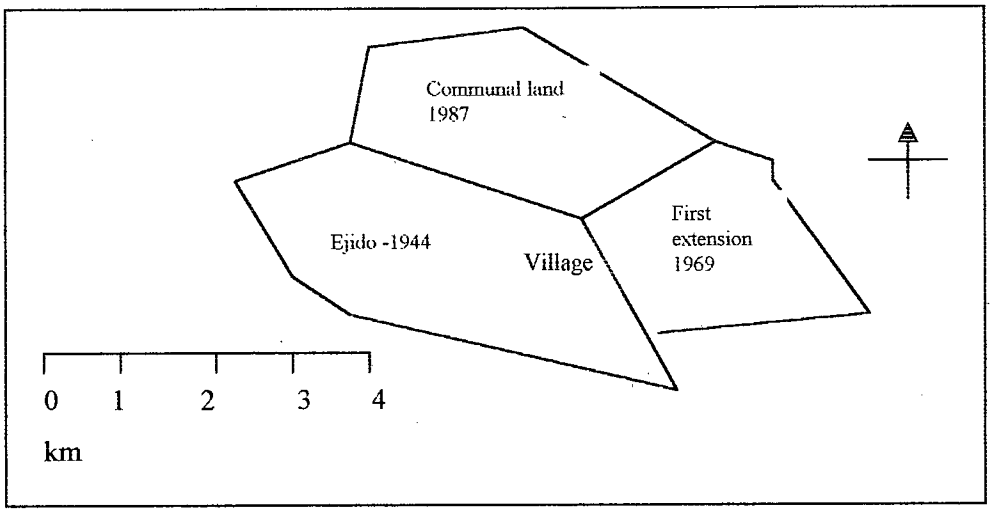
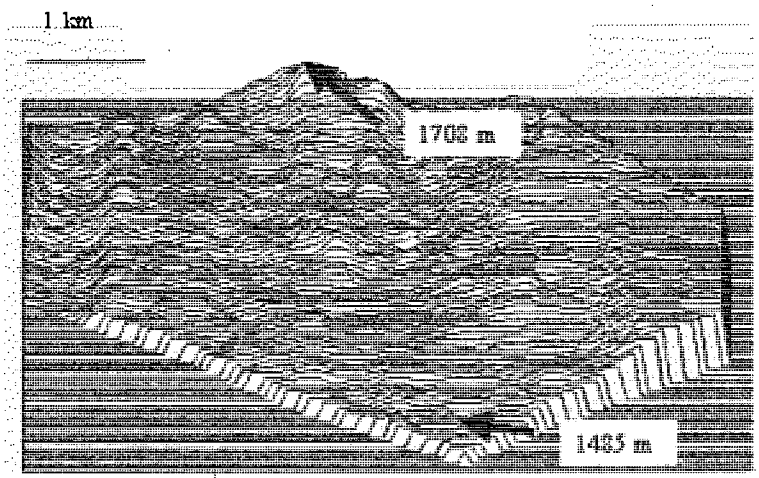


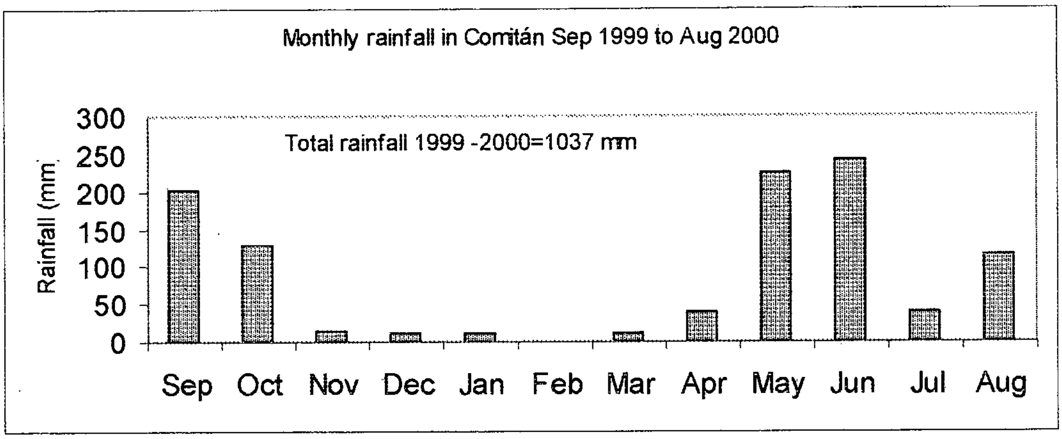
Figure 1.3. Topography of the bienes comunales derived from a digital elevation model produced as a result of measurements taken for a forest inventory.

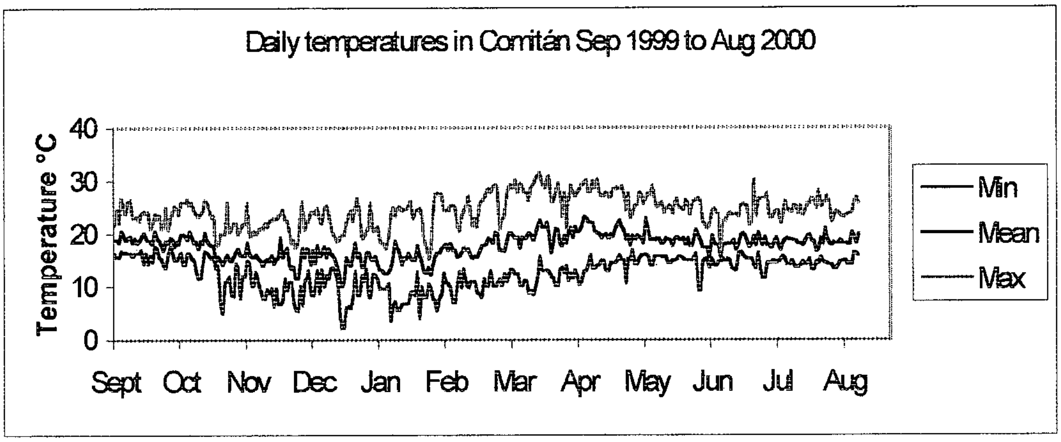


Climate

Continuous monitoring of the climate at the site was not possible during the study period. Personal observation suggest that the area is possibly rather wetter and cooler than data from the nearest local meterological station in Comitán (1,450 m a.s.l.) would suggest (figure 1.6). Precipitation is around 1200 mm per year. Rainfall is concentrated in the period between late May and early November. Plant growth is largely restricted to these months, although some deeper-rooted trees apparently continue to grow throughout the year. Temperatures during the wet season average around 20° C with daily maxima reaching 30° C and minimum temperatures of 15° C. Maximum temperatures in the dry winter months are comparable to the summer, but night-time minimum temperatures can be much lower. Ground frost occurs on at least one occasion annually. Most broad-leaved trees and shrubs have a deciduous habit. Leaf fall takes place gradually throughout the dry season and some of the previous season's leaves are generally present at the beginning of the growing season.

Figure 1.6. A summary of climatic data from the meteorological station in the city of Comitán from September 1999 to August 2000





Uses of the forested land

Given the limitations to other forms of production, forestry would appear to be the most suitable use for most of the land around Sonora. However the community has gained little benefit from previous forest exploitation. Timber companies based in Comitán extracted pine timber from the ejido and communal lands in the 1960's and early 1980's. Large pines are now scarce in accessible areas. Rides cut by the company are visible in some areas of forest, but records of timber extraction are not available and members of the community give unreliable accounts on methods used and quantities of timber removed.

The *bienes comunales* have apparently been used for slash and burn subsistence farming for many centuries. Until recently forest was allowed to regenerate between periods of brief usage for maize production. Fuelwood is also gathered from the area. A detailed understanding of the pattern of slash and burn usage and fuelwood use was found to be essential in order to trace the pattern of forest development. This is presented in chapter 4. The whole area owned by the community is grazed by around 200 head of cattle together with approximately 30 horses, a similar number of donkeys and three flocks of sheep, each made up of around twenty animals. In addition, all families have pigs and domestic chickens. Pigs rarely stray far from the inhabited areas. Other livestock are free to move throughout most of the 3,500 ha of the ejido and bienes comunales. Walls or fences surround maize fields (*milpas*) in order to protect the crops. The ejido exercises no control over ownership of live stock, numbers thus being limited mainly by the economic capacity of the population to purchase breeding stock. Overgrazing is not reported as a problem by the farmers who would like to be able to buy more livestock. There is little evidence of the soil erosion often seen in sheep rearing areas of the highlands. Nevertheless, due to the poor structural properties of the soil trampling has led to soil compaction. Grazing pressure is assumed to play an important role in shaping patterns of tree regeneration (chapter 3).

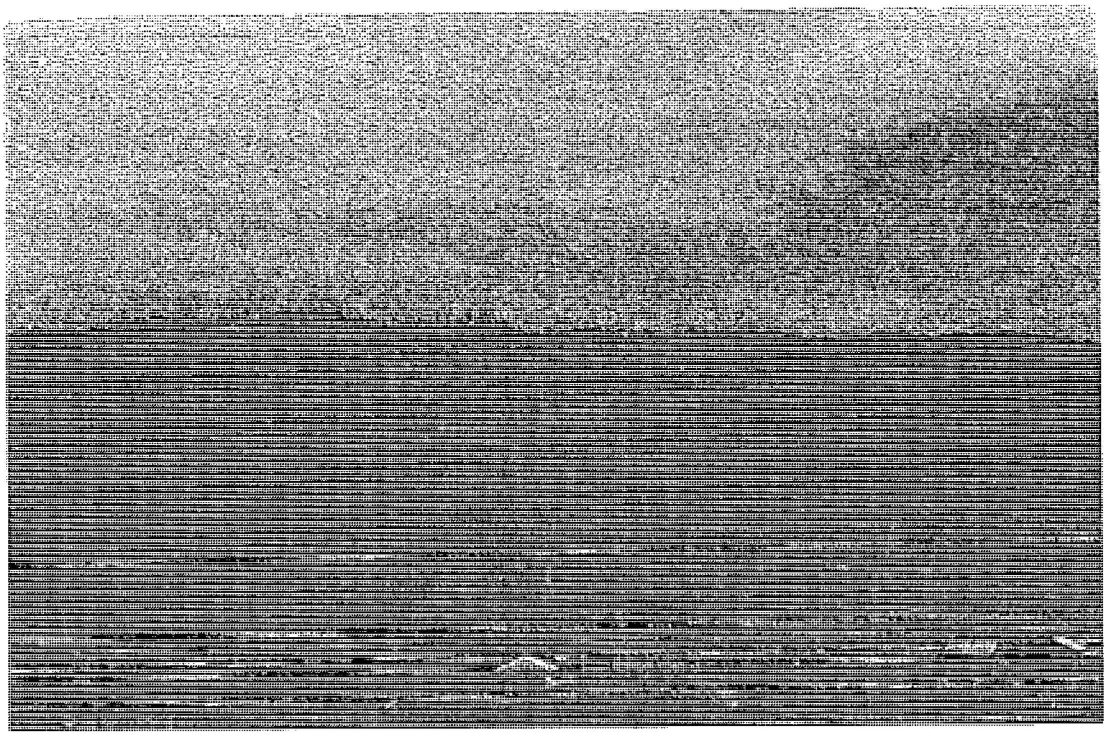
No detailed soil survey has been conducted in the area. In general the soils of Sonora are not well suited to agricultural use. Sandy alluvial deposits of low fertility are found in the valley areas of the ejido. Steeper slopes have a thin incipient rendzina over a calcareous bedrock. In a few areas the underlying geology is exposed as eroded karst or as deep potholes. However most of the *bienes comunales* is gently undulating with shallow nutrient poor sticky clay soil of uncertain technical classification that is very easily compacted. Low nutrient content and very poor structural qualities make productive use challenging. Poor drainage may impose limits on productivity in valley bottoms due to flooding.

A distinction must be made between the forested land referred to as the *bienes comunales* (communal land) which has been the object of the current study, and the area of pasture, open forest and permanently ploughed fields which comprises the *ejido* (collective farm). Legally the forested land of the *bienes comunales* belongs to the whole community. Rights to an area that was nominally state owned forest were formally granted in 1987, based on the recognition of a long established pattern of prior usage. The distinction between the *bienes comunales* and the land of the *ejido,* which is also communally owned, is now based on this date of recognition. The classification of the *bienes comunales* as forest makes clearance or logging of the area without a permit a technical violation of national forestry law (see Klooster 2000). The *ejido* land was acquired from its former owner in 1947 during the period of land reforms initiated by president Lazaro Cardenas. Prior to acquisition the *ejido* was used for extensive cattle ranching. Cattle ranching never extended to the forested *bienes* *comunales*, which were apparently only used for slash and burn maize cultivation prior to the establishment of the *ejido*. The questions addressed by this study have tested this assertion.

A practical distinction based on vegetation, soil type and usage patterns forms the basis on which the community separates the two areas. The *ejido* land (which lies to the south of the area included in this study) mainly consists of open pine savannah on well drained, sandy alluvial deposits of very low fertility. Pine dominance of these savannahs is almost certainly a consequence of soil properties, although this statement requires further confirmation as both fire and grazing have clearly played a role in maintaining the open characteristic of the savannah. There is no obvious evidence that oaks or other broadleaves have ever been a major feature of this vegetation. This area can apparently be cultivated using long rotation slash and burn farming but is mainly used as pasture. Within the *ejido* some areas of slightly richer soil are to be found, particularly in the immediate surroundings of the village. Here permanent fertilised maize plots have been established. The use of some of these plots predates the introduction of chemical fertilisers to the region, but most are more recent. Such plots are cultivated with ox drawn ploughs, a traditional method extensively used on the more fertile valley soils in the southern part of the Tojolobal region which has more recently been adopted in areas with less fertile soil.

The general aspect of the site is shown in photograph1, in which the open grazed pine savannah of the ejido with scattered permanent maize plots is in the foreground and the mixed pine-oak forest of the bienes comunales is visible on the hillside rising behind.

Photograph 1. View of the forested hillside of the bienes comunales seen from the village of Sonora. The grazed pine savannah and permanent maize plots are in the foreground, the study area is in the background.



1:2 Spatial and structural pattern in a disturbed pine-oak forest

Introduction

Pattern in forest systems can arise from underlying environmental heterogeneity or may be the result of overlying disturbance. Spatial variation itself can be essential for the coexistence of species (Tilman 1994; Huston 1999). In systems in which localised disturbances play an important role, spatial pattern may be intrinsically unpredictable (Huston 1999). Ironically local unpredictability may sometimes be the most globally predictable feature of forest systems. As the viewpoint shifts upwards from a focus on individual disturbance events this variability declines and predictability increases (Levin 1992). In order to appreciate the link between pattern and process perspectives may be necessary in which the scale of perception is constantly shifted as different processes are considered. To achieve this visual inspection of data can be an invaluable starting point (Tukey 1977; Tufte 1983). Statistical analysis helps to clarify the significance of any pattern found. This is usually by testing the null hypothesis that apparent pattern is the result of purely random effects.

Multivariate analysis is useful both for uncovering the relationship between species composition and environmental variables and summarising species composition in terms of the associations they form (Ter Braak and Prentice 1988). If species distribution is non random in space, difficulties in the interpretation of sampling data may arise when subjected to conventional multivariate analysis. Particular problems are found when the relationship between environmental variables and species composition are analysed (He, Legendre and Frankie 1997; Meot, Legendre and Borcard 1998). If species distributions are spatially auto correlated, the assumption of independence, a requirement for most standard statistical procedures, is likely to be violated. When species distributions and the distribution of an environmental factor are closely associated, the degrees of freedom in the data are limited by the number of identifiable independent patches (Legendre and Fortin 1989; Legendre 1993). This reduces the statistical power available for identifying genuine unconfounded correlation (Bellehumeur, Legendre and Marcotte1997). It was hypothesised before the study commenced that the undulating topography of the site could produce a large number of small patches with shared combinations of environmental conditions. This spatially independent level of heterogeneity could be linked to spatially independent heterogeneity in species composition. General inferences regarding the link between environmental factors and species composition were therefore assumed to be possible. This assumption was critically tested by including space as a variable in redundancy analysis.

In order to analyse the extent of spatial autocorrelation at the site a procedure suggested by Legendre (1993) was followed. Legendre states that where possible the autocorrelation present in vegetation data should be quantified and included in analyses, rather than ignored. The objective may be to demonstrate that no significant autocorrelation exists in order to take advantage of standard univariate or multivariate statistical tests of general hypotheses. Alternatively it may be desirable to demonstrate that autocorrelation is present in order to interpret it in a site specific context. Legendre suggests that either of the two commonly used canonical techniques of multivariate analysis, redundancy analysis or canonical correlation analysis, can be adapted to investigate spatial pattern by using the terms of a polynomial trend surface as pseudo environmental variables. As many polynomial terms as necessary can be included in such models and their significance tested independently or in combination using stepwise regression. Restricting the polynomial to second order terms, although reducing the fit of the trend surface if the underlying pattern is complex, produces comparatively easily interpretable models. This is particularly appropriate if a small number of strong spatial gradients are likely to be present at the site as fitting a quadratic trend surface can be used either to reveal or remove linear or unimodal spatial patterns.

If the variation in species composition falls within a short section of a wider environmental or successional gradient then the linear model assumed by principal components analysis (PCA or factor analysis) and its canonical counterpart, redundancy analysis (RDA), often explain more of the variation in the data than the Gaussian model which underlies correspondence analysis (Ter Braak and Looman 1986). The program Canoco (Centre for Biometry Wagingen, Netherlands 1997-1999) was used to carry out RDA and CCA both with and without forward selection. Forward selection is a form of stepwise regression that ranks environmental variables according to their importance for determining the species data. When automatic forward selection is used in Canoco, the best variables are selected sequentially on the basis of maximum extra fit. The statistical significance of each selected variable is judged by a Monte-Carlo permutation test (Ter Braak 1997). Thus only variables that independently explain a significant degree of the variation in species distribution are retained. If strong spatial autocorrelation is found, forward selection on a model that includes the spatial trend surface terms will lead to the exclusion of most environmental variables due to redundancy. This is especially likely when gradient analysis is based on transects along spatial gradients such as single hillsides (though see Legendre 1993 for an analytical approach which may retain more information from such studies). Because knowledge regarding any site specific correlation could still be useful for locally applicable hypothesis formation. RDA and CCA were also carried out without inclusion of the spatial terms for comparative purposes. Drawing comparisons between the results of each model allows the spatial component to be revealed (Borcard, Legendre and Drapeau 1992).

The analysis presented therefore aimed to address the following questions.

1. Can spatially defined patterns be perceived in the distribution of tree species in the *bienes comunales*?

2. Can general inferences be drawn from any patterns observed, or should inference be confined to a site specific, local level.

3. Can complex patterns be simplified in order to guide modelling of the system?

The second question is of particular relevance as answering it will help to determine whether general biological principles, or specific historical detail will best explain the observations available.

Method

Mexican forestry law requires that a detailed management plan be submitted to SEMARNAP (Secretaria de medio ambiente, recursos naturales y pesca) for approval before timber may be cut from any forested area with an extent of over 20 ha (AMPF 1993; SEMARNAP 1997). This requirement has acted as a disincentive to legal forest usage in Chiapas as the cost of the required study was beyond the means of subsistence farmers. A recent government initiative, PRODEFOR (SEMARNAP 1997) was designed to overcome this barrier through providing grants to cover the costs of inventories and the submission of management plans.

In August 1997 the authorities of Sonora applied for PRODEFOR assistance to obtain a permit to legally extract pine timber. The application was successful. An opportunity was therefore provided to obtain a substantial amount of data on the vegetation structure of the *bienes comunales*. The fieldwork was conducted from June to October 1998, immediately after the site had been affected by wild fire (see chapter 2).[2]

Transects were laid through the forest running south to north at two hundred metre intervals. The positions of the start and end points of these transect were recorded using a geographical positioning system. In order to produce a digital elevation model (DEM) for the area the slope of each 25 m sections of the transects was recorded and altitude calculated from reference points at the start of each transect. Some cumulative error is inevitable in such a method, but it was considered sufficiently accurate for the purposes of improving the detail of the site description.

Circular plots of 500 m^2 were sited every three hundred meters along each transect. Compensation was made for slope angle when plots were laid out. The diameter of all trees greater than 5 cm at breast height was recorded to the nearest cm. A total of 8,688 trees were measured in 225 plots along 24 transects. Four geomorphology classes were recorded for each plot *ridge*, *upper slope*, *lower slope* and *valley or hollow*. Slope percentage was measured with a clinometer. Aspect was recorded to the nearest 10°. Mineral soil depth was measured by pushing a 1 m long metal probe into the ground until a rock was felt (Botkin 1993). Ten measurements of soil depth were taken for each circle and the mean recorded. Humus depth to the nearest cm was recorded for each plot by digging to reveal the upper layer of the soil profile. Subjective classification of disturbance at each site was recorded, but the method used was found to reflect recent canopy opening rather than historical impact. Measurements that were suspected to be unreliable have been excluded from consideration in this study[3]. Additional data was later obtained in order to address questions that could not be answered with sufficient accuracy from this survey.

The modelling software written in Visual Basic 6 ©Microsoft 1998 (see part 3) was extended in order to incorporate a simple integrated module for mapping the inventory data. Data held in database format was read directly into the modelling software and used to produce maps

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[2] Two teams of eight members of the community of Sonora were employed. Additional financial support for gathering information of research interest was provided through the project SUCRE. Supervision and technical assistance was provided personally and by two local forest engineers. The design of the survey met legal requirements. The application for a permit to extract timber from the forest was accepted in August 2000

[3] The accuracy of the data was checked at randomly selected plots both while the inventory was being conducted and subsequent to its termination. Some errors due to the inexperience of the local crews could not be avoided. The process of estimating the height of smaller trees following measurement of top height did not lead to reliable measurement of tree heights.

showing the spatial relationship between each inventory plot. Information held in the model can be output to a dedicated GIS package such as Idrisi as data points in vector format for further analysis. The program includes a subroutine to enable this. Idrisi was used to visualise the digital elevation model (DEM) by producing trend surfaces and rendered 3D imaging (figure 1.2).

While a DEM can be manipulated using a dedicated GIS, smoothing and interpolation of tree basal areas between data points was considered to be misleading given the fragmented mosaic nature of the vegetation. Instead a routine was coded which allowed data points to be represented by circular plots drawn to scale. Because the 500 m^2 plots are small compared to the extent of the unmeasured forest around them, shading based on basal area or number of stems is extended around each circle in order to be visible. The software also was provided with an automated routine for generating size class histograms and frequencies of basal area measurements that has been used to investigate the inventory data.

Aspect was included in the multivariate models as a cosine function with the maximum shifted to the Southwest quadrant (Beers *et al.* 1960). Slope was included as the tangent of the slope angle (slope percentage) In addition following the suggestion of Stage (1976) a joint variable including aspect and slope was produced by multiplying the tangent of the slope angle by the sine and cosine of the azimuth. The other environmental variables included in the analysis were soil depth and altitude. All variables were standardised by division by the maximum value in order to take values between zero and one before inclusion in the analysis. Soil depths were log transformed prior to standardisation as this was found to reduce heterogeneity of variance. Log_{10} transformed measures of stem density per plot were used to represent the species abundance component of the multivariate data. The use of a combined measure of dominance based on basal area and stem density which can be useful in situations where self thinning occurs (Mueller-Dombois and Ellenberg 1974) was found to be unnecessary for this data set due to positive correlation between stem density and basal area.

All further data analysis and graphical output has been produced using the program Statistica (Statsoft Inc. 1996). The program has also been used in subsequent chapters unless otherwise stated.

Results

The bienes comunales form a roughly diamond shaped area of 1,027 of undulating terrain which rises gradually towards the North East (figure 1.3). The aspect of most plots is thus South Westerly, ranging between 180° and 270° although the complexities of microtopography results in areas which have easterly or even northerly aspect (figure 1.3 and figure 1.9). The land is gently sloping, with some rocky outcrops (figure 1.7). Altitude ranges from 1500 m to 1700 m a.s.l. with most of the area being between 1550 m and 1650 m (figure 1.8). Although no quantitative measurements are available, rainfall and average temperatures are unlikely to vary greatly over this comparatively small altitudinal range. However personal observations suggest that the higher areas receive more mist and cloud cover. On clear nights between November and early March ground frosts are confined to sheltered lower areas. Highly local combinations of topography and tree cover have been found to have a pronounced effect on micro climate elsewhere in the highlands (Gonzalez-Espinosa and Ramirez-Marcial unpublished data).

Of the 225 plots 20 had no trees over 5 cm in diameter. The basal area of all species of tree in the forested plots varied between 5 m^2 ha^{-1} and 50 m^2 ha^{-1} (figure 1.11 and figure 1.12). Three measurements, which are outliers from this distribution with basal areas of over 50 m^2 ha^{-1}, have almost certainly arisen as a sampling artefact due to the inclusion of trees on the edge of comparatively small sample plots.

Soils are of variable depth at a local scale with deeper pockets interspersed with some areas of exposed rock. The mean values for each geomophology class with the exception of hollows and valleys was below 30 cm (figure 1.10). At a larger scale patches in which the underlying limestone is exposed to form a fissured karst are interspersed with areas where deeper clay based mineral soil has accumulated. While geomorphology is a good predictor of soil depth, slope alone was not well correlated with soil depth (regression R^2=0.017 p=0.71) probably because very thin soils were found both on the flat plateau like summits of some low ridges and on eroded slopes. A change in soil properties occurs towards the south of the area as rendisol and limestone karst is replaced by sandier alluvial deposits at the lower elevations (pers obs). This change is not shown clearly in the data collected for the inventory.

Figure 1.7. Distribution of slope angles over the 1,027 ha of the bienes comunales of Sonora Each observation of slope was made on a 25 m section of 24 transects running S-N through the area.

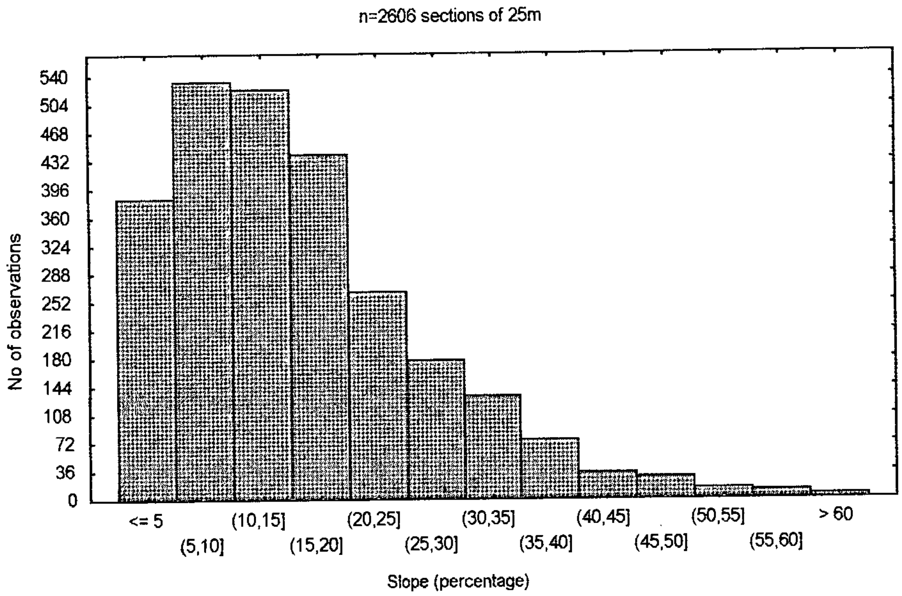


Figure 1.8. Distribution of altitudinal measurements over the 1,027 ha of the bienes comunales of Sonora. Each observation was made at the start of a 25 m section of 24 transects running S-N through the area.

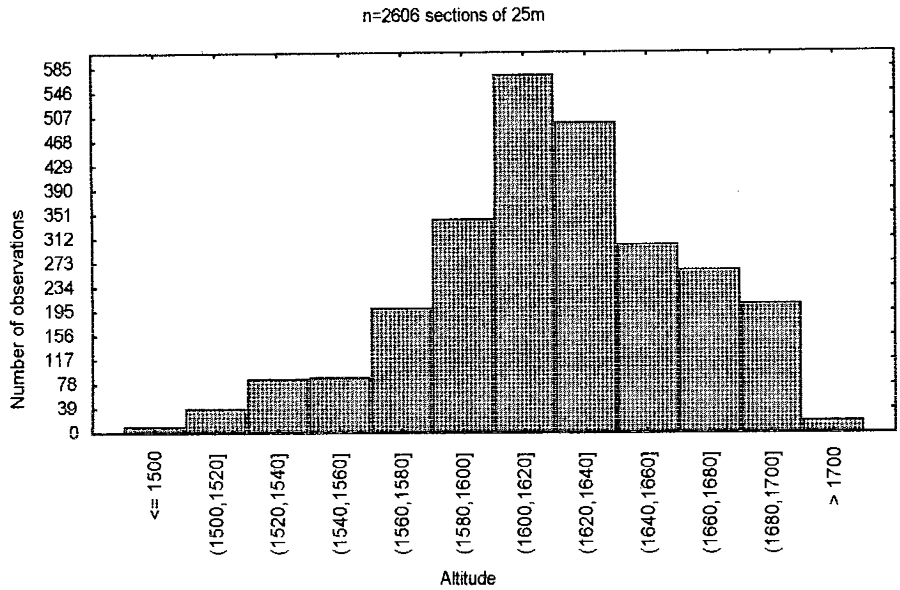


Figure 1.9. Distribution of aspect measurements over the 1,027 ha of the bienes comunales of Sonora. Each observation was made at the start of a 25 m section of 24 transects running S-N through the area

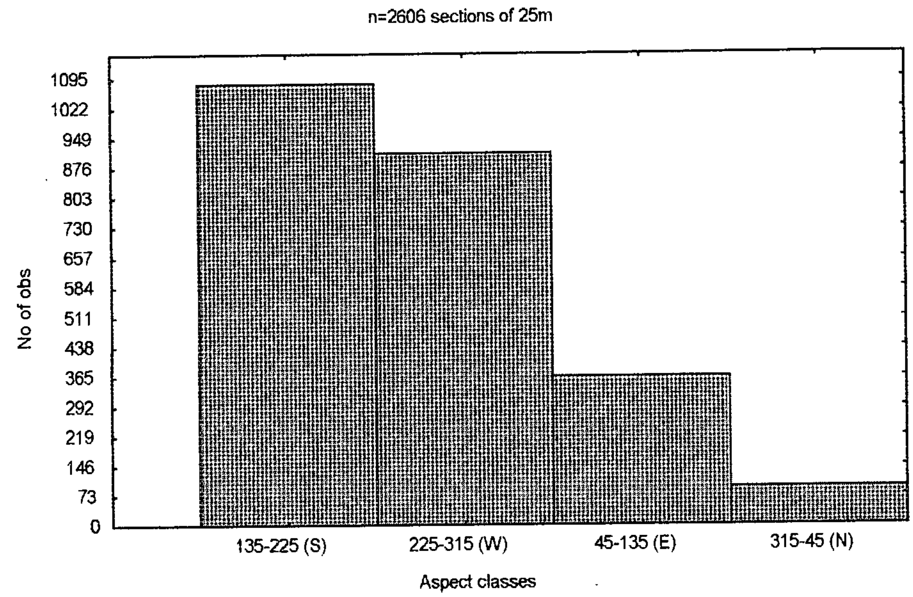


Figure 1.10. Mean mineral soil and sub soil depths stratified by geomorphology classes. Total number of measurements across all four geomorphology classes were taken from the mean of each of 6 measurements in 225 quadrats of 500 m^2. Error bars are 95% confidence intervals for each mean. The maximum depth recorded if penetration to bedrock did not occur was 1m.

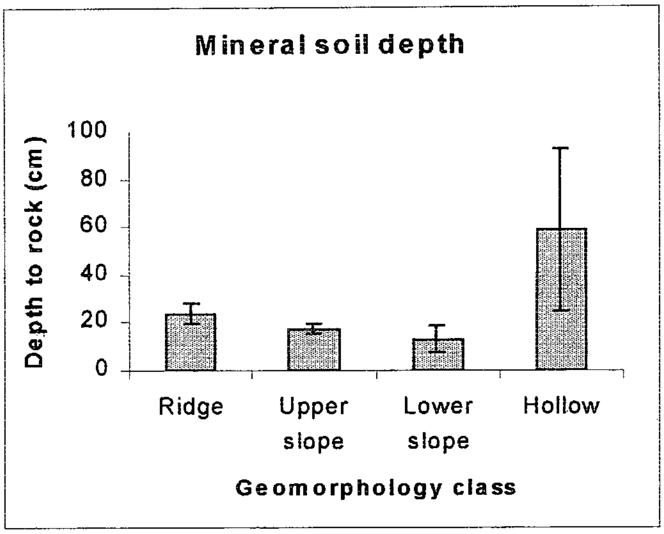


Figure 1.11 Total basal area of all species of tree in the inventory plots of the bienes comunales. Transects were spaced at a distance of 200 m apart and 500 m ^{2} circles were measured every 300 m. The irregularity in the grid is due to genuine irregularities in quadrat placement arising from the nature of the terrain. Shading tones vary with the darkest shading corresponding to the maximum basal area recorded. Unshaded plots have no trees over 5 cm in diameter.

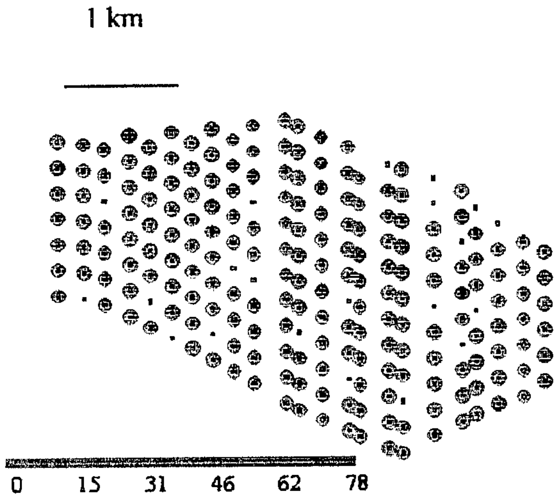
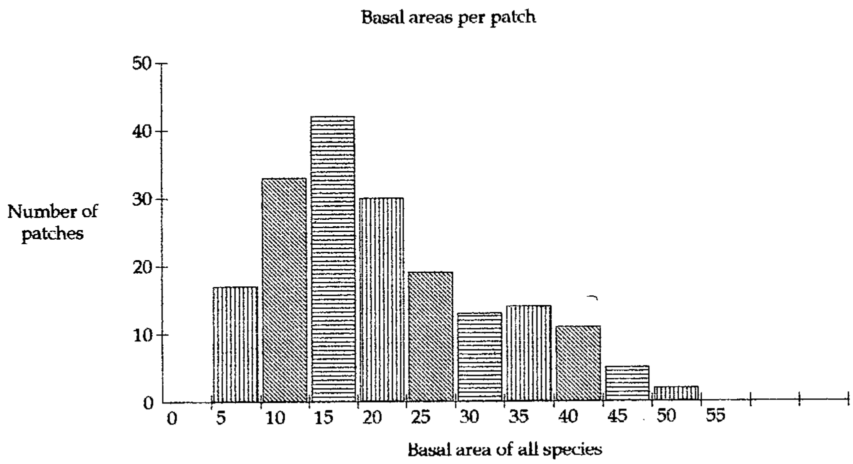


Figure 1.12. Distribution of basal areas in the 225 plots of the bienes comunales. Two outliers and 20 plots with basal areas below 5 m^2 ha $^{-1}$ are not included.



The forest canopy is dominated by three species of pine and two species of oak[4] (table 1.1) The smaller sub canopy species *Cleyera theoides* (Theaceae) and *Rapanea juergensenii* (Myrcinaceae) are also important elements of an understorey tree layer. One of the few other species to contribute to canopy basal area was *Olmediella betschleriana* (Flacourtiaceae), a species usually associated with montane cloud forest. This may have some significance in explaining the origin of this forest. It should be mentioned that five additional species of oak have also been recorded for the site outwith the measured areas, *Q. benthamii*, *Q, skutchii*, *Q. sapotifolia*, *Q. rugosa* and the shrubby species *Q. sebifera*. With the exception of *Q. sebifera* which is locally common but too small to be included in the inventory, all these species occur only as isolated scattered individuals, possibly even as single trees in the case of *Q. rugosa*. Several individuals of *Pinus pseudostrobus* have also been recorded in the northernmost part of the site. Because the total numbers of these rare species make up less than 0.01% of the tree population they were highly unlikely to be included in a sampling scheme with less than 1% total coverage.

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[4] The taxonomic status of the species reported throughout as *Q. crispipilis* Trel. and *Q. segoviensis* Liebm. could require subsequent revision, especially given the notorious hybridisation common among oaks It might be advisable to assume that the names refer to aggregates or morpho species until further detailed studies become available.

Table 1.1. Stand table for the inventory area. Note that statistical inference from means, standard deviations and standard errors requires the assumption of independent sampling units. This assumption is not valid due to spatial autocorrelation. These statistics have therefore been included for reference and comparative purposes only. Species marked with an asterisk are shrubby species or small trees that rarely reach over 5 cm in diameter. See appendix 1. for a complete species list with authors.

	Basal area (m^2 ha^{-1})	S.d.	S.e.	Stems (ha^{-1})	s.d.	s.e.
Pinus maxinioi	8.89	11.8	0.818	126	160	11.1
Quercus segoviensis	6.72	8.84	0.613	299	312	21.6
Pinus oocarpa	3.32	5.43	0.377	78.4	123	8.53
Quercus crispipilis	1.72	4.16	0.288	77.2	190	13.2
Cleyera theaoides	1.15	2.03	0.141	107	143	9.92
Pinus devoniana	0.633	2.10	0.146	11.6	43.4	3.01
Rapanea juergensenii	0.385	0.973	0.0675	41.73	91.5	6.35
Cornus disciflora	0.118	0.467	0.0323	9.23	27.93	1.94
Olmediella betschleriana	0.0906	0.313	0.0217	14.9	52.1	3.62
*Ocotea mollifolia**	0.0827	0.297	0.0206	12.5	34.5	2.39
Mosquitoxylem jamaicense	0.0818	0.405	0.0281	7.02	29.8	2.07
Rapanea myricoides	0.0744	0.242	0.0168	11.2	35.7	2.48
*Sauria scabrida**	0.0675	0.317	0.0220	10.2	50.6	3.51
*Ternstroemia oocarpa**	0.0288	0.187	0.0129	2.79	11.5	0.80
*Prunus lundelliana**	0.0187	0.160	0.0111	0.865	5.31	0.368
*Acacia angustifolia**	0.0170	0.154	0.0107	1.92	13.3	0.925
*Vernonia canescens**	0.0141	0.088	0.0061	1.635	9.79	0.679

Evidence of some recent disturbance was found in all but eight plots, but in most cases the only disturbance reported was fire. Twenty plots had no trees over 5 cm. An analysis of the spatial effect of fire based on this data is included in chapter 2. The subjective indices of disturbance by logging and fuelwood extraction were all based on canopy openness, which would be correlated with total basal area. 47 plots had evidence of recent fuelwood collection and 43 of recent logging. As the subjective criteria used to produce these indices did not appear to accurately reflect the historical disturbance regime but rather superficial recent biomass removal it was decided that they were uninformative and probably misleading when long term processes were of interest. The indices were therefore ignored in the multivariate analysis presented here. Canopy cover, while an important environmental variable for studies of the distribution of understorey trees, is correlated with the dependent variables of interest and cannot be used in an analysis aimed at explaining the variation in canopy forming tree species themselves. A modelling approach was used in the search for more effective techniques for inferring the link between species composition and disturbance history.

Figure 1.13. Distribution of the three pine species in the *bienes comunales* of Sonora. Note that the shading used for each species is based on the measured basal area in each inventory circle. Shading tones vary with the darkest shading corresponding to the maximum basal area recorded for each species. The scale therefore differs between species.

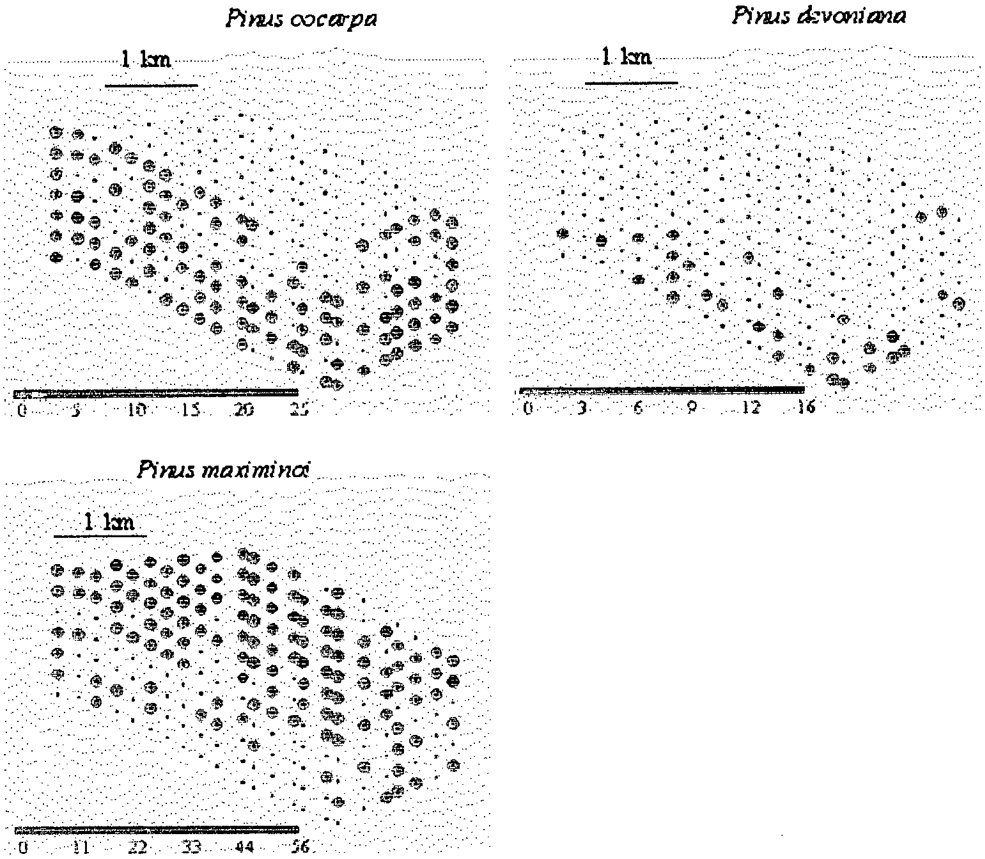


Figure 1.14. Distribution of the two principal oak species in the *bienes comunales* of Sonora. The shading used for each species is based on the measured basal area in each inventory circle.

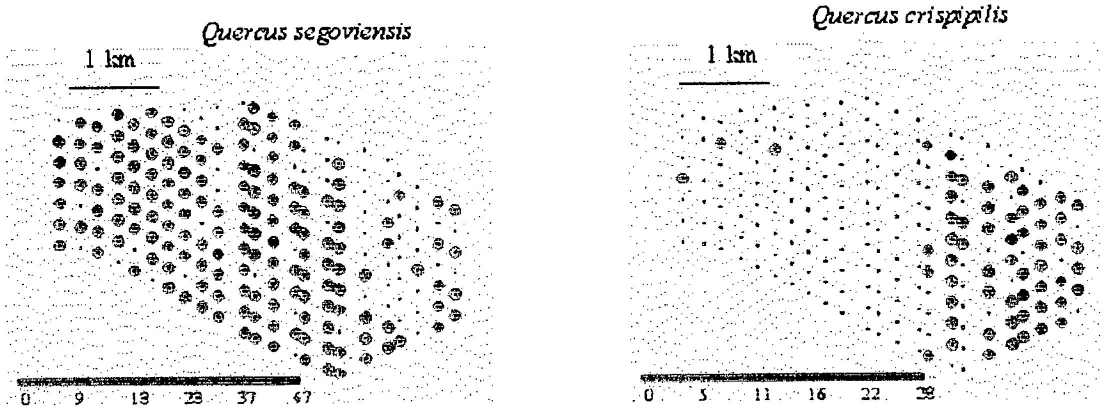


Figure 1.15. Distribution of the two genera with all species pooled in the *bienes comunales* of Sonora. The shading used for each genera is based on the measured basal area in each inventory circle

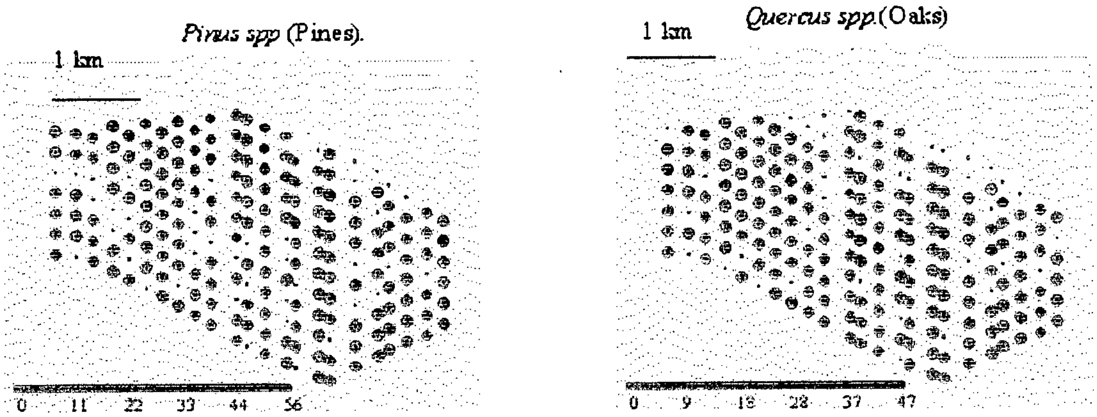
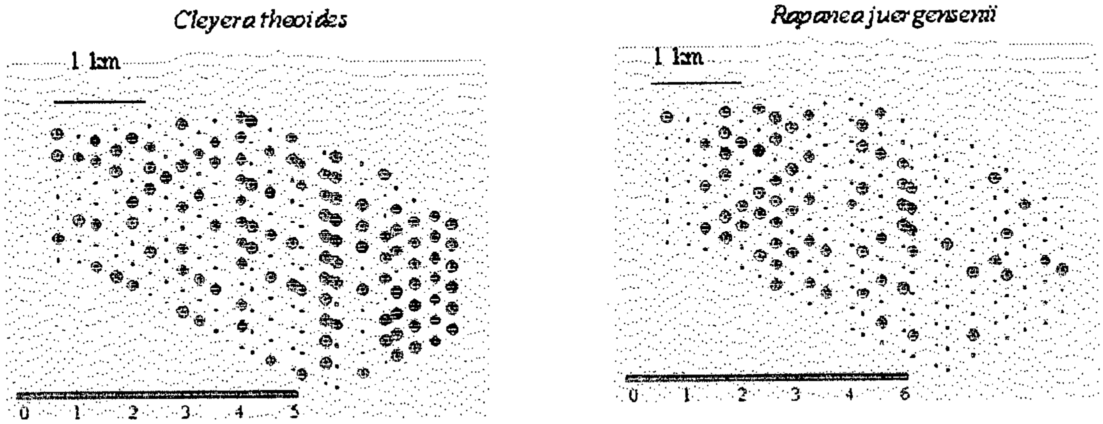


Figure 1.16. Distribution of the two sub canopy species in the *bienes comunales* of Sonora. The shading used is based on the measured basal area in each inventory circle



Maps of the species distributions given in figures 1.14 – 1.16 show a clearly marked spatial segregation between areas in which the pine component consists of *P. devoniana* and *P. oocarpa* and a higher area to the north and east in which *P. maximinoi* is the dominant species. *Q. crispipilis* is more abundant in the eastern section of the area but *Q. segoviensis* is present throughout. When all the species of pines and oaks are combined spatial pattern is less easily perceptible. This visual impression was more formally tested by RDA and CCA which includes a spatial component.

A comparison between CCA and RDA carried out on the log transformed number of stems per circle showed that the efficiency of the two methods for producing ordinations was similar. Both could only explain a small proportion of the total variance in the first two axes, meaning that much of the variability was uncorrelated with the measured environmental variables or with space as represented by a simplified quadratic trend surface model. For RDA the first two canonical axes explained 15.8% of the total variation in species composition against 12.4% when CCA was used. In both cases Monte Carlo permutation tests showed a significant ($p<0.01$) relationship between the combined spatial and environmental variables and species composition. RDA was slightly more efficient in producing an ordination of the data and therefore the results of RDA are reported here, although it should be pointed out that the order of the species scores and the general appearance of the ordination diagrams produced by both techniques were very similar. The results of RDA as an ordination biplot with the four most informative environmental variables retained are shown as figure 1.17. Note that only spatial variables are shown on this plot. This is because after the first two spatial variables are included, residual variation was found to be almost completely uncorrelated with any of the measured environmental factors. This biplot therefore turns out to be useful as a concise summary of the information provided by the maps shown in figures 1.14 – 1.16. Each species of pine and oak is separated in the diagram along one or both of the axes that are associated with the spatial patterns shown by the maps. However it might also be noted as an additional detail provided by the diagram that a comparatively large number of the non pine-oak species are associated in ordination space with *Q. crispipilis*.

The results of forward selection are summarised in tables 1.2, 1.3 and 1.4. The column headed lambda A gives the additional variance in the species data explained by the variable, assuming all other variables are already included in the model. Thus low values for Lambda A suggest redundancy. The p-values show whether any significant proportion of the variance is explained independently by each variable. From the eigenvalues in table 1.2 it can be seen that the model with all spatial terms explains only a small proportion of the variability of the species data, although the first two axes summarise most of the available explained variation. The p values given in table 1.3. suggest that after the x^2 and y terms have been included in the model, the remaining terms are redundant. This emphasises the N-S and E-W spatial pattern. If a unimodal pattern was found several higher order quadratic terms would be expected to be retained. This is because the axis is constrained to be a linear combination of terms and can therefore only represent a parabolic or more complex relationship when higher order terms are combined. If spatially independent environmental variation were present the terms representing non-spatial environmental variation would also be retained. From table 1.4 it can be seen that when spatial elements were not included in the RDA model, altitude became the only significant determinant of species composition, with altitude independent values for slope, aspect and soil depth completely uninformative. Species distribution patterns as depicted by this data set thus had no significant local component. All the variation, which could be explained in the data, was linked to larger scale overlying patterns. To some extent this result may be linked to the nature of the data set and later in this study it will be contrasted with the distribution of smaller woody species and shrubs, which does have a marked local component (chapter 3).

Figure 1.17. CCA biplot including the four best explanatory variables. These are all spatial terms produced from the quadratic terms of the plot's Cartesian co-ordinates. The diagram can thus be interpreted in terms of two superimposed second order polynomial trend surfaces. Scaling is focused on inter species correlations and centring is by species. Note that the labels attached to the points are composed of the first four letters of each half of the binomial. Thus Pinudevo = *Pinus devoniana*. See appendix 1 for a full species list and authors.

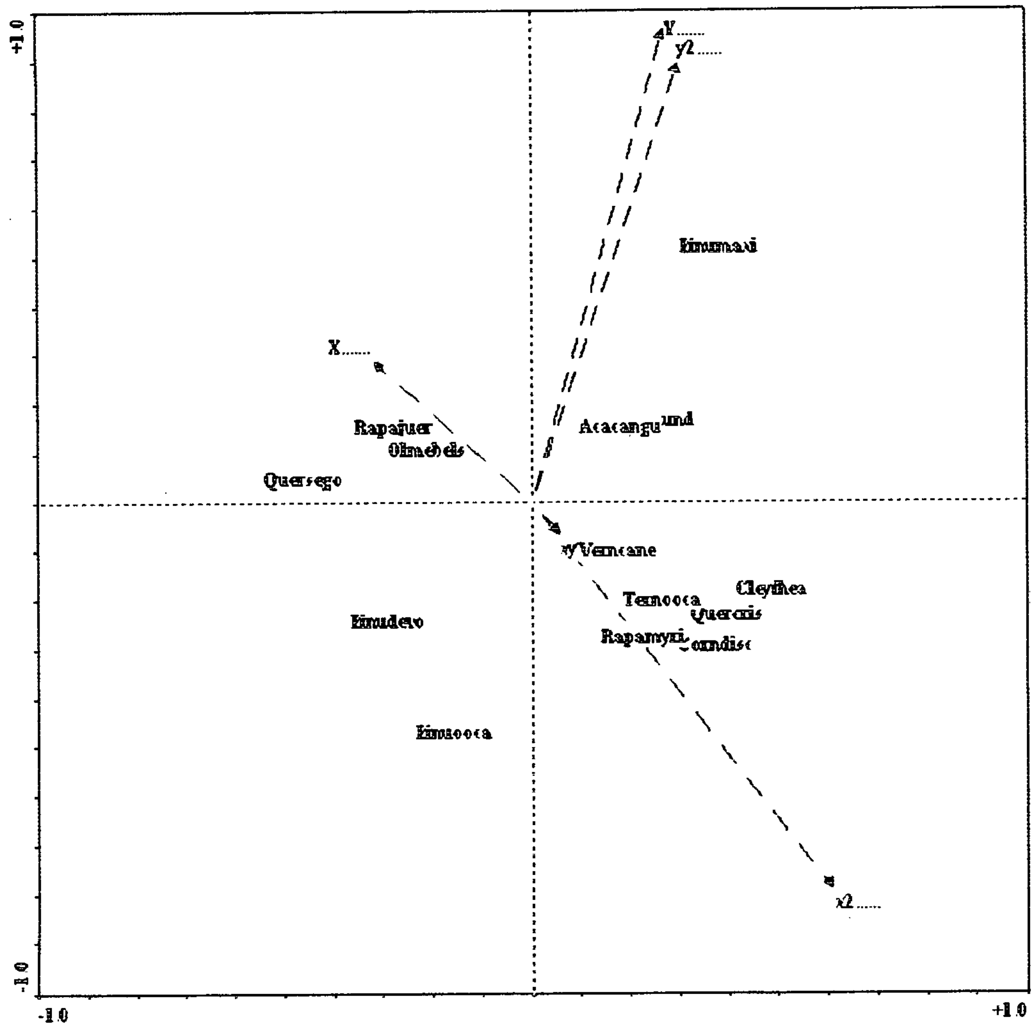


Table 1.2. Summary statistics for the full RDA model which included all environmental variables including spatial terms. The first two axes explain most of the variance in the species-environment relationship.

Axes	1	2	3	4	Total inertia
Eigenvalues :	0 .219	0 .161	0.024	0.016	0. 2397
Species-environment correlations :	0 .670	0 .691	0 .328	0 .291	
Cumulative percentage variance:					
…… of species data	9.1	15.8	16.9	17.5	
…… of species-environment relation:	51.7	89.6	95.3	99.1	

Table 1.3. Results of forward selection on all environmental variables in a combined RDA model in which spatial terms and environmental terms are included. Note that only the first two terms are significant in the full model.

Variable	Lambda A	P	F
x2	0.07	0.005	15.7
Y	0.08	0.005	20.5
y2	0.01	0.3	1.11
X	0.00	0.4	0.91
XY	0.01	0.4	0.85
Altitude	0.01	0.5	0.23
Soil depth	0.00	0.6	0.07
Slope	0.00	0.6	0.05
Aspect+slope	0.00	0.6	0.02
Aspect	0.00	0.6	0.02

Table 1.4. Results of forward selection on a model with spatial effects removed. Only altitude explains a significant proportion of the variation.

Variable	Lambda A	P	F
Altitude	0.08	0.007	17.2
Soil depth	0.01	0.2	1.56
Aspect+slope	0.01	0.2	1.08
Slope	0.00	0.3	0.95
Aspect	0.00	0.4	0.67

There was a weak but significant positive correlation between the number of oak stems in a plot and the number of pine stems ($R= 0.155$ $R^2= .024$ Adjusted $R^2= 0.0193$ $F(1,207)=5.1090$ $p<0.0248$). Figure 1.18 shows the large amount of variation found in these values. No fitted line has been added to allow patterns not connected with measures of central tendency to be perceived. For example it could be noted from the scatter of points that the pattern shown by the maximum values of pine and oak stems suggests a negative relationship between numbers of pines and oaks at very high densities. This is also suggested by the scatter of points produced when oak basal areas are plotted against pine basal areas as shown in figure 1.19. In the case of basal area no significant correlation is found ($R=0\ .0326$ $R^2= 0.00106$ Adjusted $R^2= -F(1,207)=0.220$ $p<0.63$). The pattern shown in figure 1.19 suggests that this may be because pine basal area is positively correlated with oak basal area in under stocked plots and negatively correlated in plots with a higher density of stems.

Pine basal area was strongly positively correlated with the number of pine stems $R=0\ .667$ $R^2=0\ .449$. Adjusted $R^2=0\ .446$ $F(1,207)=168.55$ $p<0.00001$. The pattern of scatter around this relationship is shown in figure 1.21. Oak basal areas was also very strongly positively correlated with the number of oak stems $R= 0.614$ $R^2=0\ .377$ Adjusted $R^2=0\ .374$ $F(1,207)=125.35$ $p<0.00001$ as shown in figure 1.20. Additionally the total basal area in each plot was positively correlated with the total number of stems $R=0\ .773$ $R^2= 0.597$ Adjusted $R^2= 0.595$, $F(1,207)=307.81$ $p<0.00001$. No indication of any negative relationships between basal area and stem density at high densities is apparent in the data. The correlations between the species groups are summarised in table 1.5.

Figures 1.21 and 1.22 show the frequency distribution of pine and oak basal areas. There are comparatively more plots with high pine basal areas than high oak basal area. Figure 1.23

shows the frequency of plots divided by a simple classification scheme. Plots are given the classification pine-oak if pine comprised the highest basal area, oak-pine if oak comprised the highest basal area and oak or pine if basal area of the second group was below 2 m^2 ha^{-1}.

Pine-oak	Pine BA> Oak BA (oak BA > 2 m^2 ha^{-1})
Oak-Pine	Pine BA< Oak BA (Pine BA > 2 m^2 ha^{-1})
Pine	PineBA> Oak BA (oak BA < 2 m^2 ha^{-})
Oak	OakBA< Oak BA (Pine BA < 2 m^2 ha^{-1})

The frequency distribution diagram produced by this classification shows that most plots contain a very intimate mixture of pines and oaks, with pines slightly more likely to be the dominant group.

Size class histograms reveal an unusual pattern. Size classes of all tree species combined show an approximation to the reverse J relationship often assumed by foresters as representing the situation in many natural forests with adequate regeneration. However the distribution of the pine size classes have a unimodal pattern with the highest number of stems falling in the ten to twenty cm diameter classes. The pattern was particularly striking for *P. maximino*i, found in the slightly more remote areas of the site.

Figure 1.18 Scatterplot of density of oak stems against density of pine stems for 223 plots of 500 m^2 in the *bienes comunales* of Sonora

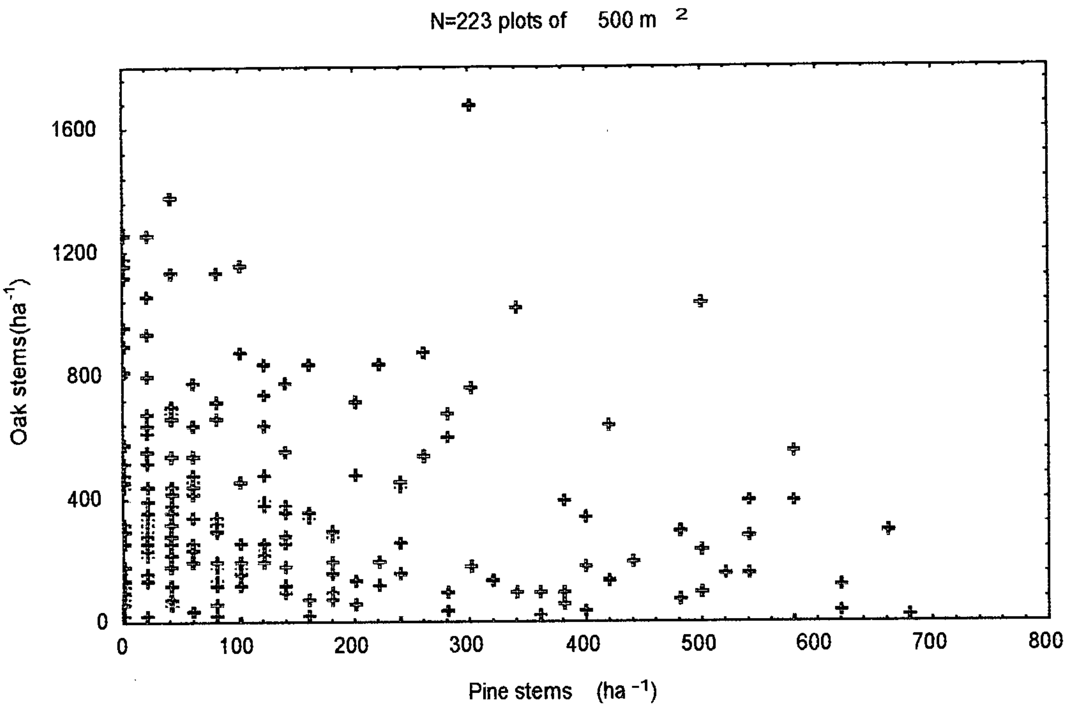


Figure 1.19. Scatterplot of basal area of oak against basal area of pine for 223 plots of 500 m^2 in the bienes comunales of Sonora.

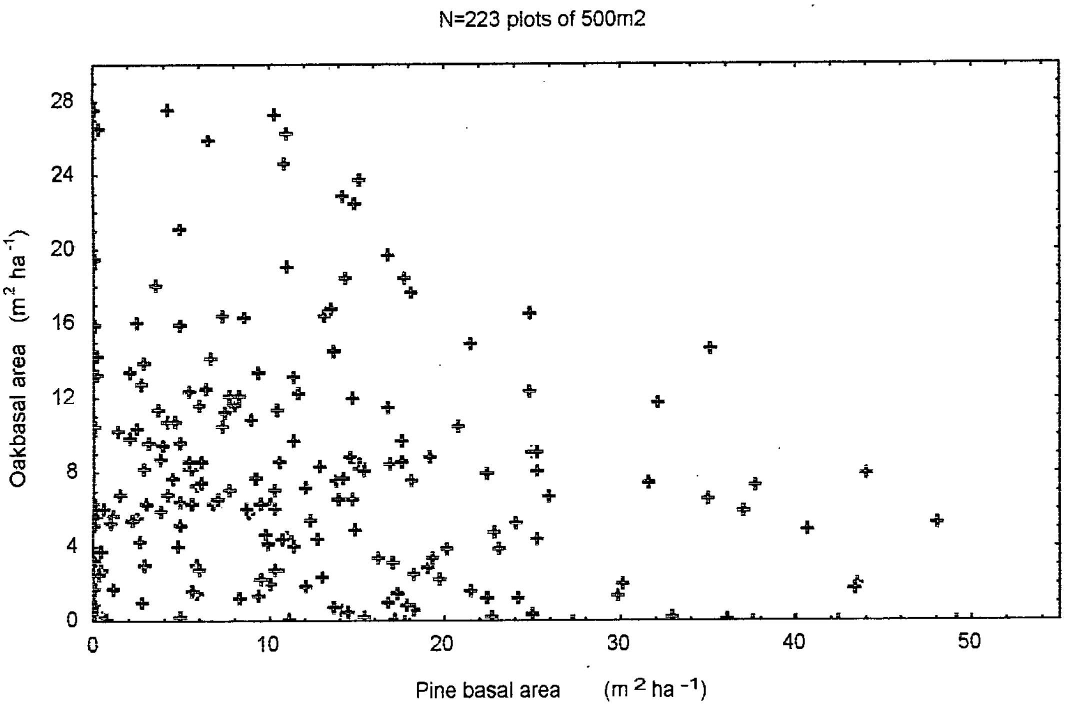


Figure 1.20 Scatterplot of basal area of oak against density of oak stems for 223 plots of 500 m^2 in the bienes comunales of Sonora

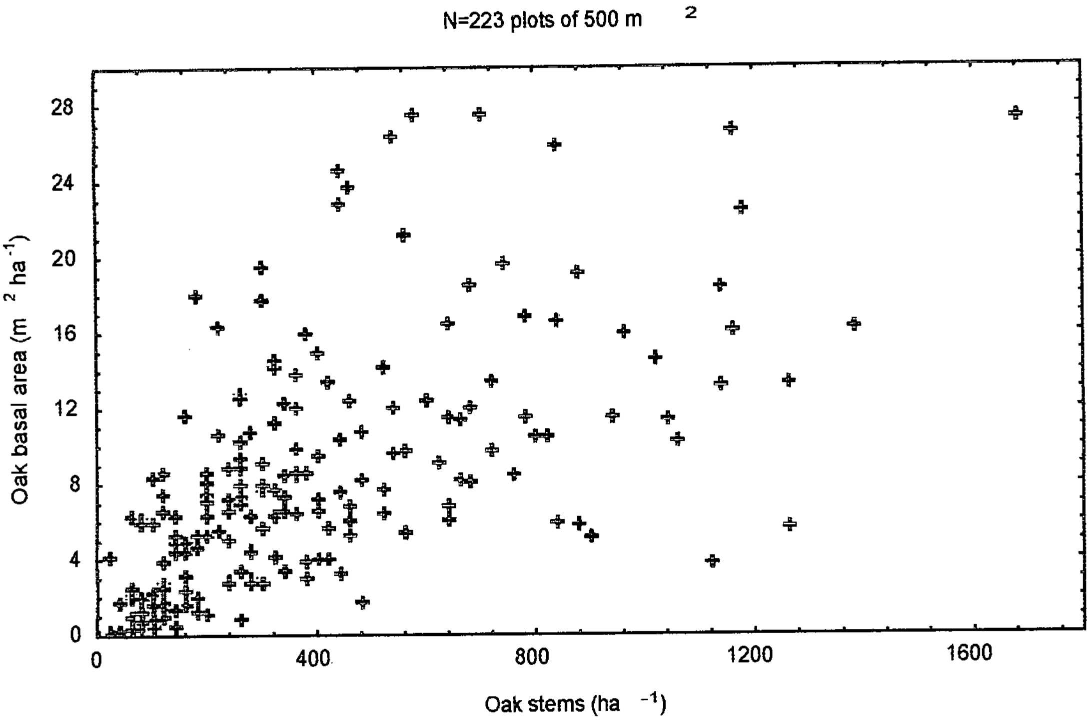


Figure 1.21 Scatterplot of basal area of pine against density of pine stems for 223 plots of 500 m^2 in the bienes comunales of Sonora

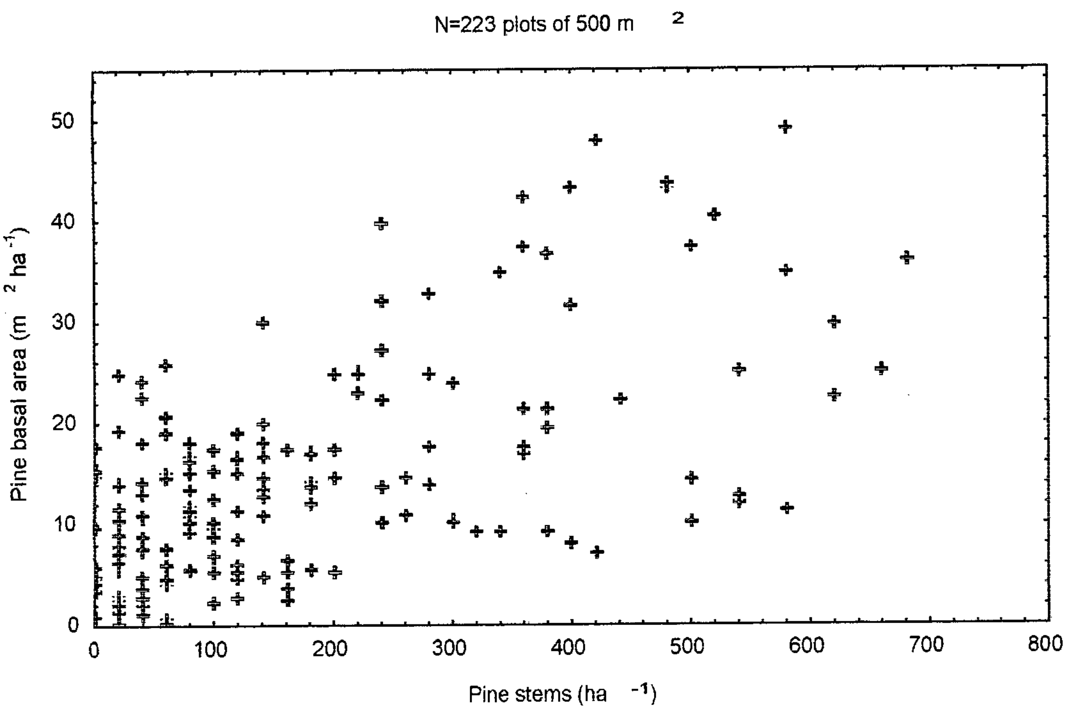


Figure 1.22 Scatterplot of basal area of all species against of stems of all species for 223 plots of 500 m^2 in the bienes comunales of Sonora

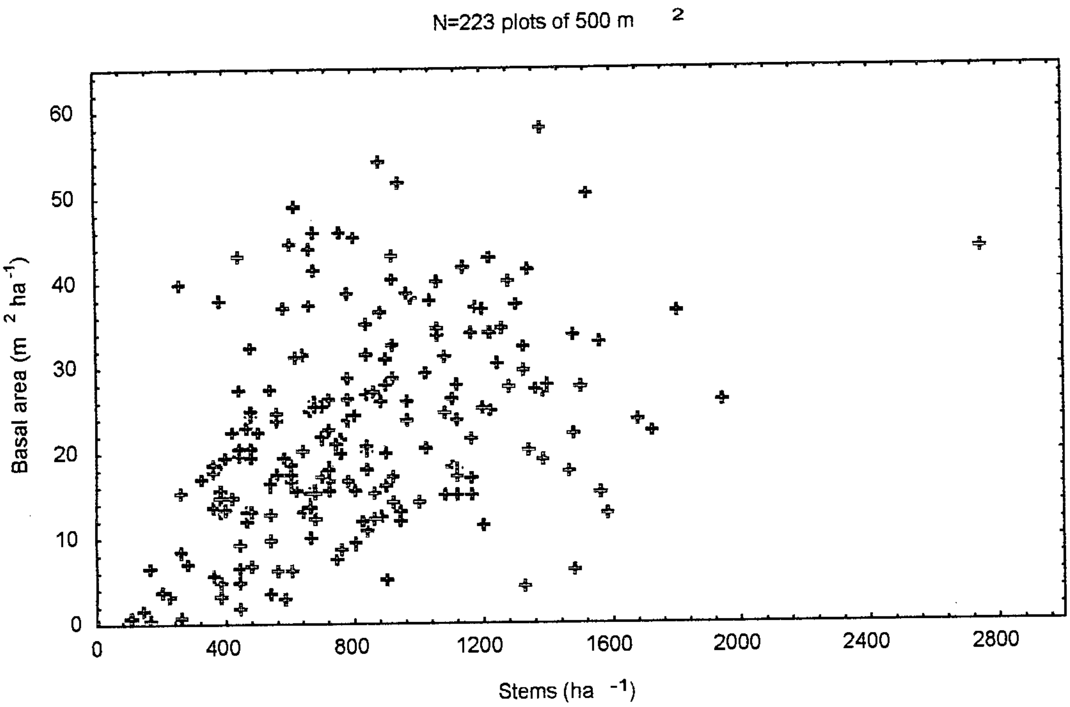


Table 1.5 Correlation coefficients between stems and basal areas of each species group. Significant correlations ($p<0.05$) are shown in bold.

	Pine stems	Oak stems	Pine basal area	Oak basal area
Pine stems	1.00	-0.16	0.67	-0.09
Oak stems		1.00	-0.22	0.61
Pine basal area			1.00	-0.03

Figure 1.21 Frequency distribution for oak basal area

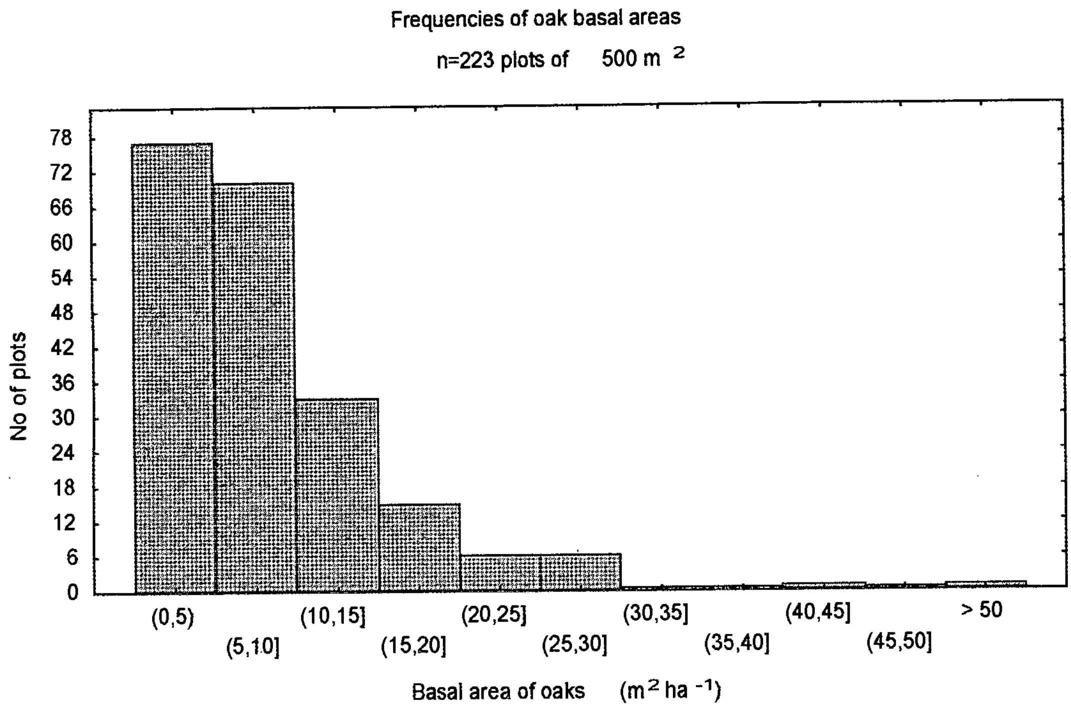


Figure 1.22 Frequency distribution for pine basal area.

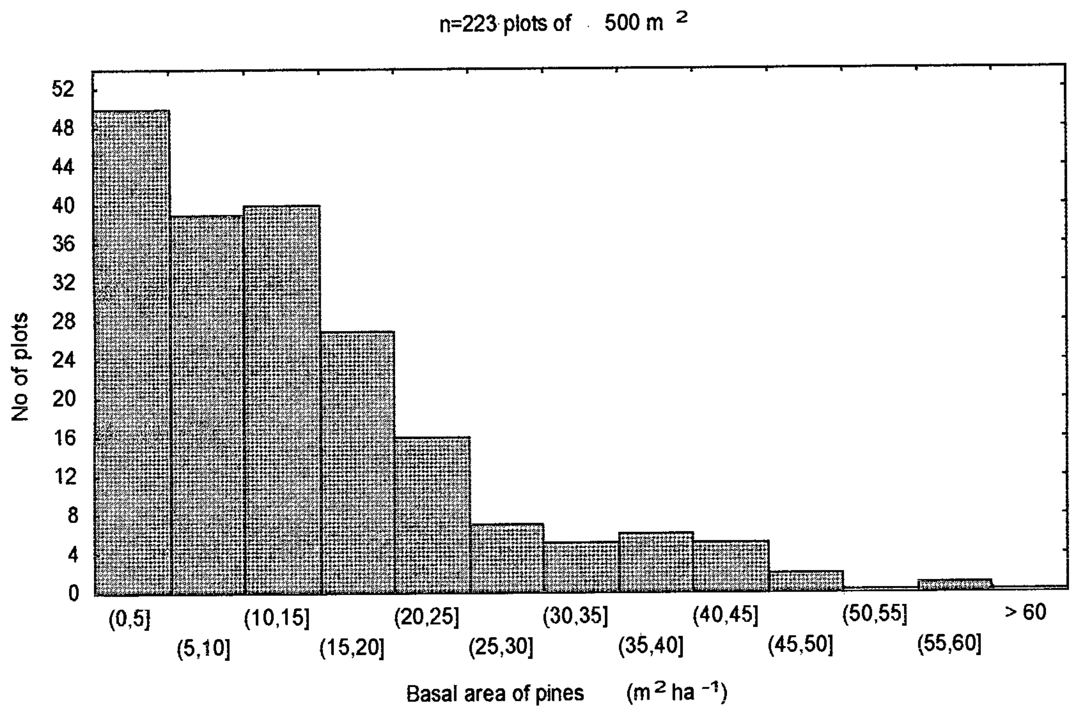


Figure 1.23 Numbers of inventory plots divided into five categories based on relative abundance

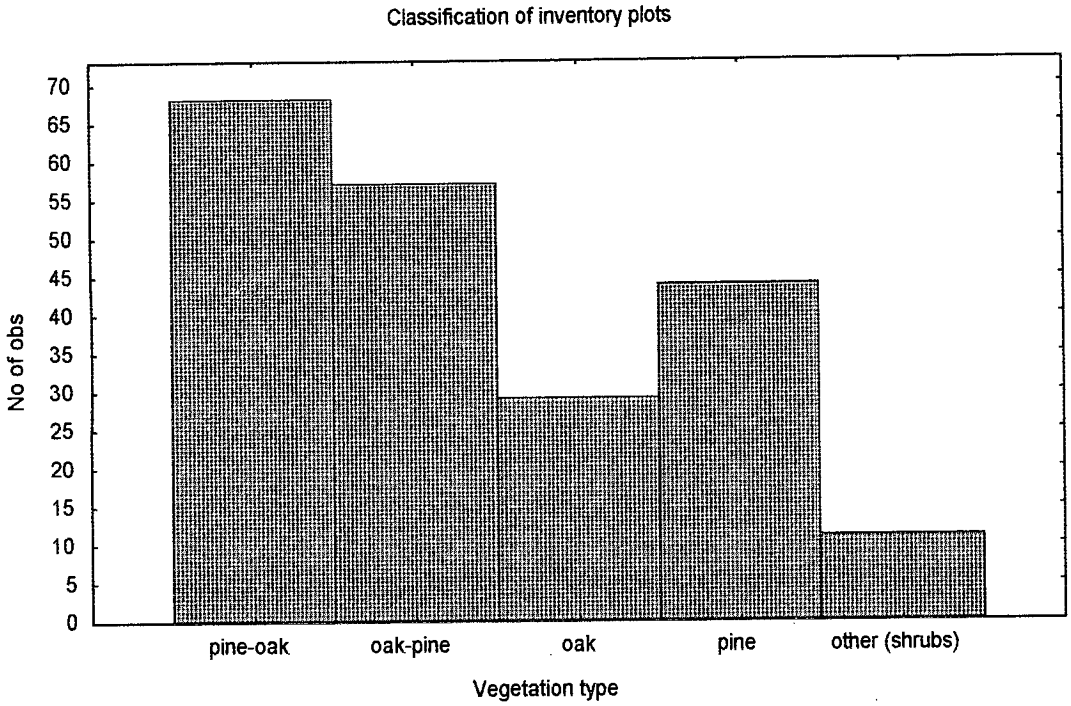


Figure 1.24 a to i. Histograms showing the diameter distribution for the principal species at the site.

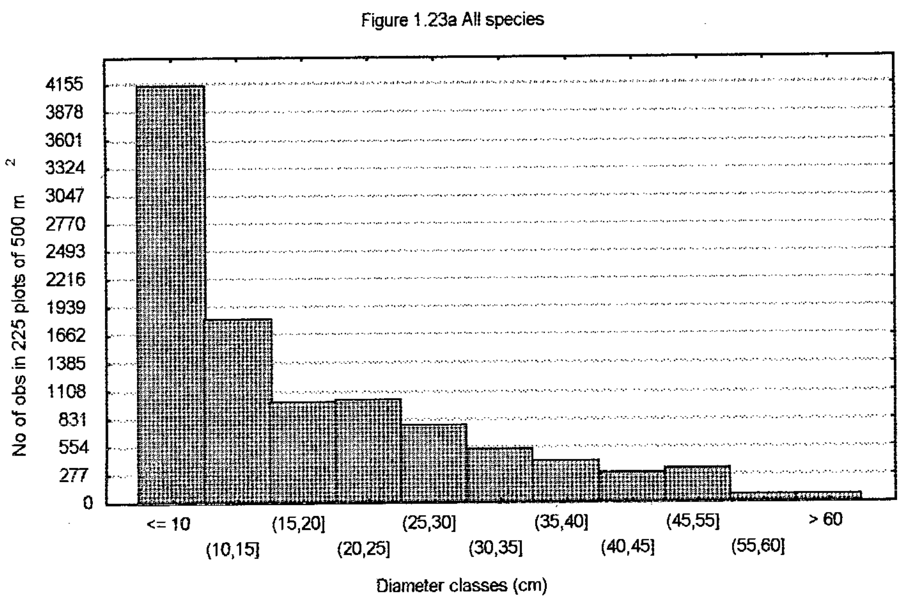


Figure 1.23b Oaks

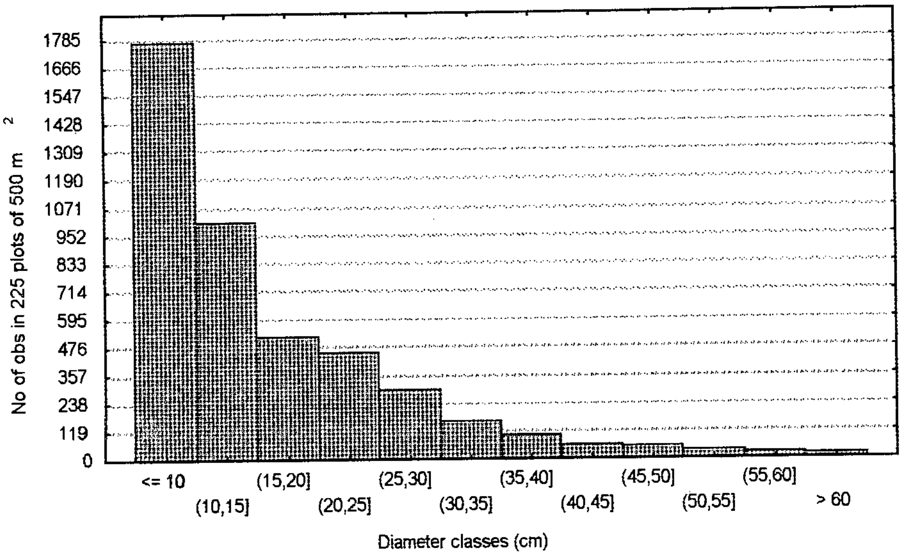


Figure 1.23c Pines

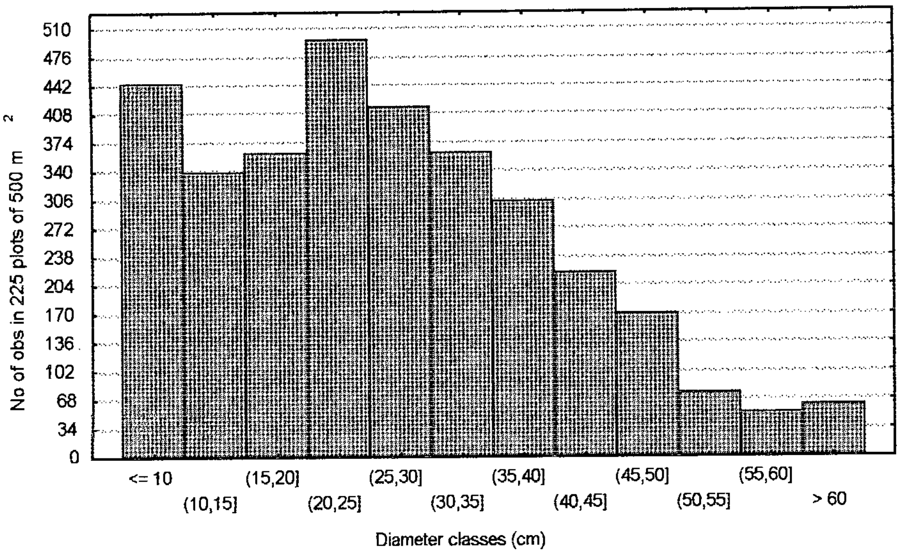


Figure 1.23d *P. devoniana*

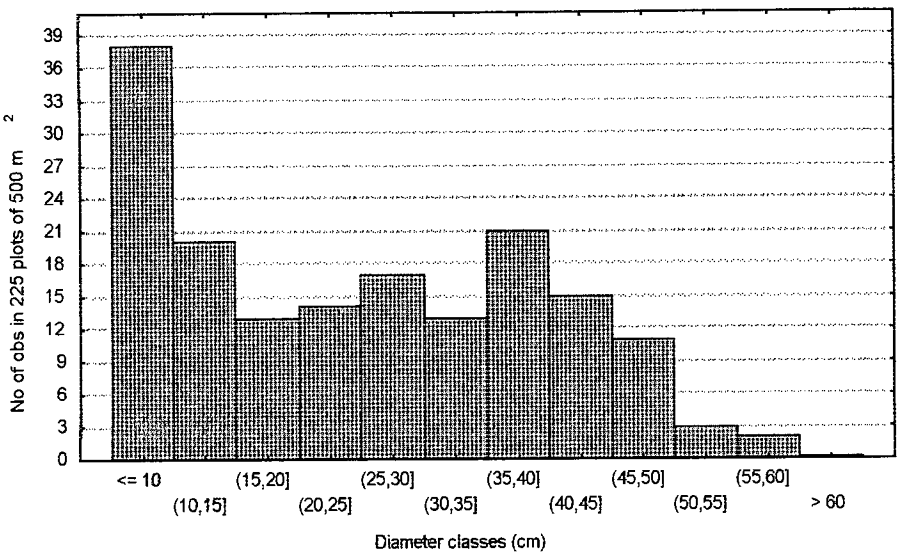


Figure 1.23e *P. oocarpa*

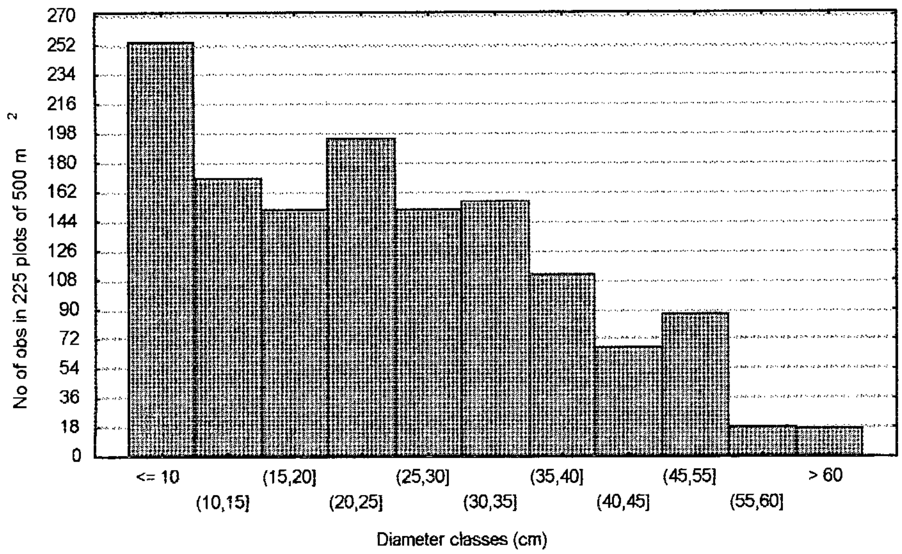


Figure 1.23f *P. maximinoi*

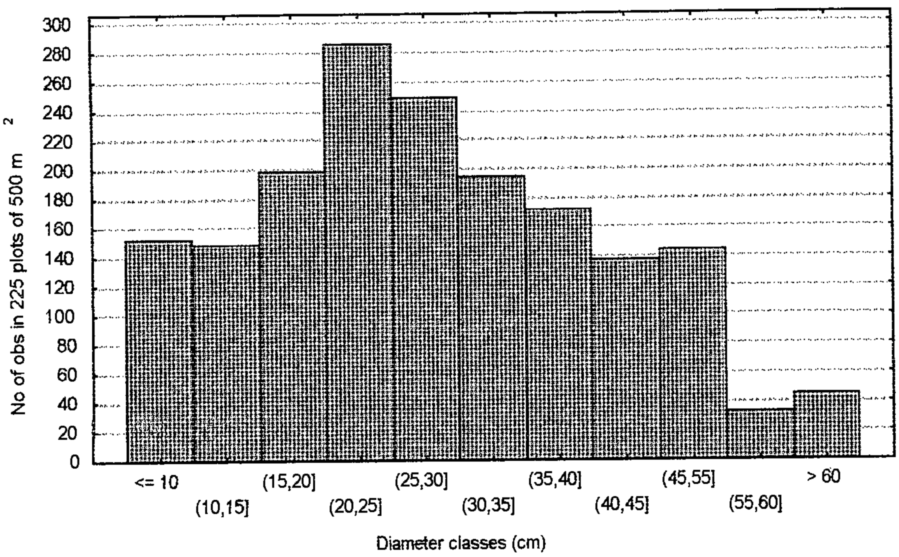


Figure 1.23g *Q. segoviensis*

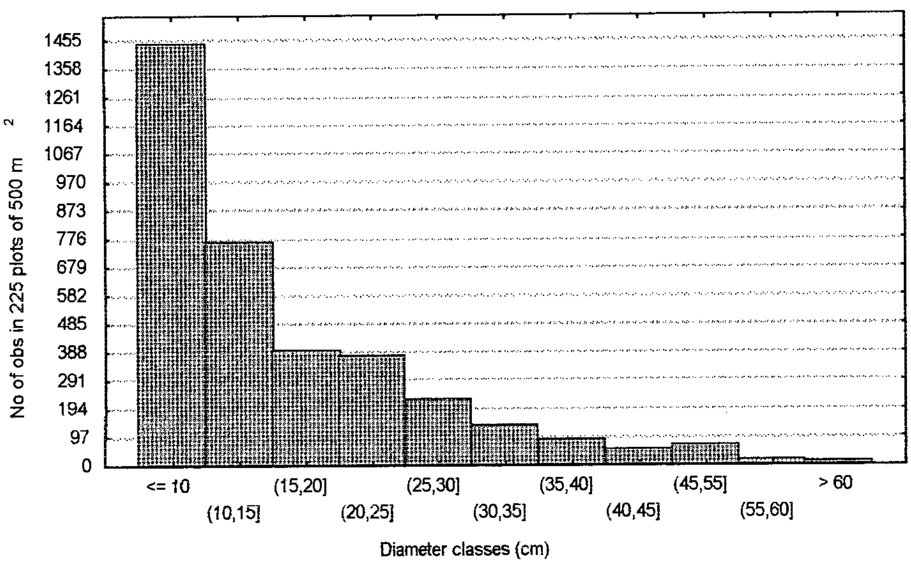


Figure 1.23h *Q. crispipilis*

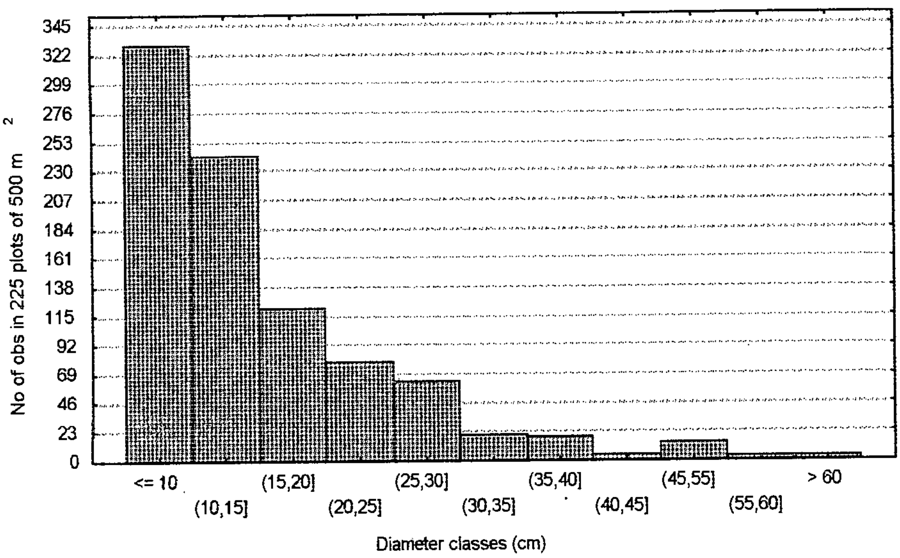


Figure 1.23i *Cleyera theoides*

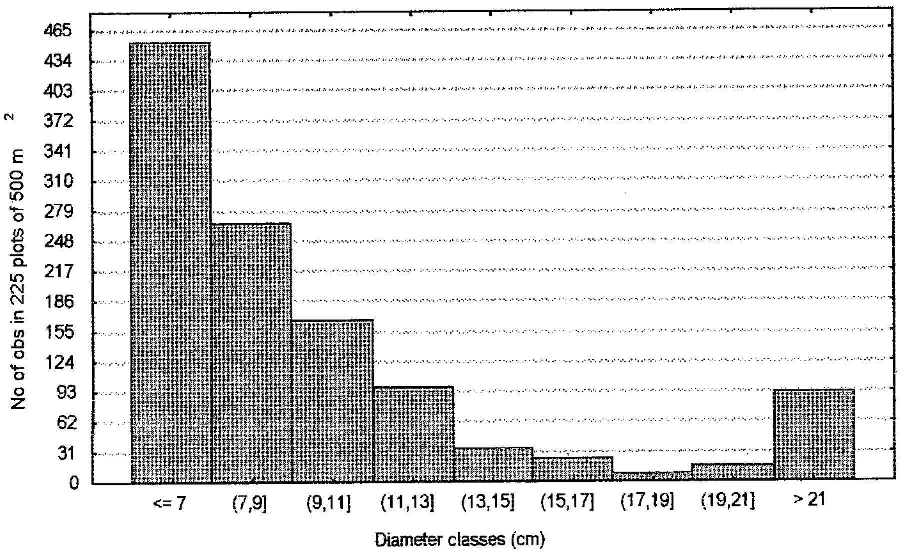
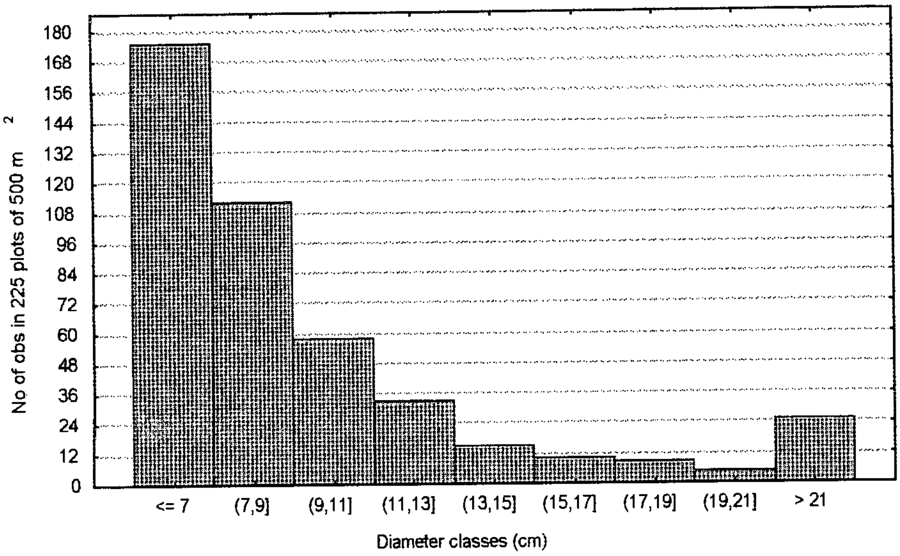


Figure 1.23j *Rapanea juergensenii*



Discussion

Methodological considerations

Simple maps of species distribution proved extremely useful in showing the level of true replication in the data set, preventing spurious interpretation of non independent data and displaying the subtleties of species distribution patterns (Driese *et al.* 1997). In some respects the maps were more effective in communicating information than multivariate analysis. Visualisation of spatial data is becoming increasingly more sophisticated as software development makes greater use of available computer power (e.g. Hu 1999). Visualisation of data in this way is not only useful for management purposes; it can also serve as a research tool, particularly when combined with a spatially based statistical analysis. Remotely sensed data cannot as yet trace intrageneric patterns of species distribution, thus the patterns shown here would not appear without extensive ground based surveying. However it may be informative to combine such data with remotely sensed information in future studies.

The statistical analysis of spatial effects in the data is an essential starting point in understanding vegetation dynamics. However spatial autocorrelation is often regarded as an undesirable phenomenon. Where it occurs the degree of independence between data points is not under the control of the researcher and cannot be easily removed through altering survey methodology. Systematic sampling always produces data points with co-ordinates, which are non-independent. However it is the spatial pattern of the phenomenon of interest that converts this lack of spatial independence into a lack of statistical independence. The problem is not avoided by random quadrat placement. Legendre (1993) believes this has often been overlooked or even that the consequences are widely misunderstood. He remarks that the extent of naturally occurring underlying spatial autocorrelation "*may come as a surprise to ecologists who have been trained in the belief that nature follows the assumptions of classical statistics, one of them being the independence of observations.*"

The problem caused by spatial autocorrelation is one of pseudo-replication (Hurlbert 1984) In such a case pseudoreplication is not due to faults in survey design. It is an inevitable consequence of a lack of naturally occurring independently replicated combinations of environmental variables within the area available for study. Both spatial autocorrelation and the non orthogonality of environmental variables potentially invalidate or confound the interpretation of many conventional statistical tests. Randomised quadrat placement cannot remove underlying spatial dependence and can lead to its effects being overlooked (Pielou 1969). Conversely if no underlying spatial pattern exists then systematic spatial positioning of quadrats of itself does not necessarily lead to any violation of statistical assumptions and has the advantage of allowing the lack of a purely spatial pattern to be revealed. Systematically collected data can then, if this were the case, be treated as if they were the product of random sampling when investigating species-environment relationships (Hayek and Buzas 1997). If spatial pattern is known to occur prior to sampling many problems can be avoided through prior stratification. This was not possible for the data set. Thus while the inventory consisted of a very large number of points, for some forms of inference it reduced to a single unreplicated observation. Provided this is accepted the data can be correctly interpreted and are of intrinsic interest. Inferences may be drawn, but can not be generalised through statistical tests of their significance.

Implications

The results describe a species poor but structurally heterogeneous forest. In general terms the reason for the low basal areas and open nature of the forest is not in doubt. It is attributable to the effects of the range of anthropogenic disturbances that have been documented throughout the highlands of Chiapas (Gonzalez- Espinosa *et al.* 1991; Ochoa-Gaona and Gonzalez-Espinosa 1999). Further lines of evidence are presented throughout this work to support this assertion. The striking lack of almost any large individuals of the two oak species, which are known to reach diameters in excess of 1 m, immediately suggests that historical disturbance has affected almost the entire site. The only alternative hypothesis is that edaphic conditions are so poor that oaks cannot reach their full potential. This is considered unlikely, although it cannot be fully ruled out. However it is not clear from the data alone which forms of disturbance have been most influential. The search for an explanatory model will form part of the work in subsequent chapters. It is also unclear how underlying heterogeneity in soils, microclimate and slope may have combined with the effects of disturbance to produce these patterns.

The data suggest that the use of a broad division of tree species into pines and oaks is a potentially powerful heuristic device. This division has been used by other researchers to produce verbal models of pine oak dynamics (Williamson and Black 1981; Barton 1999). Such a division simplifies modelling, data analysis and the communication of descriptive results and hypotheses. It also permits generalisation of conclusions drawn from data and models to a wider context of pine-oak woodlands with differing species mixes and allows studies to draw on a broader range of available literature. For the rest of this work where pines and oaks have been pooled, the term "pines" refers to *P. maximinoi*, *P. oocarpa* and *P. devoniana*. The term "oaks" refers to *Q. crispipilis* and *Q. segoviensis*. Though based on genera , in the context of the modelling approach adopted these are best considered as being divisions between functional groups (Noble and Gitay 1996). The use of this generalisation has however been approached with care as significant differences in functional attributes does also exist within each genera. These differences are discussed in later chapters and it was desirable to include the details of such variation in models even though the results reported may where convenient be summarised in terms of the dynamic between pines and oaks.

An hypothesis suggested by these results is that the relative abundance of pines and oaks is determined by processes involving disturbance, while intrageneric distribution patterns are linked to edaphic or microclimatic factors. However the results provide only indirect guidance as to the nature of these relationships. Forest species composition elsewhere has often been found to be linked to environmental factors such as aspect (Klemmedson and Wienhold 1991), slope (Ziegler 1998), soil (Barrett *et al.* 1991) or climate (Prentice, Sykes and Kramer 1991). It could be assumed that some such relationships should have been revealed by multivariate analysis. However apart from a very clear spatial effect, a consistent pattern of relationships between environmental variables and species composition did not emerge. This completely unexpected failure of multivariate techniques to explain between patch variation may be because such variation is linked to factors, which were not measured (though see Okland 1999 for a alternative explanation for the failure of multivariate analyses to explain variation). Further work aimed at producing a more detailed description of the soils of the area is required if the basis of the spatial separation between the species is to be fully understood. A detailed comparison of the nature of the differences between the south eastern area in which *Q. crispipilis* dominates and the areas in which the species is less common would be informative. It might also be productive to combine this data set with observations taken from other sites. As altitude was linked in part with the spatial pattern it may be that the slightly cooler moister conditions found on higher slopes favour *Q. crispipilis* over *Q. segoviensis* and *P. maximinoi* over *P. oocarpa* and *P. devoniana*. Such an explanation is consistent with attitudinally linked patterns found elsewhere (Ramirez-Marcial unpublished data). However it should be noted that the range in altitude at this site is not great when consideration is made of the large area the site covers. Because of more abrupt topography similar sized forest areas on hillsides in the central highlands and North of Chiapas usually cover a much greater altitudinal range.

Despite this broad spatial separation in range the two oak species mix freely within many patches where *Q. crispipilis* occurs, suggesting that any differences between their ecological optima are subtle. Observations both at this site and in surrounding areas that *Q. segoviensis* may be rather more abundant on shallower rocky soils (Alvarez-Moctezuma 1999). The two oak species do differ notably in both leaf morphology and architecture. *Q. crispipilis* has narrower leaves and taller, straighter boles. Future work should clarify many of these questions. Ordination of vegetation data is most effective when used as a confirmatory technique, where previous observations have suggested a pattern to be documented (Peet 1980; Mucina 1997). Detection of pattern through "*data diving*" (Hallgren, Palmer and Milberg 1999) is more challenging. The overwhelming confounding effects of disturbance must also be taken into account when considering the failure of multivariate techniques to clearly detect the effect of environmental variation. Disturbance does not only confound patterns through altering physiognomic and structural characteristics but may also alter large-scale species distribution patterns in pine-oak forests (Frelich and Reich 1995; Flannigan and Bergeron 1998; Foster Motzkin and Slater 1998; Brosofske *et al.* 1999). An important effect that must be taken into consideration is that where human intervention occurs it tends to be concentrated on areas with deeper soils on which a denser forest would be likely to form in the absence of disturbance. Under such circumstances statistical analyses based on the comparison of measures of central tendency will fail. Extreme values may be more informative, but few formal procedures are available which permit their rigorous analysis.

The spatial separation between pine species followed a different line to that found for oaks. This also led in part to the failure of ordination techniques to resolve the data into discrete "communities" based on dominant species. The observation is however of great interest as it suggests that different processes may be shaping intrageneric patterns of pine distribution to those affecting oaks. The area to the south of the bienes comunales consists of an open pine savannah with very few oaks. This savannah has formed on soils that are lighter, deeper and freer drained than the study area. The openness of the savannah is maintained by extremely frequent (two to three year recurrence) ground fire set to improve pasture quality. This savannah is a rather different system to the area of bienes comunales, but there seems to be an edge effect occurring. Frequent fires favour *P. oocarpa* and *P. devoniana* over *P. maximinoi* (see chapter 2) and these species may be spreading into the bienes comunales from the south.

An important clue to understanding the nature of the dynamic between pines and oaks at this site is provided by the relationship between basal area and the number of stems. The typical relationship found in unthinned forestry plantations is a negative correlation between basal area or biomass, and the number of stems, often assumed to be derived from the log (-2/3) relationship between the number of survivors and mean weight referred to as the self thinning rule (Yoda *et al.* 1963; Westoby 1984; McFadden and Oliver 1988). Self thinning and shade dependent sapling mortality occurs in natural forests with abundant regeneration (Kobe *et al* 1995; Kobe 1996). However at this site there were very strong positive relationships between stem densities and basal area. Patches with mature trees and a high basal area also contain more stems. This suggests that regeneration following disturbance occurs gradually and does not attain the densities at which self thinning occurs. One form of disturbance that appears likely to lead to such an effect is slash and burn clearance, especially if combined with grazing which prevents dense regeneration. Ground fire has also been found to lower the slope of the thinning curve (Huddle and Pallardy 1996; Fule and Covington 1998; Wirth *et al.* 1999) although classical self thinning has also been assumed when modelling fire prone pine forests (Somers and Farrar 1991).

Lack of a negative correlation between pine basal area and oak basal area suggests that competition for locally scarce resources such as light has not played an immediately important role in structuring the balance between these two groups in the present forest. Space and the access to resources that space implies is not clearly partitioned between pines and oaks. This does not imply that differential patterns of resource usage need not be included in process based models of this type of forest. The likely mechanisms for local coexistence are differences in shade tolerance (Canham *et al.* 1996), height growth (Fajvan and Seymour1993) and below ground resource usage. These differences may become critical when undisturbed succession is allowed to proceed and may form the basis for process based modelling of this system that can be used to project future change.

Whether ground fires, previous slash and burn clearance or fuelwood gathering are responsible for the open canopy and lack of self thinning is not immediately clear. Timber harvesting can however be ruled out as the principal cause of the disturbed forest structure. Timber harvesting does not affect oaks, yet most oaks were small. Furthermore stumps of recently felled pines were extremely rare in all areas beyond the immediate vicinity of access roads. The visual impression caused by the ground fires, which affected the area immediately prior to the survey being carried out (see chapter 2), led to the initial hypothesis that such events were overwhelming determinants of forest structure. However such fires may be less frequent than first believed and their impact less dramatic than it appears. Slash and burn clearance for agriculture cannot be equated with wild fire in either its spatial extent or the intensity of impact and has been regarded as a very distinctive form of disturbance for the purpose of this study. A comparable situation may perhaps be found in some pine-oak forests in the southern United States where earlier assumptions concerning the role of wildfire in maintaining open understoreys have recently been questioned (Bratton and Miller 1994). Open structural characteristic here have been attributed to the persisting effect of anthropogenic disturbance for agriculture. Grazing following canopy opening is known to be an important factor in maintaining the open stand structure (Belsky and Blumenthal 1997).

A further clue to the nature of the historical disturbance regime is given by the unusual distribution of pine size classes. There are a higher number of intermediate sized pines than small saplings. This may be due to destruction of small pines by the fire prior to the inventory. However few pines were completely consumed by the fire and dead trees were included in the inventory. An alternative explanation is that pine regeneration has been weak in recent years and that conditions favouring pine regeneration were more favourable previously. Low level chronic disturbance, which reduces establishment rates, such as grazing or ground fire, may have increased and infrequent intense stand initiating disturbance may not have occurred in recent years.

Timber extraction has certainly had some influence on forest structure, but to date it appears a comparatively unimportant factor at this particular site. The effects of extremely selective timber extraction have undoubtedly reduced the numbers of very large pines. The concentration of pine basal area and the occurrence of areas of forest with dense pine overstorey and few or no oaks in the northernmost, least accessible areas of the field site suggests strongly that timber extraction has played a role in shaping the composition and physiognomy of accessible areas of forest and could have possibly led to increased dominance of oaks in areas where extraction has been most intense. Timber extraction from the northern area is difficult or impossible because of the abrupt terrain and distance from roads. However even within this area many patches of forest have very low basal areas and are dominated by small trees. These are the result of recent slash and burn clearance followed by abandonment to successional processes. Large numbers of decaying felled trunks of pines are present in some of these clearings. The volume of decaying pine timber estimated in one plot was in excess of 200 m^3 ha^{-1}. No currently used maize fields are found within this area of the *bienes comunales*. An explanation for these observations is provided in chapter 4 of this work.

Conclusion

The forest is open, heterogeneous, species poor and mainly composed of rather small trees. Intrageneric spatial segregation of pines and oaks is not well explained by measured variables. Oak species and pine species segregate along different spatial axes. No clear pattern in the relative abundances of pines and oaks is apparent and considerable patch scale variability occurs.

There appear to be two patterns that are superimposed at this site. One is due to temporary clearance for slash and burn agriculture which causes discrete and dramatic canopy opening events. Such events reset a short successional sequence at a local level and lead to a form of coarse scale mosaic which is perceived when the spatial distribution of basal area is mapped. This form of disturbance does not seem to explain the underlying pattern of species ditribution that might be due to edaphic factors that were not measured, or more directly linked to the effect of altitude on climate. However the effect of chronic disturbance in forming spatial pattern is not ruled out. It is thought that chronic disturbance could have subtle effects, some of which may produce long lasting patterns and may even change intrageneric distribution patterns. Ground fires, grazing, timber extraction and fuelwood gathering may all be forms of chronic disturbance which do not result in complete canopy removal but may shape the spatial distribution of the species at the site. The evidence available from the description provided here is insufficient to confirm these speculations. They will be both extended and challenged through the modelling approach adopted in later chapters.

1:3 Patch level structure and dynamic

Introduction.

In order to complement the site description given in the last section of this chapter detailed permanent monitoring of a sub set of representative patches of forest commenced at the site in 1999. The preliminary results from this monitoring are presented both in order to provide a description of the vertical and horizontal structure at a patch scale and to allow a provisional estimate of site productivity to be made. The importance of the data taken from the permanent sample plots (PSPs) will increase as a longer time series of observations becomes available and will, with time, provide a basis for reliable calibration of an empirical yield model. Oaks at the site do not produce legible growth rings. This makes any available information on their growth rates particularly important for modelling purposes. As all the plots were affected by ground fire in 1998 the most immediate interest lay in recording fire induced mortality that has been reported in Chapter 2. However the following questions have also been addressed.

1. Do pines and oaks form distinct vertical strata?
2. How great is the difference in growth rate between pines and oaks?
3. How much variation in growth rate can be detected between the separate species of pine and oak?
4. How much between patch level variation in growth rates can be detected?
5. Is between patch level variation in the growth rates of pines and oaks correlated?
6. What is the productivity of the site in terms of above-ground biomass?

In addition the opportunity was taken to estimate allometric parameters used later for modelling.

Method

Twenty five permanent sample plots (PSPs) were established. The PSPs were not intended to represent a completely random sample taken from the whole forest. They were selected as being representative of the range of conditions found in the forested area. The intention when the plots were established was to stratify sites by disturbance types and time since disturbance. However it became clear as work progressed that most sites had suffered similar disturbance, but had been disturbed at differing times and had reacted in differing ways at a patch scale. Insufficient independent replication challenged generalised data interpretation and produced what appeared to be stochastic variation. Means to tackle this difficulty and draw out more general conclusions led to the modelling approach presented in the second part of this work.

The procedure for establishing the PSPs closely followed that used for the forest inventory[5]. The position of all standing trees both living and dead over 5 cm in diameter within a 500 m^2 circular area was recorded. This was calculated from measurements of the angle and distance of each tree with relation to the centre of the circle. In addition the heights of all trees were measured to the nearest 0.25 m using a clinometer. The projected crown areas of all trees were estimated by taking two orthogonal measurements of the projected crown width and modelling projected crown area (A) as an ellipse (oval).

$$A = \pi\left(\frac{D_1.D_2}{4}\right) \qquad \text{Equation 1.1}$$

Where D_1 and D_2 are the projected lengths of the major and minor axes of the ellipse.

When trees were found beneath the penumbra of other trees, the identities of any tree directly shading all or part of the crown were recorded.

Within the PSPs a total of 1,305 trees, both alive and dead, over 5 cm in diameter, were marked at breast height with numbered metal tags. Labelling of dead trees allowed their fate to be followed. Members of the community were told to treat the PSPs in the same manner as any other area of the forest. Between 15 July and 23 September 1999 the circumference of all trees were measured to the nearest millimetre and the position of the measuring tape marked

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[5] All measurements in the PSPs were carried out personally with the assistance of Jose Luis Santiz-Gomez, a member of the community of Sonora.

with a paint line. Between July and September 2000 the circumferences of all trees were remeasured. Remeasurement coincided to within a week to the date of measurement in 1999. The tape position was matched to that used in the previous year. Mortality and basal resprouting were recorded for all trees (chapter 2). Although all trees were recorded, only measurements taken from healthy trees that showed little visible effects of fire damage at the time they were measured in 1999 have been used in growth analysis.

In addition 6 rectangular quadrats of 2 m x 5 m were placed at permanently marked random points within each PSP. Stems of seedlings and saplings of all woody species within these quadrats were tallied (chapter 3) and the % cover of herbaceous species recorded (see Appendix 1 for a species list). As yet too little regeneration from seed has occurred in the plots to be used in an analysis of establishment rates.

Dawkins (1963) suggests that the crown diameter of many tropical trees is linearly related to bole diameter at breast height. This simple allometric relationship been used for dynamic modelling purposes (Botkin 1993b; Pacala *et al.* 1996). The relationship also translates into a linear relationship between projected crown area and squared diameter. The advantage of using area against squared bole diameter, rather than projected crown diameter against bole diameter, was that improved statistical properties regarding the homogeneity of variance was found in the transformed data

$$A = C_{canopy} D^2 \qquad \text{Equation 1.2}$$

Where D is diameter at breast height and C_{canopy} is some constant. The slope coefficient of this relationship was estimated for subsequent modelling purposes. The allometric relationship between height and diameter was modelled by fitting a rectangular hyperbola to the data of the form.

$$H = \frac{H_{\max} D}{a + D} \qquad \text{Equation 1.3}$$

Equation 1.2 was fitted using standard linear regression. Equation 1.3 was fitted using maximum likelihood estimation using iterative quasi Newton non-linear estimation with a least squares loss function using the program Statistica (Statsoft Inc. 1996). This model fitting procedure was chosen rather than linear regression using the Eadie-Hofstee transformation as often used for the Michaelis-Menten equation because the transformation was found to lead to residual error that was dependent on the transformed independent variable.

Standing above-ground biomass was calculated using allometric formulas given for red pine, white oak and red oak in Termikaelian and Korzukhin.(1997). Considerable variation in the constants given in this review suggests that calibration for the tree species at the site must be undertaken if accurate biomass estimates are required.

Results

The statistics describing the diameter distribution of pines and oaks found in all the PSPs are summarised in table 1.6. The mean and median diameters of oaks was approximately half that of the pines, although maximum diameters are similar.

A linear regression of projected crown areas on squared diameter provided a good fit to the data for all five principal species (table 1.7). Diagnostics showed low residual variation with no dependency of the error terms on the independent variable. To confirm the significance of the differences between the species analysis of covariance with species as a factor was followed by pairwise comparisons using the Student Newman Keuls correction for multiple tests. Both oak species have significantly ($p<0.01$) greater diameter independent crown areas than each of the three pine species. These coefficients have been incorporated as parameters in the model presented in chapter 6.

Table 1.8. gives the observed and expected frequencies of pines and oaks with respect to their positions in the penumbras of over storey trees. There is a significant difference between the two groups. Chi squared = 32.87, df=2, $p<0.00001$. More pines than predicted from the null model are found growing without direct shade from trees above them. More oaks than expected are found in the penumbra of pines. These proportions would be more markedly different if understorey trees killed by recent fire were also taken into account as many small oaks beneath large pines were excluded from the analysis. The two layered nature of the forest structure is also clearly revealed by figure 1.24. The mean heights of the pines are greater than mean heights of oaks in all but three plots. The exceptions are plots with either no, or very few pines.

Figure 1.25 shows equation 1.2. fitted to the data for the five species. The presence of outliers above this fitted asymptote should be noted and taller individuals of the species have been observed at the site. Asymptotic heights for the five species are similar, with the exception of *Q. segoviensis*, which is very clearly lower than the other three species.

Table 1.9 shows the results of a linear regression of diameter increment on the diameter measured in 1999 for all the trees stratified by FG. This analysis failed to detect a significant dependence for any of the groups. This could have been because a rather small range of diameters was included in the model. Significant between plot variation in growth rates was found for both pines and oaks. The variation in growth of the two FGs was positively correlated but not significantly so. R= 0.232 R^2=0 .0542 Adjusted R^2= 0.0112 $F(1,22)$=1.26 $p<0.273$). Analysis of variance showed significant variation between the mean growth rate of species of pines but not between the two oak species (Table 1.10). Multiple pairwise comparisons using Student Newman Keuls correction for multiple tests showed that the growth of *P. maximinoi* was significantly greater at the 1% level than *P. oocarpa* and *P. devoniana*. All other pairwise comparisons were not significant at the 5% level. Interpretation of growth in terms of direct relationships with structural attributes of each plot is impossible due to lack of power caused by the large amount of variation. Lack of independence between trees also prevents wider inferences being drawn. A more detailed investigation of pine growth rates is reported in chapter 6 where it is used to calibrate a growth model.

Standing above-ground biomass estimated for the plots ranged between 12 tonnes ha $^{-1}$ to 163 tonnes ha^{-1} with a mean value of 44 tonnes ha $^{-1}$. The estimated net above-ground production of standing biomass (trees suffering mortality between 1999 and 2000 being subtracted from the total) was regressed against the basal area. A significant positive relationship between basal area and biomasss production was found (R^2=0.299 Adjusted R^2=0 .262 $F(1,23)$=9.85 $p<0.0046$). The amount of variation in the data makes decisions regarding the best model for this relationship based only on statistical goodness of fit unreliable. A linear model, though an acceptable fit, would appear inappropriate on mechanistic grounds. Thus in order to summarise this relationship the hyperbola shown in figure 1.25. was fitted using quasi Newton non linear estimation with a least squares loss function under the assumption that productivity measured in this manner would reach a maximum value after complete canopy closure has occurred. A quadratic parabolic relationship might also be proposed under the assumption that net biomass production would decrease in plots with higher basal areas, but this may be more appropriate when changes in total biomass including above and below ground processes are measured.

Table 1.6 Distribution of live tree diameters at breast height (cm) within the PSPs classified by functional group.

	N	Mean	Median	Maximum	Lower quartile	Upper quartile	Quartile range	Std.Dev.
Pines + oaks	661	13.7	9.93	66.3	7.4	14.9	7.6	10.3
Pines	162	21.7	18.4	66.3	10.4	32.4	21.9	13.5
Oaks	499	11.9	9.6	62.0	7.2	12.7	5.5	8.5

Table 1.7 Slope coefficients and squared correlation coefficients for regressions of crown area (m) on squared diameter at breast height (cm) for trees undamaged by fire.

Species	n	B	Std error	R^2
P. maximinoi	130	0.039	0.0022	0.71
P. oocarpa	17	0.038	0.0062	0.68
P. devoniana	18	0.038	0.0026	0.92
Q. segoviensis	353	0.053	0.0012	0.83
Q. crispipilis	147	0.061	0.0020	0.85

Table 1.8 Contingency table showing observed and expected frequencies of positions of live pines and oaks in the double layered canopy. The expected frequencies are given in brackets. Chi squared = 32.87 df=2, p<0.00001

Overstorey	None	Pine	Oak	Total
Pine	78 (49.3)	56 (81.1)	31 (34.45)	165
Oak	120 (148)	269 (243)	107 (103)	496

Figure 1.24. Mean heights of pines and oaks in the 25 PSPs arranged in increasing order of pine height.

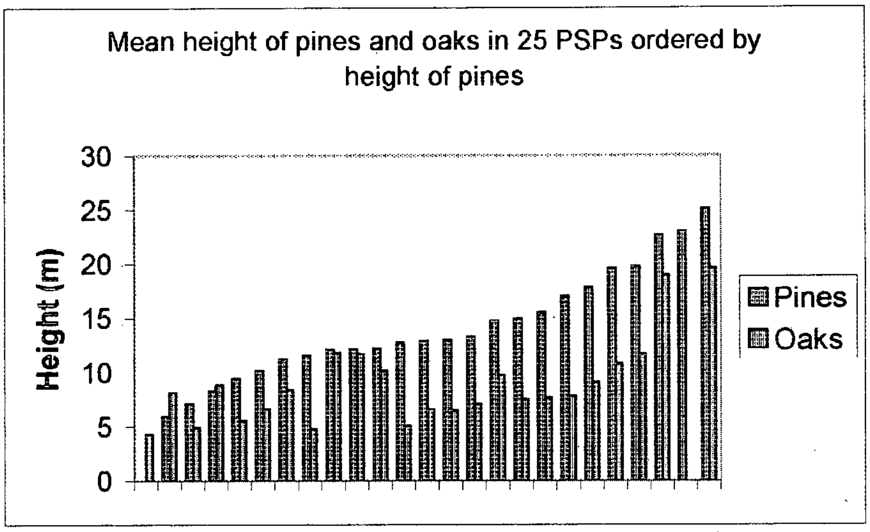


Table 1.9 Regression parameters for the dependence of diameter increment (measured over 1 year) on the diameter in 1999.

FG	n	R	R^2	p slope	Intercept (s.e.)	slope (s.e.)
Pines	162	0.095	0.009	0.22	0.70 (0.07)	-0.0034 (0.0028)
Oaks	499	0.0078	0.0006	0.87	0.27 (0.023)	0.00023 (0.0015)

Table 1.10 One way analysis of the variance in growth rate between species within each of the two functional groups

	df Species	MS Species	df Error	MS Error	F	p-level
Pines	2	1.023	161	0.224	4.56	0.012
Oaks	1	0.000618	499	0.082	0.007	0.93

Table 1.11 One way analysis of the variance in growth rate between patches (PSPs)

	df Sites	MS Sites	df Error	MS Error	F	p-level
Pines	*20*	*0.52*	*143*	*0.19*	*2.71*	*0.0003*
Oaks	*23*	*0.13*	*477*	*0.08*	*1.68*	*0.03*

Table 1.12 Diameter increments for healthy trees over 5 cm in diameter for the 1999 – 2000 growing season.

	Valid N	Mean	-95% C.I.	+95% C.I	Maximum	Std.Dev.	Std. error
Q. segoviensis	353	0.275	0.244	0.307	1.037	0.298	0.016
Q. crispipilis	148	0.278	0.235	0.320	1.055	0.262	0.022
P. oocarpa	18	0.442	0.197	0.687	1.719	0.493	0.116
P. maximinoi	132	0.677	0.594	0.760	2.165	0.482	0.042
P. devoniana	14	0.346	0.149	0.543	0.891	0.341	0.091
Cleyera theoides	89	0.225	0.182	0.269	0.764	0.207	0.022

Figure 1.25. Estimated above-ground standing biomass production in the bienes comunales at Sonora as a function of basal area of all trees over 5 cm DBH within 25 PSPs of 500 m^2

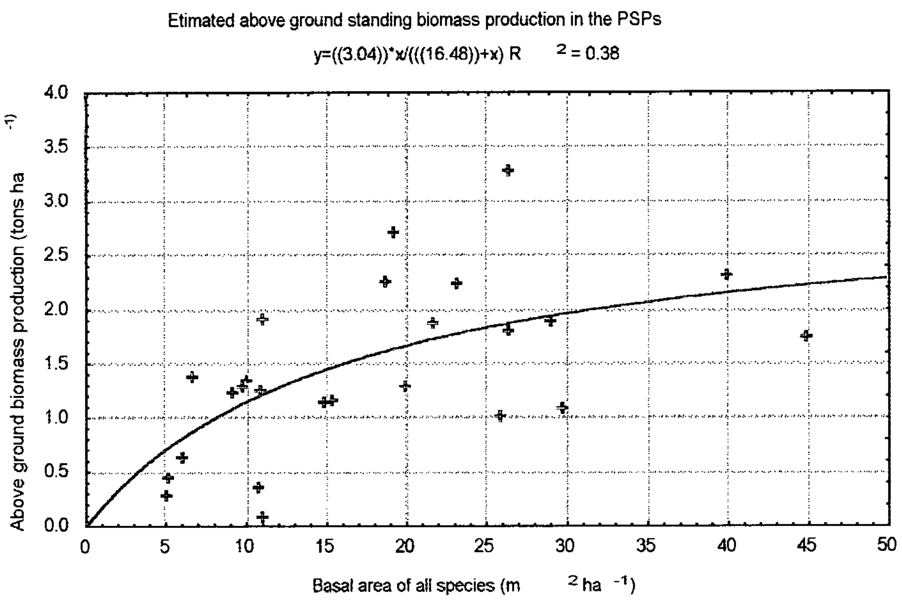
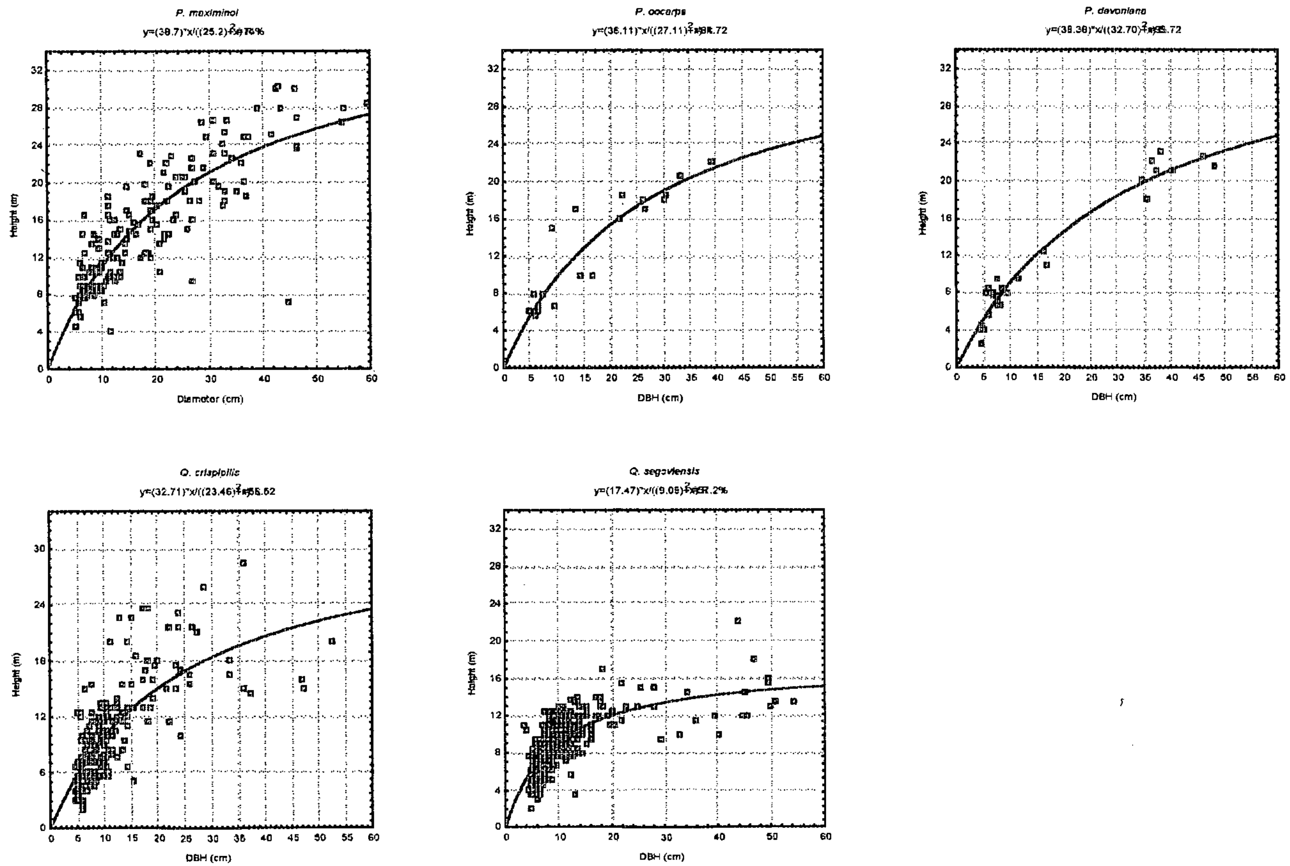


Figure 1.26 Height diameter relationships for three species of pine and two species of oak over 5 cm DBH in the 25 PSPs . Note that the asymptotic heights are given as the first term in the fitted regression equations



Discussion.

Although a great deal of variation between the patches occurs, some common patterns are apparent. Oaks form a very clear lower stratum beneath pine canopies. Even if the two groups have established simultaneously following patch level disturbance, such a pattern would naturally arise due to the slower growth rate of oaks. In the case of *Q. segoviensis*, low height to diameter ratio also would result in oaks occurring in a lower stratum. The difference in height to diameter ratio is the most obvious functional difference between the two oak species, which in many other respects, despite very clear morphological differences, seem to respond to disturbance in a sufficiently similar manner to permit models to be built which for convenience treat them as belonging to a single functional group.

A relationship between diameter and growth rate was expected from simple mechanistic considerations. That this was not found must be ascribed to type two error arising when samples are taken from a population of observations with a high intrinsic variance. Many of the smaller trees were killed by the fire, leaving a reduced range of diameters from which to establish the relationship. Other sources of information have been used to establish this relationship for modelling purposes (chapter 6).

The variability and unpredictability in growth rates at the site is an interesting phenomena in its own right providing it can be shown that it is due to process error rather than observation error (*sensu* Pascual and Kareiva 1996). No tree was recorded as having undergone a reduction in diameter over the measurement period. Despite an inevitable degree of imprecision inherent in the methodology used, measurement error was not the principal cause of the variation. Suppression through shading is only a partial explanation for the variation given the rather sparse open nature of most of the PSPs. Failure of some trees to fully recover following the ground fire may well have contributed to the variation in growth rate observed. The failure to detect differences in growth between the two oak species may also be attributable to type two error, although the data set was large enough to detect a significant difference between the growth of the three pine species and variation in productivity at the patch level did follow an expected pattern.

Both the diameter increments and the overall productivity of these patches appears low when compared with the results of studies conducted on plantations and other disturbed tropical forests (Lugo 1992). This may be attributable to the residual effects of the fire, but it could conversely be argued that the flush of nutrients and canopy opening following fire could have enhanced growth of the surviving trees. Scatena *et al.* (1996) report 21.6 tonnes ha $^{-1}$ yr $^{-1}$ for Puerto Rican forests recovering from hurricane damage. Cuevas Brown and Lugo report production of 19.2 tonnes ha $^{-1}$ yr $^{-1}$in a pine plantation and 19.4 tonnes ha $^{-1}$ yr $^{-1}$ in a comparable broadleaved forest, although in the second case 46% of the biomass production occurred underground. The estimate here may however be more compatible with observations made on other pine or oak forests growing on poor soils. Standing above-ground biomass has been estimated as only 60 to 100 tonnes ha $^{-1}$ in natural 200 year old Scots pine stands (Wirth *et al.* 1999). Coppicing holm oak is reported as producing 8 tonnes ha^{-1} yr $^{-1}$ of fresh material calculated over 30 years. This translates into around 4 tonnes ha^{-1} yr $^{-1}$ of dry biomass (Leonardi and Rapp 1990). Reed *et al.* (1999 report 0.25 tonnes ha^{-1} year^{-1} to 4.01 tonnes ha^{-1} yr $^{-1}$ of biomass production in the pine forests of Yellowstone park recovering from natural fire. Secondary vegetation recovering from slash and burn cultivation in the Brazilian Amazon may produce 6.6 to 8.7 tonnes ha $^{-1}$ yr $^{-1}$ (Alves *et al.* 1997).

Above-ground biomass production by pines translates into lower long term biomass accumulation than occurs in hardwood stands (Gower *et al.* 1997) as hardwoods partition more of their primary production to below ground (Cuevas Brown and Lugo 1991). Litter production by hardwoods is also greater than the litter production of pines (Cuevas Brown and Lugo 1991).

Conclusion

Pines form a distinct upper strata above oaks at the site. Pine radial increment is approximately double that of oaks. There is a significant difference between the growth rate of pine species, and between pines and oaks, but the two oaks species grow at comparable rates. Growth rates vary between patches. The site appears to have a low intrinsic productive potential, possibly due to nutrient limitations. As knowledge of the site improves monitoring of litter production and below ground productivity could be used to build up a fuller picture of biomass production. This information can be then linked if individual based models of tree growth are available which accurately reproduce the complex and variable details of patch structure.

Chapter 2. Fire induced mortality in disturbed pine-oak forest

Introduction

During the month of April 1998 a wild fire burnt through a contiguous area of approximately 12,000 ha of forest including the study area. Most of the forest's understorey and advance regeneration was affected. Wild fires were particularly extensive in Southern Mexico at this time due to the unusually prolonged dry season. This drought appears to have been a consequence of the 1997-1998 El Niño Southern oscillation (Groetzner, Latif and Dommenget 2000; Buizer, Foster and Lund 2000). Such events may be increasing in frequency. The impact of these fires caused immediate concern. The resulting poor air quality led to the closure of schools throughout southern Mexico. Studies of the impacts of fires were initiated at a regional and national scale. However the longer term consequences of fire for forest structure and composition has not been documented. The fire at the study site thus provided an opportunity both to further develop hypotheses regarding the underlying causes of patterns in species distribution discussed in chapter 1 and to study and document the effects of a phenomena with wider implications.

Although fire is a common natural feature of many forest systems, anthropogenic influences often cause the cycle of fire disturbance to differ in both frequency and intensity from a natural regime (e.g. Fuller *et al.* 1998). Vegetation composed mainly of species with adaptations that allow persistence in the face of fire is a feature of many areas with seasonal or unpredictable fluctuations in precipitation. (Keeley 1986; Goldammer and Jenkins 1990; Braithwaite 1996). In fire prone communities differences between species' vital attributes (*sensu* Noble and Slatyer 1980) can combine with patterns in the periodicity and intensity of fire events to produce complex temporal dynamics. The community level consequences of differences between species that either resprout or possess seeds with dormancy broken by fire have been intensively studied and modelled (Keeley and Zedler 1978; Malanson and O'Leary. 1982; Malanson 1985; Rego, Pereira, and Trabaud 1992). The dominant canopy forming species of mixed pine-oak woodland display a similar contrast between differing modes of fire survival.

It is believed that the formation and maintenance of mixed pine and oak forests throughout the North American continent is linked to both natural and anthropogenic fire (Bergeron 1991; Cowell 1995; Fuller *et al.* 1998; Batek *et al.* 1999; Bonnicksen 2000). In southern Mexico this linkage has special significance given the continuing practice of slash and burn agriculture. The impact of slash and burn farming is clearly distinct from that of fire alone and can be regarded as a different disturbance type (chapter 3). Nevertheless the two types of disturbance are connected, as the use of fire in slash and burn plots often leads to the unintentional ignition of neighbouring uncleared forest in dry years. Ground fire is also used as a management tool in the more open pine savannah that adjoins the southern part of the site. In this savannah area frequent fires are set to improve the quality of grazing. Thus the vegetation at the study site has almost certainly been subjected to previous unintentional fires.

The heterogeneous open nature of the forest (chapter 1) suggests that any recently occurring fires are unlikely to have been the major stand replacing events that occur in some North American forest systems (Barrett, Arno and Key 1991; Barrett 1994). However even ground fire can cause extensive mortality of large trees (Mutch and Parsons 1998). Although the immediate effects of low intensity fire will usually be concentrated on smaller trees, ground fire is still capable of playing a substantial role in shaping landscape level pattern (Miller and Urban 1999). Ground fire may be responsible for maintaining the open nature of the forest. Juvenile trees that survive a fire are likely to reach the canopy before seedlings that establish in its aftermath. These intraspecific differences in the mortality rates of juvenile trees, combined with competitive effects, can prove decisive in shaping post fire composition. Quantification of species' specific mortality is thus a first step in understanding the processes leading to forest change. Simulations, which combine this information with models of growth and competition, can then be used in order to explore how the composition of the vegetation might respond to alterations in fire recurrence and intensity. The similarities between contemporary patterns of change in the disturbance of Mexican pine-oak forest and historical change in other regions may also provide a valuable opportunity to study some of the processes involved in determining the formation, structure and distribution of analogous forest types across the continent. In order to compare the results with previous work elsewhere, analogies may have to be drawn based on morphological similarities between species.

Fire is unlikely to produce conditions that directly favour oak regeneration from seed (Cain and Shelton, 1998). Resprouting from epicormic buds does however allow the persistence of oaks on fire prone sites (Arthur, Paratley and Blackenship 1998: Barton 1999). Pine species are able to exploit fire prone environments as a result of a variety of morphological and life history attributes. Details of the nature of the fire regime appear to determine the distribution of pines possessing differing combinations of features (Keeley and Zedler 1998). While intense crown fires may result in considerable mortality of all pines, they produce conditions that tend to favour regeneration of species with cones that disperse their seeds following fire (Agee 1998). In contrast ground fires may favour species that resist the effects of fire. *P. devoniana* is very similar to the long leaf pine, *P. palustris*, found in the Southern United State. Both species possess a thick bark, long (>30 cm) needles and a juvenile grass stage. The grass stage morphology of juvenile long leaf pine has long been considered an adaptation to mild ground fires (Chapman 1932; Keeley and Zedler 1998).In contrast *P. oocarpa* has a thinner bark, and smaller diameter twigs. Unlike *P. devoniana, P. oocarpa* often (though not always) bears serotinous cones that open after fire. This trait is found in a range of pines associated with fire, examples of commercially valuable species being *P. contorta* (lodgepole pine) and *P. banksiana* (jack pine). Intraspecific variability in the trait is always high and seems to be linked to past fire regimes (Tinker *et al* 1994, Gauthier Bergeron and Simon 1996). Serotiny can arguably be best regarded as a local, population specific trait rather than a species specific characteristic (Givnish 1981).Like *P. echinata* , *P. serotina* and *P. rigida* smaller individuals of *P. oocarpa* resprout, sometimes vigorously, from the root crown following fire (Keeley and Zedler 1998). Keeley and Zedler have suggested that this combination of traits is an adaptation to moderate to extreme crown fire. Thus while *P. devoniana* may be expected to persist after mild fire, *P. oocarpa* may be adapted to recolonise areas following more intense crown fire. In contrast *P. maximinoi*, which dominates the northern area of the site, has brittle, non serotinous cones and thinner bark and twigs than *P. devoniana*. This species does not resprout and appears to have no special adaptations to fire beyond those common to most pines such as wind dispersed seeds, that can reach newly disturbed areas easily, and rapid growth.

In addition to its effects on the distribution of pine species, fire may also mediate competition between pines and oaks. In long leaf pine communities mortality of turkey oaks (*Quercus laevis*) is apparently higher among individuals located close to large (>20cm diameter) pines, due to increased fire intensity under the canopy of mature trees (Williamson and Black 1981; Rebertus *et al.* 1989).

The response of other North American pine-oak systems to fire has thus become rather well documented. As prescribed burns present opportunities for designing controlled experiments, formal hypothesis testing has now become possible (Glitzenstein, Platt and Streng 1995). The dynamic of the specific mix of pine and oak species at the study site has not however been the subject of any previous study, although the response of pure stands of *P. oocarpa* to controlled burning has been documented in Honduras (Hudson *et al.* 1983a). The study therefore aimed both to document and describe the effects of the fire at the site and to test a series of more general statistical hypotheses regarding the differential effects of fire on juvenile pine and oak trees. Description of the fire's effects was achieved through analysis of the forest inventory and monitoring the permanent sample plots over the space of two years following the fire. However in order to test general hypotheses data were required which possessed suitable statistical characteristics. Trees taken from within the comparatively small number of permanent sample plots could not be considered as independent sample points, thus reducing the degrees of freedom available for statistical analysis. Also it was apparent from initial observations that mortality was concentrated in the smaller size classes. Small pines were not well represented either in the inventory or the PSPs. Therefore an additional study was designed in order to produce a sample of sufficient size to produce adequate statistical power.

The following hypotheses were identified :

1. Crown kill of pines and oaks due to ground fire is a function of diameter.

2. Crown mortality, after compensating for the effect of diameter, is higher closer to mature pines for both pines and oaks.

3. Significant diameter independent intergeneric differences in fire induced mortality can be found.

4. Significant diameter independent intrageneric differences in fire induced mortality can be found.

5. Oak resprouting ability is related to size.

Note that these hypotheses do not include *P. maximinoi* due to limitations in the data set. Some of the implications of fire for this species can however be derived from the descriptive analysis of the inventory and PSP data.

Method

Three sources of data were used to provide a comprehensive picture of fire impact.

1. The inventory data set presented in chapter 1.2

2. The PSP data presented in chapter 1.3

3. Independent juvenile trees selected in a 40 ha homogeneous area.

1. Inventory data. The height of bark scorching and the proportion of leaves scorched and killed were recorded on every tree in the inventory data set. Based on these measurements and on observed damage to the understorey inventory plots were placed into six fire damage classes.

1. *No damage*

2. *Low intensity ground fire*. Leaves and small woody debris consumed. Leaves of understorey shrubs and bushes scorched.

3. *Moderate ground fire*. Twigs and leaves of understorey shrubs and bushes consumed. Leaves of small canopy trees and the lower branches (<15 m) of large canopy trees scorched

4. *Severe ground fire to mild crown fire*. All canopy elements scorched to 20 m and lower leaves burnt.

5. *Moderate crown fire*. Leaves and small twigs in canopy burnt.

6. *Severe crown fire*. Branches burnt.

This data provided a large scale indicator of the extent and intensity of the damage and allowed the analysis of spatial pattern of the fire. However it was not possible to follow the fate of all the trees in the inventory, and interpretation of the immediate damage in terms of long term mortality required corroboration.

2. The PSP data. This was used principally to follow mortality in the two years following the fire, and corroborate assumptions made regarding mortality based on immediate post fire damage. Although this data provides a useful description of the fire effects, lack of statistical independence of trees within the PSPs limits the inference that can be drawn from this data set.

3. Data from juvenile trees in a homogeneous area. To overcome the statistical limitations imposed by the small number of PSPs a further data set was obtained by evaluating the immediately visible impact of fire on juvenile trees a few months after the fire. The survey was conducted within a uniform 40 ha area situated 320 m to the south of the area included in the inventory. The area was chosen as being the most appropriate "*natural experiment*" (*sensu* Diamond 1986) available. The area had a mixture of size classes and species. Abundant juveniles of *P. devoniana, P. oocarpa, Q. segoviensis* and *Q. crispipilis* occurred within this area, although *P. maximinoi* was not found. At this site scattered large individuals of both *P. oocarpa* and *P. devoniana* form a very sparse overstorey, growing to 20 m in height. *Q. crispipilis* and *Q. segoviensis* form a lower strata of small trees, together with a shrub layer dominated by *Rhus schiedeana*. General inferences drawn from this limited data set must be regarded with caution. The area is not typical of the site as whole. However the similarity of the fire intensities experienced by all the individuals in the area permitted a more reliable assessment of species specific differences than can be obtained from analysis of the PSP data. Localised patchiness in fire intensity at this scale was presumed to be due to concentrations of fuel around larger pines. This effect was of interest in potentially mediating competition between pines and oaks.

This survey was conducted between July 20 and August 31 1998, three to four months after the fire. This allowed survival of crowns to be assessed together with any immediate signs of basal resprouting. Some small individuals may have been completely consumed by the fire and therefore not recorded. Fire damaged trees are normally quickly removed for fuelwood, but the area had not yet been harvested at the time of the work. The majority of the fire killed stems could therefore still be found and these provided the only indication of pre fire structure available.

Individual trees were selected at random within this study area based on proximity to randomly selected points along randomly spaced transects. Where clumping of individuals occurred the individuals within each clump were numbered and one selected at random. This produces a close approximation to a completely random selection of individuals (Pielou 1969). The proportion of dead (fire scorched) leaves and presence of new crown shoots was noted for each individual. Trees were defined as top killed if all leaves were scorched and no evidence of new shoots in the crown were observed. The number and height of basal resprouts were recorded if present. Diameter was measured at ground level in order to include all juvenile individuals of *P. devoniana* in the grass stage. Some juveniles of this species may reach a diameter of 5 cm before attaining breast height. Height diameter relationships of juveniles were analysed in order to document this observation. In addition the distance of each individual to the nearest large (over 20 cm DBH) pine was recorded.

Multiple logistic (Logit) regressions (Hosmer and Lemeshow 1989) were used to model crown survival. The independent variables used in the model were diameter of the affected tree or sapling and the distance from the tree to the nearest large (defined as over 20 cm DBH) pine. This definition for the second predictor of the logistic model followed Rebertus and Williamson (1989) who documented a significant link between oak mortality and proximity to large pines in long leaf pine communities.

A stepwise technique was employed to determine the significance of the second predictor (distance to pine) in the model. The improvement of the fit of the model when the second parameter was added was measured by comparison of the maximum likelihood (-2 log likelihood) ratios. Colinearity between the independent variables was checked before the analysis was conducted and was found not to be significant.

Results

The fire, which occurred between April 21 and May 2, was a low to moderate intensity ground fire. Most trees suffered visible scorching of the bark reaching a maximum of 12 m, but this was mainly confined to below 2 m. Leaf scorch extended into the canopy up to a maximum height of 12 m to 17 m, though flames did not spread into the crowns of mature trees. Leaves and needles on larger trees were not consumed. Trees that were recorded in the inventory as having 100% leaf scorch were assumed to have been crown killed. This assumption is shown here to be an adequate approximation based on evidence from longer term monitoring of the PSPs.

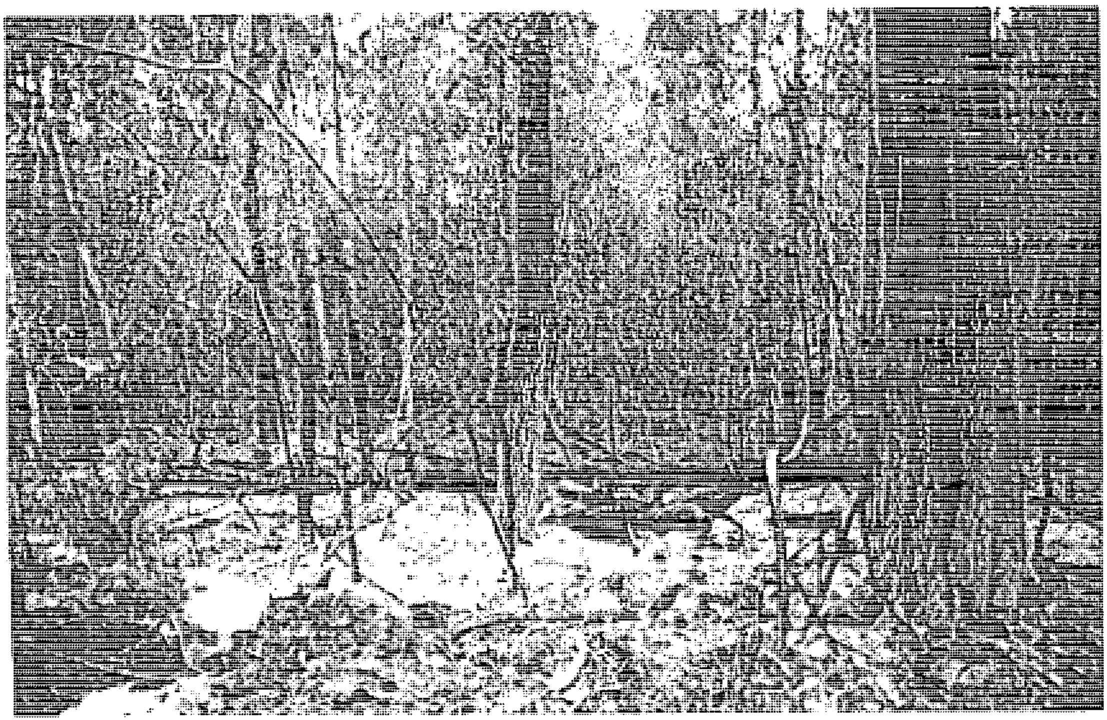
In order to summarise trends and gain some insight into the spatial pattern of fire severity, the proportion of dead trees in each inventory circle was given an arcsine square root transformation in order to remove heterogeneity of variance. A regression of this transformed variable on the arc sine square root transformed proportion of pines to oaks in the circles detected a small but significant positive correlation between the transformed mortality and the transformed proportion of pine stems $R= 0.257$ $R^2= .0664$ Adjusted $R^2= 0.0619$ $F(1,208)=14.807$ $p<.00016$. Thus plots dominated by pines suffered significantly greater fire induced mortality than plots dominated by oaks. However regression of the transformed index of fire damage on pine basal area showed no effect ($R=0.073$ $R^2=0.0054$ Adjusted $R^2= 0.00064$ $F(1,207)=1.13$ $p<0.28$).

In order to trace spatial effects this transformed variable was then regressed on the x and y co-ordinates of the inventory circles together with the corresponding quadratic terms derived from these co-ordinates (see the previous chapter for a justification for a similar methodology). This revealed a weak, but significant, trend towards increased fire severity in the southern and western area of the site. The Y and X co-ordinates were retained in the model, but higher quadratic terms were not significant when a stepwise selection procedure was followed. The full model gave R= 0.252 R^2=0 .063 Adjusted R^2= 0.050 F(3,204)=4.682 p<0.00347. A significant multiple correlation with the first two RDA axes summarising species distribution which were produced by the analysis in chapter 1 was also found R= 0.272 R^2= 0.0740 Adjusted R^2= 0.0651 F(2,207)=8.28 p<0.00035. It should be noted that these RDA axes are only partly constrained by the quadratic trend surface. The RDA scores in this data set are very similar to unconstrained PCA scores, in other words they represent a summary of species composition. Stepwise forward selection retained only the second RDA axis. Stepwise forward selection on a model including spatial co-ordinates and the summaries of species composition represented by the RDA axes retained the second axis but showed the other terms to be redundant. This axis is more closely associated with pine distribution then oak distribution (see figure 1.17). This rather elaborate procedure only gave weak support to the postulate that the intrageneric separation of pines detected in chapter 1 may be connected with the pattern of fire severity. Cause and effect clearly cannot be directly inferred and the effect was too weak to be shown by more direct analytical techniques.

Large scale spatial effects were thus weak and ambiguous, due to heterogeneity in forest structure preventing the detection of a signal within the local noise. However at the local level fire effects were predictable. Fire affected almost all the forested area with very few patches escaping completely, but few areas were very severely damaged (figure 2.1). Heterogeneity in fire impact followed a predictable local pattern with large trees in closed canopy areas being largely unaffected while open areas with many juvenile pines suffered high mortality rates. However because these local effects were also related to patterns in size structure it was more informative to concentrate the statistical analysis on the relationship between tree size and species identity and fire damage. The longer term consequences can then be inferred through modelling (chapter 7).

Photograph 2 shows the general aspect of most of the site at the time when the study began and photograph 3. shows the unusual resprouting response of *P. oocarpa.*

Photograph 2. Fire affected area of the forest May 1998. When the study period started very few areas of forest could be found which the extensive ground fire had not affected. This photograph shows one of the most severely burnt areas. Note that the fire did not spread into tree crowns and the larger trees were not killed.



Photograph 3. An unusual response to fire for a pine species. Resprouting from root crown of *Pinus oocarpa*

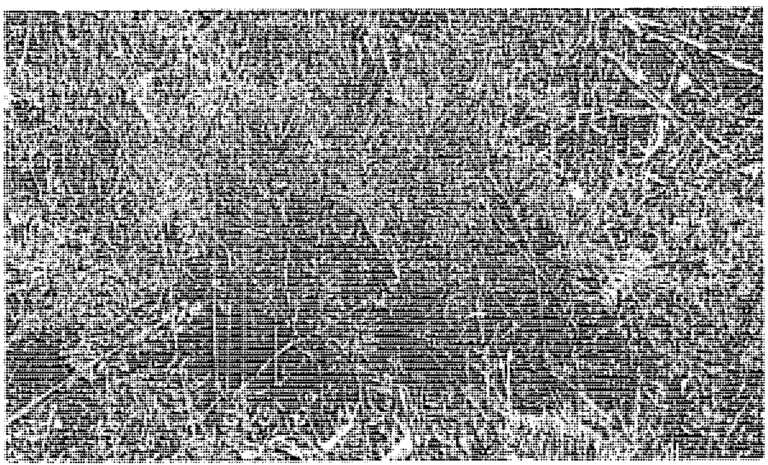
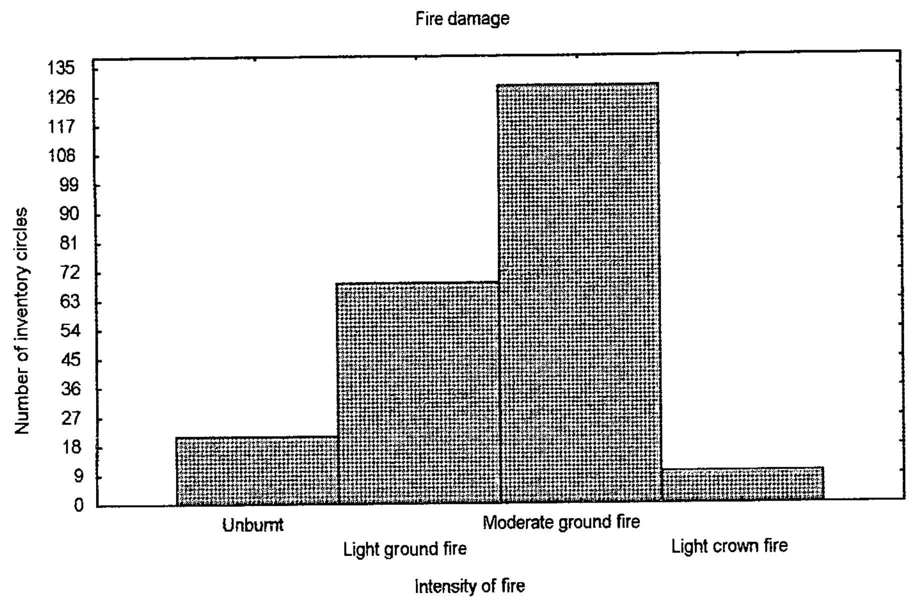
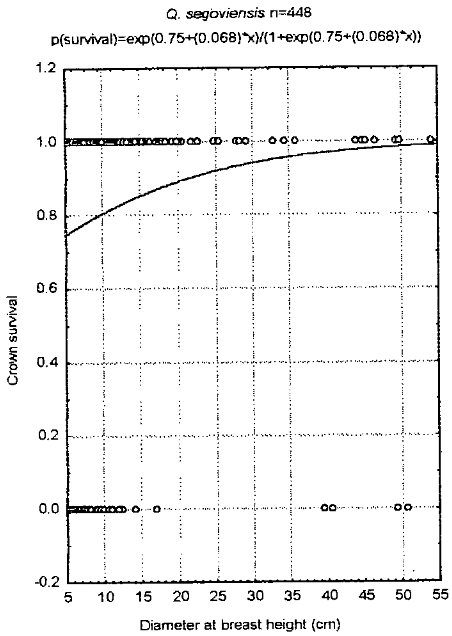


Figure 2.1 Numbers of inventory plots which experienced each type of fire intensity.



The results obtained from monitoring the PSPs over two years showed that complete mortality, defined as stems which were crown killed and did not show any signs of basal resprouting two years after the fire, was restricted largely to pines (Table 2.1). Oaks and the smaller sub canopy broad leafed species all resprouted vigorously after crown death. There was a low level of delayed crown mortality in the year following the fire. Trees registered as dead in 1999 had all been recorded as 100% leaf scorched in 1998. Few trees with this level of damage survived into 1999. Most of the mortality between 1999 and 2000 was of trees that had been 100% leaf scorched and were thus weakened in 1999. These observations supported the assumption that 100% leaf scorch was equivalent to tree death that had been used in earlier studies carried out before longer term monitoring had taken place. Rather unexpectedly the pine species which suffered the greatest mortality in the PSPs was *Pinus devoniana*, a species which was assumed to be well adapted to survive fire and which is later shown here to be resistant as a juvenile tree in open areas. This result may have been linked to the spatial distribution of the species that was concentrated in plots that were severely burnt or due to suppression of the shade intolerant juveniles prior to the fire. The lack of adequate replication in the PSPs does restrict the general interpretation of these results. Figures 2.2 and 2.3 summarise the results of logistic regressions of crown kill on diameter for the data from the PSPs. It should be noted that because of high resprouting rates, models of absolute mortality cannot be produced for comparison and all models shown are based on crown kill. Although statistical comparisons between species based on this data would not be valid, the equations produced can be valuable for modelling site specific mortality, and complement the results from the less representative area which was used to study only juvenile mortality. It should be noted from figure 2.2, that in the PSPs small individuals of *Q. segoviensis* have a higher crown survival than small individuals of *Q. crispipilis*. This difference was not detected in the study that concentrated on juveniles in a more homogeneous area, but could have great relevance when attempting to draw inferences regarding processes acting over the wider area.

Figure 2.2 Logistic regression models of the relationship between diameter and crown mortality for the two oak species found in the 25 PSPs.



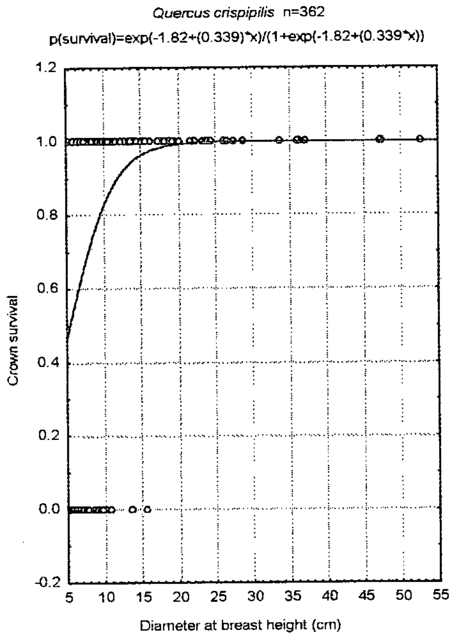


Figure 2.3 Logistic regression models of the relationship between diameter and crown mortality for the three pine species found in the 25 PSPs.

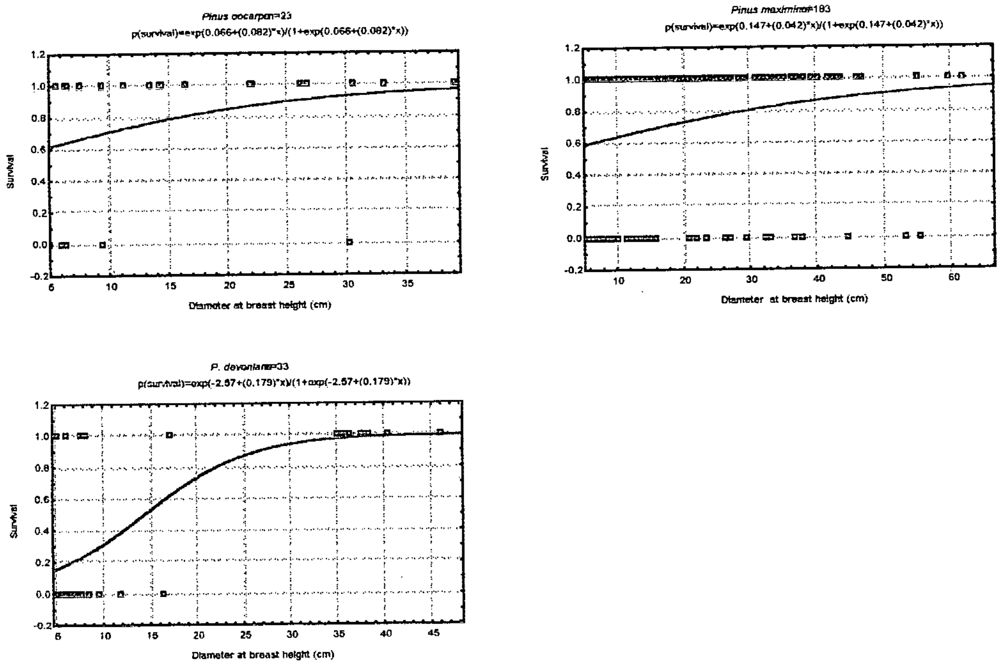
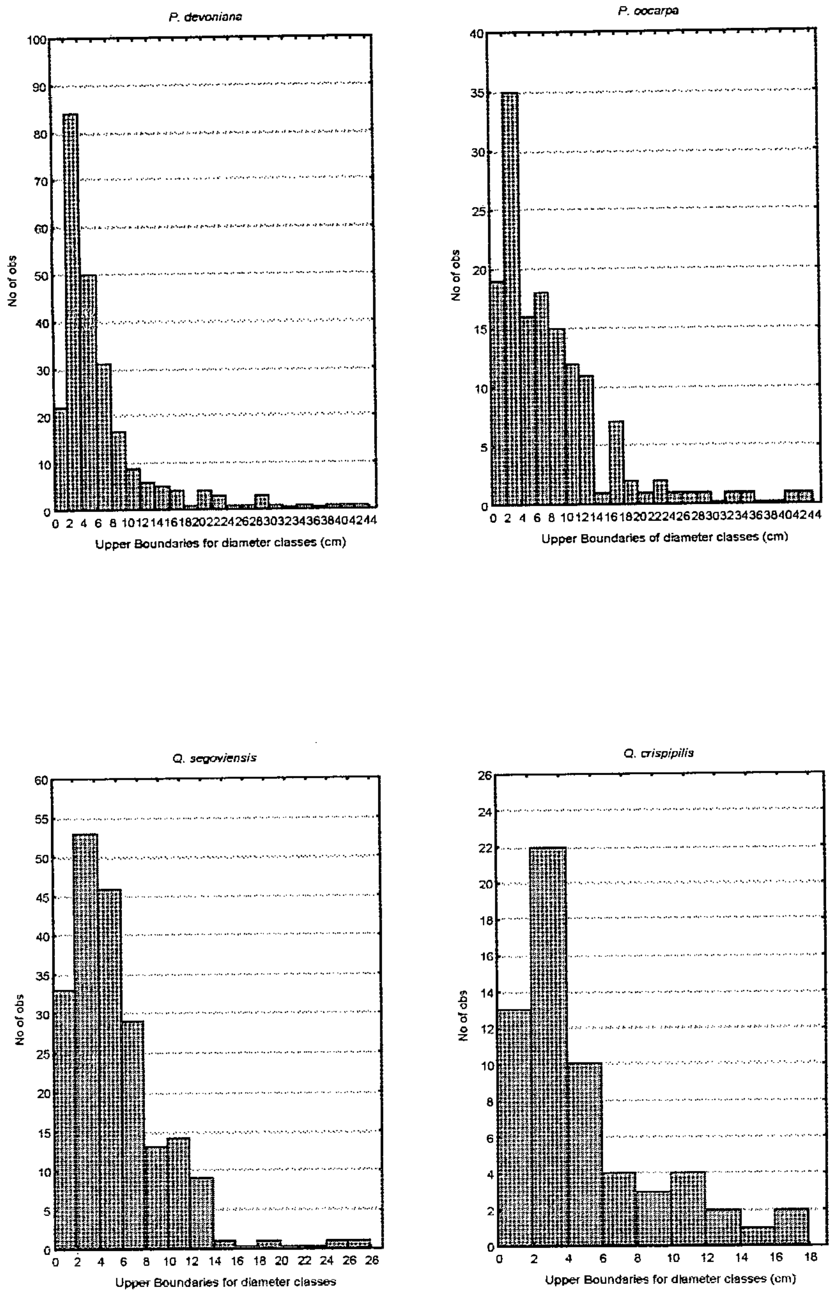


Table. 2.1 Survival of trees in 25 PSPs measured over two years. Basal areas are based on measurements of tree circumferences to the nearest mm and are $m^2\ ha^{-1}$ Heights of resprouts are in cm.

	All trees 1998		Live trees 1999		Live stems 2000		Resprouts 2000		Mortality		Crown kill
Species	**Basal area**	**Stems**	**Basal area**	**Stems**	**Basal area**	**Stems**	**Mean ht**	**Number**	**Stems**	**%**	**%**
Pinus maximinoi	8.73	185	6.81	138	6.70	132	0	0	53	28.6	28.65
Quercus segoviensis	6.20	501	5.28	379	4.95	360	72.7	279	22	4.4	28.14
Quercus crispipilis	3.06	201	2.86	153	2.85	151	68.2	96	8	4.0	24.88
Cleyera theaeoides	1.16	182	0.758	97	0.74	92	65.2	110	25	13.7	49.45
Pinus devoniana	1.14	33	1.07	16	1.047	14	0	0	19	57.5	57.58
Pinus oocarpa	0.775	23	0.697	17	0.689	17	65.4	5	0	0.00	26.09
Acacia angustissima	0.560	17	0.538	13	0.521	12	60.0	1	4	23.5	29.41
Rapanea myricoides .	0.400	47	0.072	11	0.071	12	83.1	30	5	10.6	74.47
Rapanea juergensenii	0.245	41	0.180	21	0.126	11	67.0	32	20	48.8	73.17
Olmediella bestchleriana	0.123	7	0.123	7	0.123	7	25.0	1	0	0.00	0.00
Saurauia scabrida.	0.051	3	0.049	2	0.047	1	91.5	2	0	0.00	66.67
Vernonia canescens	0.008	2	0.000	0	0.000	0	115.0	2	0	0.00	100.00
Cornus disciflora	0.004	2	0.000	0	0.000	0	70.0	2	0	0.00	100.00
Clethra suaveolens	0.004	2	0.000	0	0.000	0	180.0	2	0	0.00	100.00
Total	22.475	1246	18.427	854	17.854	809	962.686179	562	156		

The survey designed to investigate the impact of fire on juveniles within what was assumed to be a more homogeneous area did provide sufficient statistical power to detect unambiguous species specific differences providing the assumptions of independence between trees and random sampling were met. As most of the survey points fell over 10 m apart these assumptions were unlikely to have been seriously violated. Prefire size distributions for the populations display the incipient nature of the vegetation in this more intensely disturbed area of the site. The populations of both pines and oaks were dominated by juveniles between 1 cm and 6 cm. The smallest juveniles and any previous years seedlings are likely to have been completely consumed by the fire, and thus not recorded in the post fire survey.

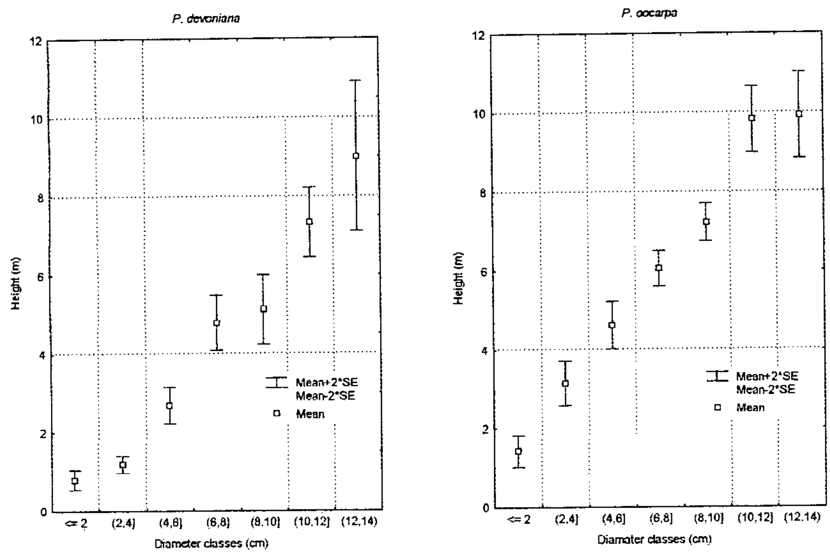
Figure 2.4 Population structures of juvenile pines and oaks in the 40 ha area of the site chosen for a comparative study of fire induced mortality of small trees.



Although the density of stems of the two species of pines in the study area was very similar, the population structures of *P. oocarpa* and *P. devoniana* were significantly different (chi squared $p < 0.001$). The difference was due to a larger proportion of population of *P. oocarpa* falling into 10- 20 cm diameter classes. If similar rates of diameter increment may be assumed for the two species, recruitment of *P. oocarpa* following the last major disturbance may have been initially faster than *P. devoniana* either due to survival by resprouting or establishment from seeds stored in the canopy. Alternatively early growth of *P. devoniana* may be slower.

A significant morphological difference between juveniles of the two pine species linked to the grass stage of *P. devoniana* is revealed by a comparison of the relationship between diameter and height. Figure 2.5 shows the mean height and associated standard error for juveniles classified by diameter. Although the height diameter relationship for the two species becomes similar for larger size classes, smaller diameter classes of *P. devoniana* have clearly significantly lower mean heights.

Figure 2.5 Height diameter relationships for juvenile pines. Error bars represent 2 s.e. units around the mean for each diameter class.

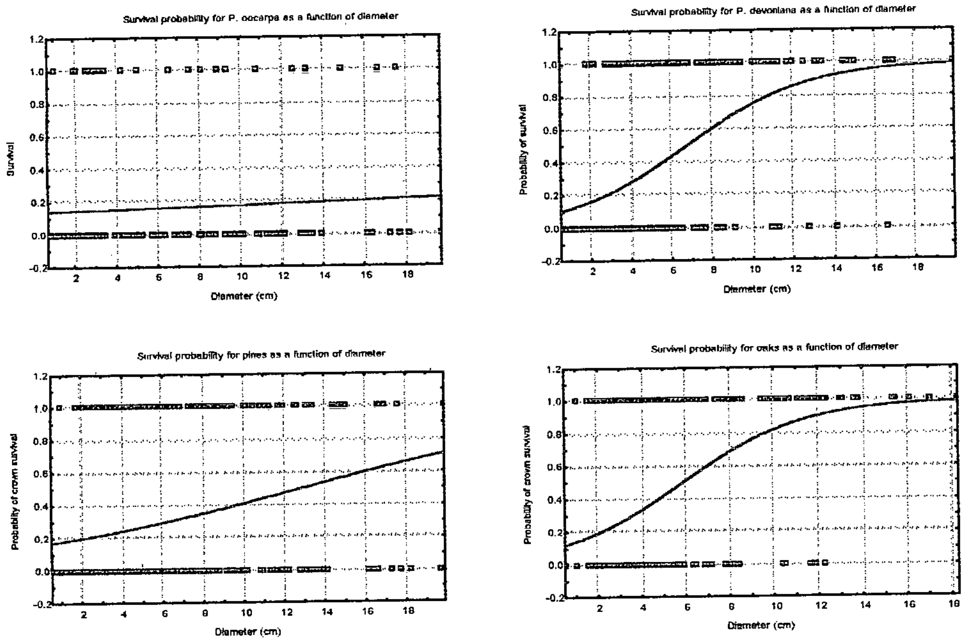


As was found in the PSPs, crown killed oaks displayed vigorous resprouting in this area. Only three individual oaks that suffered crown mortality were recorded as completely failing to produce basal sprouts. Again, as in the PSPs, the almost universal survival of oaks did not permit any quantification of a relationship between oak diameter and the likelihood of surviving through resprouting. A Gaussian relationship in which mid-sized oaks had the highest resprouting rate was expected. This could not be tested as larger oaks, which may have failed to resprout, survived with minor damage to the crown. It is possible that the smallest seedlings, which may also have failed to resprout, were consumed by the fire and so were not included in the survey. The observed effect of fire on oak juveniles which were crown killed was to cause a set back to their growth rather than to remove them from the population.

As expected crown kill of all species was a statistically significant function of diameter. Logistic regression models (table 2.2) provide a concise summary of survivorship patterns. The test of significance of the model is based on the –2 log likelihood statistic. Low p values indicate that the data are unlikely to have been obtained if the null model of no relationship between the dependent variable and the independent variable obtains. As in linear regression the model is constrained by the form of the equation used and any underlying relationship may differ in shape from that suggested by the best fitting logistic model. The stepwise procedure used allows the significance of the second predictor to be assessed after fitting the first model.

Top kill of trees below 18 cm in diameter was found to be significantly dependent on diameter (figure 4). In contrast to the results found for the larger trees in the PSPs no significant differences could be shown between fitted models for the two species of oak therefore the species were pooled in order to increase the power of the comparison which could be made with pines. Oaks showed significantly higher diameter independent crown survival than pooled pines ($p<0.001$). However the two pine species were different in their pattern of survival. Comparatively few individuals of *P. oocarpa* below 18 cm in diameter survived. This resulted in a regression model with a non significant slope. The inclusion of mature individuals in the analysis does produce a significant result as most individuals over 20 cm survived but these trees were not included in the model used for comparative purposes. The model for *P. oocarpa* differs significantly from that produced for *P. devoniana*. Juveniles of *P. devoniana* were more likely to have survived the fire than *P. oocarpa* juveniles ($p< 0.001$). The diameter independent survival of *P. devoniana* and the pooled oaks was not significantly different ($p= 0.21$).

Figure 2.6 Logistic regression models of the relationship between diameter and crown mortality for the four species in the 40 ha area of the site chosen for a comparative study of fire induced mortality of small trees.

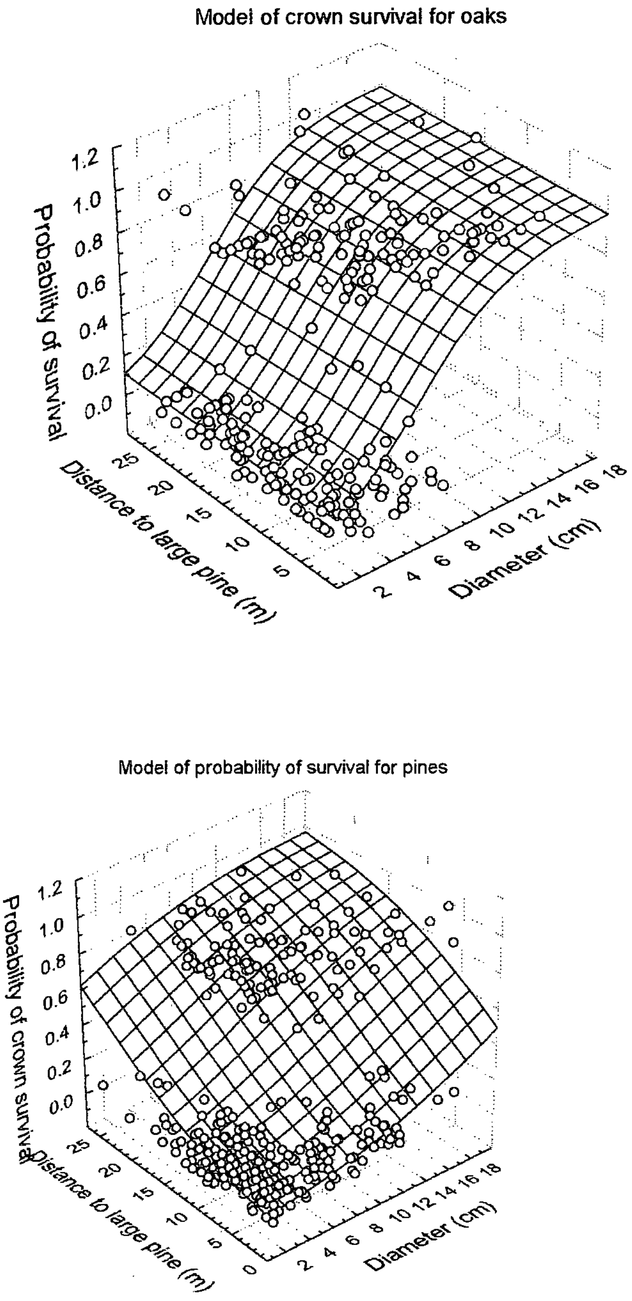


Adding a second predictor, the distance to the nearest large (> 20 cm diameter) pine, to the model significantly improved the amount of variability explained in the case of pines, but not oaks. The lack of significance in the case of oaks could have been due to a difference in the mean distances to the nearest pine for the two groups or in the variability in distances. This hypothesis was tested by a t test of the significance of the difference between the mean distance of juvenile pines and oaks to the nearest large pine. The means of 8.5 m for pines and 10.3 m for oaks were not significantly different (p= 0.23). Levene's test for homogeneity of variances, p= 0.093 confirmed that the spread of distance to the nearest pine for the two groups was comparable, though the difference was significant at the 10% level.

Table 2.2 Logistic regression models of the relationship between diameter and crown mortality for the species in the 40 ha area of the site chosen for a comparative study of fire induced mortality of small trees.

Species	Model	C1	C2	C3	-2 log likelihood	Chi squared	p	Odds ratio	p value (difference from previous model)
All oaks	Diameter	-2.155	0.367		283.7	71.1	<0.0001	7.19	
	Diameter + distance to large pine	-2.046	0.364	-0.0081	283.6	71.27	<0.0001	7.71	0.64
All pines	Diameter	-1.63	0.127		423.1	21.94	<0.0001	2.24	
	Diameter + distance to large pine	-2.872	0.144	0.121	396.4	48.65	<0.0001	4.74	<0.0001
P. devoniana	Diameter	-2.307	0.342		249.7	54.42	<0.0001	8.8	
	Diameter + distance to large pine	-3.34	0.334	0.1078	238.1	66.04	<0.0001	8.52	0.0006
P. oocarpa	Diameter	-1.84	0.03		120	0.36	0.54	----	
	Diameter + distance to large pine	-2.84	0.045	0.1	114.54	5.84	0.052	----	0.019

Figure 2.7 Logistic regression models of the relationship between diameter, distance to large (> 20 cm DBH) pine and crown mortality for pines and oaks in the 40 ha area of the site chosen for a comparative study of fire induced mortality of small trees



Discussion

Evidence that fire did not reduce the number of surviving oaks in secondary vegetation due to vigorous basal resprouting appears to contradict the view that disturbance inevitably leads to a landscape dominated by pines (Gonzalez-Espinosa *et al.* 1991). Diameter independent crown mortality of oaks was lower than that of pines, but pines pass through the vulnerable juvenile stage more quickly due to faster growth rates (chapter 1) Growth of juvenile oaks was clearly set back by crown mortality. Surviving juvenile pines and seedlings establishing after the fire may rapidly overtop resprouting oaks during interfire intervals (chapter 1, chapter 3 and chapter 7). This would lead to a restoration of a double layered vegetation structure, with pines as the dominant canopy tree. Such vegetation may be regarded as pine dominated when basal area is considered, even though oak populations are largely unaffected by fire.

The role of fire in mediating competitive interactions between pines and oaks has been extensively discussed (Streng, Glitzenstein and Harcombe 1989; Barton, 1999; Glitzenstein *et al.* 1995; Williamson and Black, 1981). Some ambiguity can arise due to the terminology used. As is usual with ambiguity in ecology, the problem is resolved by defining the scale of perception and more careful definition of the variables to which terms are applied. Barton (1999) states that pines are more resistant to fire than oaks. This is an accurate statement as the definition of resistance and resilience used by Barton is taken from Rowe 1983 and refers to top kill. However if the whole system of pine-oak dynamics were of interest it might suggest behaviour that has not been observed. The terms inertia and resilience used in the introduction to this study were derived from system theory (Hollings 1973; Westman 1978; Pimm 1991). Resilience could refer either to basal area, or to numbers of individuals. When longer term dynamics, and the interactions between pines and oaks are considered to form a system of interest it could sometimes be appropriate to apply the terms *inertia* (sensu Westman 1978) and *resilience* (sensu Pimm 1991) to the population of stems in an area. They then communicate information regarding the ultimate effects of fire on temporal and spatial patterns in the system as a whole over long time scales. Pine populations tend towards resilience and thus oscillate, while oak populations have a high level of inertia and are rather static when numbers of stems are considered. Inertia can be overcome by chronic stress, which can degrade the entire system, but not by the point effect of a single fire. Analogies may be drawn with the seeder-sprouter dichotomy in Mediterranean shrublands. The long term resilience of populations could not be fully assessed in this short term study. However the distance of displacement of the population from its original condition in terms of mortality was measured. In terms of population size this displacement was very small for oaks, but comparatively large for pines.

The resilience of oaks at an individual level leading to inertia at the population level appears to be a very general phenomenon. Oaks are particularly vigorous resprouters under semi-xeric conditions. Examples of documented situations in which fire has led to the loss of oak from an area are not easily found in the North American pine-oak literature. Repeated fires over a short time interval may well exhaust the capacity of oaks to resprout leading to a reduction in the number of stems, although scarlet oak has been shown to sprout repeatedly (Cobb, Miller and Zahner 1985). Though the effect of resource exhaustion can be incorporated into models of the systems (Dey, Johnson and Garret 1996) it has not been well documented. The extremely vigorous resprouting observed at this site suggested that no reduction in oaks' capacity to resprout has occurred due to any previous disturbance. This may be because sufficient time has passed since previous fires to allow stored resources to build up, or because these oaks resprout vigorously regardless of past history. No evidence was provided which could test these hypotheses. Similarly, although an effect of size on resprouting ability would be expected, it was not detected. Some early research reported an increase of oaks in pine dominated areas following burning (Heyward 1939). A consideration of the temporal perspective being adopted is needed when the results of studies are interpreted. Although an increase in oak stems was observed at the site it was assumed to be a temporary phenomena as self-thinning would lead to a reduction as succession proceeds.

Although fires in pine-oak woodlands do tend to increase dominance by pines the mechanism by which this occurs is not fire induced mortality of oaks. Rather it seems to be the short term effect of a reduction in live oak basal area following fire. Fire suppression in North American pine-oak woodlands has led to many well documented instances of increased hardwood dominance (Palik and Pregitzer 1992; Roy and Vankat 1999; Gilliam and Platt 1999; Motzkin Patterson and Foster 1999). Thus in the longer term fire acts to prevent the eventual competitive displacement of pines by oaks during the course of succession and thus should tend to restore a pine-oak mix in undisturbed areas in which closed oak canopy is suppressing pine regeneration.

The failure of the survey to establish a relationship between diameter independent oak top kill and distance to a large pine is difficult to explain and contradicts the findings of a classic study (Williamson and Black 1981). Because the study was a survey rather than a controlled experiment, site specific effects cannot be excluded. An unrepresentative sample of individuals may have been included in the data set causing erroneous results, although the finding did not appear to be inconsistent with visual impressions of the fire effects over the study area and beyond. A possible explanation may be provided by the clumped distribution of young oak stems due to previous resprouting. Hardwood litter is not easily ignited and burns at a lower temperature than pine needles (Vose *et al* 1999). Fire intensity within a clump of oaks may have been determined by the build up of fuel provided by the oaks themselves rather than litterfall from neighbouring pines, or oak clumps may tend to trap wind blown pine litter in a way that small pines do not. In chapter 3 it is shown that oaks may be associated with tall herbs that dry to produce a further source of inflammable litter that is not usually associated with isolated juvenile pines. The generality of the observed pattern of mortality and its underlying causality need further investigation. Experimental manipulations in similar vegetation would allow more rigorous testing of hypotheses based on the observations made in this study.

The effect fire may have on determining relative abundances of pine species has been largely confined to discussions of rather larger scale patterns of pine distribution than would be found at a single site (Keeley and Zedler 1998). However these results show how quite local spatial structure may emerge in a community following fire. The hypothesis that fire mediated mortality of juvenile pines is influenced by their position with regard to adults is supported. The evidence suggests that the ground fire burnt at a lower intensity in areas away from large pines, or clumps of shrubby vegetation. Juvenile pines provide very little combustible material themselves and are therefore extremely sensitive to variations in fire intensity caused by litter build up from neighbouring large individuals. This effect is likely to produce an open, savannah type community if fire recurrence is less than the time needed for individuals to reach a diameter at which they may survive the fire.

Of the four species that were intensively studied, *P. oocarpa* was apparently the most vulnerable to fire induced mortality. Although the comparative mortality of *P. maximinoi* was not assessed as rigorously, the results from the PSPs suggest that top kill of this species under comparable conditions would not differ markedly from that found for *P. oocarpa*. The species is superficially very similar in general morphology to *P. oocarpa* (Farjon 1984). with comparatively slender terminal branches (5- 7 mm vs 8- 14 mm in *P. devoniana*) and thin (< 10mm) bark. On the basis of the results from the comparative study, repeated ground fires with recurrence times of below 10-15 years would be expected to move a mixed community towards one dominated by *P. devoniana*. However the key characteristic that allows the persistence of *P. oocarpa* in the face of a fire regime which otherwise favours *P. devoniana* is the species ability to resprout. Although resprouting was not recorded in the first few months following the fire, vigorous resprouting from root crown was noted in a large proportion of smaller individuals of *P. oocarpa* later in the year, continuing into the spring of the following season. This unexpected effect should be considered when future studies of fire impact in the region are planned.

In the absence of frequent fire the comparatively rapid height growth of both *P. oocarpa* and *P. maximinoi* would be expected to lead to a competitive advantage over *P. devoniana* during inter fire periods. This advantage would be especially marked as closed canopies begin to form. In such a community stand replacing crown fires, rather than ground fires, would be more likely to occur. The results obtained from the PSPs, which suggested comparatively high mortality of *P. devoniana*, appear to contradict the findings from the statistically more rigorous study. However the effect may not have been merely an artefact. There is a suggestion that although *P. devoniana* can resist low intensity ground fire, the species is rather poor at surviving the rather more intense ground fires which occur in denser forest. Alternatively, even if fire intensity is comparable in denser forests the result may be due to low shade tolerance in the species. This could result in poor pre fire growth and consequently increased vulnerability to fire induced mortality in areas with canopy closure. These speculations cannot be confirmed from the available data, but provide an interesting topic for future research.

Stand replacing fire should result in conditions that favour regeneration of *P. oocarpa* due to its serotinous cones. Slash and burn clearance may provide similar favourable conditions for regeneration of *P. oocarpa*, providing some individuals of the species are already present within the burnt area. However the serotinous cones of *P. oocarpa* could be disadvantageous for invasion of slash and burn sites as seed release from surrounding unburned areas would not occur. Only oaks and other very vigorous resprouters can survive the intense disturbance of slash and burn clearance *in situ* (see chapter 4). *P. maximinoi* may thus be the most favoured pine species to colonise areas following the abandonment of slash and burn sites. Interestingly regeneration of pine in the northern are of the bienes comunales only became noticeable two years after the fire and has not as yet not been documented. This delayed colonisation is probably due to low seed availability immediately following the fire. Mature trees of *P. oocarpa*, which would have provided the most immediate seed source, are not numerous within this area.

The results have implications for forest management. Prescribed burning is used in the Southern United States in order to restore long leaf pine savannah (Glitzenstein *et al.* 1995). Controlled burning is also used in the management of less fire resistant species of pine (McRae *et al.* 1994; Cain *et al.* 1998; Vose *et al.* 1999). The effect of prescribed fire has been assessed for *P. oocarpa* stands in Honduras (Hudson *et al.* 1983a; Hudson *et al.* 1983b). Clearance and associated burning was probably associated with the initial establishment of pines at the study site. However the study demonstrated that wild fire produces both short and long term effects that differ from those of slash and burn clearance. The high juvenile mortality observed at the site does not suggest an immediate positive role for fire at this already understocked site. Repeated burning at this point would probably lead to a reduction in standing pine timber over time, unless active steps were taken to improve regeneration, possibly through a reduction in grazing. The species favoured by a frequent fire regime, *P. devoniana,* is also a rather less desirable species than *P. oocarpa* as timber. If future burns were combined with the removal of seed sources, which may occur as a result of timber extraction, they could potentially encourage a move towards an oak dominated understorey. Oaks would then tend to exclude recolonisation by pine as their canopies develop. On the other hand, if situations arise where such oak dominance has already reduced pine recruitment, fire could be used as it is in the United States, to open the canopy and improve pine regeneration. This would only be a suitable course of action if a good pine seed source were available. Thus any prescribed burning programs contemplated for the region must be site specific and must take into account the potential complexities of underlying ecological processes associated with fire.

Conclusion

Fire mainly affected the smaller trees at the site. Small pines close to larger pines were particularly likely to suffer mortality. Pines were distinguished by species specific differences in fire survival, while the two oak species were rather similar in their mortality patterns. No relationship between tree size and resprouting vigour was found. Almost all the oaks suffering top kill survived as resprouts. The inertia of oak populations to the effects of ground fire leads to the conclusion that such a disturbance type is unlikely to explain spatial pattern in oak distribution. In contrast, pines show significantly different responses to ground fire. The north-south divide in pine distribution found at the site may have arisen as a result of fire adapted pines spreading into the area from the historically fire prone pine savannah to the south. While fires may affect the short term physiognomy of the vegetation and prevent long term competitive exclusion, they are unlikely to have a major effect on the pine-oak balance in already disturbed areas. Incorporation of fire into a dynamic modelling framework will help to clarify its long term effects.

Chapter 3.Regeneration following slash and burn clearance

Introduction

In the previous chapter the role of fire in disturbing the vegetation at the field site was documented. It became apparent as work at the site progressed that fire alone could not have caused the immature status of the forest which has been described in chapter 1. Fire was found to kill mainly small trees, yet the notable feature of the data was the absence of large trees. Furthermore, clear signs of disturbance by slash and burn milpa farming were apparent throughout the forested area. In this chapter the effects of this unique form of disturbance are documented.

Pine-oak woodland has been found to regenerate readily on land that has previously been used for agriculture both in North America (Peet and Cristenson 1988; Bratton and Miller 1994; Compton *et al.* 1998; Motzkin, Patterson and Foster 1999) and in Europe (Carcaillet *et al.* 1997). Many patches of forest at the site are recovering from the effects of recent slash and burn agriculture. The rate at which recolonisation from the surrounding vegetation takes place and the extent of *in situ* survival through resprouting provides vital information needed to model stand development and structure. In addition a study of vegetation growing on sites with a known history of agricultural usage will help to resolve questions regarding the impact of slash and burn agriculture on the floristic diversity of the area.

Slash and burn clearance can form part of a cyclical system if followed by vigorous regeneration. However grazing could prevent tree survival and establishment or reduce growth of regenerating trees through a negative impact on soil properties. Grazing pressure at the site has increased from approximately 0.01 animals ha $^{-1}$ in the 1980s to approximately 0.1 animals ha $^{-1}$ in 2000 (farmers comments and personal observations). Consideration of the results of a model produced for European broadleaved forest suggests that grazing of this intensity would have only a marginal direct effect on regeneration if the impact were evenly distributed over the whole site (Jorritsma, Van Hees and Mohren 1999). However because cattle and sheep are selective in their grazing and do not spend much time in areas of closed canopy woodland, their impact is concentrated on areas which have been previously opened by slash and burn farming (personal observation). Highly local patchiness in intensity of grazing thus arises.

Although the direct effect of grazing is mechanical damage to establishing trees which might prevent forest regeneration, repeated cycles of clearance would also be expected to lead to some degradation of the productive potential of forest soil (Martens *et al.* 1991; Killian 1998; Garcia-Oliva, Sanford and Kelly 1998). Soil organic matter, which accumulates under oaks, is lost following canopy removal (Dahlgren Singer and Huang 1997). This process occurs more rapidly if shrubs and tall herbs are unable to quickly restore a closed canopy above-ground level. Grazing also causes soil compaction, which directly prevents recolonisation by trees. Unequivocal quantification of degradation through grazing is impossible without a reference point provided by historical measures of productivity. While heterogeneity in the growth rate of regeneration between patches would be consistent with the hypothesis that some degradation in soil properties has taken place, other causes could be proposed. Nevertheless it may be useful to test for such heterogeneity, either in order to begin to build a set of observations that can form the basis for hypotheses to be examined more rigorously through experimentation, or to estimate parameters that can be used in a modelling context.

Although the previous chapters have focused on the dynamics of canopy trees, the vegetation of abandoned milpas is initially dominated by a more diverse assemblage of shrubs and smaller trees, some of which later form the forest under storey as stand development progresses. The diversity of this vegetation could be related to the degree to which usage has led to degradation in soil properties. Successional patterns may also be apparent in such vegetation. Open grazed areas will have fewer stems of woody species than areas that are ungrazed. Quantifying the relationship between grazing and indices of diversity, which summarise community attributes such as equitability and dominance, provides insight into differences between the vegetation of each area that go beyond the more superficial measure of stem density. It was hypothesised that diversity of woody plants would be significantly lower in plots in which stress is high. Stress is assumed to be caused directly by defoliation associated with grazing and indirectly by soil compaction, nutrient loss and the extremity of the micro climate in open areas. The hypothesis of a positive relationship between diversity and productivity follows from the unimodal model of the relationship discussed by Huston (1994). The site as a whole is known to have very poor edaphic qualities and it is assumed that the negative relation which is often found in very productive situations is less likely to hold. Hypotheses regarding indices of diversity could also be studied in greater detail by concentrating on the actual identities of the species found. Thus composition itself might be correlated with grazing or could be the result of a degree of successional replacement in the time since milpa abandonment.

Key parameters required in later chapters of this work for modelling purposes were 1)The size of milpa plots 2)The rate at which colonisation of milpas by pines and oaks takes place 3)The rate of re growth of pines and oaks in milpas. It was also hypothesised that 1)Variation in growth rates of juvenile trees between milpas is higher than the variation in growth rates within milpas 2) Spatial variation in growth rate of juvenile pines is correlated with variation in growth rate of oaks 3)Growth rate of juvenile trees is negatively correlated with grazing intensity. 4) Diversity indices for tree and shrub species are negatively correlated with grazing intensity 5) Diversity indices for tree and shrub species are positively correlated with site quality. 6)Tree and shrub species composition is related to site quality 7) Tree and shrub species composition is related to grazing intensity.

Method

The survey was conducted during the months of February to May 2000. Thirty seven accessible milpas, which had been used within the last twenty years, were found within the study site from which a random sample of twenty five was selected. One milpa was recleared after work begun and only partial data collected. The history of each milpa was determined through interviews with the farmers. Reliable dating of the time of clearance was possible for thirteen of the twenty five areas. In the remaining areas discrepancies of up to five years were found in the accounts. Consequently the reported time since abandonment was taken as a guide to data interpretation and used to produce a classification of the milpas, rather than as a continuous independent variable for regression analysis. Time since last abandonment ranged between 8 and 20 years. Comparisons were further complicated because several of the milpas had been either partially or completely recleared in the time since initial abandonment. In addition the 1998 fire had destroyed some of the evidence of post abandonment regeneration.

The perimeter of each milpa was measured by standard surveying techniques and the position of the centre recorded using a GPS. A plan of each milpa was produced and its surface area calculated. The presence of mature individuals of the principal tree species in the surrounding vegetation was recorded and the proportion of the perimeter made up of each species estimated.

Two orthogonal transects were cut through the vegetation in each milpa, one running from N-S and the other E-W. Quadrats of 5 m x 2 m (10 m^2) were selected at intervals of 10 m along each transect and at a random lateral offset to the quadrat of up to 30 m in either direction. Transects were cut for convenience of access as the vegetation in many milpas was dense and contained species bearing thorns.

The survey design maintained the number of quadrats in each milpa as an approximately constant proportion of the milpa size. This was considered desirable in order to reduce the heterogeneity of estimates of within milpa variability which might arise in this patchy vegetation if smaller milpas were sampled more intensively than larger milpas. The difficulty of patchiness causes non independence of sampling units. The issues concerned should be considered when the results are interpreted. Balanced sample sizes were not obtained, but while they are desirable, they are not essential for one way ANOVA (Underwood 1997). Data obtained from surveys rather than experiments can rarely fully meet all the criteria for ANOVA, which is more suited to an experimental setting. Violation of the criteria of lack of independence could not be completely avoided. The statistical models that were tested must be regarded as exploratory techniques comparable to multivariate analysis.

The survey produced a total of 478 quadrats of 10 m^2 in the 24 milpa plots. In each quadrat all individuals of tree and shrub species over 1 m in height were tallied. Woody stems were found in 465 of the quadrats. A total of 7,182 individuals were recorded. Trees or shrubs were defined as perennial species with free standing woody stems which do not die back to ground level during the dormant season. Multiple stems arising from a common rootstock were counted only once. The discreteness of each individual was usually apparent, although the number of individuals of species such as *Quercus sebifera*, which spreads extensively through root sprouting, may have been overestimated. All species were identified with reference to collections held in the herbarium of El Colegio de la Frontera Sur where voucher specimens were deposited. A full list of species recorded at the site is provided in appendix 1

The definition of woody species excluded sub-shrubby annual and perennial plants such as *Eupatorium* spp. *Melampodium* spp. and *Calea* spp., which were dormant at the time of the survey. The abundance of stems of these sub shrubs and tall forbs was however noted as was the abundance of *Pteridium aquilinum*. These species taken together are responsible for the formation of a matrix of unpalatable stems and foliage during the growing season that may affect the grazing pattern of animals at a local scale. Where taller herbs are not present a sward of grasses and sedges forms which encourages continued browsing and trampling. For each quadrat the proportion of tall herbs was recorded according to a classification that used the previous year's dead stems to estimate the cover of herbs that would be expected to develop during the growing season. 0) No tall herbs 1)Tall herbs < 5% cover 2) Tall herbs >5% cover but < 50% cover 3) Tall herbs > 50% cover . This index was negatively related to the proportion of the ground covered by grasses and sedges that was also recorded but has not been reported in subsequent analyses due to redundancy. Direct grazing damage to shrubs through browsing could not be recognised in the field, either because damage was slight, or because browsing occurs during the growing season. The most appropriate index of the localised grazing impact on each milpa was thus assumed to be the mean of the ordinal values of tall herb cover.

The soil in each quadrat was classified into four simple qualitative classes.0) *Exposed rock or* subsoil 1) *Poor*: Soil surface compacted with a dark stained layer less than 5 cm in depth 2)*Normal*:Dark stained layer 5 cm to 15 cm in depth 3) *Good*: Dark stained layer over 15 cm in depth. The mean of these scores was used as a quantitative measure of overall soil quality for each milpa. Slope was also recorded for each quadrat. Mineral soil depth was measured by pushing a 1 m metal rod into the soil at random positions within the quadrat until it met a rock and recording the mean of three readings.

Because of the comparatively small area covered by the quadrat survey in each milpa, a limited number of pines and oaks and the larger sub canopy species such as *Cleyera theoides* and *Rapanea juergensenii* fell within the quadrats. To provide a large enough sample to typify size distributions for each milpa, measurements of height and diameter 30 cm above-ground level were taken on a random sample of twenty trees of each of the canopy forming species in each milpa. Because some did not contain twenty specimens of each of the five species of interest, balanced sample sizes could not be obtained. Saplings reaching over 2 m in height were selected on the basis of proximity to the randomly placed quadrats. Where clumping of trees occurred a single individual was selected from each clump by numbering the stems and choosing one at random, except in the case of a clear group emerging from a single common rootstock in which case the dominant stem was measured.

A complete count of the number of pine and oak saplings and trees over 2 m in height was also made for each milpa. This was possible as such trees emerge from the surrounding vegetation and were easily visible from a suitable vantage point or were tallied as work proceeded on quadrat placement. Trees killed by the 1998 fire were included in this count in order to estimate regeneration rates in the time since clearance. Because the study aimed to measure parameters of importance for subsequent forest development, clumps of stems of resprouting oaks were counted as single individuals under the assumption that self thinning later in succession would reduce their number.

In addition to the qualitative assessment of soil properties, site quality was estimated by an indirect analysis that used measurements of tree growth. Height-diameter relationships are the basis of site indices widely used in forestry. Though many methodological variants have been proposed (McDill and Amateis 1992; Meng *et al.* 1997; Zeide 1999) an assumption common to most site indices is that poor edaphic conditions reduces height gained for a given stem diameter (though see Wang 1998). Because of the wide range of ages of the trees in the milpas, direct comparisons of the height of the vegetation are confounded. However analysis of variance of the residual variation in height after statistically compensating for the effect of diameter can be used to test for significant variation in growth conditions between milpas. In order to allow full diagnostic checks the procedure was carried out in two stages. Regression equations for height on diameter at 30 cm above ground level were fitted to the complete data set for each of the four tree species with broad representation in the milpas, *P. maximinoi, P. oocarpa, Q. crispipilis,* and *Q. segoviensis*. The highly anomalous species *P. devoniana* (chapter 2) was not included. In order to reduce bias in the residual variation due to non-linearity of the relationship a quadratic equation was fitted of the form

$$H = b_1 + b_2.D + b_3.D^2 \qquad \text{Equation 3.1}$$

Where H is height, D diameter and b_1, b_2, and b_3 are constants. Cutting of oaks for fuelwood, and pollarding of live stems in order to use then as support for climbing beans results in individuals which are very clear outliers with much lower heights than predicted. These unusual individuals were not included in the analysis. After fitting the equations for each species the usual diagnostics were carried out by inspection of scatter plots showing predicted values against observed values, predicted values against residuals and normal probability plots. It was expected that a logarithmic transformation of one or both axes would improve statistical properties, but no trend was identified in the residuals that suggested that transformation of either of the variables was necessary. Species specific relationships, rather than pooled data for pines and oaks, were fitted. This was preferable as clear intrageneric differences have already been documented (chapter 1 and chapter 2). However once species specific equations had been produced, the residual heights after removing the effect of diameter were pooled into the two broad functional grouping of pines and oaks in order to summarise patterns of differences. As most milpas had equal number of the two oak species this is unlikely to have caused bias, but it could have slightly exaggerated the site indices in a small number of milpas in which the taller oak species *Q. crispipilis* was the only oak present.

One way analysis of variance of the residual heights after the predicted height from the regression model had been subtracted was used to test the null hypothesis that the variation in growth conditions between milpas was no greater then the variation in growth conditions within milpas (Underwood 1996). The residuals were then also analysed using linear regression to test for correlation between SI as measured for each of the two FGs and between SI and the soil and grazing indices produced independently.

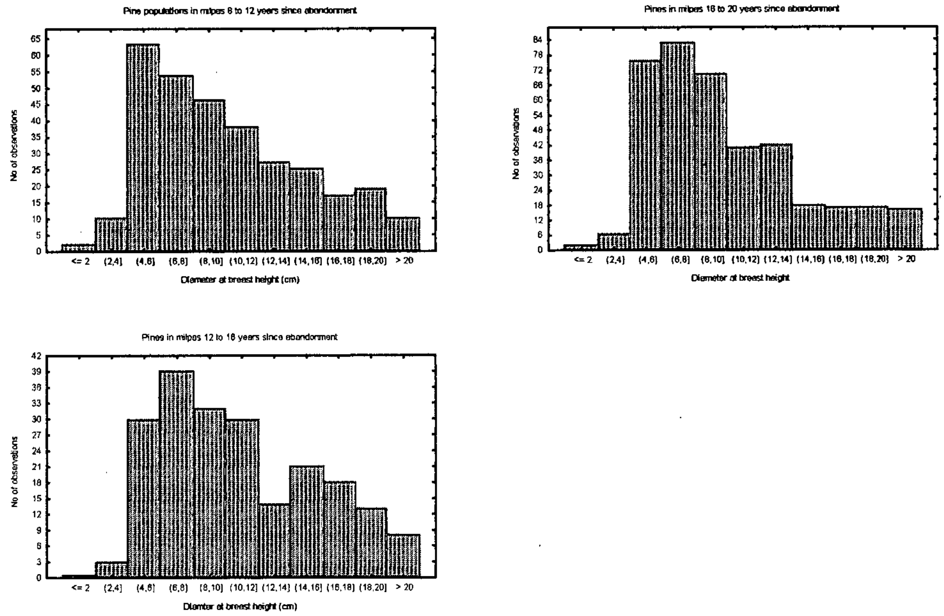
Two diversity indices are reported. Shannon's H which has a strong richness component, and the reciprocal of Simpson's D which is negatively related to dominance of one or a few species (Magurran 1988). The standard error associated with the diversity indices for each milpa was found by calculating jack-knife pseudovalues following the procedure after Pielou (1975) in Magurran (1988). A macro written in visual basic linked to MSAccess data base was used. Diagnostic checks showed that pseudovalues could be treated as being normally distributed around the mean, therefore the significance of between plot variations in diversity was evaluated by analysis of variance of the pseudovalues. This tested the simple null hypothesis that variation in diversity between milpas was no greater than variation within milpas (Underwood 1996). Because analysis of diversity in terms of numbers of species (S) was found to raise some additional issues it will be presented in more detail in the subsequent chapter.

An ordination through detrended correspondence analysis (DCA) using the program Canoco was used to summarise the species data. Relationships between species composition and environmental variables were tested by evaluating the significance of correlations between DCA scores, grazing and soil indices. The unconstrained ordination produced by DCA was found to be more efficient in summarising species-site relationships than constrained ordination used in chapter 1 for analysing spatial pattern.

Results

Mean size of milpa plots was 1.21 ha (sd=0.67 se=0.14). The mean diameters for all species in the pooled milpas are given in table 3.1. The mean diameter of *Q. crispipilis* is quite clearly significantly greater than that of *Q. segoviensis,* although this should be seen as a context specific observation rather than a statement regarding underlying differences between the two species. In order to summarise general patterns in the data oaks and pines have been pooled. The pine population structure shown in figure 3.1 shows a unimodal distribution that becomes slightly more pronounced in plots that were assumed to be older based on farmers comments. This suggests that a gradual recruitment of pines over the space of five to ten years after clearance could be followed by a reduction in new recruits in older milpas as shrubs and oaks begin to form a closed canopy. The largest pines found (not presumed to have been left standing when the milpa was cleared) have reached a diameter of 28 cm since milpa abandonment.

Figure 3.1 Diameter distributions for stems of pines over 2 m in height in milpas abandoned to regrowth between 8 and 20 years ago.



Oak regeneration as shown in the size distributions in figure 3.2 was mainly due to resprouting from the root crowns of what appeared to have been small to medium sized trees (10- 40 cm diameter) at the time the milpas were cleared. The size distributions show that diameter increment has been comparatively slow and variable. Of the total of 342 individuals of *Q. crispipilis* selected for measurement 281 were clearly derived from a previous stump or root crown. Of the 452 individuals of *Q. segoviensis* 428 were clearly resprouts. It was not clear if the remaining oak saplings had established from seed or by adventitious suckering from rootstocks. Evidence of spread through suckering was found around many mature oaks at the site, particularly following fire damage. Mean heights of the regeneration in each milpa (figure 3.3) showed no obvious relationship with the reported time since last clearance.

Figure 3.2 Diameter distributions for stems of oaks over 2 m in height in milpas abandoned to regrowth between 8 and 20 years previously.

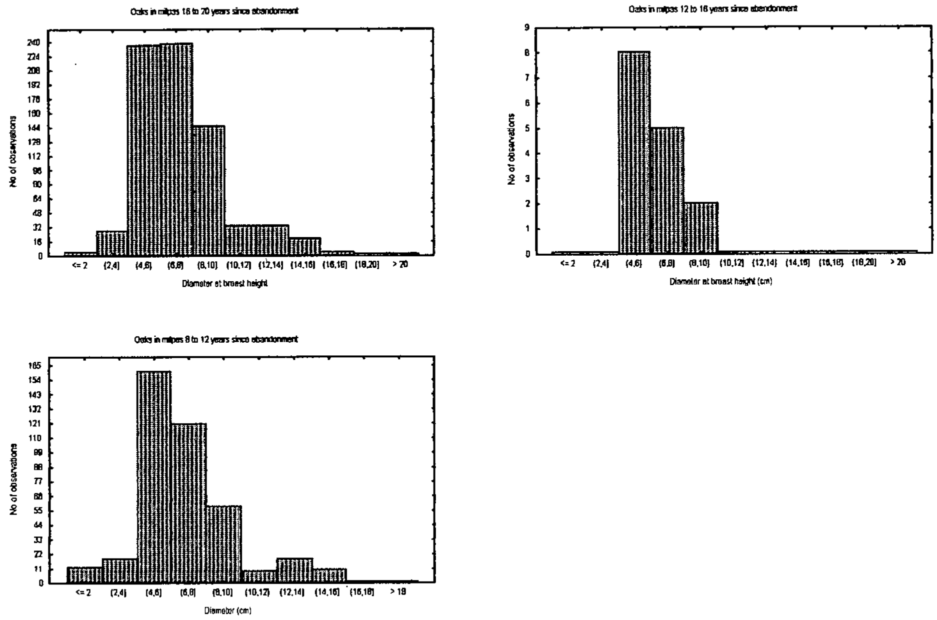


Table 3.1 Mean diameters of forest trees regenerating in 24 milpas of reported ages between 8 and 20 years. Note that the total sample size for each species varies.

Species	Mean	95% CI	N
Cleyera theaeoides	5.79	0.49	76
Olmediella bestchleriana	6.99	1.40	24
Pinus devoniana	9.62	1.52	72
Pinus maximinoi	10.82	0.49	424
Pinus oocarpa	9.07	1.06	88
Quercus crispipilis	7.77	0.35	342
Quercus segoviensis	6.83	0.23	452
Rapanea juergensenii	5.12	0.20	48
Rapanea myricoides	4.78	0.96	13

From figure 3.3 it can be seen that pines were taller than oaks in all except one of the milpas in which the two groups were found together. However in three milpas the difference in mean heights were not significant. In one exceptional 17 year old milpa, oaks quite clearly grew over pines. The oaks (*Q. crispipilis*) were apparently older than the pines that may have established following a ground fire around seven years previously caused by clearance of a neighbouring milpa. This particular milpa had been cut from comparatively mature forest and had a deeper (20 cm) layer of organic soil than the other areas.

With the exception of clumps of resprouting oaks which were treated as single individuals, the stems of all species in most milpas were well spaced with little possibility of direct competition at this early stage of forest development. No significant relationship between the number of individuals of any species and the reported time since clearance could be established. A maximum density of 348 pine stems ha $^{-1}$ was found and a maximum density of 732 oak stems ha $^{-1}$. Figure 3.4 and figure 3.5 show how pine and oak densities relate to the mean index of tall herb density, which is assumed to be the best indicator of grazing intensity. There is slight positive correlation between pine density and grazing and a small negative correlation in the case of oaks. However neither of these are statistically significant. The peak density of pines stems was however found in a milpa that appeared to be heavily grazed, and the peak density of oaks was in a lightly grazed milpa. Figure 3.6 shows the very close correlation between the presence of a matrix of tall herbs and the number of stems of all woody species including smaller shrubs. This suggests that the visual impression of vigorous regeneration in many milpas might be less closely connected to their longer term dynamic in terms of the development of canopy trees than would initially be assumed. An impression of vigorous regeneration can arise as a result of multiple stems of smaller species, which will not become trees. Table 3.2 shows the estimated maximum rates of establishment on a species specific basis, which may be used as a guide for constraining the rates of regeneration used in the model, presented in chapter 6 and 7. Mean establishment rates would be less informative as they would be biased by milpas with no nearby seed sources.

Figure 3.3 Mean heights of pines and oaks in milpas abandoned to regrowth between 8 and 20 years ago. Error bars are 95% confidence intervals based on samples of between 20 and 40 individuals per milpa. Milpas are arranged in order of reported time since clearance.

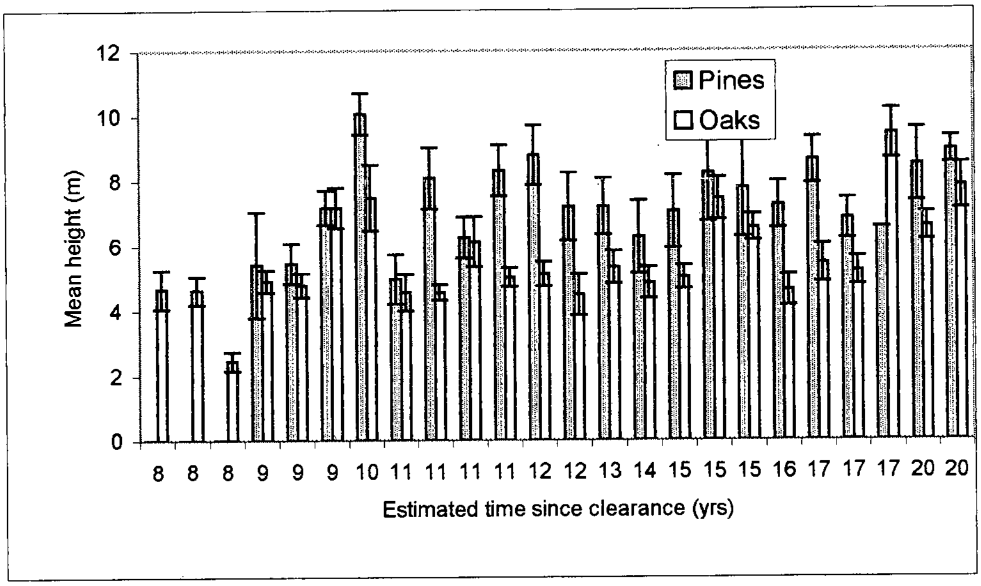


Figure 3.4 Density of pine stems in 24 abandoned milpas related to an index of the density of tall herbs. Areas with tall herbs are assumed to receive a lower grazing impact.

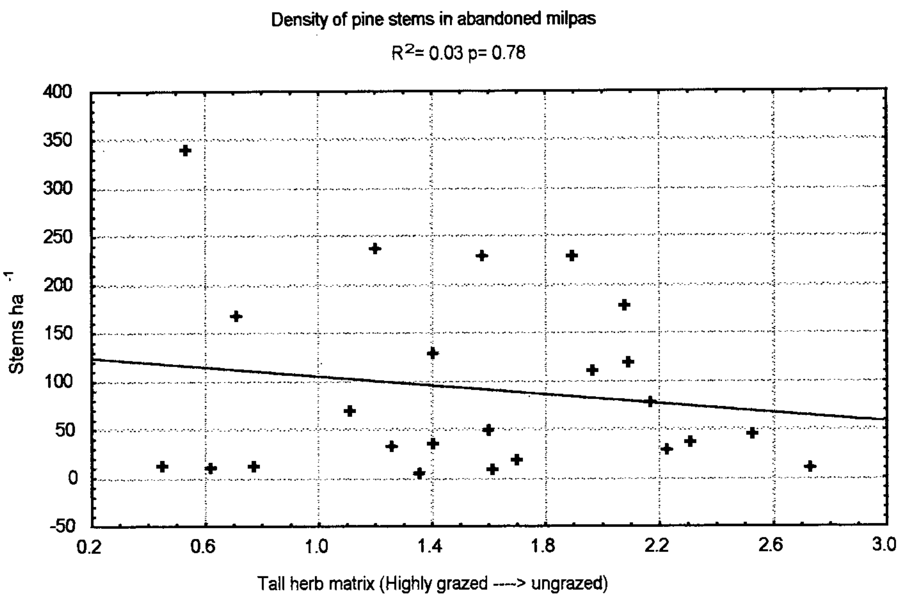


Figure 3.5 Density of oak stems in 24 abandoned milpas related to an index of the density of tall herbs. Areas with tall herbs are assumed to receive a lower grazing impact.

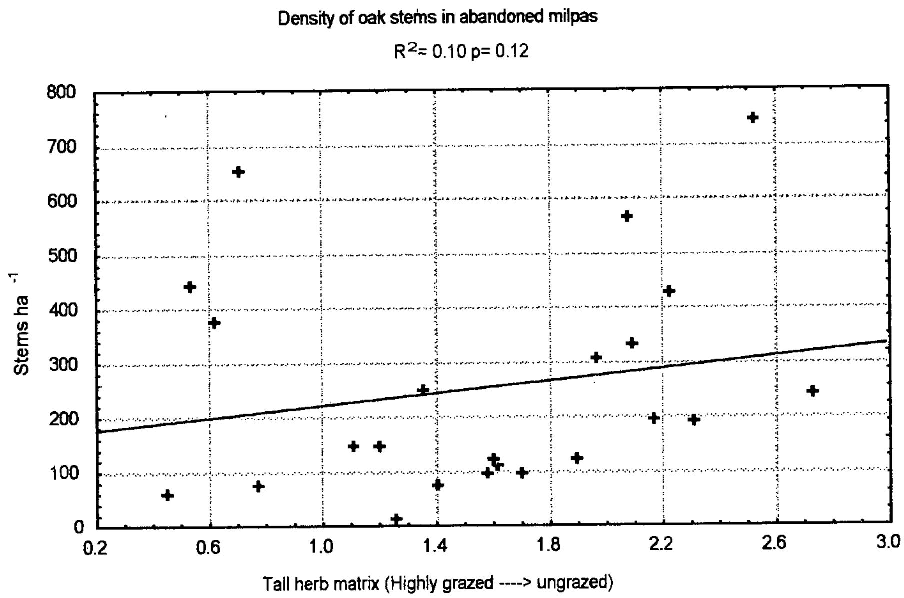


Figure 3.6 Density of all stems of shrubs and trees in 24 abandoned milpas related to an index of the density of tall herbs. Areas with tall herbs are assumed to receive a lower grazing impact.

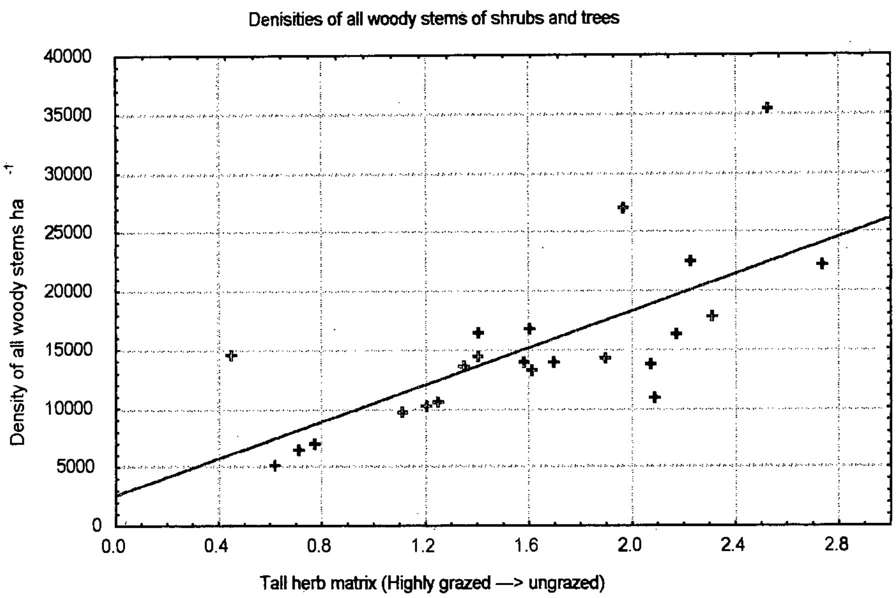


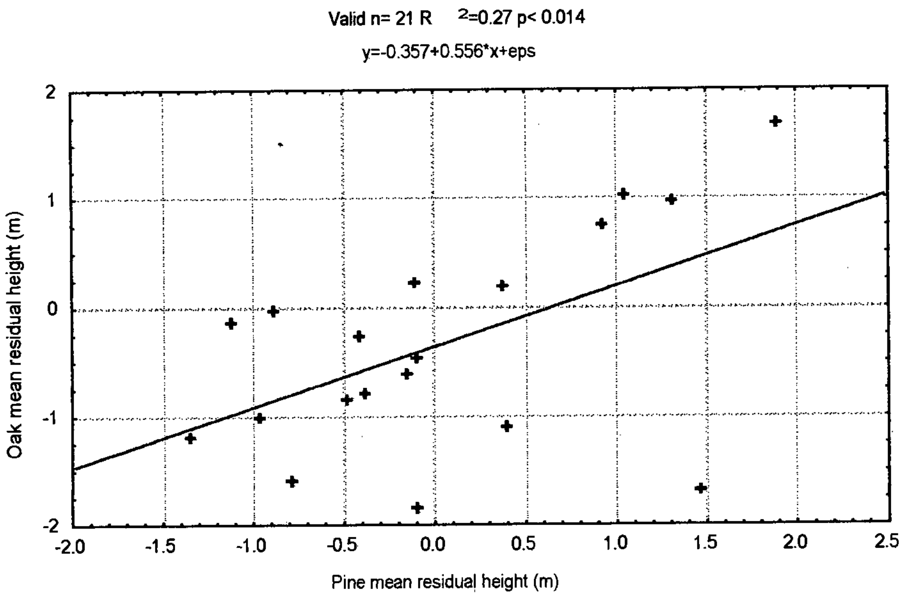
Table 3.2 Maximum rates of establishment estimated for the tree species found in the milpas. Due to unreliable dating of the time since clearance these figures are imprecise, but are included as a guide for modelling the system. Minimum rates for all species are zero, mean rates are thus not an appropriate measure for modelling. Estimated rates assume 16 years since clearance.

	Maximum number of stems recorded ha^{-1}	Estimated maximum rate of stem establishment ha^{-1} yr^{-1}	Estimated maximum rate of establishment from seed. Stems ha^{-1} yr^{-1}
Q. crispipilis	478	29	5.6
Q. segoviensis	532	33	2.3
P. maximinoi	297	18	18
P.devoniana	127	7	7
P.oocarpa	122	7	7
Cleyera theoides	325	20	3.2
Rapanea juergensenii	276	16	4.2

The relative proportion of pines to oaks in the milpas was significantly but weakly correlated with the relative proportion of pines in the surrounding vegetation R=0 .43 R^2= 0.18 Adjusted R^2=0 .14 F(1,23)=5.096 p<0.034. However the correlation between the absolute number of pines in a plot and the absolute number of pines in the surrounding vegetation was not significant R= 0.23 R^2=0.054 Adjusted R^2=0.0129 F(1,23)=1.31 p<0.26. Pine regeneration was found in milpas with no mature pines in the immediate surroundings. A potential pine seed source within 200 m of the plot was always found, except in the case of four milpas with no pine regeneration.

The estimate of site index (SI) for each milpa was taken as the mean residual heights of pines and oaks after statistically compensating for the species specific effect of diameter. Note that as no dependence of the residual variation on diameter was found, the residuals were not standardised and are thus expressed in metres. The SI values are therefore directly interpretable as the difference between the mean height observed and that expected given the measured diameters. SI's for pines and oaks shown in figure 3.7 were positively correlated (R=0.52 R^2= 0.27 Adjusted R^2=0.23 F(1,19)=7.22 p<0.014. The SIs for the two species of oaks were also strongly correlated with each other ($R= 0.53$ $R^2= 0.28$ Adjusted $R^2= 0.24$ $F(1,19)=7.43$ $p<0.013$)

Figure 3.7 Mean residual heights (height after compensation for dependence on diameter) random samples of 20 to 40 pines and oaks in each of 21 abandoned milpas in which the two groups co-occur. Note that some unusually low values for oaks may be artefactual due to the effects of cutting for fuelwood.

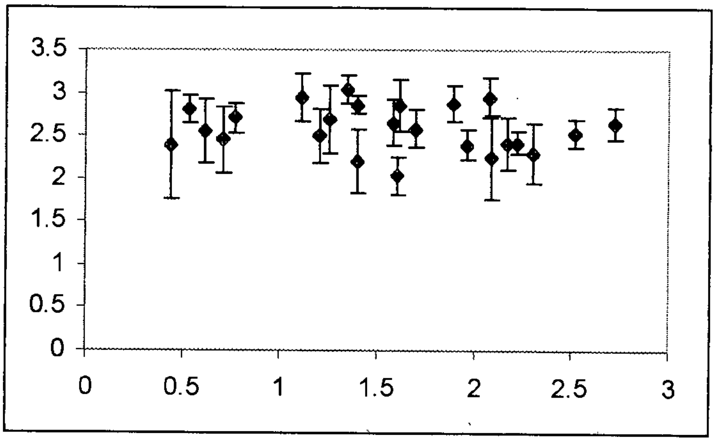


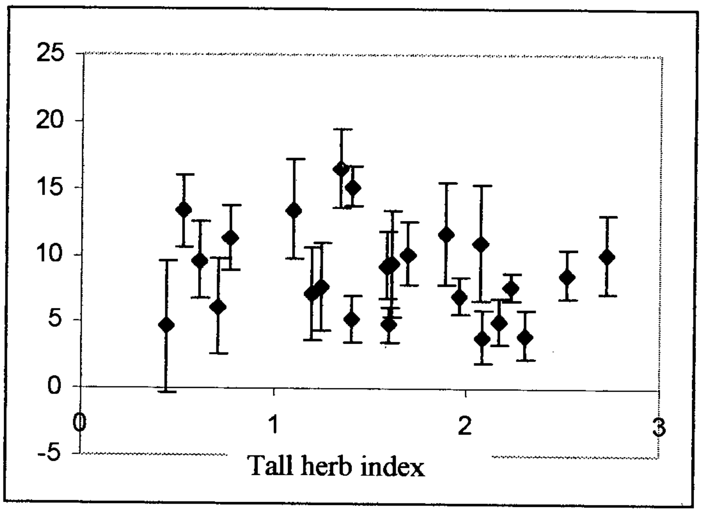
The range in the residuals for oaks was unexpectedly large. Some unusually low residuals were present in the data for both oaks, which despite attempts to avoid the choice of unrepresentative individuals had almost certainly arisen as a result of including oak stems which were artificially shortened due to either partial top kill by burning or cutting for firewood. Stems that had been recently slashed were more common in open grazed areas and this artefactual effect, not connected with soil properties, may explain part of the observed correlation. It may also have lowered the slope of the fitted relationship thus producing higher residual heights than might be expected in some of the milpas where cutting or burning had not occurred. However this artefact could not explain differences in heights of pines. Differences in tree form were visible, with some milpas having very noticeably shorter trees to the eye even though trees had not been cut. As both the pines and the oaks emerged above the shrub layer the possible effect of increased height growth due to competition for light with shrubs was not thought to have been responsible for differences between milpas in residual heights.

Despite the recognised anomalies caused by outliers, the pattern of the residual heights appeared sufficiently well typified to permit an overall SI to be calculated as the mean of the SIs calculated independently for each species. The correlation between pines and oaks increased confidence that SI as measured in this way corresponded to some underlying difference in growth conditions. SI was then used to test the statistical hypotheses concerning relationships between site productivity and diversity.

Analysis of variance found significant variation between milpas in both Shannon's and Simpson's indices. $F(23,465)= 3.93$ $p<0.0001$ and $F(23,465)= 8.95$ $p< 0.0001$ respectively. However this variation did not translate into a significant relationship with any of the measured site attributes including age since clearance. Regression of the pseudovalues on SI found no significant dependence of either of the two diversity indices on the estimates of site quality for tree growth. Similarly no clear relationship could be established between diversity indices and the index of grazing impact provided by the coverage of tall herbs or the direct index of soil quality. Thus these diversity statistics alone gave no indication of any relationship between site quality and species composition. The lack of a pattern in diversity as measured by the two indices can be seen by inspecting figure 3.8.

Figure 3.8 Variability in a) Shannon's index of diversity and b) Simpson's index of diversity calculated for each milpa and plotted against tall herb index. Error bars are 95% confidence intervals calculated for jack-knifed pseudovalues for each milpa.





DCA using log transformed abundance values was found to be efficient in summarising the species composition. Table 3.3 shows that the first two axes combined explained 36 % of the variance in the species data . In table 3.4 a summary is presented of the correlations between the various site indices calculated from soil depth, soil quality, tree growth (SI) tall herbs and the first axis of the DCA ordination. The clearest relationship was with the index of tall herbs (figure 3.10), but the axis was also significantly correlated with the site index as measured by tree growth (figure 3.11). Multiple regression of the first DCA axis on the environmental variables representing site quality produced partial correlation coefficients which were significant for the tall herb index and the site index derived from the growth analysis, showing that SI independently explained a significant fraction of the total variance in species composition after the major influence of tall herbs had been extracted. Because slope and soil depth varied very locally within the milpas, as did tall herb cover, the relationships between them at the quadrat level are also reported. Soil depth was negatively correlated with slope $R= -0.33$ $R^2= 0.11$ Adjusted $R^2= 0.10$ $F(1,478)=59.343$ $p<0.00000$ Figure However at the quadrat scale a regression of the index of tall herb cover on slope and soil depth showed that soil depth was redundant as a predictor of tall herb cover. All the available variability in tall herb cover could be explained by a very high correlation with slope alone (table 3.6).

Figure 3.9 Relationship between mineral soil depth and slope in abandoned milpas. Soil depth was measured by pushing a metal rod into the soil until it met a rock. Each point is the mean of three such readings at random point within 10 m^2 quadrats.

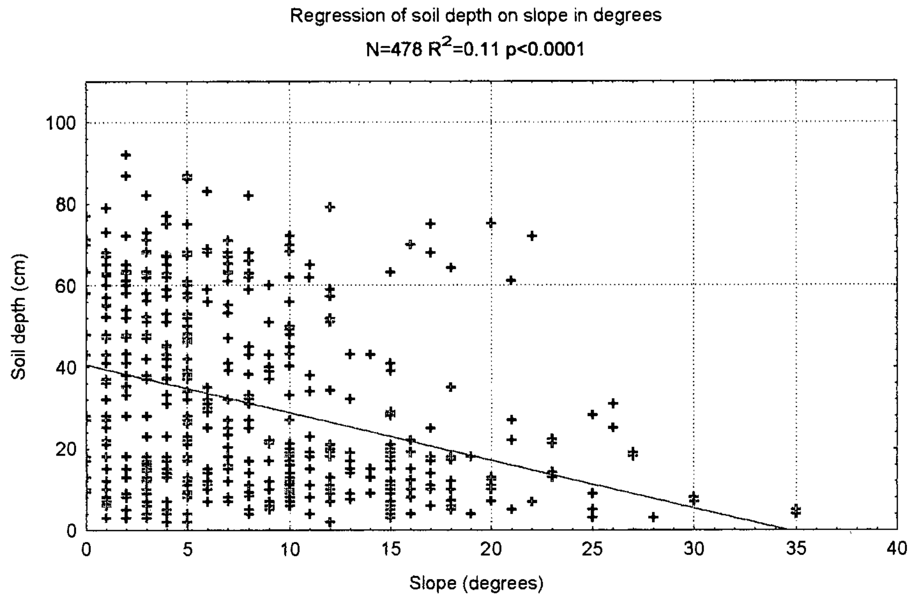


Table 3.3 Variance in species data explained by DCA on log transformed data

Axes		1	2	3	4	Total variance
Eigenvalues	:	.208	.158	.117	.088	1.000
Cumulative percentage variance of species data	:	20.8	36.6	48.2	57.0	

Table 3.4 Correlation coefficients (R) summarising correlations between site indices and site first axis DCA scores. Values shown in bold are significant at the 5% level.

	Soil depth	Direct soil index	Tall herb index	DCA score
Site Index	0.011	0.004	**0.203**	**0.37**
Soil depth		**0.81**	0.153	0.158
Soil index			0.165	**0.22**
Tall herb index				**0.89**

Table 3.5 Results of multiple regression of species composition summarised by the first DCA axis on the indices of site characteristics. Significant partial correlation coefficients are in bold.

	Partial correlation	**Tolerance**	**t(18)**	**p-level**
Site Index	**0.462**	**0.804**	**2.214**	**0.039**
Soil depth	-0.162	0.325	-0.696	0.494
Soil index	-0.252	0.324	-1.106	0.283
Tall herb index	**0.844**	**0.471**	**6.686**	**<0.0001[6]**

Table 3.6 Quadrat level multiple regression of tall herb index on soil depth and slope.

	Partial correlation	Tolerance	T(477)	p-level
Soil depth	0.017	0.89	0.41	0.678122
Slope	0.35	0.89	8.38	0.000000

Figure 3.10 Relation between species composition as represented by the first DCA axis and site index as estimated by the residual heights of regenerating trees for 24 milpas

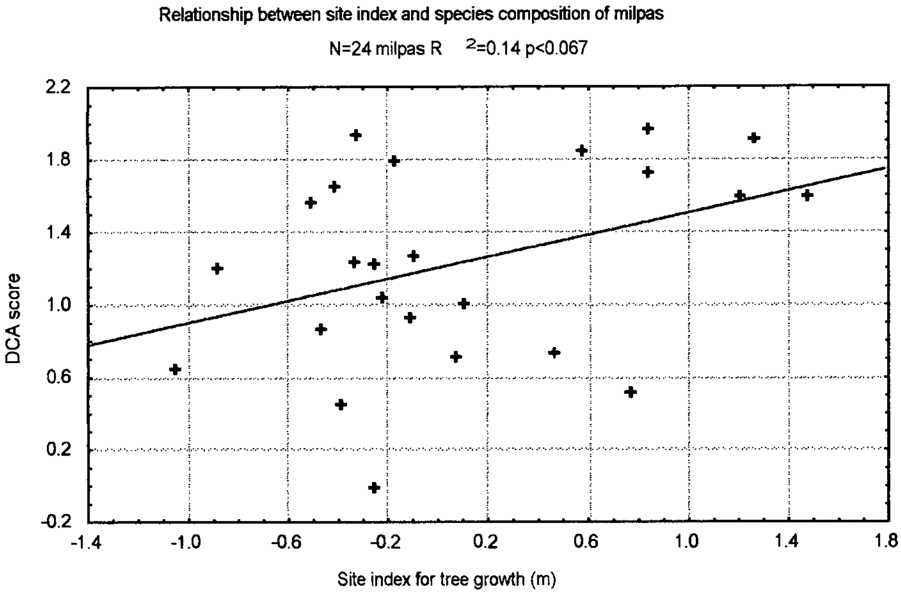
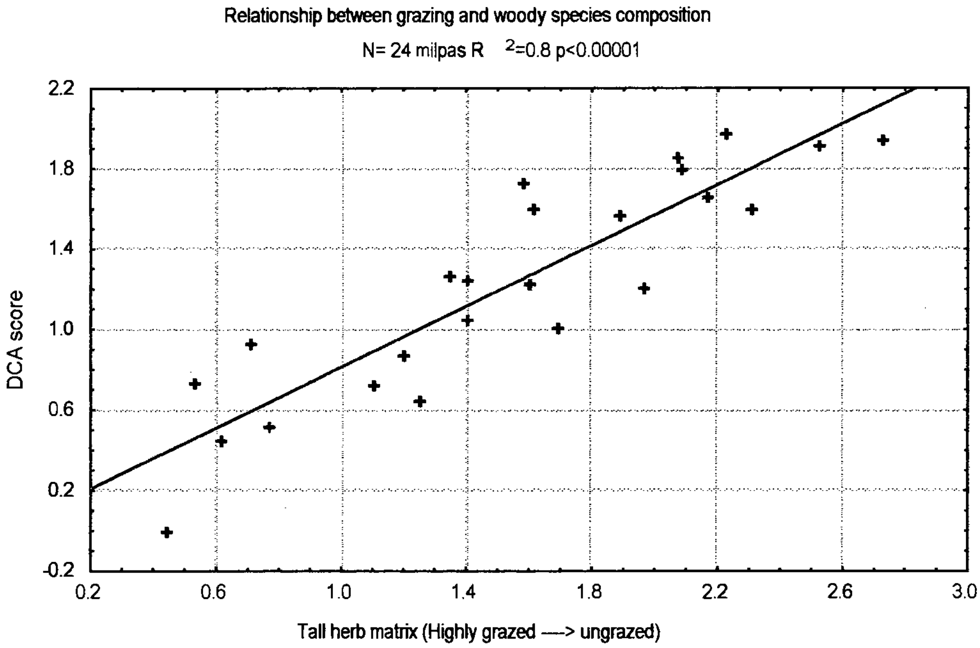
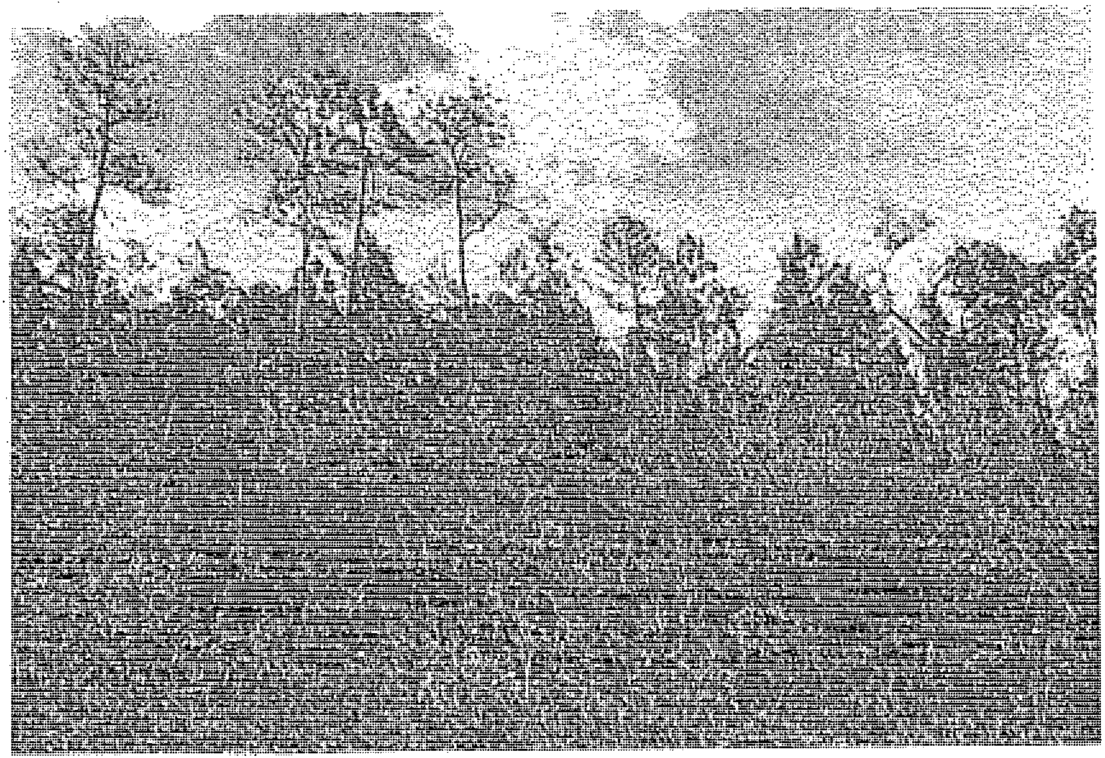


Figure 3.11 Relation between species composition as represented by the first DCA axis and an index of tall herb cover for 24 milpas



The species and sites arranged along the first axis of the DCA ordination are shown in table 3.7. At the top of the table appear clearly xerophytic species with scerophylous leaves such as *Pinus oocarpa, Quercus sebifera, Baccharis vaccinioides, Rhus schiedeana* and pubescent leafed species such as *Vernonia canescens* and species armed with spines such as *Sageretia elegans, Crataegus pubescens* or *Harpalyce formosa*. Species at the foot of the table such as *Miconia mexicana, Saurauia scabrida, Monnima xalapensis, Chiccoca alba, Daphnea americana* are more commonly associated with the forest interior and tend to have larger thinner leaves. In general terms the ordination matches classification schemes that have been produced for the local flora based on successional status (Gonzalez-Espinosa *et al.* 1997; Ramirez-Marcial en prep.) However it should be noted that this ordination is not directly related to time since clearance of the milpa and is not a chronosequence as such. A large number of species fall in a central region of the ordination, where a diagonal structure to the matrix is less apparent. Thus a rather short gradient is found in the data, and most of the discrimination between sites is based on relative abundances of comparatively common species. The most ubiquitous species, *Solanum lancelatum* is a rather small shortlived shrub that may have been favoured by the recent fire. However the similar but larger *Solanum hispidum* appears as an indicator of plots undisturbed by grazing. This species is indeed common in the forest only in shaded areas where the soil has a high organic matter content. Both species are armed with sharp spines. The ordination is not related to the degree of obvious herbivore defence in an easily interpretable manner.

Photograph 4 Regrowth of oaks and shrubs in a twelve year old milpa.



Photograph 5 Cattle grazing leading to the formation of a closed short grass sward which prevents regeneration.

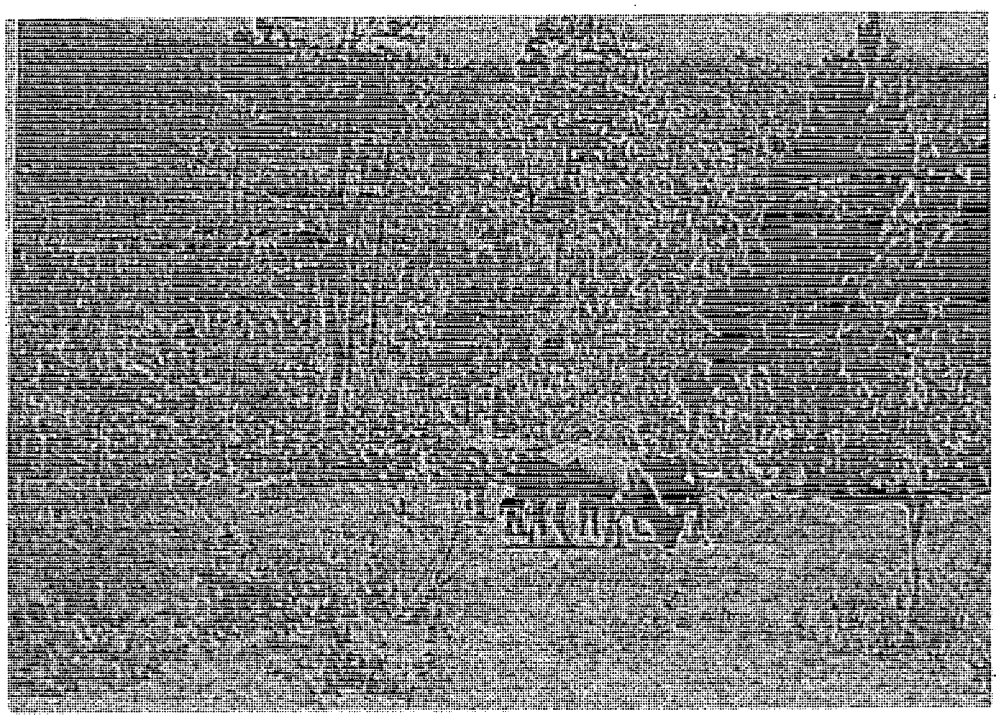


Table 3.7 Ordination of sites and species using DCA for 24 milpas. The figures given for each species is the proportion of stems in each plot expressed as a %.The DCA scores are positively correlated both with an index of site quality and negatively correlated with an index of grazing intensity. Thus species at the top are assumed to be associated with grazing. Sites to the left are more heavily grazed.

Milpa number		**15**	**13**	**11**	**14**	**10**	**4**	**17**	**2**	**20**	**25**	**19**	**21**	**16**	**12**	**7**	**9**	**5**	**8**	**18**	**1**	**6**	**24**	**22**	**23**
DCA scores		0.01	0.45	0.52	0.65	0.72	0.74	0.87	0.93	1.01	1.05	1.20	1.23	1.24	1.27	1.57	1.60	1.60	1.66	1.73	1.79	1.86	1.92	1.94	1.98
Crataegus pubescens	-2.06	5.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pinus oocarpa	-1.60	6.1	-	-	-	-	-	0.6	3.9	-	0.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Quercus sebifera	-1.23	40.8	-	-	-	-	7.8	-	-	-	-	4.0	-	-	-	-	-	-	-	-	-	-	-	-	-
Baccharis vaccinioides	-0.51	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.7	-	-	-	-
Rhus schiedeana	-0.49	0.4	4.4	1.1	3.8	1.6	-	-	-	0.5	-	0.3	-	0.3	0.8	-	-	-	-	-	-	-	-	-	-
Pinus devoniana	-0.49	0.8	4.4	1.1	0.5	0.5	-	-	-	-	0.2	-	-	-	-	-	-	0.5	0.3	-	0.3	-	-	-	-
Fleischmanniopsis leucocephala	-0.48	-	-	-	0.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Phyllanthus glaucescens	-0.45	1.9	-	1.1	3.8	-	-	3.9	-	3.8	2.8	1.4	2.4	0.3	-	-	0.8	0.2	-	1.5	-	-	-	-	0.2
Psidium sartorianum	-0.39	1.9	7.4	1.1	2.8	3.8	-	3.2	2.0	-	1.4	-	0.4	-	1.2	-	1.3	-	0.3	0.4	-	-	0.2	-	0.2
Sageretia elegans	-0.34	-	-	-	-	2.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Harpalyce formosa	-0.34	-	-	12.6	4.7	4.3	15.6	-	11.8	-	-	-	-	-	5.9	0.8	-	0.7	-	-	0.3	-	-	-	-
Vernonia canescens	-0.06	1.5	17.6	6.9	0.9	3.3	1.2	4.5	2.0	3.3	4.9	0.2	0.4	2.8	1.6	1.6	0.4	1.0	1.4	1.5	6.5	2.6	-	0.7	1.0
Ximenia americana	0.06	2.3	1.5	12.6	5.2	12.0	1.2	4.5	3.9	1.1	1.0	1.7	-	2.8	5.1	2.7	4.2	1.5	2.0	0.8	-	2.1	0.3	0.1	-
Ternstroemia oocarpa	0.07	-	-	2.3	-	8.7	-	-	-	-	-	0.2	-	0.3	0.4	-	-	1.0	2.7	-	3.4	-	0.2	0.6	-
Rhus terebinthifolia	0.25	5.7	13.2	10.3	17.4	16.3	9.0	5.2	3.9	7.7	2.4	4.7	11.1	3.8	7.1	6.2	6.3	5.8	2.7	2.3	1.0	3.1	2.5	1.7	-
Clusia flava	0.28	-	-	-	-	-	-	-	-	-	-	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-
Quercus segoviensis	0.37	5.0	-	5.7	29.6	5.4	12.6	3.9	7.8	18.7	11.4	2.0	7.5	2.1	3.5	8.1	1.7	4.1	1.0	1.5	0.7	2.6	-	0.1	-
Rubus hadrocarpus	0.57	1.9	2.9	8.0	-	3.8	1.8	1.9	3.9	1.1	2.6	0.3	0.4	2.8	4.7	0.4	2.5	0.2	1.0	0.8	1.7	1.0	2.0	-	0.5
Viburnum jucundum	0.87	0.4	-	1.1	1.9	2.7	3.0	-	-	0.5	-	0.5	0.4	-	4.3	1.9	1.3	0.7	1.0	0.4	-	4.1	-	-	-
Rapanea myricoides	0.92	6.9	-	-	1.4	1.6	8.4	3.9	-	4.9	4.3	3.6	8.7	2.1	7.1	1.9	0.4	1.2	3.4	-	1.0	1.0	3.5	3.2	12.4
Mimosa albida	0.97	6.5	20.6	-	3.8	2.7	2.4	30.3	11.8	18.1	10.1	23.6	38.7	18.3	5.1	7.4	4.6	-	-	1.5	1.7	2.6	20.2	13.0	16.3
Smilax lanceolata	1.04	-	4.4	-	0.9	2.2	-	16.8	-	-	7.5	11.7	-	14.1	3.5	-	-	-	15.7	16.6	-	-	-	-	-
Pinus maximinoi	1.08	0.4	1.5	1.1	0.9	1.6	-	-	-	0.5	0.8	0.2	0.8	-	-	-	0.4	-	1.4	0.8	0.7	1.0	0.3	0.8	0.7
Erythrina chiapasana	1.11	-	-	-	-	1.1	-	-	-	-	-	-	-	-	-	0.4	0.4	-	-	-	-	-	-	-	-
Quercus crispipilis	1.14	4.2	11.8	2.3	2.3	1.1	4.2	1.9	3.9	9.9	10.8	0.6	1.6	1.0	3.1	2.7	2.5	1.9	2.0	10.2	6.5	13.4	5.0	3.5	3.5
Acacia pennatula	1.30	-	-	-	-	-	-	-	-	-	-	-	-	-	0.4	-	-	-	-	-	-	-	-	-	-
Litsea neesiana	1.34	0.4	-	-	0.5	-	0.6	-	-	-	-	-	-	-	0.4	0.8	0.8	0.2	0.3	-	1.0	0.5	-	-	-
Senecio deppeanus	1.43	-	-	-	1.4	0.5	-	-	-	-	0.2	-	-	-	-	0.4	-	0.5	-	1.9	-	-	-	-	-

Cleyera theaeoides	1.49	-	-	5.7	3.8	-	4.8	0.6	-	2.2	-	0.3	-	0.3	10.2	1.9	5.0	0.7	0.7	0.4	3.4	4.1	0.2	0.8	0.2
Calliandra grandiflora	1.78	-	-	-	4.2	-	10.2	-	3.9	-	7.1	0.3	0.8	0.3	-	-	0.8	-	-	-	-	1.0	20.7	7.4	11.6
Solanum lanceolatum	1.79	6.9	-	18.4	0.9	10.9	6.0	9.0	35.3	4.4	7.5	25.4	17.0	35.9	15.7	20.9	25.5	46.5	41.3	21.1	48.3	23.7	12.4	21.7	25.5
Salmea scandens	1.91	-	-	6.9	-	8.7	0.6	1.3	-	11.5	7.1	2.6	-	1.0	3.9	10.9	15.1	10.2	0.7	6.0	-	2.6	2.1	2.8	3.0
Acacia angustissima	2.10	0.4	-	-	1.4	0.5	1.8	0.6	3.9	4.9	7.5	3.3	5.5	0.3	2.0	3.5	4.2	4.6	2.4	4.9	2.0	2.6	5.3	9.1	4.5
Rubus adenotrichus	2.13	0.4	1.5	-	0.5	0.5	1.8	1.3	-	3.8	2.6	0.3	2.4	0.7	6.3	4.3	1.3	3.9	3.1	1.9	2.7	2.6	1.5	5.0	7.9
Rapanea juergensenii	2.16	0.4	8.8	-	6.1	-	4.8	-	-	-	0.4	0.2	0.4	0.3	0.4	1.6	0.8	1.5	0.7	4.5	0.7	3.6	0.8	0.4	0.2
Vernonia leiocarpa	2.28	-	-	-	-	-	2.4	-	-	-	0.6	-	-	-	0.4	5.4	2.5	2.2	1.0	-	-	2.6	-	-	-
Randia aculeata	2.53	-	-	1.1	0.5	1.1	-	-	-	-	-	4.0	1.6	3.1	1.6	1.9	0.8	1.5	3.8	1.9	3.1	3.6	1.5	1.5	1.2
Parathesis belizensis	2.60	-	-	-	-	1.6	-	5.8	-	-	5.7	4.9	-	6.9	4.7	8.9	6.7	4.9	5.8	14.3	6.5	6.2	6.9	7.8	2.2
Senecio cristobalensis	2.73	-	-	-	-	-	-	-	-	2.7	0.8	-	-	-	0.8	0.4	1.3	0.5	-	1.1	-	0.5	-	0.6	-
Eugenia sp.	2.90	-	-	-	-	-	-	0.6	-	-	-	3.8	-	-	-	1.9	0.8	-	1.4	-	-	4.6	1.5	3.6	-
Perymenium grande	2.95	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.8	-	-	-	-	-	-	-	-
Eugenia acapulcensis	2.95	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2	-	-	-	-	-	-	-
Olmediella bestchleriana	2.95	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.5	-	-	-	-	0.2	-	-
Ocotea mollifolia	3.30	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.4	-	0.2	-	-	-	0.5	-	-	-
Cestrum aurantiacum	3.32	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.5	-	-	0.3	-	-	-	-
Smilax jalapensis	3.38	-	-	-	-	0.5	-	-	-	-	-	-	-	0.3	-	0.4	0.4	1.0	2.4	1.5	1.4	-	1.3	3.4	1.7
Dodonaea viscosa	3.50	-	-	-	-	-	-	-	2.0	-	-	-	-	-	-	-	-	-	-	-	-	-	7.3	2.1	3.0
Senna sp.	3.60	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.5	1.4	-	-	-	0.8	-	0.5
Saurauia scabrida	3.61	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.4	0.4	-	-	-	2.0	-	-	0.4	-
Monnima xalapensis	3.63	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.3	-	-	-	-
Chiccoca alba	3.66	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.9	5.9	1.0	-	2.3	3.7	5.2	3.5	9.1	2.7
Daphnea americana	3.81	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.5	-	-	-
Psidium guajava	3.81	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.1	-	-	-
Solanum hispidum	4.26	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.4	0.7

Discussion

Although an explanation for the state of the vegetation in each plot based on a detailed knowledge of site history could be found, repeated patterns were less easily discernible. Some evidence of degradation seemed evident, yet no clear overall trend emerged. A successional model based on the assumption of a chronosequence along a disturbance gradient could not be found. Each milpa patch had to be considered as equivalent to a single experimental unit subject to a complex combination of treatments. Factors involved in this complex experiment include the vegetation preceding clearance, clearance methods, intensity of use, grazing pressure following abandonment, distance to seed sources, and unintentional fire among others. Statistical analysis was challenged by a study that produced "*the curse of middle order numbers systems*" (Allen and Hoekstra 1994). Because every milpa was different, a simple comparative study between any given pair of milpas would always show statistically significant results if enough power was obtained, although further inference regarding the causes of the differences would be limited. Clearer patterns might emerge if sufficient statistical power were obtained from a survey of several hundred milpas which could treat each milpa as a sampling unit. However the data set fell between these extremes and unequivocal statistically supported statements regarding the data were limited in number due to the variable nature of the system. Nevertheless some robust generalisations emerged that can be incorporated into a general model of the system.

The pattern of pine size classes found in the milpas has clear similarities to that found in the forest as a whole (chapter 1). Drawing a distinction between forest and abandoned milpa, though convenient for some purposes, may be artificial when long term dynamics are considered. Some of the oldest plots included in this survey were beginning to have structural characteristics which were similar to the surrounding forest. It seems likely that pine establishment, if grazing is light, takes place within a comparatively brief window of opportunity following milpa clearance and before oak and shrub canopies close. A linkage between pine abundance in the neighbouring vegetation and pine regeneration could not be discerned in this data, although at the limit some connection trivially must exist and a simple rule is assumed when a process based model is produced. A likely explanation for the lack of documented pattern is that obvious pine seed sources have been removed by anthropogenic disturbance since the establishment of juveniles, but some long distance dispersal may also have occurred.

Contrary to expectation no vegetation characteristics were predicted by the reported time since abandonment of the milpas. This is either because farmer's accounts are not reliable or due to patch level heterogeneity in processes such as growth and establishment. Evidence of significant differences in growth conditions between plots supports the latter explanation. These observations reveal the complexity of the competing processes in operation at a local level.

A key to understanding the cyclical dynamic of secondary vegetation under slash and burn regimes may lie in identifying which species can persist through the disturbance event and which cannot. Neither slash and burn farming nor ground fire seem to produce discrete catastrophic disturbances which act to completely reset a successional clock. The dramatic biomass destruction associated with slash and burn disturbance suggests a greater initial impact than it seems to have. Slash and burn's initial role is as a filter that removes individuals not able to withstand its immediate effects. The degradation that arises later through soil erosion and chronic nutrient loss then causes stress to the surviving trees. A large proportion of the woody species found in slash and burn plots are the result of persistence through resprouting. Initial floristic composition has been found important for other slash and burn systems where both residual species, either resprouters or species present at the site in buried seedbanks, and rapid colonisers dominate post disturbance vegetation(Halpern 1989; Kammesheidt 1999; Miller and Kauffman 1998; Miller 1999) Thus the chronosequence view based on a linear pattern of successional replacement is only partially applicable to this form of vegetation.

If species are lost, recolonisation becomes difficult. Open areas are extremely hostile areas for seedling establishment. Species which cannot survive the effects of milpa disturbance are at risk of local extinction unless they are well adapted to recolonising stressful environments. Even in temperate regions, temperatures close to bare soil surfaces can be 20° C above ambient levels (Bazzaz 1996). Diurnal fluctuations of over 40 °C have been recorded at ground level in comparable open areas at montane sites in the region (Gonzalez-Espinosa unpublished data). If a short grazed grass sward forms this will be an extremely hostile environment for tree seedling establishment, made even more so by accompanying soil compaction and repeated mechanical damage by grazing animals. Seeds that are dispersed by birds and small mammals will not arrive at sites unless the habitat is attractive to the dispersing organisms. A short grass sward offers little cover for rodents and birds. The extremity of the regeneration niche (Grubb 1977) in a tropical montane climate leads to an intuitive expectation that the vegetation in grazed milpas should consist only of light demanding pioneers with xerophytic adaptations and wind dispersed seeds. However a few individuals of species that would appear unable to establish from seed in such conditions can usually be found in the vegetation. Such individuals must either have persisted through resprouting from stumps or root crowns or found a suitable micro habitat for establishment.

A suitable micro environment for establishment of many species may be provided if a layer of vegetation above ground level forms. The matrix provided by fast growing tall herbs such as *Eupatoriun* spp. and *Melampodium* spp. seems to play an extremely important role in providing conditions for establishment of a range of woody species, as may *Pteridium aquilinum*, which here does not form the dense monospecific stands associated with a species that have been implicated in preventing oak regeneration in Scottish woodland (Humphrey and Swaine 1997).

Whether the variability in growth rates and species composition between milpas can be attributed to degradation or underlying edaphic variability is unclear. Tree growth rates and vegetation composition are linked to the presence of tall herbs, but this only displaces the variability a step back in a causal chain. Why do some milpas have a denser cover of tall herbs than others? The proposed explanation is slightly speculative as it is based on undocumented site specific field observations but it does coincide with patterns in the data. At a local level the pattern seems to be caused by the behaviour of cattle and horses. The tall herb matrix tended to be found on steeper slopes. Steeper slopes deter grazing cattle if alternative areas are available. However steeper slopes have thinner soil, hence the independent relationship of the DCA axis with site quality. Under light unconstrained grazing there is a complex and highly contradictory set of factors influencing growth rates and floristic composition which are extremely difficult to unravel from the data alone. The most inherently productive areas with deep soil receive more attention from grazing animals and thus can degrade more quickly and lose more woody species than the essentially less productive slopes that regenerate woody cover more quickly. A further element to be considered in the complex mix is that recently abandoned areas on flat ground have often been partly ploughed during the cultivation stage. This requires the removal of woody stumps and causes a much clearer punctuation of a successional cycle than the more traditional form of usage (chapter 5). Ploughing has tended to occur on milpas closer to the village. After abandonment of a ploughed plot the early colonisers are often palatable grasses, particularly if N based fertiliser has been used during the cultivation phase. This can lead to increased grazing. Pines colonise such areas as do xerophytic composites such as *Vernonia* spp. and *Bacharis* spp., but few forest understorey plants can be found. If the areas remain undisturbed a pine forest may form. Grazing alone has been shown to have little effect on the growth of slash pine (Cutter, Hunt and Haywood 1998) No negative effect of grazing on the growth of established pines emerged in this data.

From the point of view of modelling future forest dynamics most of the previously ploughed areas would fall outwith the traditional iterated cyclical system of disturbance followed by recuperation of canopy species. Once woody stumps have been removed these areas often become used for semi permanent agriculture with chemical fertilisers being used to compensate for lost inherent fertility. Any regeneration does not lead to full forest restoration. In the areas where trees do re-establish between clearances the situation may be complicated as iterated clearing of plots over a long time period causes chronic degradation, making comparisons of soil properties based on current properties or reported age since the last clearance misleading. Improved methods to more accurately assess the full history of this vegetation are clearly needed. Highly variable data which challenges simple generalised interpretations must be expected from such situations

A very clear relationship between grazing intensity and species composition was thus found, and a convincing mechanistic argument may be proposed for this link. However it is also possible to challenge the evidence supporting any causal interpretation of the relationship when merely the presence or absence of any given species is considered. Chapter 1 showed how species distribution patterns could be the result of large scale edaphic patterns. There is no evidence here that shows conclusively that a comparatively low level of grazing has the direct influence on species composition suggested by the ordination, although the localised link between slope and tall herbs does support this interpretation. It could still be proposed that grazing and species composition may be linked through a third factor such as unmeasured underlying edaphic conditions. A suitable statistical technique to analyse the spatial trend in this data was not found due to the low number of independent samples. The DCA arranged canopy forming tree species in similar positions in ordination space to that produced by the ordination in chapter 1. Again it may be difficult to separate general explanations based on plant traits from explanations based on land use, either contemporary or historical. The pattern of species distribution could well be linked to a very long term historical degradation through grazing and fire, as some of the highly grazed areas are close to the marked boundary with the area which made up the former hacienda and which seems to have been burnt and grazed for several centuries. Alternatively the explanation may lie in underlying differences in soil properties and climate due to altitudinal effects.

The difficulties associated with unambiguously separating these factors are familiar to researchers in the region. The situation does lead to a tendency to use natural history as a basis for explanation, rather than systematic generalisations. The modelling approach that is presented in this work was developed specifically to begin to reconcile these two views of the system for at least a subset of the species involved and a subset of the possible land use scenarios. The key seems to be to model changes in abundance as a local process and changes in occurrence as a larger scale process. Further progress will become possible as more detailed functional classifications of shrubs and trees are produced for the regional flora. Also as the system becomes better understood, *a priori* stratification criteria will become available which may help to increase the power of future surveys

The most notable feature of the abandoned milpas for modelling vegetation change was the simple observation that oak resprouting after slash and burn is vigorous and universal. Because traditional slash and burn farming does not use the land for more than two years, it can not easily remove oaks, or any species capable of resprouting from the landscape. Again this marked inertia of oak populations, which was also found for situations where fire alone affected the site, can lead to iterated slash and burn resulting in a form of oak coppice. This has been reported in comparable situations in North America (Mikan Orwig and Abrams 1994). Pines take advantage of the reduction in overstorey to establish between oaks, and rapidly overtop oak resprouts. Over longer periods, pines may well turn out to be transient members of the vegetation of each patch, but this may only be studied through a simulation approach. Stands of similar origin in North America have regained old growth characteristics as self thinning occurs (Nowack and Abrams 1997).

Evidence of former slash and burn farming is found within mature areas of this forest in the form of multiple stemmed oaks emerging from common rootstocks. This has been observed in other Mexican forest types subjected to slash and burn (Miller and Kauffman 1998). Some areas of this forest have a very similar appearance to old European oak coppices (Rackham 1976). This observation must be included in forest models. Resprouting will have important implications for understanding how forest dynamics can diverge from that predicted by models which assume either permanent or temporary deforestation following milpa clearance. Inappropriate models could be proposed if no direct field experience of the system is available. Although easily documented, the subject can be a potential cause of controversy if overlooked. For example in a strongly worded statement on how historical processes shaping the wooded English landscape have been misinterpreted Rackham (1976) lamented that historians who attempted to trace landscape pattern without the benefit of field experience had built "*a huge inverted pyramid of argument on the belief that trees die when cut down – a factoid which flatly denies the whole basis of woodmanship as practised over the last 5000 years*". Statements such as this show the strength of feeling the subject can provoke. There is a need for further field work in the area to fully document the ability of species to persist through slash and burn and forest fire.

Conclusion

Each milpa plot used by a single family comprises an area of between 0.5 and 1.5 ha. There are significant differences between milpas in growth and colonisation rates of both pines and oaks. Regrowth can be vigorous. If milpas are not recleared or heavily grazed a pine-oak forest system will re-establish. Grazing can inhibit colonisation of milpas by oaks, but many oak root crown survive clearance and resprout. Pines either colonise immediately following clearance or take advantage of the opening caused by grazing to colonise more slowly. As was found when fire alone was investigated (chapter 2) oak populations show considerable inertia, but are less resilient than pines. The composition of shrubs and trees is closely related to grazing, but the underlying causes of the relationship require some further investigation.

When pine-oak woodland undergoes a single discrete clearance through slash and burn, surprisingly few trees are killed outright, and most are pines. A simple regenerative mechanism exists which can quickly repopulate cleared areas, not only with shrubs but also with canopy trees. Most contemporary degradation associated with slash and burn is linked to grazing and deliberate land conversion. The consequences of repeated cycles of slash and burn farming which occurred in the last two hundred years during a period when grazing, ploughing and fertiliser use did not occur within the *bienes comunales*, would not be immediately apparent to the casual observer. If historical slash and burn impact produced a shifting mosaic (Watt 1925; Watt 1947), the variability which has been documented here shows that the pattern would not be perceived as a visually striking mosaic of patches. Instead very subtle local pattern would be found as the tiles of the mosaic blend into each other over time and internal processes within each take over as determinants of forest structure. This theme will be returned to and extended in chapters 7 and 8 when models are presented which represent the process in action.

Chapter 4. The performance of species richness estimators: Implications for estimating woody species diversity.

Introduction

In chapter 3 the pattern of woody species diversity in abandoned milpas was analysed. The aim was to identify a successional sequence for the woody species at the site. However a pattern based on age since clearance was not apparent. Areas with differing disturbance histories have differing densities of stems of shrubby plants. This automatically leads to different numbers of species being found in the same sized area. Collections of woody species from the area are still incomplete. A full picture of the floristic diversity of the site has yet to emerge. Estimating the true number of species in any habitat from a sample is a non-trivial problem that raises interesting questions. If a clear successional chronosequence cannot be identified, can a sharper dichotomous contrast be used to draw conclusions? Can differences be found between the vegetation found in milpas before canopy closure has occurred, and the forest understorey? The two types of vegetation are visually distinct due to tree canopy closure above them. Although they are linked by dynamic processes they would receive different habitat classifications. Is it likely that the forest as a whole contains more woody species than the more recently disturbed open milpas? How many more species might be found in the forest as work continues? What tools are available which may help to provide answers to these questions from partial data?

An analysis of species richness of a habitat should provide answers to three distinct but related questions. 1) How many species does a habitat contain? 2) What is the pattern of relative abundance of species within a habitat? 3)How is habitat size related to species richness?

The first question is a common challenge for research in tropical forests. Many areas of tropical vegetation are as yet only partially surveyed. Extrapolation from incomplete data must often be attempted to avoid underestimating true species richness. A series of promising analytical techniques have recently been developed which allow such extrapolation to be carried out using a minimal set of assumptions (Colwell and Coddington 1994; Chazdon *et al.* 1998). If these methods prove to be effective, rapid progress may be made in poorly studied regions of Chiapas. Yet producing an estimate of the number of species addresses only part of the problem. The remaining questions regarding patterns of relative abundance may test the strength of theoretical models that have been criticised as weak predictive tools for applied conservation (Peters 1991; Schrader-Frechette and McCoy 1993). The three questions are closely linked, but there are advantages to be gained from applying separate but complementary methods of data analysis to each.

The need for this procedure is revealed by a consideration of the issues which arise when the questions are combined in a single analysis. The most direct form of estimating the true number of species in a defined area involves simple extrapolation of the species-area curve to areas larger than are actually observed (Holdridge *et al.* 1971). In order to extrapolate from the curve some model must be fitted. A set of models are often selected *a priori* from theoretical considerations (Soberon and Llorente 1993). When the performance of a range of models has been compared species-area distributions have been found to fit differing theoretical models depending both on the nature of the organisms being studied and the region in which the survey has been conducted (Miller and Wiegert 1989; Palmer 1990; Williams 1995; Flather 1996; Veech 2000). No clear rules regarding which model applies to which community have yet been developed. A common *a priori* choice is the log-normal model of species abundance (Preston 1948; MacArthur and Wilson 1967) which predicts a linear relationship between the logarithm of area and the logarithm of the number of species (May 1975). However Connor and McCoy (1979) have suggested that species area curves produced using the log-log transformation provided no empirical evidence in support of the log normal distribution and concluded "*as yet no significance can be attached to any particular model*". No major advances have apparently been made which would lead to a revision of this view. Although Tokeshi (1993) sees little to be gained from "model free description" it may be advantageous to retain only models which have proven useful as tools to answer specific questions (Peters 1991).

A further difficulty is faced by all methods that involve direct parametric extrapolation. There appears to be no reliable method for curve fitting available. Least squares and maximum likelihood methods have been used (e.g. by Flather 1996). However as Colwell and Coddington (1994) point out "*using successive values of S(n) and n to supply the supposedly independent sample variates X and Y makes statistical nonsense of the variate estimates*". Thus although different models do produce differing fits to the data, there appears to be no way of confidently differentiating between them based on well known statistical procedures.

The statistical and theoretical weakness of parametric curve fitting and the frequently encountered need to extrapolate from collections in which non area based measures of effort are used led to the development of a range of non-parametric estimators of species richness. For a review of these methods and a full description of each see Colwell and Coddington (1994) and Colwell (1999). The aim in developing non parameteric methods has been to provide estimators which are robust both to assumptions concerning underlying patterns of species abundance and to the size of the sample obtained. All such estimators are based on an asymptotic model of species accumulation. If viewed as a statement regarding underlying pattern the assumption of an asymptote represents a static, bounded view of community composition which is at odds with contemporary views of vegetation which stress dynamic processes at varying scales (Shugart 1998; Huston 1994) However a more pragmatic operational interpretation is that the asymptote is merely a convenient device for preventing unrealistic extrapolation. Such techniques are thus designed to provide an answer to the most straightforward of the three questions of interest. They give no guidance regarding the other fundamental concerns and deliberately ignore the spatial distribution of organisms. Nevertheless they offer a potentially powerful basis for evaluating the performance of species-area models where the true number of species is unknown.

The use of robust estimates for species accumulation curves could potentially resolve the extrapolation problem. Yet it might still be informative to determine the relationship between species and area. Species-area curves can be constructed from nested quadrats or sequential addition of equal sized randomly placed quadrats. Because nearby quadrats tend to contain more similar species than distant ones, using spatially nested quadrats has the effect of reducing the initial rate at which species accumulate and accentuating the rate of later species additions (Palmer 1988). This automatically leads to an improved fit when a log-log transform is applied. Random sequential addition removes this artefact (Coleman *et al.*1982; Palmer 1990). However the form of any species-area curve will depend on the arbitrary order in which quadrats are added. Iterated randomisation can be used to avoid this (Simberloff 1979; James and Rathburn 1981; Coleman *et al.*1982).

Fitting curves to such data using the least squares procedure is invalid due both to lack of independence and heterogeneity of variance. Heterogeneity of variance follows a predictable pattern and its effect can be removed using maximum likelihood or weighted least squares procedures (Flather 1996). However this does not resolve the problem of non independence. Weighting data points with respect to the variance compounds inherent bias caused by non independence by forcing the curve to pass through points with most dependence on the preceding data. A formal solution to this problem is not provided in the ecological literature.

Both the milpa plots and the 25 PSPs covered a range of different conditions (chapter 1 and chapter 3). If quadrats are taken in randomised order from the complete sample for each type of habitat this heterogeneity will affect the mean rate at which new species are added. Comparisons between the slopes of the curve, or the extrapolated species number from non parametric estimation might provide a guide to underlying differences, if any, both in the species richness of the two types of vegetation and the pattern of species accumulation. In effect the slope of the curve would give an indication of beta diversity. Open disturbed communities tend to show a pattern of species accumulation associated with an underlying log series or geometric series of species abundance (Magurran 1988). It was therefore hypothesised that the species area relationship in the milpas would fit a log linear model, whereas the relationship within the forested area would be better modelled by a power curve.

An additional tool for evaluating the relationship between species is provided by species abundance histograms. These are obtained by plotting frequencies (number of species) in abundance classes. A log (base 2) scale is used as proposed by Preston (1948) to divide the abundances into classes. If this reveals a distribution that fits a log series then the log-linear species area relationship is expected to apply (Williams 1947). However if the distribution is unimodal and approximately normal then it has been assumed that the log-log transformation will linearise the species area curve (Connor and McCoy 1979)

It might be proposed that the fit of competing models to the abundance data could be tested using standard statistical tests. The difficulties of fitting species area curves have been discussed. Species relative abundance histograms pose a similar set of problems that prevent a correct statistical interpretation. A range of methods have been proposed for testing the goodness of fit of the truncated log normal model including the chi squared statistic (Pielou 1975) the Kolmogorov-Smirnoff test (Tokeshi 1993) and the Hellinger Distance test (Amanieu *et al.* 1981). The results of such procedures have deliberately not been included in the results. In part this is because the assumptions of all these methods tend to be violated when they are applied to the type of data usually obtained (Tokeshi 1993). More seriously, an inference problem arises which makes the interpretation of such tests potentially misleading in this context. They test the probability of the data arising given the model, not the probability of the model given the data (Johnson 1999; Ellison 1996). Type 2 error is thus the most likely cause of retaining a model. The data are best assessed by visual inspection as argued by Hughes (1986). Inference is made at the discretion of the reader using the full information available, rather than with reference to a summary statistic.

The study aimed to test the hypothesis that species richness as measured by the total number of species found in the habitat as a whole is higher in the closed canopy forest than in the open milpa plots. It was also aimed to assess the performance of eight non parametric indicators of species richness (Colwell 1999). The criterion on which they were judged is given by Chazdon *et al.* (1998) as "*independence of sample size (beyond some minimal threshold) leading to stability as sample size increases*". In addition the predictive utility of two classical non asymptotic models of species accumulation was evaluated. The two models, which were chosen for their contrasting statistical properties rather than for theoretical considerations, were the power law (Preston 1948) and the log-linear model (Gleason 1922; Williams 1943; Williams 1947).

Method

The data sets used were provided by the study carried out on the milpa plots reported in chapter 3 and the quadrats placed in the PSPs reported in chapter 2. In each of these data sets the number of individuals of free standing woody species over 1 m in height had been tallied. The survey produced 465 quadrats in the milpa plots and 150 quadrats in the PSPs. This difference in sample size caused a clear difficulty for simple comparisons of species richness and thus provided a suitable test of the efficiency of the methods proposed.

Non parametric indices of species richness were obtained using the program EstimateS (Colwell 1999). The program was run using the default options which produce 50 iterated species accumulation curves. The program output produces the mean number of species observed and the estimated number from the 50 iterations for each of an increasing number of quadrats up to the total included in the entire sample. These values were plotted to test the criteria that non parametric estimators should quickly rise to an asymptotic value and then become independent of sample size. A log (base 2) scale has been used for the abscissa.

In order to partially overcome the problem of non independence, an alternative curve fitting procedure was also used. A modified algorithm for drawing bootstrap samples was written in Microsoft Visual Basic. Independent samples of size n= 1, n= 2...n=2^n without replacement were taken. Because each sample in the series shares half the information with its predecessor the number of repetitions was halved for each point along the series as an informal compensation for non-independence. Where log or log/log transformed data appeared to fit a linear model least squares regression was then used as a convenient summary of trends. This procedure is proposed as a partial solution to the problem of non independence, as the least squares procedure is weighted by the appropriate degrees of freedom. However its validity requires more detailed investigation. Where transformation led to non linear trends they were given qualitative interpretations.

Histograms of species abundances were produced based on log (base 2) classes using the procedure outlined in Hayek and Buzas (1996). No models were fitted to the histograms.

Results

In Figure 4.1 the observed mean number of species against area produced from averaging 50 curves using the program EstimateS is shown for both habitats. It should be noted that a greater number of quadrats were included in the milpa study. The plot shows a consistent pattern of greater mean species richness for a given area in the forest plots, even though stem density was almost double in the abandoned milpas at 16,433 (95% CI+-2915) stems ha^{-1} in the milpas compared with 7,023 (95% CI +-1,892) stems ha^{-1} in the forest.

Figure 4.1 Mean richness of woody species in quadrats from milpas and forest PSPs. The points are the means of 50 iterated species area curves. No reliable error estimate is available

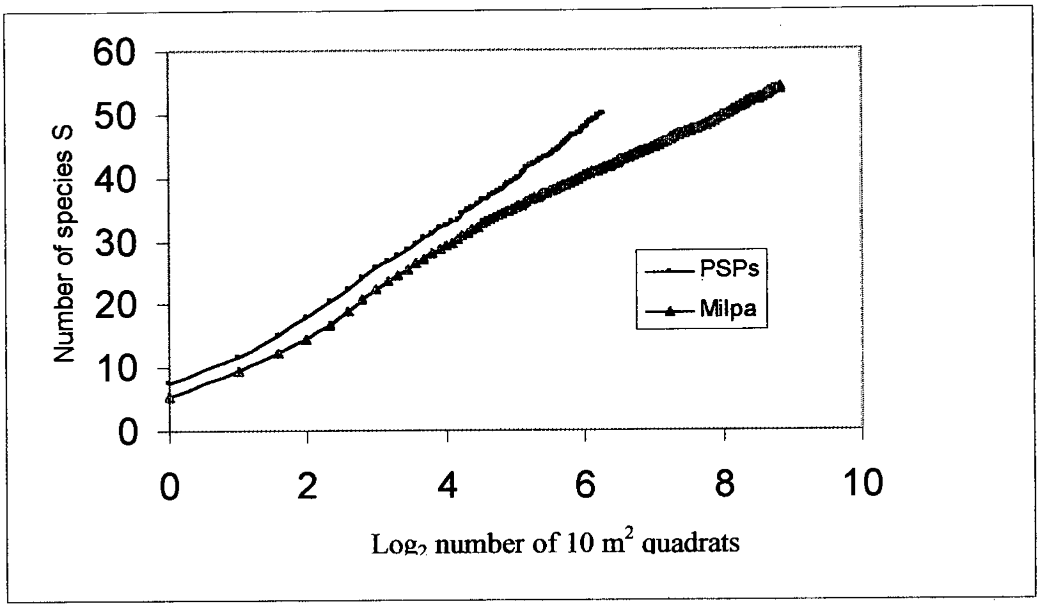


Figure 4.2. shows that with the exception of some anomalous behaviour at low sample sizes, all the indicators maintain a constant relationship with the observed species richness throughout the range of sample sizes drawn iteratively from the whole sample. There is no evidence of any of the indicators rising to an asymptotic value. When all the quadrats are included the indicators provide a range of estimates for S between 54 and 65 species (Table 4.1). The log-linear model seems to provide a good fit to the species-area relationship (Figure 4.3), whereas transforming both axes and fitting a linear regression produces a model which clearly passes over the points at the top of the curve (figure 4.4). Extrapolation from a log-log transform thus would be expected to overestimate species richness. The species abundance histogram shows that many of the species found in this data set are represented by numerous individuals. Nine species fall in the modal class of between 512 and 1023 individuals. However eight species were represented by three or fewer individuals and four species by a single record. There was a clear indication that more species would be found if a larger area were included in the survey.

When the data for the forest is analysed a rather similar pattern emerges, but with some clear differences. The non parameteric estimators still maintain a constant relationship with observed S, although the estimates are comparatively higher than those produced for the milpa data, with final estimates ranging from 64 to 83 species. Again a log-linear model provides the best fit to the species area relationship although in this case the fitted line appears to slightly underestimate the number of species in the complete data set. When species lists for the two areas are compared it emerges that there are only four species found in the forest plots which do not occur in the milpa plots and all the species found in the milpa plots are found in the forest. Species composition alone as such does not form a basis for separating the two habitats. Shade tolerant forest species such as *Miconia* spp., *Eugenia* spp. and *Olmediella bestchleriana* were all found occasionally in milpa plots. Light demanding species were found in forest plots. The species abundance pattern in the forest is however markedly different to the pattern found in the milpas. The modal class with nine species is the class of singletons. There are comparatively few common species.

This difference is also reflected in significantly higher values for Simpson's diversity index in the forest plots than in the milpas, although no difference is apparent for Shannon's index (Table 4.1). Thus the forest understorey differs most noticeably from the milpas in a reduction in the dominance of a small number of species which are very common in open areas.

There is no indication that all the species have been found in either of the two habitats. Although a total of 7,182 stems were tallied in the comparatively homogeneous vegetation of the milpa plots, four species were only represented by a single individual. Such rarities must be expected to be continuously encountered, and would appear less exceptionally rare if the common species were not included in the data set. On an area basis species accumulation rates are not greatly different between the two habitats. The milpa quadrats only covered a total area of 0.465 ha and the PSP quadrats 0.15 ha. Extrapolation from the log linear model can be used to produce both an estimate of the number of species which would be found in the area from which the sample of quadrats was randomly drawn, and more speculatively, an estimate of the number of species that might be found in the complete 1,027 ha of forest if the species accumulation followed the patterns found in the PSP quadrats or the milpas. There is only a small difference between the extrapolated figures. If species accumulation over the whole area follows the pattern found in the milpas the *bienes comunales* would be expected to have a total of 117 woody species, while if accumulation followed the pattern found in the PSP quadrats 128 species would be found. The actual total of woody species recorded for the area in October 2000 is 106 species but continues to rise as new collections are made.

Figure 4.2. The relationship between the eight non parameteric indicators and the observed species richness plotted on a logarithmic scale for the milpa data set of 465 quadrats

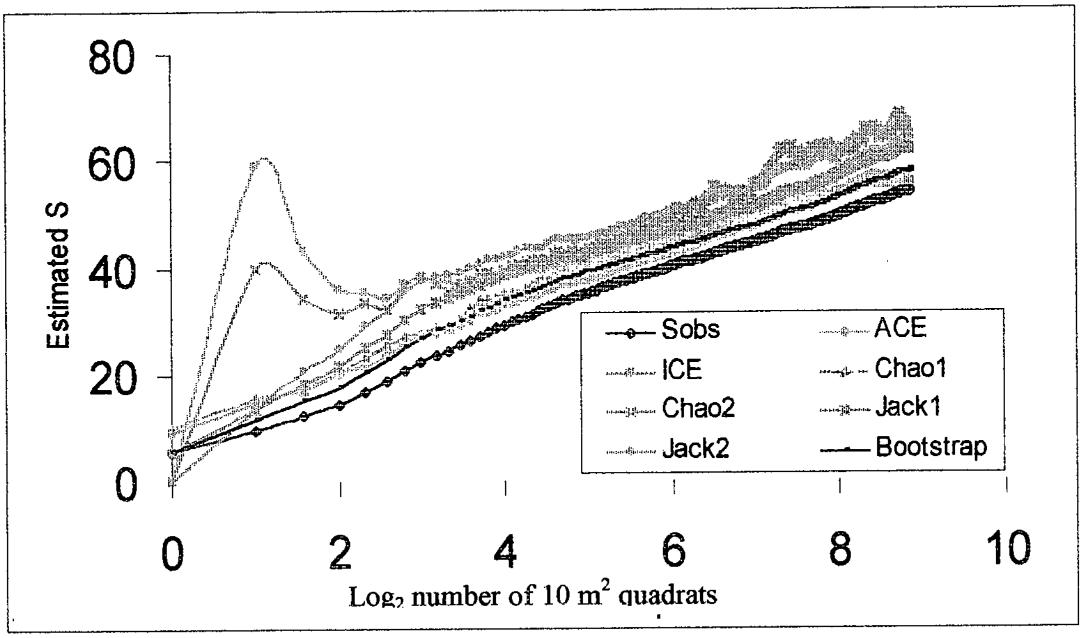
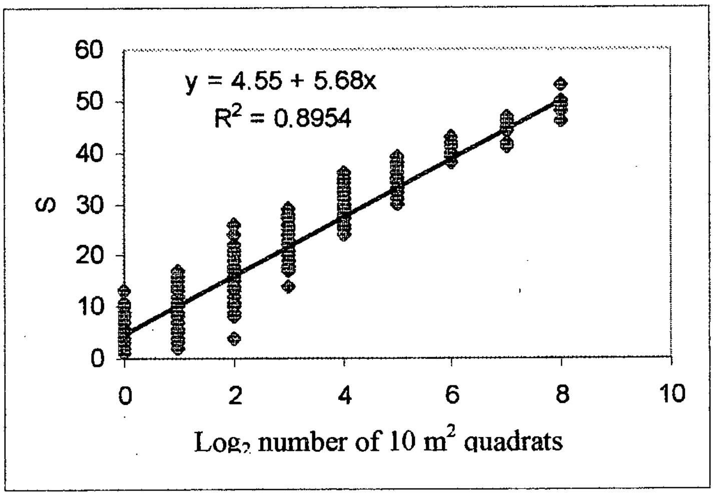


Figure 4.3 Species area relationships for the milpa data set produced through fitting a regression to log transformed number of quadrats data with weighting proportional to the degrees of freedom for the milpa data. a) log linear b) Log-log transform



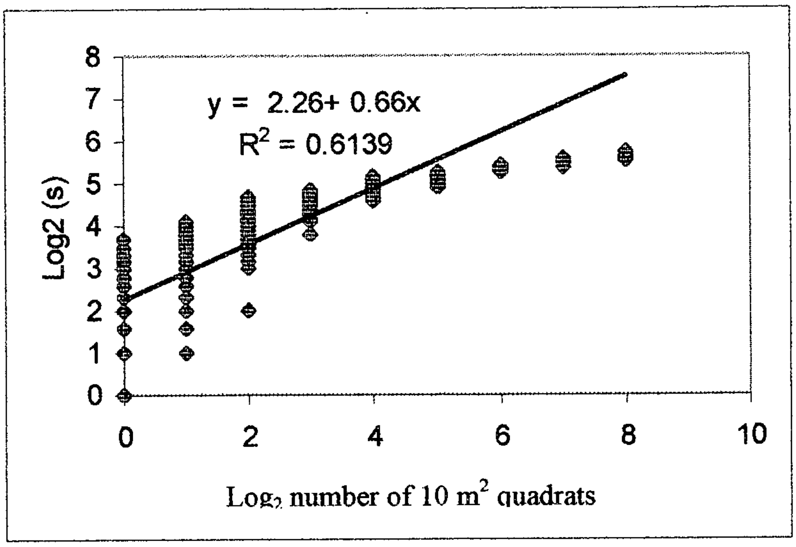


Figure 4.5 Species abundance frequencies for woody plants in the milpa data set. Bars show the number of species falling in each of the log 2 abundance classes.

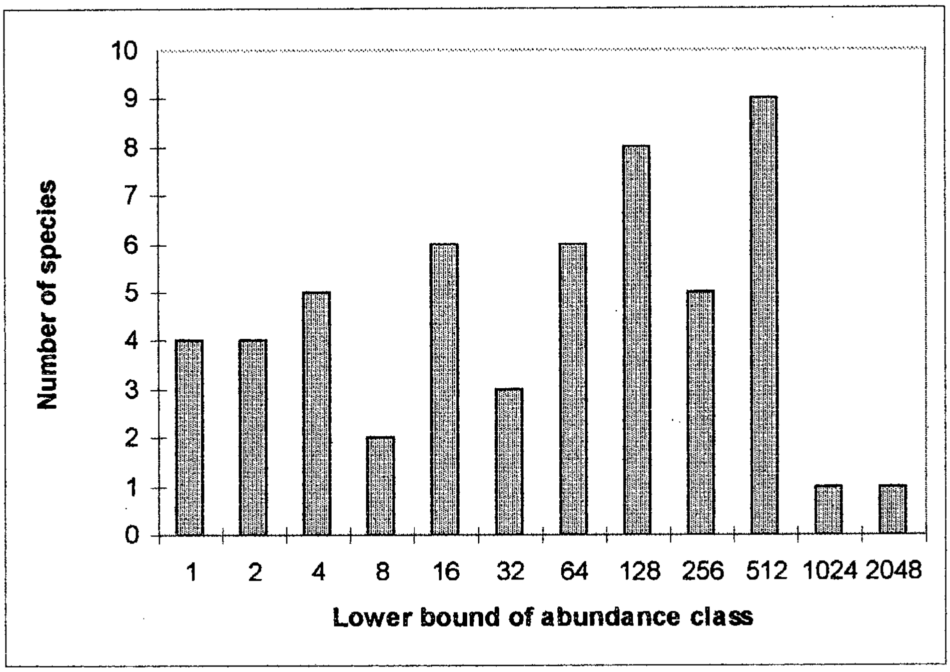


Figure 4.6 The relationship between the eight non parameteric indicators and the observed species richness plotted on a logarithmic scale for the forest data set (PSPs)

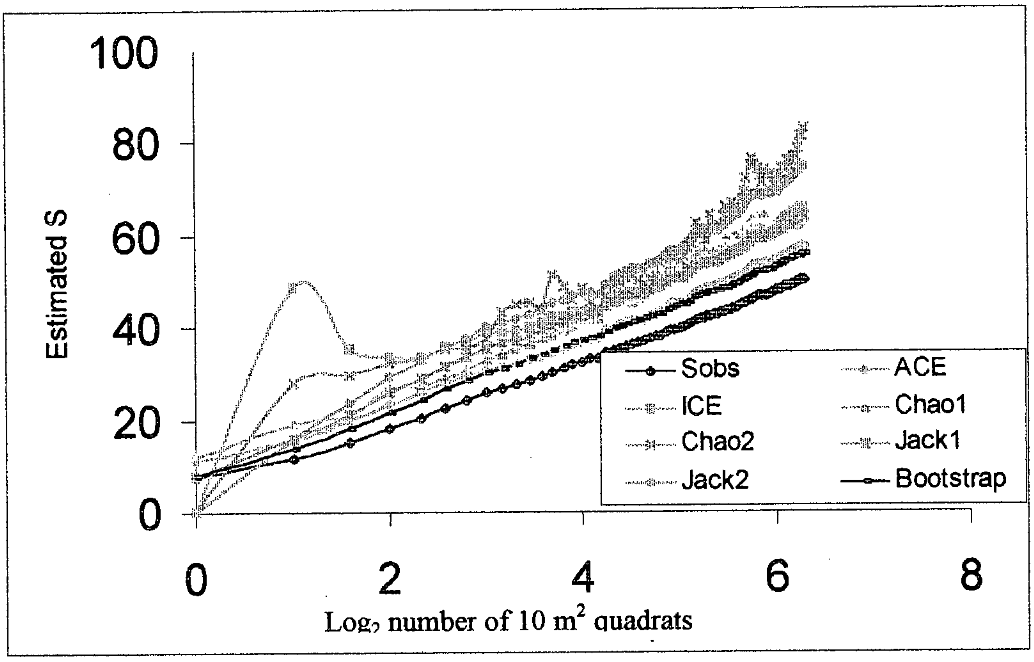
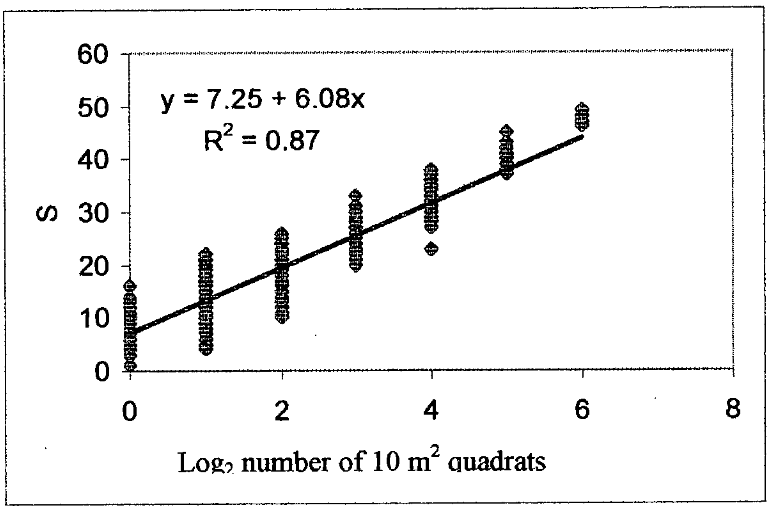


Figure 4.7 Species area relationships for the forest data set produced through fitting a regression to log transformed number of quadrats data with weighting proportional to the degrees of freedom. a) log linear b) Log-log transform



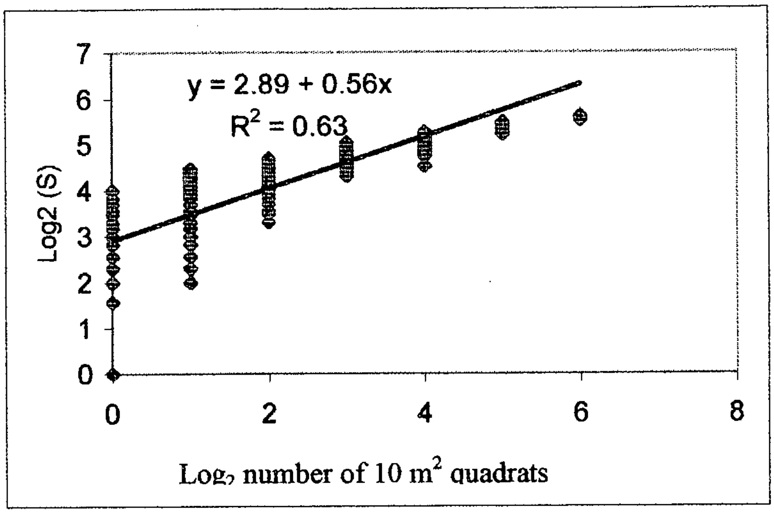


Figure 4.8. Species abundance frequencies for woody plants in the forest data set. Bars show the number of species falling in each of the log 2 abundance classes

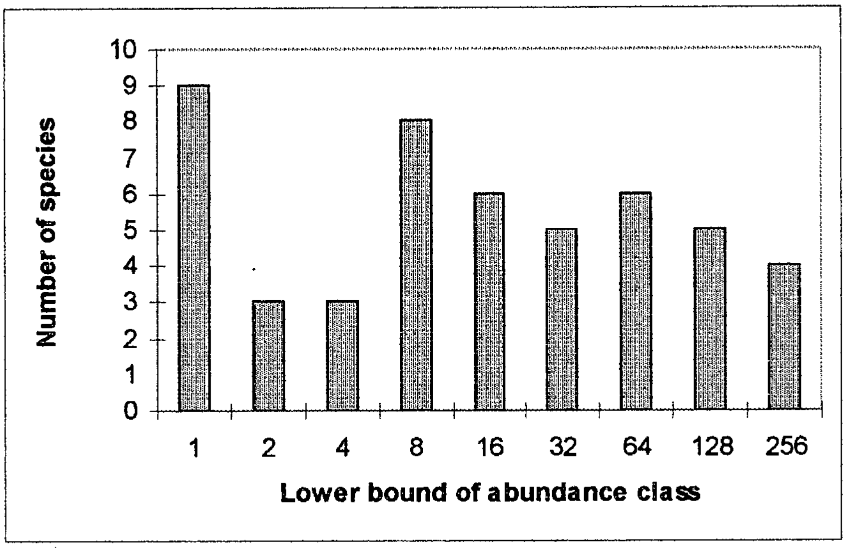


Table 4.1 Estimates of species richness rounded to nearest integer. The lower figures have been calculated from extrapolating the log linear model to 1) the area from which a random sample was drawn and 2) the total study area of 1,027 hectares. Standard errors given for estimates of Shannon's H and Simpon's D are calculated from jackknifed pseudovalues

Estimator	Milpa (s.e)	Forest (s.e.)
Sobs	54	50
ACE	56	57
ICE	63	66
Chao1	56	64
Chao2	65	83
Jack1	62	64
Jack2	67	75
Bootstrap	57	56
Shannon's H	2.99 (0.09)	3.01(0.07)
Simpson's D (reciprocal)	13.58(0.15)	11.89(0.16)
Log linear intercept	4.55	7.25
Log linear slope	5.68	6.08
Log -linear extrapolated to sampled area	89	69
Log-linear extrapolated to whole forest	117	128

Discussion

None of the non parameteric indicators met the criteria established for their use. For both data sets the indicators were dependent on sample size and did not rise to an asymptote. The indicators closely followed the pattern of the observed species richness. Thus the estimators could not provide the solution to the sample size problem that was hoped. The underlying asymptotic model on which the estimators were based gave no guide to how the estimation procedure should proceed if a dependence on sample size was found. Thus it was unclear how any inference could be based on these estimators. Extrapolation from the slopes of the species area curves seemed a more efficient means of detecting differences between the two habitats, and the inferences drawn were based on species area relationships rather than the non parameteric estimates of species richness. However difficulties with the statistical model used to fit the curves was apparent. The commonly used power curve was a poor predictor when fitted using the procedure proposed.

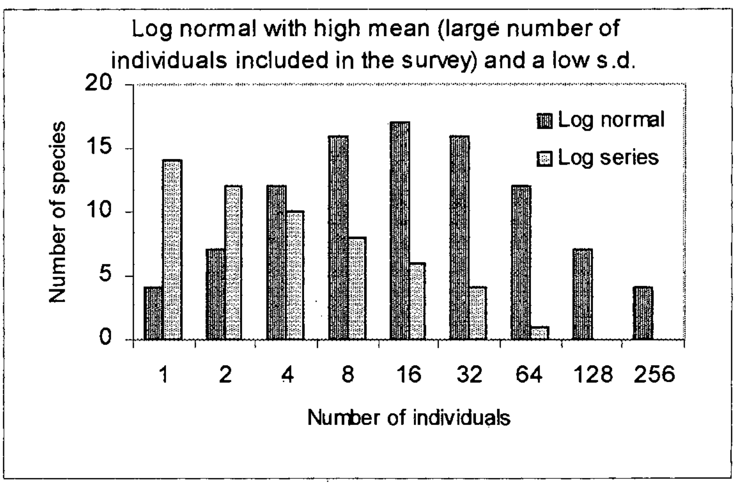
Colwell and Coddington (1994) suggest that the jack-knife estimators have upper bounds of twice the total species included in the data and should thus correlate with sample size until half the total number of species is observed. Other estimators vary slightly in their upper bounds. Incompatibility between the sampled distribution and the assumptions made by the estimators for most of the range of the data may thus be responsible for the correlations between estimators and observed S.

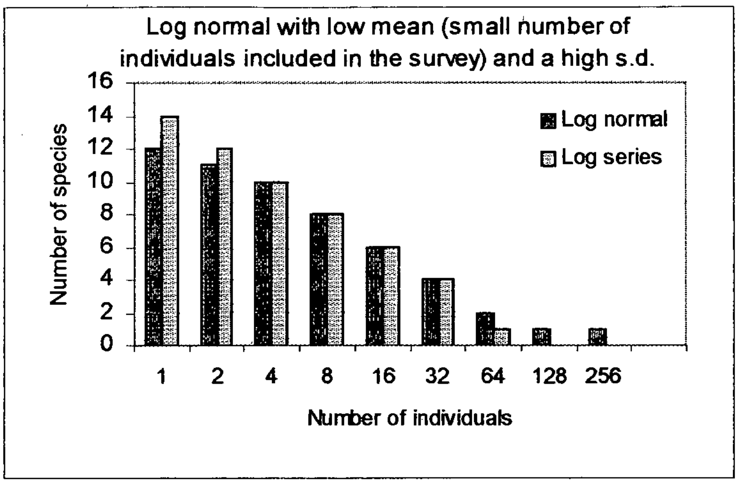
Both areas produced species area relationships that did appear to fit a log linear relationship. The question arises of how this might have occurred when quite large underlying differences in abundance patterns were found in the two data sets. The species area curves might have been expected to follow different trajectories defined by differences in the species abundance patterns. However when fitting a species area curve from sampled data of this type the underlying relationship may well turn out to be unimportant when small sampling units are used. A purely statistical argument might explain the results based on a consideration of the sampling procedure.

The argument involves a brief consideration of the development of the use of the power function. Preston (1948) was instrumental in developing the log normal model as a paradigmatic feature of ecosystems (Sugihara 1980). His arguments were incorporated into the theory of island biogeography (MacArthur and Wilson 1967) and led to a widespread acceptance of the power function for fitting species-area curves which has been extended to circumstances where the original criteria of community isolation is not met (Hayek and Buzas 1996). The test of the model originally proposed by Preston involved fitting a normal distribution to a frequency histogram of the number of species in logarithmic abundance classes. However to solve the problem of under representation of rare species in samples, Preston suggested the use of a veil line or truncation of the log normal curve. This has the effect of blurring the distinction between a log normal model and competing distributions (Magurran 1988; Hayek and Buzas 1997). Furthermore the log normal distribution has unusually robust properties which leads it to be easily fitted to many empirical data sets regardless of the true distributions from which they have been drawn (May 1975). Though more formal procedures for fitting the distributions than those used by Preston are now available (Hayek and Buzas 1997) the underlying problems remain. Preston's method accepted that small samples produce what are in effect acceptable approximations to log-series from distributions that are assumed to be log-normal. This seems to be the key to understanding why the log-linear species area model is so universal at a small scale.

Once all the quadrats were included the data for the milpas provided a visibly better fit to a log normal model while the data for the forest suggested the log series model. Although no tests were used, this would also be concluded from any statistical comparison that might be proposed. However if small samples are drawn from a log normal distribution with many species and a high variance the result is a distribution which is initially operationally indistinguishable from a log series when the inevitable stochastic and process error found in field data is added. A species-area curve which superficially fits a log linear model can thus arise in several ways. When less than half the species have been sampled from a symmetrical log normal distribution the modal class will usually be the class of species with just one individual. As the mode for a normal distribution equals the mean the effect is as shown in figure 4.12 . The mode shifts to the right as larger data sets are available. Non parametric indicators might then begin to give better estimates, the log linear model may begin to overestimate species accumulation and the log-log transformation may become appropriate for linearising the data. However the regression would have to ignore earlier data points. Clearly if individuals are clumped, clonal or of very different sizes, as occurs with forest trees, the mode may be artificially shifted to become two or several individuals. Other confounding patterns of variation are likely to arise with real data. None of these incidental effects are likely to lead to an improved performance by non parametric indicators or an improved fit to the power curve.

Figure 4.12 An example of the effect to be expected when small samples reduce the absolute value of the modal class of a log-normal species abundance distribution





The suggestion is that the log linear fit arose in both cases initially from a simple sampling artefact and has no biological significance. It may thus be difficult to defend direct extrapolation from this model. In the case of the milpa data the sampling effect was beginning to weaken. A considerable proportion of the species pool had been included. There was a slight suggestion that the log-linear model would overestimate species richness if extrapolated. New species were perhaps accidentals. In the forest data there was no suggestion that a limit had been reached. The log linear model still underestimated the true species number. Nevertheless the fit for both models might be used as a useful rule of thumb guideline for future research, or as a comparative figure in the absence of better data.

In both cases the power curve proved a poor model which seriously overestimated species richness if fitted to the whole data set. It might be argued that doing so was inappropriate and the power curve should only be fitted to the top of the curve when the sampling effect has been overcome. However to confirm this requires considerably more effort. To add four more $\log_2$ classes to the distribution would require sixty four times more quadrats than were used. In other words, the failure of the power curve to provide a realistic estimate of species richness could be related to the failure of the non parametric estimators to meet their principal criteria. There may be too many rare species in the data, simply because fractions of individuals cannot be found when sampling is limited. As this will always tend to be true until a large proportion of the species have been sampled, it may be difficult to identify circumstances in which the non-parameteric indicators will solve the extrapolation problem more effectively than plotting iterated species accumulation curves or the more statistically robust variant used here.

Overall it must be concluded that the forest habitat is richer in woody species than the milpa habitat. This occurs despite an obvious increase in stem densities in open areas and an almost complete overlap of species distributions. Milpas are dominated by a comparatively small number of woody species. The initial steady, log linear accumulation of species does seem to be flattening out in the data set. The species richness of the forest is due principally to rare species. The statistical analysis was very strongly supported by field experience. As work continued it became apparent that only a very small proportion of the total number of species found in the forest had fallen within the quadrats in the PSPs. Field collections are constantly adding new species to the list found at the site. Often the collection is made from a single individual and despite searching, no further specimens can be obtained. This observation does tend to support the proposed log series model. Log series are traditionally associated with disturbed habitats while a log normal distribution which was hinted at for the milpas is taken as a sign of stability (Magurran 1988). The possible explanation for this seemingly paradoxical reversal may lie in the fact that the forest is in fact far from its original undisturbed state and contains remnants of species which were once more abundant. The milpas also contain these remnant species, but the commoner species form a more coherent community in which active niche partitioning has led to a model which approximates more closely to a log normal species abundance distribution.

If interest lies in testing the log-normal model in its appropriate theoretical setting it may be necessary to move up to the scale at which its premises better apply. The fit of the model to species numbers found in large discrete sampling units represented by whole forest fragments may be revealing. This test has not as yet been possible for the montane forests in Chiapas. The first requirement for such analysis is clearly that reliable estimates of the true species number in each fragment be available. However the spatial extent of sampling will still tend to determine which model provides the best fit to data sets of finite size. This leads to an inference problem that will require very careful attention. As research in the region progresses it may not always be clear whether different processes act at different scales (Schmida and Wilson 1985; Rozenweig 1995; Huston 1999 see Hubbell in press), or different patterns in the data result as artefacts of sampling.

The principal concern in this study was not to test theory, but to find an effective tool for rapid assessment of species diversity in a changing landscape. Some consideration of competing species-abundance models had to be made in order to explain the failure of the estimators, but more detailed comparison of species abundance models is clearly premature. These models are based on theories regarding niche partitioning. Alternatives to classical niche partitioning may explain the co-existence of plants (Tilman 1990; Tilman 1994; Pacala and Tilman 1994). Establishing the role that niche partitioning plays in structuring forests has proven challenging (Duncan *et al.* 1998; Hubbell *et al.* 1999).

Conclusion

Producing robust empirical estimators of species richness is currently of greater value to ongoing conservation efforts in this understudied region than tests of underlying theoretical models. It was hoped that non-parametric indicators would provide such tools. Unfortunately their performance was less robust than had been hoped. Based on these results such estimators cannot be generally recommended for uncritical application to data sets of modest sizes drawn from species rich forest communities. The log-linear model provided the best fit to the species area curve for both data sets. The underlying reason for this may be unimportant. The model can be considered the most effective operational instrument available for rapid assessment of the return in terms of species found for time spent collecting in such forests. The model is particularly effective for small data sets because an approximation to the log series will be initially drawn from almost any distributions. In other words at the beginning of a new survey the log-linear model will be a very robust guide to the number of species found. The fit of this model does however provide little insight into underlying pattern.

The forest at Sonora does perhaps contain more woody species than more open shrubland, but the difference in absolute numbers of species is slight. Because of the well mixed heterogeneous vegetation structure, dispersal of propagules between patches and persistence through disturbance seems to have maintained diversity in disturbed areas. It is this feature of the current vegetation that may be the key to future conservation efforts aimed at preserving representative patches of habitat as refuges for scarce species.

Part 2. Models of decision making which predict the historical and contemporary disturbance regime of pine-oak forest: Introduction

It is now clear that the cause of the heterogeneity of the forest structure that has been documented in the previous chapters is the result of a historical pattern of disturbance associated with rotational slash and burn farming combined fuelwood collection and more recent grazing impact. The important question that must be answered in order to model the system is what criteria are used to decide whether the forest is disturbed in this way?

Approaching this topic poses special challenges, especially when slash and burn is discussed. The use of fire either in rotational systems or to clear new land became a highly sensitive issue in Chiapas following the 1998 fires. The wild fire which affected the forested area of Sonora (chapter 2) was undoubtedly started by slash and burn farming, even though the community placed restraints on slash and burn activities in order to protect their forest resources. Sale of pine timber is a source of income for the community. The practise of slash and burn farming varies widely at the regional scale making generalisations from published studies hard to draw. Soils, cultural and social systems, external restraints, population density, climate and forest type all influence the details of how rotational farming systems are practised. Evidence from regional scale studies based on remote sensing do provide a framework for assessing the impact of slash and burn farming, but cannot provide insight into how it may be modelled as a process (Ochoa-Gaona and Gonzalez-Espinosa 1999). Short term studies may be unable to distinguish rotational slash and burn from permanent land conversion. These inherent challenges associated with the studies of land use change in Chiapas inevitably lead published accounts of slash and burn methods to draw on anecdotal qualitative evidence (Pool Novelo 1997, Konstant *et al.* 1999; Hellier, Newton and Gaona 1999). In order to model this system effectively some means must be found of predicting the disturbance regime associated with slash and burn farming.

This section consists of one chapter which summarises the knowledge obtained from the people of Sonora regarding their forest and their decisions on its use. A little used means of linking and summarising probabilistic data is evaluated as a tool for modelling the decision making process. Most of the chapter concerns slash and burn (milpa) farming which was found to be the major disturbance affecting the forest. In the second part of the chapter the impact of fuelwood collection is briefly evaluated and quantified.

Chapter 5. Modelling the decision making process leading to forest disturbance

5.1 Slash and burn farming

Introduction

An accurate picture of slash and burn practice can best be obtained from interviews with farmers. However reliable information cannot be obtained by questioning a random sample drawn from the population. Because the researcher's intentions may not be fully understood misinformation is likely to be given unless trust has been established (see Lynam 1999 for a further example of the problems with the use of questionnaires in rural appraisal). Slash and burn is regarded by its practitioners as wasteful of forest resources, but is an effective means of producing subsistence crops. There is thus a marked and understandable reluctance of farmers to provide details on the practice. Farmers are most sensitive to questions regarding the most traditional form of rotational slash and burn clearance in which high forest with potentially valuable timber is used.

As work at the site had progressed it became apparent that most of the forest had been disturbed by slash and burn previously. Yet no recent disturbance of intact forest had taken place. It emerged that the community had placed a moratorium on forest clearance at the time when they applied for a permit to cut timber. This was largely due to concerns regarding the loss of timber that could be sold once the legal permit had been obtained (chapter 1). Decision making is thus directed by the framework provided by the ejido system and the wider legal framework of land tenure. However these constraints act by modifying the options available to individual farmers. Thus a bottom up approach was adopted to attempt to reveal and model how the decisions that directly affect the forest are actually made.

The case study thus provided an opportunity to attempt to answer two important questions that will need to be answered more generally if forest models are to be linked to disturbance regimes.

1. How did/do farmers decide which plots were/are suitable for slash and burn clearance?

2. Will slash and burn continue to play its historical role in disturbing forest vegetation?

The following work addresses these questions and evaluates the potential of a novel tool for modelling rural decision making and moving low level observations taken from field work up into a more general context. Bayesian belief networks (or probabilistic causal networks) offer a promising framework for synthesising and modelling qualitative or semi quantitative probabilistic information (Pearl 1988; Neapolitan 1990). Software, which facilitates the construction and analysis of such networks, has only recently become generally available. Bayesian networks represent believed relations between a set of variables that are related to some phenomenon of interest or problem to be solved. Variables may be considered to be related to the problem because their values alter the outcome of some action that affects the problem, or because their values are altered by actions associated with the problem (Norsys 1998). Belief networks may be constructed using variables which are uncertain, stochastic, or imprecise. They thus represent a formal structure for connecting what may be informal knowledge regarding causal mechanisms and correlated phenomena

Belief networks are being increasingly widely applied to building expert systems, particularly in the medical domain. To construct a belief network nodes are used to represent variables. Variables may be discrete, continuous, or propositional (true or false). Nodes are connected by directed links, which are interpreted in a different manner to the influence arrows used in compartment flow modelling. Links are indications of conditional dependence. A link from node A (parent node) to node B (child node)indicates that A causes B, that A partially causes or predisposes B to take some value, that B is an imperfect observation of A, that A and B are functionally related, or that A and B are statistically correlated. Nodes are related by Bayes theorem that states

$$p\langle y|x\rangle = \frac{p\langle x|y\rangle.p\langle y\rangle}{p\langle x\rangle}$$

Where y and x take the values of the possible states of the nodes A and B. Changes in the probability distribution for the states at node A are reflected in changes in the probability distribution for the states at node B. Estimation of conditional probabilities is thus required in order to construct belief networks. When networks are compiled the application of Bayes theorem results in appropriate changes in the probability distribution of linked nodes if further knowledge is acquired. Software used for network construction checks for consistency and prevents trivial but common logical fallacies which arise from assuming p(y|x) can be translated into p(x|y) when relevant information regarding p(x) or p(y) is not provided.

Formal definitions of conditional probability are not easily translated into operational guidelines for network construction for non-specialists in the field of artificial intelligence (Anderson 1998). The directionality of the arrow used for the link does not necessarily impose an order in which new knowledge is placed in the network and does not necessarily imply causality, although the value of nodes which receive arrows often reflects higher level knowledge which is more difficult to acquire. Following causal pathways may be an efficient means of determining conditional dependence, but it is not the only way in which belief networks may be structured. Normally a network is used to predict the value of nodes that cannot be known directly from knowledge of the values of variables whose values can be estimated with a greater degree of certainty. For example, in a medical diagnosis changes in the value of symptom nodes will change the believed probability that the patient suffers from a given illness.

The familiar medical example demonstrates how a chain of causality is not necessarily used to structure the network. If symptoms may be observed without the presence of disease they may be conditionally independent observations. Influence arrows could be used in the network that run in the reverse direction to underlying mechanistic causality. The disease may cause symptoms, but observation of symptoms implies the presence of the disease and alters strength of belief in the diagnosis. The application of Bayes theorem when networks are compiled reflect this relationship and the structure of the network can depend on the available knowledge used to produce estimates of p(x),p(y), p(x|y), p(y|x). Bayesian networks can thus be used to model systems in which an *a priori* chain of cause and effect cannot be established or the only evidence available concerns correlative relationships. The utility of belief networks in applied situations arises from exploiting their potential to convert easily obtained knowledge into probability distributions for unobservable or unmeasurable variables. Networks can be built in which expert knowledge of the connections involved in conditional probabilities is used to provide a structure which links measurable and observable variables to predict the value of a node which is not directly quantifiable.

A difficulty faced when constructing networks is the fact that the number of discrete conditional probabilities that must be provided for a child node is a geometric function of the number of parent nodes. In some network applications automated learning of probability tables may be possible from large data sets of prior observations. However if each probability must be elicited in turn operational considerations require that networks be built through the application of Occam's razor. The process of network design inevitably requires the elimination of weak correlative or causal links from consideration in order to produce an operative framework. This procedure does not necessarily result in the loss of structural detail. Even simple networks display complex interconnectivity through the application of Bayes theorem when the network is compiled and used.

Two Bayesian networks were constructed in order to investigate the separate but related questions of relevance to modelling the forest dynamics of the field site. In order to correctly interpret the results of Bayesian networks the questions of interest have been reworded in order to refer to probabilities.

1. *What is the probability that a randomly selected patch of communal land is suitable for slash and burn farming?*

2. *What is the probability that a randomly selected member of the community is in favour of enforcing a moratorium on slash and burn forest clearance?*

Bayesian networks could provide a solution to some of the difficult problems associated with asking these questions. In the first case the network can combine known information on forest structure with the farmer's own criteria for use and thus reveal underlying details of the way slash and burn may impact a forest. In the second case asking a direct question to each farmer in turn is impractical due to the delicate and controversial nature of the subject matter. Information regarding the underlying factors which influence the farmer's decisions can however be more easily obtained.

Method

Notes were taken continuously during each visit to Sonora over the space of over two years of fieldwork. Many hours of conversations with farmers who worked as field assistants were used to produce a description of traditional farming practises and their replacement by permanent cultivation. Relevant comments were noted, transcribed and translated. This information was then assembled to produce a descriptive account and formed the basis of the first network.

Information of relevance to the second network was gathered from the opinions expressed at communal meetings. Direct incorporation of this information was unfortunately not possible due to poor understanding of the Tojolobal language. Therefore a sub set of the active participants gave information regarding the issues discussed. It was important to explain that questions did not concern the participant's personal views, but referred to the views of the community as a whole. Additional analysis of economic and agronomic information was also carried out in order to provide some quantitative support for the otherwise largely qualitative information. A non-linear optimisation model which incorporates information available to the individual farmer was used to investigate economic constraints to the decision making process.

Once understanding of the basic issues involved had been obtained, the construction of the two Bayesian networks was carried out with the help of a focus group of six farmers ranging in ages from twenty to fifty five including a former comisariado of the community and the present secretary of the ejido. Networks were constructed using the program Netica © Norsys Software 1997. A list of potential nodes was first compiled during a "brainstorming" session. The connections between them were established by attempting to estimate the probabilities of each taking a set of possible values without making any reference to the other nodes. It became apparent in most cases which nodes had unconditional probability tables (parent nodes) and which required conditional information in order to be predicted (child nodes). After a period of network structuring and refinement in which the focus group participated, probability values for the tables were elicited at a series of focus group sessions. Model building and refinement took place over the space of four months from May 2000 to September 2000. Networks were constructed in Spanish and translated first into Tojolobal for discussion and later into English.

Although it is important not to view Bayesian networks as deterministic structures referring to frequencies, cognitive errors are commonly encountered when eliciting single event probabilities for Bayesian analysis (Anderson 1998). The most common are over estimation of single event probabilities and conjunction violations. Anderson suggests that many of these problems may be overcome by eliciting probabilities in a frequentist format as proportions rather than as single event probabilities. Conjoined probabilities were therefore elicited by building verbal scenarios involving proportions. Questions were phrased in a standard manner which allowed estimation of believed probabilities using the convention shown in table 5.1.

Table 5.1 Conversion between qualitative modifiers and quantitative probabilities used when eliciting probabilities in terms of frequencies for Bayesian network construction

Modifier	Proportion
All	100%
Almost all	90%
Most	70%
Half	50%
Some	30%
A few	10%
None	0%

When the networks were built some adjustment of the values given by this scheme were required to ensure that probabilities summed to 100%. The ordinal relationships between values given by the farmers were always retained.

The information obtained from the farmers was combined with the quantitative information provided by the forest inventory. The combined network produced an estimate of the total amount of land that was judged suitable for slash and burn. In the case of the network concerning the moratorium, farmers' perceptions of the composition and value of the forest were as important to their decisions than its actual state. It was therefore decided that the network that the nodes representing forest properties were parameterised by using what was reported to be the general belief concerning the forest even though in this particular case more accurate information was available and was initially used for parameterisation. The two modes of parameterisation could be compared to analyse how differences between perceptions and measurements could influence decision-making.

Additional challenges had to be overcome in order to produce functioning networks. It became clear that the farmer's knowledge was often subtle, and great care was required not to use subjective interpretations or mistrust what was being conveyed. Some suggestions for structural connections and parameterisation appeared counter intuitive, but on examination were found to be consistent statements of observations and beliefs.

Results

1. Narrative account of slash and burn practices.

The distinction between the forested bienes comunales and the land used by the community for grazing and permanent maize plots has been pointed out in chapter 1. While the *bienes comunales* consists almost entirely of pine-oak forest it appears likely from many independent lines of evidence including farmers comments that almost all this area has been previously used for slash and burn farming at some time. However until recent times it was largely ungrazed. Decisions regarding use of communal land for forestry and grazing are made at meetings in which all members of the community participate. Externally imposed legal restrictions constrain commercial forest exploitation and large scale change in land use but have no direct influence over subsistence activities in which no material from the forest leaves the village.

Each field is owned and managed by a single farmer. All farmers use at least one plot of land within the ejido for permanent maize production. Although the forested land is nominally communally owned, patches of forest are considered by the community as having an owner. This ambiguous and rather loose right of ownership is informally recognised if the land was originally cleared by a family member. If older members of the community recall where they cleared land their sons and grandsons are recognised as having first rights on the use of such areas for agricultural purposes, although fuelwood collection, timber harvest and grazing remains a communal right. Unwritten knowledge regarding ownership can be lost when the last farmer to remember the clearing of a plot dies. The large area of the bienes comunales, 1,027 hectares plus 800 hectares of pine-oak woodland in the *ejido*, might suggest that more remote areas could have remained in an undisturbed state. However even the few unclaimed patches of communal land are not old growth forest, although they have not been cleared in living memory or were used by farmers from neighbouring communities before formal land rights were established. Farmers without a recognised right to any suitable site for a new milpa in the forested area must ask permission from the owner of any site they select for clearance, or seek land whose ownership has been forgotten. Permission to use land is rarely refused making recognised "*ownership*" a rather poor predictor of the identity of the farmer who last used a patch on a temporary basis.

The criteria used to judge the suitability of a site for cultivation depends on the crop that is to be sown and the availability of external inputs. If fertilisers and herbicides are to be used in order to grow maize on what will then become a permanent plot, the existing tree cover is of little importance. However only areas with closed forest cover produce an acceptable maize crop without any chemical fertiliser input. It is easier to reclear an area once canopy closure and self thinning has reduced the number of stems. Extremely large oak trees are difficult to fell and are sometimes left standing, plots with a large number of such trees may be avoided, although the organic matter in the soil of such areas makes them attractive sites and they may be partially cleared with isolated remnant trees left standing. Larger pines are also sometimes left standing, but if the plot is accessible they may be harvested for timber. Farmers using recently cleared high forest sow a traditional variety of maize (*maiz del monte)* rather than the improved varieties used in the permanent plots or plots cleared from young secondary vegetation where some fertilisation is required. No ploughing or digging is needed on slash and burn sites, seeds are planted in holes made with a sharpened stake. Yields decline sharply after the first year. Plots are usually abandoned after two years cultivation unless chemical fertilisers and herbicides are used, in which case they may be semi-continuously cultivated using a very short rotation consisting of one year of maize followed by two or three years fallow (*año y vez*). Occasionally an intermediate rotation (*roza quema*) is used. This lies somewhere between the very short rotation fertilised system and the unfertilised forest fallow system. *Roza quema* relies on the dense shrubby vegetation which forms after 5 to 7 years fallow and is usually used for bean production. However in general there is little pressure to adopt very short rotation in the *bienes comunales* where a large amount of uncultivated land remains. Recently abandoned plots are undesirable sites for maize farming and are unlikely to be re cleared within ten years unless farmers are constrained in their choice of alternative sites. A clear distinction can thus be made between traditional methods requiring very long tree fallow periods which were the main means of maize production before fertiliser use and are still occasionally used in the *bienes comunales* and the permanent to semi-permanent production systems used in the *ejido*.

Beans are usually planted in pockets of soil on areas of rocky karst. Areas of shrubby re-growth which would produce a poor maize crop are reported as suitable for beans, presumably as the crop is not dependent on accumulated nitrogen. Beans are never planted without burning. Beans and maize are never intercropped, which is a common practise in areas with greater intrinsic soil fertility. Beans do not produce any crop if planted in the permanently cultivated fields of the ejido. A recent (2000) government initiative in the Tojolobal region has provided some communities, including Sonora, with subsidies (982 pesos per family) to buy fertilisers with higher ratios of potassium and phosphate in order to attempt cultivation of beans without the use of fire.

Nitrogen based chemical fertilisers and improved maize varieties began to be adopted in the area at the end of the 1970's. Since that time government extension workers and subsidies have encouraged the switch from slash and burn agriculture to the use of permanent plots. Currently a subsidy of 690 pesos (US $67) per *ejidatorio* is available if it can be demonstrated that at least one hectare is under permanent cultivation. No subsidy is received for the illegal use of forested land for slash and burn cultivation. This has been a point of contention in the region and it has been claimed that the payment of subsidies has been subject to political manipulation.

In the absence of chemical fertiliser less than half the maize planted may reach anthesis on the nitrogen deficient soils of the permanently cultivated areas. Farmers use around 200 kg (4 costales) of urea (48% nitrogen) per hectare of permanently cultivated ploughed land. Yields are rarely above 1000 kg per hectare (20 costales) and a rule of thumb mean is 750 kg (15 costales). Most of the applied nitrogen is thus being lost to surface runoff, leaching or de-nitrification. Losses are compounded by inaccurate timing of application and unpredictable often highly unfavourable climatic conditions. Leaching apparently occurs readily on these soils once they have lost their organic matter. This may be because their highly weathered mineral elements provide very low cation exchange capacity. Farmers report that unusually high rainfall can cause low, spatially variable yields that may be worse than those in drought years, an observation consistent with the hypothesis that yields are low due to loss of nutrients through leaching. The very high level of nitrogen application is apparently a "brute force" approach to fertilisation, ensuring some uptake by the crop despite a large wastage. The extent to which yields are limited by other soil nutrients cannot be easily assessed as only urea or ammonium sulphate are used.

A farmer therefore is faced with a choice. He may cultivate permanent plots which require subsidised inputs, or he may clear forested plots which give an immediate return with no external input, but must be either abandoned after two years or assimilated into the permanently cultivation system through increased application of fertilisers and herbicides. Some combination of these two strategies may also be used.

A simple non-linear optimisation model was used to compare the economic return of using the legally recognised permanently cultivated plots of the ejido to that obtained from rotational slash and burn in the forested area. The model solves for two sets of equations which calculate the yield and cost for each type of plot in order to find the optimum partitioning of effort between permanent plots and slash and burn plots using the spreadsheet package MsExcel. The aim is to produce a simple null model of farmers behaviour. Constraints and parameters were altered to build a series of alternative scenarios. Due to the unusually high levels of fertiliser loss a mechanistic model of crop N uptake that was first considered was replaced by a simpler but more realistic hyperbolic function which better matched the farmer's reported yields and crop responses. Box 1. shows one example of an optimised solution for a possible scenario and includes data on prices and reported yields in the area in 1999. The model uses an empirical measure of soil fertility based on fertiliser equivalence that is easily communicable This is an approach adopted by fertiliser companies and agricultural advisory bodies to suggest optimal fertiliser use following fallow or leguminous crops. The conclusions of the model are uncomplicated and robust to minor changes in parameterisation. They are summarised in Box 1. Currently a mixed strategy involving some slash and burn clearance will be desirable in order to both obtain subsidies and a good maize yield. If subsidies are withdrawn a strategy of pure slash and burn may be optimal. Slash and burn ceases to be viable if soil fertilities are intrinsically high or the value of timber is taken into account.

Box 1. Solving a non linear optimisation model to predict farmer's behaviour based on economic considerations. Is slash and burn an economically optimal strategy?

The problem: A subsidy is available to produce maize from legally recognised, clearly demarcated permanent plots. However these fields require high nitrogen inputs and their yield is uncertain. Slash and burn forest plots produce a relatively good maize crop at a low cost and with less risk. Land used for slash and burn is not legally recognised and a subsidy is not paid. The farmer can only cultivate a small amount of land due to time constraints. If he cannot show permanent cultivated plots when inspections take place the subsidy might not be paid. Seen from the farmer's perspective and only using information at his disposition how might he decide to optimise the return? Are economic considerations useful predictors of the farmer's behaviour?

Example parameterisation:

Taking the local November 1999 prices in the market city of Comitán: 1 peso=9.35 US$

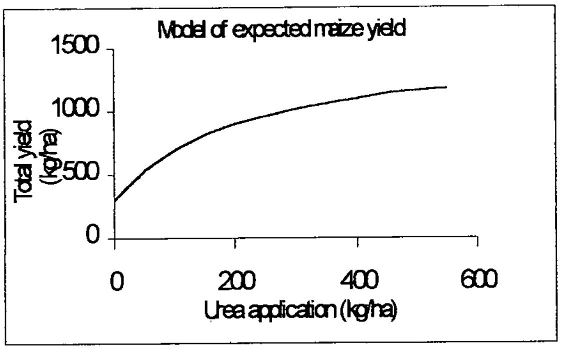
	Kg	Ton	"Costal" (50 kg sack)
Maize	1.72 pesos	1720 pesos	86 pesos
Urea	2.10 pesos	2100 pesos	105 pesos

Herbicide (gramoxone - paraquat) -Price per litre = 60 pesos 2-3 litres per hectare

The response to the addition of nitrogen fertiliser is modelled as a rectangular hyperbola, parameterised from yield reports in order to represent the very low nitrogen use efficiency obtained. There are very high levels of wastage in this system. Assuming that a small yield could be produced without fertiliser, the yield becomes some baseline yield + a response to added fertiliser. Slash and burn plots accumulate additional soil **N** during the tree fallow phase. This is empirically represented in terms of an estimated "fertiliser equivalent" which in this context is taken from reported yields to produce a simple deterministic empirical model in which slash and burn clearance reduces the need for fertiliser use. This figure can be altered to test the model's sensitivity to the length of the fallow period.

Estimated yield model: The surprisingly low yields and high fertiliser input are taken from direct field observation.

Fertiliser which produces half the maximum response (kg ha-1)	200.
Asymptotic response to fertilisation (kg of maize ha-1)*	1200
Base yield (kg of maize ha-1)	300
Slash and burn plots "bonus" N in units of fertiliser equivalent (kg ha^{-1})	312



Constraints: The maximum amount of land which can be cultivated and weeded is around 2 hectares. No money above the PROCAMPO subsidy is available. If the permanent plot area falls below around 0.6 hectares the payment of the subsidy may be at risk. Thus there may be an incentive to use two plots, one of which is used to ensure the payment of subsidies. There is an opportunity cost associated with timber destruction due to slash and burn, but the extent to which this is taken into consideration may depend on exogenous factors. In some cases it may be ignored, in other cases the whole community may take additional constraints into account. It is assumed that land availability is not a direct constraint.

PROCAMPO (credit) available***	690 pesos	Total area cultivated	2 ha

One possible view of the opportunity cost: Assume pure self interest as a null model. The farmer regards the value of any lost timber due to slash and burn as being divided between all families in the community and only counts his share. This may apply if no permit for forest use has been obtained or if monetary considerations are secondary to subsistence. The timber lost is assumed to be advance regeneration that may be harvestable within a person's lifetime as some standing timber may be extracted prior to burning.

	Volume (m^3)	**Stumpage**	**Timber value**	**Divided between 72 families**
Opportunity cost of lost pine timber	50.00	300 pesos m^{-3}	15,000 pesos ha^{-1}	208 pesos ha^{-1}

Example: Optimisation calculations: Fertiliser use, and area cultivated are adjusted to optimise yield or profit. An optimised solution is found using the MS Excel solver macro. The farmer may be assumed to be attempting to optimise either total maize yield or economic criteria. Here the model is solved for net profit. Note that labour only enters the model as a constraint. It has no economic cost to a subsistence farmer. Additional fixed costs are very small and set to zero for simplicity. With this set of parameters the optimal solution "flips" to use of only permanent plots if an improved response to added N is assumed or if opportunity costs are increased.

	Permanent plot	**Slash and burn plot**	**Total**
Area (ha)	0.6	1.4	2 ha
Fertiliser (kg ha-1)	290.47	0.00	
Total fertiliser use (kg)	174.29	0.00	174.29
Yield (kg of maize)	606.41	1444.39	2050.80
Fertiliser cost	366.00	0.00	366.00
Herbicide	72.00	252.00	324.00
Costs	438.00	252.00	690.00
Maize gross value (pesos) 1999	1043.03	2484.34	3527.37
True net profit (pesos) 1999	677.03	2484.34	2837.37
Realised net benefit (maize gross value + unused credit)			3527.37
True net benefit (-opportunity cost)			3235.70

Summary of model results. The model is sensitive to changing economic and productive scenarios. It is also sensitive to alterations in the farmer's optimisation goals. It is summarised here in terms of optimum strategy for each optimisation goal

Optimisation goals

A) Optimise maize yield (pure subsistence

B) Optimise immediate net benefit from maize production (subsistence + short term view of economic benefit

C) Optimise long term net benefit (maize production - opportunity cost of lost timber viewed from an individual perspective

D) Optimise benefit and minimise cost to the community (maize production -opportunity cost viewed from a community perspective).

Possible strategies.

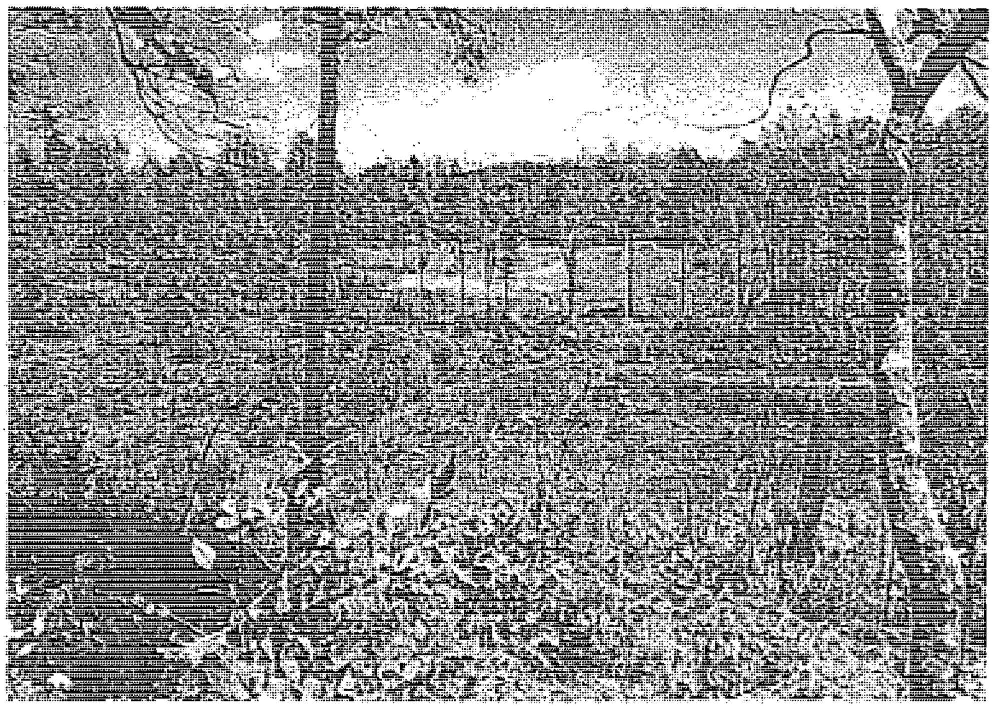
1)Cultivate only recognised permanent plots in the ejido (no new forest clearance.

2)Cultivate only slash and burn plots cut from the forest.

3)Cultivate the minimum area of permanent plot necessary to ensure the payment of the subsidy and concentrate remaining effort on production from a slash and burn plot.

	A	B	C	D
Current situation	3	3	3	1
Lower productivity (bad year)	2	3	3	1
No subsidy	2	2	2	1
Increased timber value	3	3	1	1
Lower maize prices	3	3	1	1
Higher fertiliser prices	3	3	3	1
Lower fertiliser prices	3	3	1	1
Higher intrinsic fertility	1	1	1	1

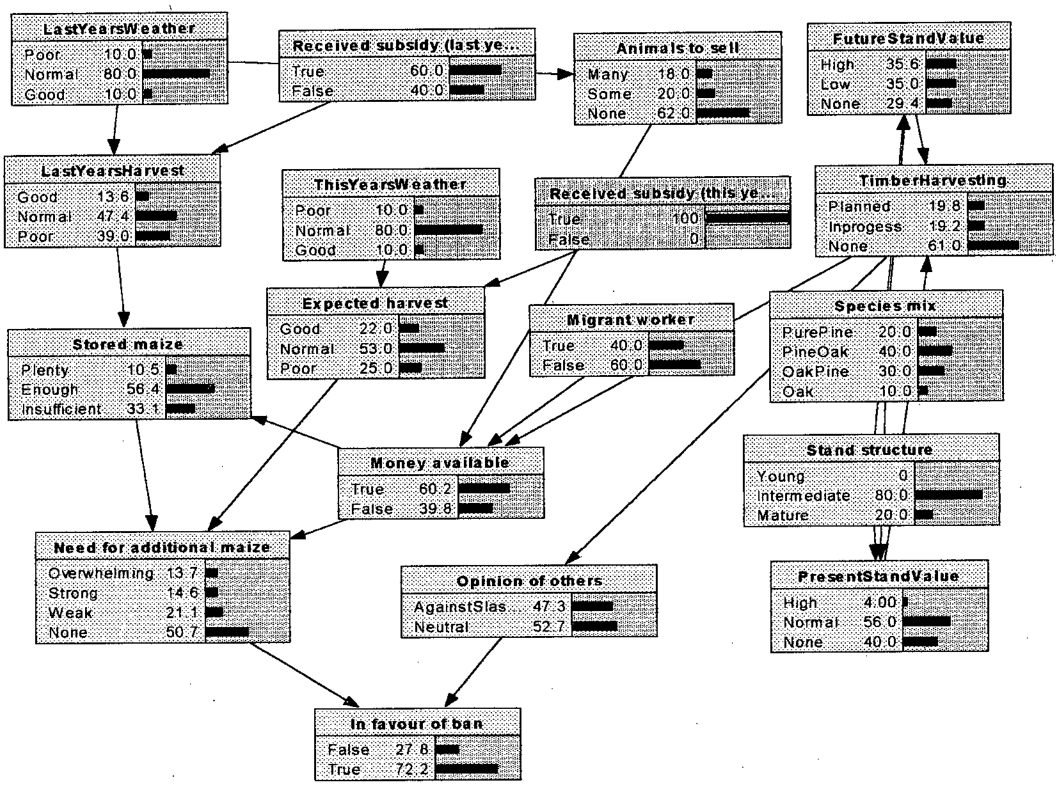
Photograph 6. Ploughed permanent plots in the ejido of Sonora on the edge of the forested area



3. Bayesian belief network

The delicate issue of farmers' opinions on the community enforced moratorium on slash and burn farming is presented as a Bayesian belief network in figure 5.1. In this network the political and religious elements, which accentuate divisions and lead to conflict, have been excluded to allow the underlying resource use issues to emerge.

Figure 5.1 Bayesian network showing the probability of variables representing elements which influence the decision a farmer may make on whether to support a moratorium on slash and burn farming. In this example the certain knowledge incorporated is that the farmer has received the Procampo subsidy. Other nodes take probabilistic values.



In figure 5.1 the value of the node "*In favour of ban*" represents the strength of belief that a randomly selected ejidatorio will either be in favour or against the communally imposed moratorium on slash and burn farming. A formally incorrect, although useful, interpretation is that it displays the proportion of the population that are likely to hold views in favour of or against the moratorium. If the frequentist perspective is taken the network can be used to investigate how changes in the value of parent nodes alter the consensus of the community as a whole, providing the level of uncertainty inherent in the network is recognised (see the later discussion of this difficulty). The network is a working model to which information may be added. As more information is known, the strength of belief in the farmer's position is altered

Proximate reasons for rejecting or supporting the moratorium are the farmer's desire for additional maize and his expectation regarding the opinions of others. The opinion of others is assumed to be influenced by considerations of the forest structure and composition and the legal position regarding commercial exploitation. The belief that additional maize (i.e. maize not produced from the permanent plot in the *ejido*) is required for subsistence is influenced by the previous years' harvest and factors affecting this years harvest such as the availability of subsidies and the actual or believed weather conditions.

This network is comparatively small but still contains a large amount of information that may be analysed in many different ways. As with all moderately complex models it quickly becomes impossible to explore systematically the whole of the available parameter space. This can make communication of networks properties challenging. In many respects their properties are best discovered through exploration by potential users of the information. This is a common problem with the presentation of expert systems. However one of the advantages of the network structure is that it allows automated sensitivity analysis to be carried out which can provide a convenient summary of their properties.

The interpretation of the sensitivity of the model requires considerable care, as subjective decisions regarding network structure and decisions made regarding the discretisation of nodes will influence sensitivity indices. Also the findings that have been incorporated into the network for any one case will affect sensitivity. Sensitivity is thus a scenario specific property. Sensitivity analysis gives a guide to how small changes in one node affect the node of interest, but not necessarily which processes are most important in determining the current value taken by that node. Some nodes may tend to "flip" from 100% in one state to 100% in an alternative states, while others change more gradually.

Table 5.2 shows the sensitivity of the node "In favour of ban" to small changes in the probabilities at unconditional nodes when the network is parameterised from knowledge of the actual situation in August 2000. Most of the unconditional probabilities have been estimated from frequencies, such as the proportion of farmers who have worked in Cancún. It suggests that a person's opinion on the current ban on slash and burn farming in *the bienes comunales* is most likely to be altered by this years weather, the availability of migrant work, the number of animals he has to sell (alternative income) and the forest composition. The relative importance of these factors was validated in discussions with farmers. Weather was indeed found to have a direct effect on farmers support for the moratorium, even if an official permit to cut timber had been obtained. Slash and burn plots produce reliable yields most years. Worries regarding maize supplies are highly influential in determining some farmers' views, even when the majority wish to preserve timber for future sale. In the focus group meetings the view was expressed that older members of the community felt that buying maize, even if money was available to do so, was shameful and a sign of failure. Younger farmers who are often migrant workers are less concerned if their milpas fail, providing they have enough money with which to buy maize.

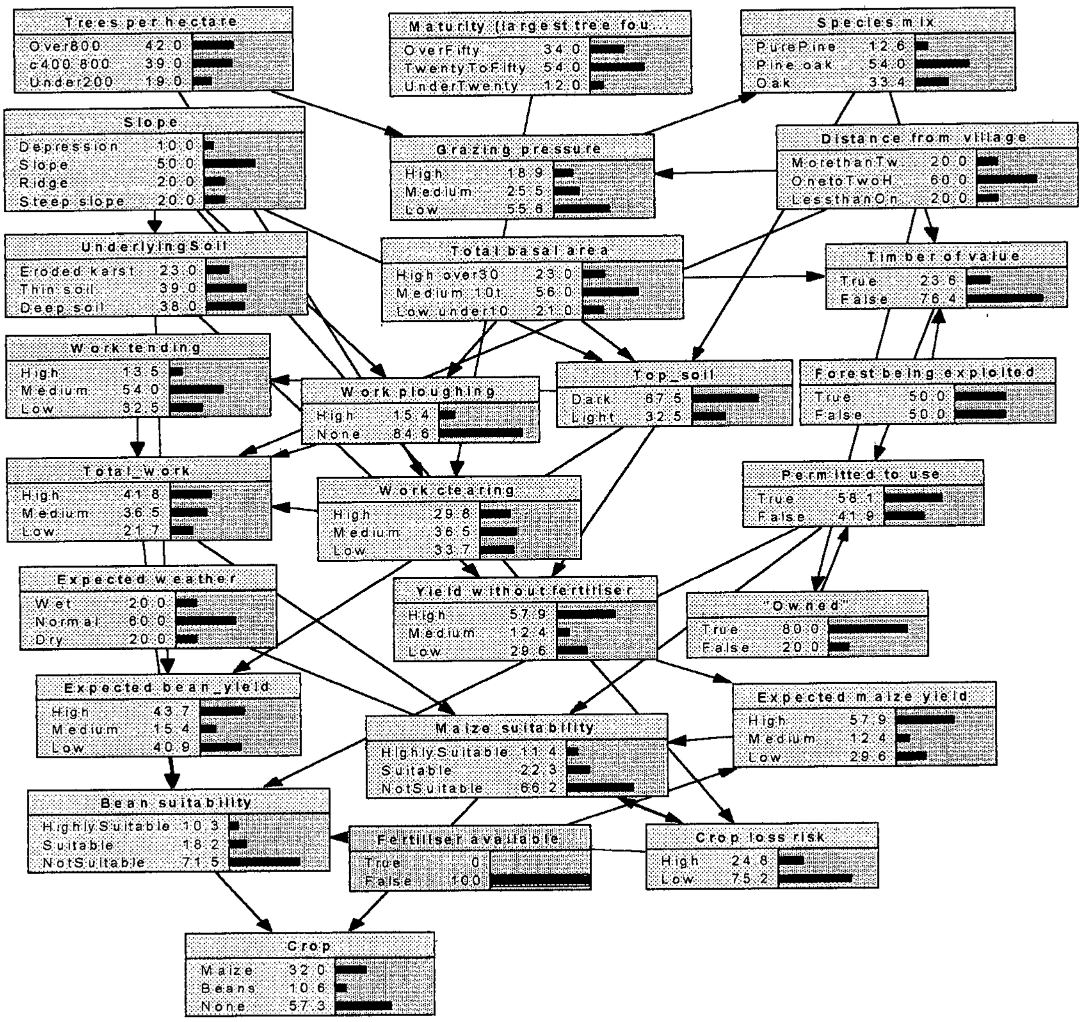
This result shows the value of the belief network in drawing out initially unexpected but useful conclusions, in this case that a run of poor years might cause the slash and burn moratorium to collapse, even if timber harvesting provides a motive for enforcing it. However uncritical interpretation of the sensitivities of belief networks is misleading. For example it might be assumed from table 5.2 that this years subsidy has little influence. This is in fact due to the fact that when the model was parameterised it was already known that the subsidy had been received by all farmers and the value at the node was set to 100%. Small changes then have little effect. Altering the initial parameterisation to make the probability of receiving the subsidy 50% results in a model which is highly sensitive to change at this node. One solution to this form of problem may be to analyse the model using a scenario in which all states of unconditional nodes are assumed to be equally likely. However sensitivity analysis will then only reveal information concerning the structural sensitivity of the network rather than the sensitivities of actual scenarios.

Table 5.2. Sensitivity of the node "In favour of ban" to changes at nodes with unconditional probability tables in a Bayesian network model of farmers decision making regarding enforcing a moratorium on all slash and burn.

Node	Mutual information	Quadratic score
This year's weather	0.0468	0.0141495
Migrant work	0.02478	0.0066267
Animals to sell	0.01007	0.002586
Stand composition	0.00562	0.0015732
Last years weather	0.00439	0.001264
Last years subsidy (PROCAMPO)	0.00245	0.0006865
Stand maturity	0.00012	0.0000343
This year's subsidy (PROCAMPO)	0.00000	0.0000004

The second network (figure 5.2) forms a small expert system for assessing the suitability of any single small patch of forest for slash and burn farming. It also may be interpreted as a tool for predicting the proportion of the forest considered suitable for clearance. This interpretation becomes especially valuable as the network has been parameterised using information regarding structural attributes from the forest inventory of the area (chapter 1).

Figure 5.2 Bayesian network diagram showing the connections between nodes and a representative parameterisation which predicts the probability of a given 1 hectare patch of the bienes comunales being considered a suitable site for slash and burn clearance.



Although the network appears complex, a number of nodes are used simply for the purpose of "bookkeeping" and simplifying further connections. Table 5.2 shows the sensitivity of the node "crop" to values at the other nodes. The ranking of the sensitivities reflects not only whether the plot is suitable for cultivation, but also which crop would be planted if cultivated. One interesting finding is that distance to the village has little influence on the farmers decisions for choosing a slash and burn plot. The decision is of course most sensitive to the constraining factor of whether the individual farmer has the right to use the plot or not, although this is seen at the local level and not determined by formal legal strutures imposed from without the community. Thus if land ownership follows a clear pattern this is reflected in the landscape. In the case of the *bienes comunales*, land "ownership" may have played a secondary historical role in determining which plots were actually cleared when pressure on available land was lower. This would have been especially true in the period before legal control over the bienes comunales was granted to the ejido.

Table 5.2 Sensitivity of the node "crop" in a Bayesian network model of farmers decision making in a slash and burn system. Note that the nodes with the highest sensitivities may be child nodes of others (i.e. they have conditional probabilities) and that decisions involved may be both whether the plot can be used, and which crop to plant. For example the slope and underlying soil largely influence the choice between beans and maize.

Node	Mutual	Quadratic
----	Info	Score
Allowed to Use	0.58207	0.1352886
Timber value	0.25984	0.0631992
Risk of crop failure	0.05631	0.0120574
Underlying soil	0.05491	0.0022372
Slope	0.03565	0.0026997
Forest composition	0.02922	0.0081283
Work tending crop	0.02397	0.0014966
Top soil quality	0.02363	0.0014133
Fertiliser availability	0.01875	0.0027777
Forest cover (BA)	0.00963	0.0005147
Work ploughing	0.00372	0.0001619
Tree density	0.00202	0.0005774
Likely weather	0.00124	0.0003491
Work clearing trees	0.00087	0.0000806
Distance from village	0.00055	0.0001556

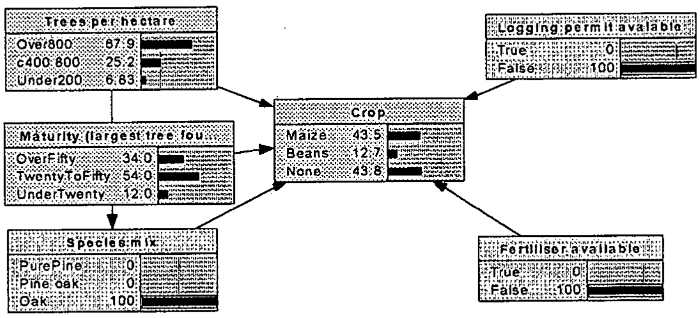
An alternative to automated sensitivity analysis for reducing the complexity of the networks is node absorption. Node absorption is a network transform which removes nodes from a belief network or decision network, and makes any necessary adjustments to the resulting network. Any inference yields the same results as before the nodes were removed. The local representation is changed, but the global relationships are not changed. The variables are "summed out", but the full joint probability distributions of the remaining nodes remains unchanged. This results in much more concise and easily communicable diagrams, though the underlying model remains as complex as it was prior to absorption. A series of reduced models may be produced from a single original model and used for scenario building exercises in which key nodes in the model are changed by external forcing functions. Key forcing nodes should normally be nodes with no or limited conditional probabilities. This feature offers considerable potential for interdisciplinary studies, as it may be used to expand

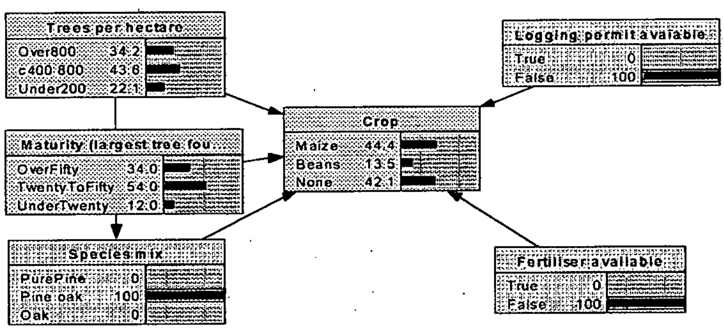
and contract the level of detail in a network as needed in order to produce modules which can be incorporated into a dynamic simulation or spatial modelling using GIS.

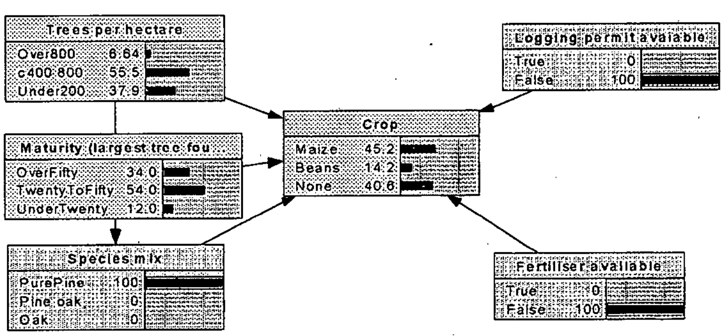
Figure 5.3 shows an example of this approach being used to form a simplified module which may be linked into a forest succession model based on the model shown in figure 5.2. After node absorption a series of scenarios are built. In the first three scenarios it is assumed that no logging permit is available and fertiliser is not used. The decision regarding whether a patch is suitable for slash and burn is almost completely insensitive to the species mix. In the second set of scenarios a logging permit is available and fertiliser can be used. The decision to slash and burn now depends on the species mix. Areas with pine would not be used, but mixed areas may. Note however that the decisions are probabilistic, the model does not result in a simple dichotomous rule and the underlying complexity of the situation has not been removed through node absorption. If the model were used for prediction the probabilistic nature of the model would result in stochastic noise around the deterministic signal. The remaining unknown factors contribute to the system variability and constrain the reaction of the model to the forcing factors. In Figure 5.4 node absorption is taken a step further to produce an extremely simple kernel that may be suitable for inclusion in a forest dynamic model. Probability of clearance is reduced to dependence on findings at the nodes representing fertiliser availability and tree basal area.

Figure 5.3 Demonstration of the use of node absorption. Five key nodes with unconditional probability tables are shown. A series of scenarios are built through assuming knowledge regarding their states. The model must be seen as predicting the probability of suitability for use of a randomly drawn 1 ha patch of land in the bienes comunales, not the whole stand.

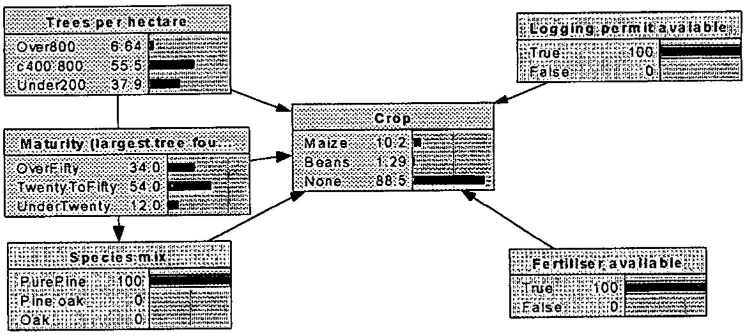
a) Scenarios with no logging permit and no fertiliser use.

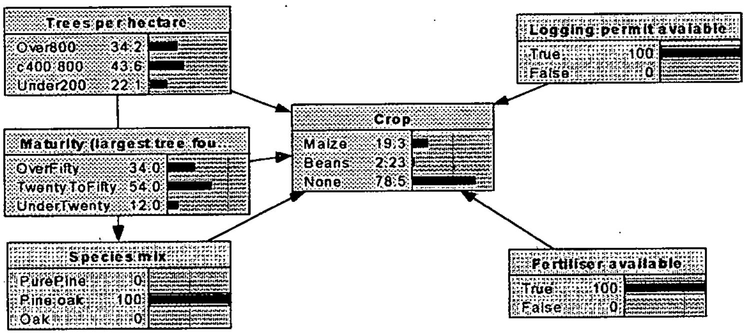






b) Scenarios with a logging permit obtained and fertiliser available.





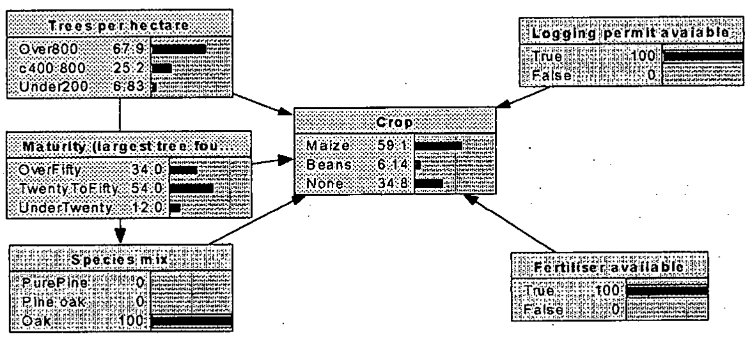
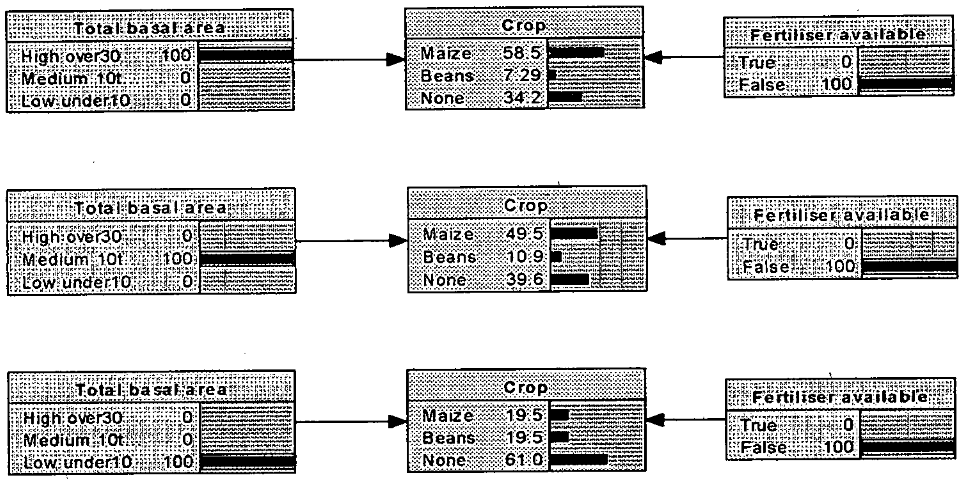
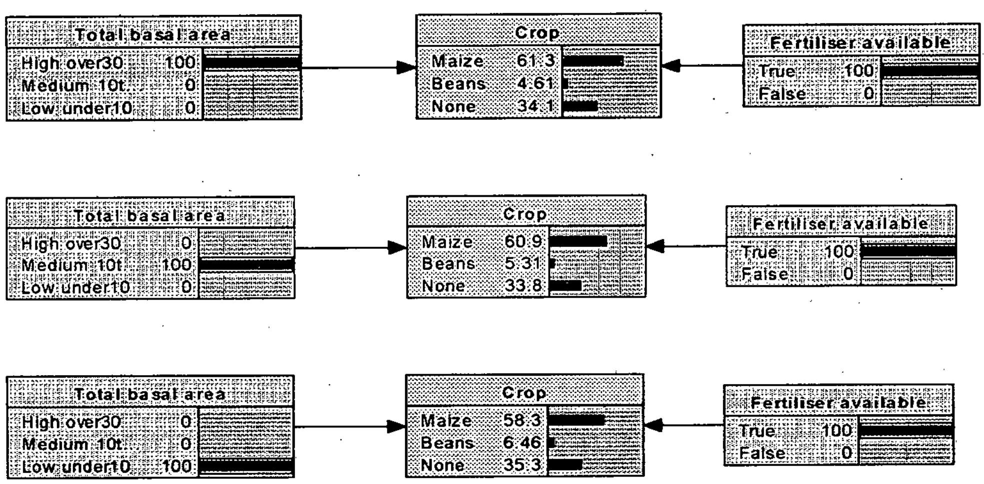


Figure 5.3 Demonstration of the use of node absorption 2. The model has been reduced to two key nodes with unconditional probability tables are shown. The effect of combinations of findings for these key nodes is shown.

a) No fertiliser used



b) Fertiliser available



Discussion

Methodological considerations

An inherent conceptual challenge must be faced when interpreting the results of Bayesian networks (Anderson 1998). Bayesian networks incorporate probability distributions, not frequencies. In some cases probability distributions can be usefully interpreted in a frequentist manner. For example it might be assumed that the network provides an estimate of the proportion of land that is suitable for slash and burn or the proportion of the community in favour of a decision on forest use. Nevertheless this natural interpretation, though useful is not formally correct. The information contained in belief networks is probabilistic. Interpreting the output of a belief network in this way could give a misleading impression of certainty. Binomial theory could be used to estimate error when single event probabilities are converted to frequencies but this would still underestimate the amount of structural uncertainty included in the network. Alternative methods for estimating error and uncertainty are available but they are advanced statistical topics that fall outside the scope of this work. The models would be best used to represent a real situation through using an individual based modelling approach involving iterated model building to avoid aggregation error (chapter 6).

An unexpected advantage of the approach was that Bayesian probabilistic reasoning seemed to be a very natural reflection of the Tojolobal decision making process. In one of the few published works on the Tojolobal culture, Lenkersdorf (1999) has investigated in depth the relationship between Tojolobal linguistics and the indigenous world view. His analysis stresses the importance of the "*inter subjectivity*" of the Tojolobal language in defining their view of other members of their community. For example the phrase "kala awab'yex" which could be translated as "I told them" is more literally translated as "I told them, they listened". It could be argued that a form of inter subjectivity is a feature of Bayesian networks.

Lenkersdorf also provides an interesting account of the decision making process used in communal meetings. [6]"*Suppose we are at a communal meeting convened to resolve some problem. Either the comisariado or one or other person puts forward the business to be discussed. On finishing the presentation all those present begin to talk simultaneously. Voices are raised. Some have questions, some answers, others want to convince the crowd of their point of view......Gradually the voices soften, and the meeting enters into a quieter* *phase. The last voice is silenced and a calm descends on the meeting. No one speaks and no one gets up. Finally the silence is broken. The president or elder announces .. ... we have thought and we decide.*" This decision making process has been witnessed on many occasions at Sonora. On no occasion was a vote or show of hands observed, nor do the participants state their final opinion. Stating a definitive position is regarded as divisive. Yet it is agreed that the majority position is known at the end of the meeting. Communal meetings are held at least once a month, and are always convened if any new concern which may affect the community arises. Thus all the male members of the community are constantly estimating the opinions and viewpoints of others. The process through which this is achieved is clearly rather well modelled by a Bayesian network. In effect the senior members of the meeting interpret the value of a single node which represents the majority position of the community from a large number of parent nodes representing frequencies of opinions and beliefs. This can be contrasted with a secret ballot in which the ultimate value of the highest level node is perfectly known after the vote is cast, but the reasons for the choice are not. This observation reveals why methods of assessing beliefs on sensitive issues through replicated questionnaires or replicated structured interviews are neither advisable nor effective. Asking individuals in private to express views on issues of importance is regarded with extreme suspicion. In neighbouring communities misunderstandings regarding the intentions of outsiders have resulted in expulsion (Konstant *pers comm.),* or communally imposed punishment (Taylor *pers* comm). Also, whatever privately held opinions may be, they will not be expressed if not in accord with a known majority view. Therefore a true picture of the degree of variation in the values of controversial beliefs is difficult to ascertain. This has proved to be an important barrier to implementation of rural development projects in the area (Taylor *pers* comm).

The belief network approach did overcome some of the delicate problems associated with alternative methods for assessing this issue. Nevertheless the inherent difficulties could not be completely bypassed. As an example, determining the values of a conditional probability table that represented the way in which conflicting influences might affect the farmer's final position was extremely challenging. In this case the information required demanded that questions be asked that could not be phrased easily in the readily understandable frequentist format without being understood as referring to deeper divisions in the community. The problem could be bypassed by using the researchers beliefs to determine the relationships, but this was considered undesirable. Initially attempts to illicit the information as a scenario

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[6] Translation from the original Spanish text

involving non controversial beliefs failed. The following format for the questions was first used;

"If a person (strongly, weakly etc.) felt that they needed more maize, but the community wanted to preserve the forest, how likely is it that the person would be in favour of the moratorium on slash and burn?"

This form of questioning was misunderstood. It was naturally assumed that holding a viewpoint contrary to the majority position would be a sign of a dissident political or religious alignment. However it was desirable to treat these factors as proximate causes and exclude them from the network structure.

An alternative phrasing was found to address the true underlying resource use question.

"If a person (strongly, weakly etc.) felt that they needed more maize, but the community wanted to preserve the forest, how likely is it that the person would be allowed to use the forest for milpa?"

In effect this is the same question, but this slight change allowed it to be interpreted as referring only to resource use issues. If a large enough proportion of the population are allowed to cut the forest then the moratorium collapses. If a person feels that there is no possibility of their view being accepted then it is unlikely to be expressed. Once the difficulty of establishing a conditional probability table for the highest level node was overcome a rather small network with a few easily parameterised nodes was found to be a useful predictive tool and summary of the system.

A common difficulty encountered when researching indigenous agricultural systems is misinterpretation of information. Norton, Pawluk and Sandor (1998) , reporting work with indigenous groups in the Southern United States stated "*sentences about some aspect of farming or natural ecology seemed inappropriate, only to be substantiated when the Zuni way of thinking and the unique landscape ecology were more fully understood*". The process of constructing Bayesian networks can help to clarify and draw out such issues. Researchers trained in the natural sciences may have a grasp of how processes influence crop growth, but do not have the contextual knowledge regarding how they apply in the area which is possessed by the farmers. There is a clear linkage here with some of the surprising results found in the vegetation data that suggests synthesis may be necessary which crosses scales of observation. The researcher may supply a knowledge of generalities, but the site specific situation demands local natural history understanding. For example, it was stated that the yield of beans was low from almost all plots with deep soil, but high from most plots with shallow soil. This appeared to be unlikely as a causal link, but a similarly unlikely correlative relationship was found in data from the natural vegetation of the area. On closer inspection the result could be predicted from consideration of the other properties usually associated with plots with deep and shallow soils.

It appears that the concept of shallow soils used by the farmers refers to sub soil depth, and thus rock outcropping, rather than top soil depth. Shrubby regrowth which is a source of potassium and other cations upon burning forms quickly on rocky slopes (chapter 4). Although rocky slopes give the appearance of having little agricultural potential, top soil and ash following burning does accumulate in fertile pockets between the rocks. Weathering of rock may also provide mineral input which is absent in areas with deeper sub soils. A good yield of beans is a relative term, yields are extremely low in the area. Because maize is the preferred crop beans would not normally be planted on the most fertile plots. These considerations combined lead to the correlative relationship expressed. The knowledge used in the network is thus contextual. It is clearly important that both the structure and parameterisation of the model is determined as much as possible by the accurate empirical knowledge being provided by the farmers. Nevertheless the use of a mechanistically consistent structure is advantageous for extrapolation and scenario building. Causal linkage is not required in order to incorporate information in a belief network, but purely correlative linkages can block further expansion of the network through deduction rather than induction.

A synthetic process of network construction was therefore found to be necessary in which both the farmer and the researcher provided some of the incorporated beliefs. The best solution found to this specific problem was to redesign the network linkages in order to separate soil depth and soil fertility. The set of conditional probabilities in the network then led to the conclusion that beans would indeed grow well in fertile, deep, well drained soil on a recently burnt plot if maize was not preferred, but such a combination is rarely found at the field site. The correlation was retained but the network became more extensible. The flexibility of the network approach allows such dynamic re-evaluation during the construction phase but this is challenging when the level of network complexity becomes non-trivial.

Belief networks offer an extremely powerful methodology for synthesising disperse information and forcing logical consistency. Simple graphical presentations are tautological qualitative constructs that cannot produce more information than used in their construction. In contrast belief networks become complex working models with emergent properties. However this complexity means that their construction and interpretation requires care. Researchers inevitably incorporate their own prior knowledge when building belief networks based on the beliefs of others. This is a potential weakness of the approach, particularly as the process by which this takes place cannot be analysed by a third party if belief networks are produced through focus group sessions rather than with reference to data from questionnaires. One manner of regarding the synthetic process is to take a Bayesian perspective regarding not only the network structure, but also the process of network construction. The process of synthesising beliefs which occurs during network construction could be regarded as analogous to the synthesis used in Bayesian statistical analyses and criticised on the same grounds (Edwards 1996; Dennis 1996). The researcher provides a prior conception of the network that is combined with the empirical knowledge provided by the farmers to produce a joint network. Unbiased, precise priors improve the precision and accuracy of the final result, biased precise priors lead to biased precise posteriors, imprecise priors whether biased or not have little effect on the posterior result but do not improve precision. Thus if the researcher has very precise prior beliefs the structure of the resulting network will be dominated by these beliefs. This is undesirable unless the researchers beliefs are based on expertise regarding processes rather than preconceptions regarding local patterns which are best understood by the farmers.

The extent to which synthesis has occurred should be made explicit. One solution is to insist that a network constructed using only the researcher's prior beliefs be provided for evaluation together with the synthetic network. This would permit external assessment of how much additional information has been incorporated. This was not possible in this study as a great deal of the synthesis had occurred as a result of two years of field experience prior to network construction. Field experience itself had led to a degree of shared natural history understanding with the farmers who provided the information for the network.

The two networks presented are initial steps in developing the approach. The networks may be extended in a range of directions. If used as tools in sociological or anthropological research a greater level of detail could be added in order to gain a deeper understanding of underlying mechanistic details leading to decision taking. The level of detail will be in part determined by considerations associated with the structure imposed by the relevant academic discipline. In the models presented variables have been defined as parent nodes because their values may be easily found. This is the most efficient rule for network construction but these nodes may become objects of investigation to be further disagregated if it is more important to know the reasons why they take a certain value than the value itself.

An important application may be in regional scale modelling of land use change. Belief networks may be parameterised from regional databases or GIS sources by exploiting their ability to learn from cases (Stockpile 1993). Although learning from cases offers a more powerful and objective means of parameterisation that eliciting beliefs alone, it does require detailed field work to be undertaken in a subset of communities in order to define the connections built into network structures. It is this element that distinguishes the belief network approach from more commonly used empirically based multivariate analysis techniques. Belief networks require knowledge of processes and structural linkages to be defined before parameterisation from cases, whereas factor analysis or path analysis (Sokal and Rolf 1995) does not.

If decision network modelling is to be extended into a tool for guiding management decisions greater attention needs to be paid to providing quantified documentation of the parameterisation process and to verifying and validating the output. In the case of the two models presented some knowledge regarding the values of the higher level nodes was available. For example it was known that the community recently decided to forbid slash and burn clearance. If the model suggested that this would not have occurred its structure and parameterisation would require revision. This process could benefit from the use of a more formalised procedure for model validation and optimisation. However this may not always be possible. The complexities and unique nature of the system being modelled places logistical limits on model validation. Improved quantification of structural uncertainty and improved methods for reducing bias in parameterisation are arguably more important goals at this stage in research.

In summary, these Bayesian networks are a form of expert system, in which knowledge is in part provided by the researcher and in part by the forest users. The level of field experience gained by the researcher will inevitably influence their reliability, but this criticism applies equally to any alternative methodology for formalising similar knowledge. Because belief networks can be constantly revised and updated as new information becomes available their construction should not be regarded as a static process, but used as platform for further research. This view of network building is compatible with the philosophy underlying Bayesian approaches to uncertainty in which hypotheses are refined rather than rejected and competing views given differing levels of credibility (Ellison, 1996).

Implications of the results

While deforestation patterns can often be accurately predicted by models based on land tenure and road development (Dale and Pearson 1999), the more complex patterns occurring within forests that may emerge in areas with a long history of communal land use are not predictable from cartographic information (Gilruth *et al.* 1995) combined factors such as slope and distance from settlement in a model designed to predict patterns of slash and burn clearance in West Africa. They concluded "*the model did not simulate the farmers' selection behaviour for topography and village proximity successfully*". This also appears to be the case in the study area. The key node in the Bayesian network was found to be largely insensitive to the node representing the distance from the village. Clearance for shifting cultivation, if no societal constraints are in place, is mainly determined by the state of the vegetation, with more mature sites being preferred over less mature sites . This suggests that iterative slash and burn farming results in a semi-closed system with behaviour partly determined by internal feedbacks, rather than an open system driven by external forces. It also suggests a conveniently simple deterministic model, even though the underlying system is far from simple and considerable stochastic variability around any deterministic signal would be needed to realistically model it.

The poor agricultural performance of the soils of the Tojolobal region is notorious. It has been suggested that the land was ceded to the indigenous population because it was of such low intrinsic fertility (Lenkersdorf and Van der Haar 1998; Lenkersdorf 1999). Maize grain contains 1-2% N, depending on variety and growth conditions. The extremely low, < 10% nitrogen use efficiency contrasts with an estimate of global NUE for cereal crops of 33% (Run and Johnson 1999). The most important factor responsible for recent alterations in patterns of forest use has undoubtedly been the introduction of nitrogen based fertiliser to the region. Without nitrogen input neither permanent nor short rotation farming could be attempted in the poor soil of the area. Farmers are unanimous in their accounts regarding the dramatic change that took place when chemical fertilisers were first used. Even so traditional slash and burn clearance of mature forest remains an attractive option, perhaps because loss of organic matter has already resulted in a very low cation exchange capacity in permanent plots and a poor response to fertilisation. Economic analysis suggests that in the absence of restraints or external inputs slash and burn would still be the preferred method of farming.

The economic based model of the farmer's decision-making processes may be a poor predictor of the observed situation because it is unclear whether farmers actually aim to optimise yield, or simply to provide enough maize for their own use. The Bayesian network approach only partially confronted this problem, but did provide insight. Both the actual situation and the predictions of the Bayesian networks differ from that predicted by the economic model. No new slash and burn plots have been cleared since 1997, though some recently cleared secondary growth has been reburnt. This is due to the communally imposed moratorium on the practise aimed at preserving timber resources. Although the moratorium is respected, it is not popular among all members of the community, although dissent is not expressed directly. Slash and burn clearance had declined to a very low level in the 1980s but was increasing in the period immediately prior to the community applying for a permit for legal timber extraction. The proximate causes may have been a breakdown in community unity due to the political turmoil of the time, but the state wide moratorium on timber sales imposed between 1990 and 1994 may also have contributed by reducing the perceived value of the forest. During this period internal division in the community also led to inequalities in the distribution of subsidies for buying fertilisers. There is a potential for serious conflict over resource use issues in all communities with political and religious divisions.

The economic model was found to be sensitive to soil fertility. If valley soils were inherently fertile, hill slopes would be reserved for timber and fuelwood production until population pressure led to all available valley plots being cultivated. Only a small proportion of the valley land in Sonora is cultivated. Long rotational slash and burn farming is a feature of poor soils, but is less likely to have been practised recently in areas where comparatively rich soil is available for use. This could be important for understanding extant patterns of forest cover throughout the region. Areas with intrinsically low fertility are likely to have extensive, superficially unbroken forest cover which on closer examination are found to be a complex mosaic of patches in differing stages of development which have arisen through historical disturbance by slash and burn. However, where richer soil allows permanent farming to develop, forest cover may be more markedly discontinuous. In such a situation each fragment may be much more heavily exploited for timber and fuel wood than forests growing on poorer soils, but may develop without cyclical felling. Generalisation from one type of forest to another is misleading because of these differences in disturbance regime. There is not a single model applicable to the whole of the highlands of Chiapas. The nature of the forest on any given hillside is influenced not only by the soil type on which it forms, but also on the soil type in its neighbouring valley. Conclusions drawn from other investigations of forest usage in the comparatively densely populated, more fertile areas of the central highlands will not apply to the situation at the field site. Identifying whole landscape patterns from remotely sensed data will help to predict forest structure if the variability of the agricultural context in which forests survive is taken into account.

Some confirmation of the farmers' comments can be drawn from direct observations of the site. These have revealed that timber harvesting has affected a much smaller area than initially assumed from a superficial interpretation of its structure. Disturbance caused by timber harvesting appears to explain little of the current compositional or structural attributes, beyond the absence of large pines in more accessible areas. Fuelwood collection is also likely to have had little direct impact on forest structure (see the supplement to this chapter). Forest structure does however appear consistent with the assumption that unconstrained slash and burn farming had occurred prior to fertiliser introduction. Fewer large trees are found at this site than in woodland fragments in the central highlands.

Conclusions

Decisions regarding slash and burn clearance were found to be made at two levels. Patch level impact may be determined by individual farmers' personal criteria for clearance. These criteria are complex and variable and the belief network presented includes only a subset of possible considerations. Any further simplification of the process of decision making will still only include a small fraction of this total variability. Nevertheless, if no external considerations or constraints are included a useful generalisation that may be used for parameterising disturbance regimes used in forest dynamic models may be that plots with the highest tree basal area were most desirable for clearance under the long rotation historic slash and burn regime, particularly if topography is reasonably homogeneous. More recently constraints have been imposed on site choice by considerations related to community interest. Thus although the most attractive sites for an individual to clear for temporary use are semi mature or mature forest these sites are now more likely to be regarded as a potentially valuable community resource due to the timber they contain.

There are also linkages between forest structure and composition and recent history of usage. The presence of valuable timber has temporarily halted slash and burn clearance. The relative proportion of pine in the species mix is an important determinant of forest value, as is stand maturity. The models show that complex feedbacks between the ecological processes of forest formation following disturbance and the decision making processes which lead to disturbance are an intrinsic part of the system. These results are essential for interpreting forest structure and modelling forest change. They provide an explanation for many of the contradictory observations reported in the previous chapters.

5.2 Estimating the impact of fuelwood consumption

Introduction

The previous section placed the emphasis on slash and burn farming as the major disturbance at the site. However it may be argued that the potential effect of fuelwood collection has been ignored. The only previous estimate of fuelwood consumption for the area is given by Montoya-Gomez, (1995) who reports that a tercio of fuelwood which measures 0.35 m^3 is used per family per day. This figure which is repeated by Alavarado (1995). This suggests that fuelwood gathering could be the major disturbance causing factor. In order to test this a small study was conducted to produce an estimate of daily fuelwood consumption. Observations on the pattern of fuelwood gathering at the site are also included and modelled as a Bayesian network.

Method

The daily fuelwood consumption of three families was measured on ten separate occasions in November and December 1999. Households were visited before the fire was lit and all pieces of wood that were used during the day were measured. The cross sectional area (including bark) and length of each piece of fuelwood used was recorded together with the reason for its use (cooking or warmth).

Results

Despite the fact that the study was conducted during the coldest part of the year, very little of the fuel wood was used for heating. Most fuel is used in a single long lasting fire, which is lit early in the morning (6.00 a.m.,) and used to boil maize for tortillas and to cook beans. Later in the day a small additional amount of fuel is added to the embers in order to cook the midday meal and heat the tortillas. 9.3% of the fuel (by volume) consisted of pine which was used for starting the fires. This quantity included small quantities of the resinous pine wood "*ocote*". Ocote is produced for the purposes of lighting fires through stripping the bark of mature pines and lacerating the underlying timber. The trees respond by producing resin which is absorbed by the wood.

All the oak fuelwood used during this period was obtained from *Quercus segoviensis*. However *Quercus crispipilis* is also commonly used as fuelwood and no preference between the two species was expressed.

A notable feature of the statistics on fuelwood use was the lack of variability in the quantity used from day to day and between families. This suggests that the women responsible for tending the fire are careful in their use of the resource. No significant difference was detected between the families (ANOVA $p>0.2$). The pooled estimate for fuelwood use, assuming that the small data set could be treated as a random sample, had only a small associated error. The mean daily usage was 1.67×10^{-2} m^3 per day +- 3.6×10^{-5} (95% C.I.). The uniformity in the daily quantity used led to an unexpectedly high level of precision being obtained from a small sample. This level of precision does however only estimate the fuelwood use by the three families incorporated in the study. Other sources in variability in usage between families require further investigation.

Table 5.3 Daily consumption of fuelwood by three families in the village of Sonora during 10 days in the months of November and December 1999.

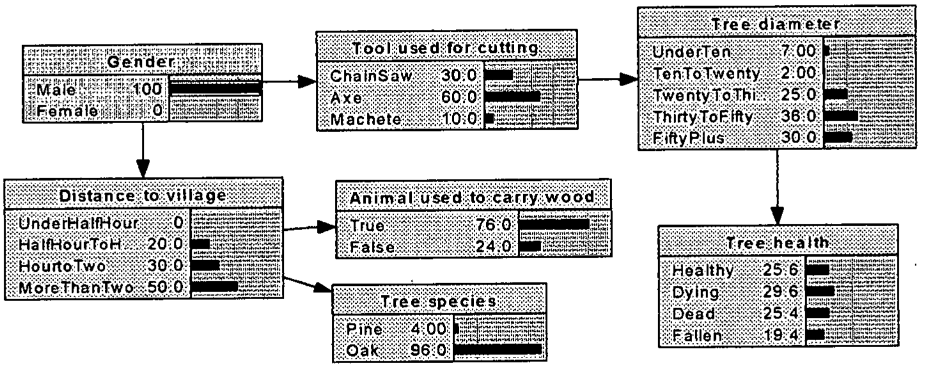
Family	Family size	Days	Mean daily usage (m^3)	Std dev	95% C.I	Mean Number of pieces
Jose Luis Santiz Gomez	7	10	0.0169	0.0013	0.000894	16.5
Arturo Santiz Gomez	10	10	0.0157	0.0007	0.000481	18.3
Francisco Lopez-Gomez	10	10	0.0172	0.0018	0.001238	17.5

Fuelwood gathering at this site is a purely subsistence activity. No fuelwood or charcoal is collected for sale. Day to day fuelwood gathering is usually carried out by women who carry the timber on a head strap, but may also use donkeys. Women either collect fallen branches or cut small diameter trees with a light machete. Green wood is undesirable as it cannot be used immediately and is not easily carried. A large proportion of the large diameter fuelwood is collected by men using chain saws, axes and animals (usually donkeys) to carry the wood back to the village. This activity is carried out when no other work is available, often in the winter months. Fuelwood gathering by men usually involves felling larger trees. Nevertheless most trees chosen are either dead or senescent. Felling large live trees is prohibited by the rules imposed by the community but occasionally occurs, although it is normally associated with milpa clearance.

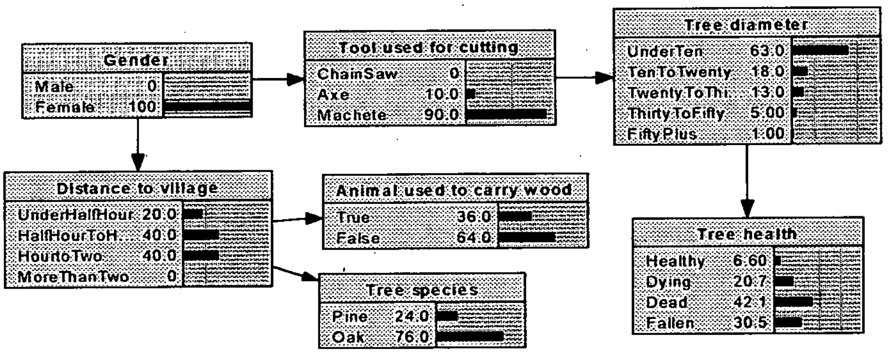
Figure 5.4 is a concise summary in the form of a belief network information gathered from interviews and notes taken during two years of field work at the site. The proportions shown in the diagram should be interpreted as estimated figures rather than measured data, being calculated from a series of conditional probability relationships. It shows how the pattern of fuelwood gathering differs between gender. There is an inconsistency which is known to researchers in the area and has been reported to arise in other indigenous communities when questions are asked regarding fuel collection (Ramirez-Marcial pers comm). Direct observations show that over 90% of the fuel used is collected by women from small dead trees. However interviews with farmers would lead to the conclusion that most fuel is cut by men from larger trees. Here direct personal observation has been used to attempt to avoid this inconsistency, but the diagrams must be regarded as a subjective model.

Figure 5.4 Bayesian network showing the connection between the gender of the fuelwood collectors and the choice of tree cut for fuel. A large, but undefined, proportion of the fuel used in the village is collected by women.

a) Fuelwood collection by men



b)Fuelwood collection by women



Photograph 7. Fuelwood collection by women of the village of Sonora.

Discussion

The results do not agree with previous reported figures for fuel wood usage in the highlands. The amount of fuelwood observed to be used in the village is an order of magnitude below the figure reported by Montoya-Gomez (1996). The term *tercio* as used by the inhabitants of Sonora refers to the amount that can be carried on a head strap. The density of oak fuelwood varies depending on the degree of moisture it contains. The density of dry oak fuelwood (n=50 pieces) was measured at 0.69 +- 0.09 g cm^{-3} including bark. Thus 0.35 m^3 would weigh approximately 200 kg. This raises serious questions regarding the basis of Montoya-Gomez's estimate. Montoya-Gomez suggests that a family uses a "*large tree*" every ten days. Based on the results obtained in Sonora a large tree (45- 65 cm diameter) providing 0.7 to 1.5 $m^3$of fuelwood would meet a families' needs for at least two months.

Montoya-Gomez's estimate would place fuelwood consumption of the 73 families in the community at 9,325 m^3 p.a.. The data suggest an annual consumption of 442.3 +-9.67 m^3. Unfortunately the error range attached to this figure is too narrow as random sampling from the entire population of fuelwood users in the village was not carried out. Wood density may also vary. Nevertheless widening the margin of error beyond the statistical estimate to allow for errors due to the weak survey design translates the figure for annual fuelwood consumption into an estimate of between 200 and 400 tonnes of dry biomass. It is unlikely that the true figure falls outside this range. This is well within the productive capacity of the 1,027 hectares of forested communal land (chapter 1). In addition to the communal land there are areas of pine-oak woodland within the 2067 hectares of the ejido. Fuelwood shortage is not a problem and natural mortality can currently meet all immediate needs. No concern was expressed by any member of the community regarding fuelwood supplies. Fuelwood gathering is not reported as having become more difficult in recent years.

Because the forest had suffered an extensive ground fire prior to the period in which observations were taken almost all the fuelwood that was observed to be collected was taken from dead or dying trees. Such timber may not always be available in such quantities. However it was also reported that a large proportion of the fuelwood is usually gathered from slash and burn sites. Slash and burn leaves much of the wood charred, but otherwise available for use. It appears that most fuelwood collection for subsistence needs does not cause disturbance to large growing trees, or when it does it is combined with slash and burn for agricultural purposes in order to exploit canopy opening. This observation clearly cannot be generalised to communities nearer to large population centres where fuelwood is cut for sale or charcoal production.

Fuelwood collection may however play a secondary role in the disturbance regime. The collection of large woody debris would be expected to reduce the severity of forest fires. It has been reported that fire induced mortality in Northern Mexican pine forests is considerably lower than that found in comparable forests in the United States, possibly as a result of reduced fire intensity as a result of traditional fuelwood usage (Savage 1997)

Conclusion

Fuelwood consumption was found to be low considering the large quantity of available material. Women are surprisingly frugal in their use of the resource when cooking, due perhaps to the work involved in gathering wood. Previous estimates of fuelwood use seem to have been based either on a consideration of commercial exploitation or a mistaken conversion of units. Fuelwood gathering alone cannot explain the disturbed nature of this forest site. Subsistence fuelwood usage, as distinct from commercial exploitation for sale to the populations of urban areas is unlikely to be a direct cause of deforestation. The impact of fuelwood gathering can be examined in more detail by incorporating its effects in the simulation model of forest dynamics. Further work is required to measure the regional scale consumption of this resource.

Section 3: Simulation of the dynamics of pine-oak woodland: Introduction

The previous part of this work documented some of the spatial and temporal patterns of forest development found at the field site and investigated the disturbance regime. It demonstrated that a great deal of apparently "random" variation exists at the site. Slash and burn disturbance of the forest is spatially and temporally localised in its direct impact, although ultimately it has large-scale effects. Could local variability have been predicted from a knowledge of underlying process? Is the variation random, in the sense that it can only be treated as stochastic "noise", or is the variation an inherent part of a larger system? In other words, could pattern at a higher level of organisation be predicted from interactions occurring at lower scales (O'Neill 1989; Levin 1991; Levin 1992; Allen and Starr 1982; Allen and Hookstra 1994)? If a framework can be built which predicts the heterogeneity that was found in the case study, then wider generalisations regarding change in other pine-oak woodlands may be made.

The aim of the following section of this study is to assess whether a representation of the dynamic of the system can be produced based on linkages between scales (Bascompte and Sole 1995). It is postulated that stand level structure could be predicted from knowledge of the response of patches of forest to disturbance. It is further proposed that such knowledge can be used to simulate novel scenarios, extract generality from the particular and form a basis for predicting patterns of forest change in response to disturbance. This section consists of three chapters.

In the first chapter a framework for modelling forest change based on the properties of individual trees is reviewed. The method used to build and parameterise the model is presented. The model is shown to be sensitive to decisions regarding its structure, and the implications of this are discussed.

In the second chapter the relationship between the model and the system of interest is analysed. Scenario building is used to address the central questions involving forest change which have motivated the research.

In the third chapter of this section the model is simplified in order to investigate ways in which it may be extended to address some broader questions.

Chapter 6. Design of an individual based forest simulator

1. Individual based modelling: A review of concepts and applications

The basis of individual based modelling

An increasingly common method of predicting the response of patches of forest uses knowledge of the properties of the trees that compose them. Individual based approaches have a long history in forest modelling. The earliest such model to successfully capture interactions in a mixed forest was the JABOWA "gap" model (Botkin *et al.* 1972), although Ek and Monserud's (1974) FOREST model was developed simultaneously and in many respects foreshadowed the development of more complex spatially explicit simulators. The term individual based model (IBM) was formalised by Huston *et al.* (1988). Individual based modelling acknowledges two fundamental biological principles. The first is that individual organisms are all potentially distinct due to genetic or environmental influences. The second is that interactions between individuals are inherently local. Sedentary organisms such as trees are influenced mainly by other nearby sedentary organisms. IBMs can be contrasted with some other detailed forest simulation models in which the numbers of trees in size classes is used as a state variable (Bossel and Krieger 1994; Vanclay 1994)

Representing individuals

The simulation of many individual organisms can place considerable demands on computational resources (Bugmann 1996). It also leads to detailed output, which requires additional routines to produce automated summaries. However the equations used by IBMs can be relatively simple. This simplicity arises from the fact that individuals usually can be represented quite naturally as having a limited set of key properties which determine the outcome of a limited set of key processes (Judson 1994). The link between processes and properties can often be expressed as mathematical equations with a small number of terms or as logical rules that apply to specific situations arising during the lifetime of an individual organism. Although the formal representations of processes which change individual's properties may be intuitive, when they are applied iteratively to many individuals over time even apparently simple IBMs can generate phenomenological realistic and often complex behaviour (DeAngelis *et al.* 1986; Huston *et al.* 1988). More highly detailed individual tree models are not usually IBMs *sensu* Huston (1988). IBMs are *based* on individuals. They are not models *of* individuals (see Deutschman Levin and Pacala 1995).

Representing individuals' interactions

If a suitably simplified core model, which represents an idealised individual, can be designed, the next step in individual based modelling is to produce a structure that links these individuals and allows interactions between them to be modelled. There are two key questions at this stage. 1)How much "*relevant detail*" (Levin 1992) is required in order to produce a realistic structure? 2)Do arbitrary decisions made for convenience or computational tractability alter model behaviour? Contemporary debate regarding forest models has revolved around whether the precise spatial position of an individual tree must be known in order to produce realistic behaviour (Pacala and Deutschman 1995; Deutschman *et al.* 1997). Descriptions of forests as a mosaic of gaps and nongaps (Watt 1925; Watt 1947; Shugart 1984, Hubbell and Foster 1986; Whitmore 1989) suggests a natural framework for modelling localised interactions. A gap or patch model assumes that while spatial heterogeneity is important in structuring forests, sufficient detail can be captured by dividing the stand into arbitrarily small units within which the position of the modelled individual is unimportant.(Botkin *et al.* 1973; Shugart and West 1980; Shugart 1984; Urban *et al.* 1991; Solomon and Cramer 1993). The term patch model is in many ways a more appropriate description of the FORET-JABOWA class of models, but the use of the description gap model is now so well established that it will be retained in the following discussion. Gap models can be contrasted with a more detailed form of spatial representation in which the precise position of every tree is known. The best known recent model of this type is SORTIE (Pacala *et al.* 1996), but explicit tree positions have also been used in models by Luan (1994) and Young (1998) among others.

Criticisms of gap models

Gap models have been found to be sensitive to small changes in parameters which may be difficult to measure directly (Leemans 1991). Attention to calibration of the underlying growth model is a requirement if successional models are to play a role in guiding management decisions. When IBM simulations have been validated against data they have often been found to under perform when compared with methods of aggregated yield projection developed for forestry applications (Desanker, Reed and Jones 1994; Lindner

Sievanen and Pretzsch 1997; Yaussy 2000). Alterations have been suggested in order to improve gap models' representation of growth (Moore 1989), linkage between growth rates and the light environment (Smith and Urban 1988), allometry (Lindner, Sievanen and Pretzsch 1997) gap size (Smith and Urban 1988) and temperature response (Fischlin Bugmann and Gyalistras 1995; Bugmann 1996). However the extent to which these changes can improve the model's stand level performance remains unclear. When a contemporary challenge to the gap model paradigm, the spatially explicit simulator SORTIE (Pacala and Deutschman 1995; Pacala *et al.* 1996) was developed greater attention was placed on calibration than had been previously attempted (although see Ek and Monserud 1974). A stated aim of the SORTIE approach was to improve the linkage between direct observation and model structure (Kobe 1996; Deutschman 1999). These criticisms suggest that if FORET-JABOWA type models are used for site specific prediction a great deal of attention should be focused on the model's empirical base.

Linking IBMs to site specific data

Gap models were originally designed to be highly general representations of forest systems. The weak empirical basis of some of the parameterisation used for gap model applications may have arisen either as a natural consequence of a search for simplicity and generality (Acevedo Urban and Shugart 1996; and see Shugart 1998) or because detailed information required for site specific parameterisation was not available (Botkin 1993). This led both Dale, Doyle and Shugart (1985) and Liu and Ashton (1995) to draw distinctions between models used for investigating forest succession and those used for yield prediction when reviewing a range of forest models. In the current study, change in species composition is of principal concern. This suggests that a forest succession model would be the most appropriate tool. However , despite differences in the temporal scales at which questions regarding yield and succession apply, drawing a distinction between the two types of model appears artificial. Common questions arise regarding natural forests. Successional developments may be closely linked to the yield of desirable species (Vanclay 1995). Even if improving yield prediction is not the question which motivates research, if a model does not accurately predict forest productivity, it is unlikely to accurately reflect the phenomenon of successional change. It has been suggested that the poor empirical performance of gap models is not necessarily the result of weaknesses in the form of the equations used. It seems to arise mainly because the scope of applicability of any single model is more limited than was once thought (Bugmann *et al.* 1996). If this is the case, then difficulties can be tackled through attention to the process by which models are linked to site specific data.

Hybrid models

IBMs can be linked to more aggregated models at the whole system level (Friend, Running and Shugart 1993). Such models are designed to answer rather different questions to those addressed by the more restrictive framework of purely individual based modelling. In these models short term stand level change is often of greater interest than long term successional change. The individual components in the model are used to produce contextually appropriate inputs into system dynamic models and may also receive a degree of top down control from the whole system model (Makela *et al.* 2000; Green, MacFarlane and Valentine 2000). Makela *et al.* (2000) discuss circumstances in which using system level empirical information in a process based model may be necessary to improve accuracy. This could be some measure of gross productivity at the stand level. If the maximum basal area recorded for the forest type under consideration is available, it might be included in the model as a constraining parameter. This example of a whole system constraint is a feature of JABOWA-FORET gap models, though it has not been emphasised in published accounts of their structure. The difference between pure IBMs and hybrid models may lie mainly in the level of detail used to simulate top down constraints.

Constraining and optimising models

Imposing some top down control on IBMs can be useful for forestry applications as it results in models which robustly reproduce known growth patterns while realistically responding to forcing factors such as stocking levels, fertilisation, pollution or climate. However if system level attributes constrain the behaviour of an IBM, the model could have weaknesses for basic research applications. Many models built for research purposes aim to use only lower level information in order to fully investigate the ultimate consequences of changes in underlying processes. Constraining such models' behaviour could lead to uninformative tautology, especially if the ability of a model to reproduce known successional endpoints is used as a validation criteria. Nevertheless not all forest research asks questions regarding only underlying biological processes and not all forest simulations are allowed to run to endpoints without disturbance. Incorporating some constraints need not prevent a model from producing informative dynamic behaviour. Accurate reproduction of the phenomenon of interest is a natural criterion against which a models' utility is judged. Where this is of prime concern, as in the current study, it may be desirable to use some available prior information regarding stand level properties in order to improve the models' accuracy and realism. If such a procedure is followed it should be documented. Calibration data should remain independent from data used to assess a model's performance. If this independence is not achieved the model would only reproduce prior knowledge, as does an expert system. The procedures used will be discussed in some detail when model parameterisation is described.

The application of gap models

Few applications of gap models have been reported for regions beyond the geographical limits for which the original software has been developed and parameterised. Shugart (1998) tabulates 37 published variants on the gap model structure. Of these, 25 have been applied to forests found within the United States, 5 in Europe, 5 in Australasia, and 3 in Africa. Neotropical forests are undergoing extremely rapid change, yet the lack of application of the potentially powerful gap model approach to investigating forest dynamics in the region is apparent. A gap model produced for Puerto Rican forests did successfully predict the effects of disturbance by hurricanes (Doyle 1981). However the application of gap models to poorly studied areas such as the African Miombo ecosystem appears to be have had more limited success (Desanker 1996). It may be that gap models are too data intensive for preliminary research situations where data from time series is not available (Liu and Ashton 1995).

This perspective is however not shared by an originator of the gap model paradigm. Botkin (1993) describes how parsimonious principles regarding data needs were applied to the process of model formulation when JABOWA was being developed. Gap model parameterisation was clearly intended to be achievable without detailed knowledge. In the same work the need to use realistic models rather than precise but unrealistic empirical relationships which cannot be extrapolated beyond their spatial and temporal bounds is strongly emphasised. Thus, rather than assuming that lack of detailed knowledge makes all prediction impossible, Botkin takes a more optimistic viewpoint. Insufficient knowledge makes precise prediction impossible. But prediction regarding forest change may have to be imprecise. The challenge lies in the development of protocols which do not lead to model predictions which are more precise than can be justified on the basis of limited knowledge.

The commonest operational barrier to extending an existing model's field of application is that recent extensions of the IBM approach have shown the "*inevitable tendency to clutter a model with the particular attributes of a favourite field system*" (Pacala 1997). Available software contains "hardwired" assumptions concerning specific species and forest types(Bugmann 1996). Schrader-Frechette and McCoy (1994) warn of dangers when computer models are applied to case studies. They suggest that the use of externally supplied software leads researchers to "*rely on computer results without understanding all the associated hypotheses and assumptions built into the software design.*". This study therefore follows the protocol recommended by Pacala *et al.* 1997. Software design and data collection were carried out simultaneously as complementary activities. This approach allowed software to be built which met limitations imposed by available data. Thus the model and the data combined represent a single statement regarding the state of knowledge on the system under consideration. Where uncertainty arose due to unavailable data or inherent variability the simulation was adapted accordingly. Designing and testing software permitted a detailed evaluation of hidden assumptions in model design and allowed data collection protocols to conform with the model's structural assumptions. The software was based loosely on the Fortran code for FORET included in the appendix of Shugart (1984). However the code was redesigned in order to follow a contemporary object oriented structure.

2. Implementation of the gap model

Introduction.

The software addresses the following question. "How do the structural and compositional characteristics of pine-oak woodland respond to differing anthropogenic disturbance regimes." The software allows the comparatively simple successional patterns in this species poor system to be investigated in depth and produces quantitative output that could be suitable for guiding management decisions. For the purpose of the model, pine-oak forest is defined as vegetation cover in which members of the genera *Pinus* and *Quercus* of all size classes represent over 90% of the total basal area. Thus the software can be applied to predict the dynamics of the canopy forming vegetation present at the majority of forested sites in the highland of Chiapas between 1500 m and 2400 m a.s.l.The dynamics of vegetation classified as secondary or non forest on physiognomic grounds is not excluded. Abandoned milpa, pine savannah, or resprouting oak coppice may all be simulated using the software.

A distinction must be made between the scope of the modelling framework provided by the computer program, and the scope of the locally parameterised model presented as an example for this particular case study of pine-oak dynamics. The computer program could be parameterised for other sites using comparatively easily available measures of tree growth and disturbance regimes. However, once parameterised the model becomes site specific. Thus although the model results may provide insight into the generalised question of the dynamics of pine oak woodland in the region, extrapolation of the specific findings presented here to the regional level must be approached with caution.

Model design

Treatments of the structure of gap models are provided by Shugart (1984) and Botkin (1993). These works provide detailed discussions and justifications for equations used which are common to many gap models. The reader is referred to Botkin 1993a for a particularly detailed defence of the gap model concept. Rather than repeating this treatment, the novel features of the model and the methods used to overcome challenges associated with site specific parameterisation are discussed in more detail here. Unless otherwise stated equations used for growth, allometry and light response have followed Shugart 1984. Equations and rules not referred to in the main text may be found in the annotated Visual Basic code included in the appendix.

The program differs from the classic JABOWA-FORET implementations in the following respects.

1. Object oriented programming techniques were used.
2. An interface linked to a relational database (MSAccess) was produced for parameter input and data storage.
3. Probabilistic error was incorporated.
4. Parameters were linked to data taken from a single site

Object oriented programming

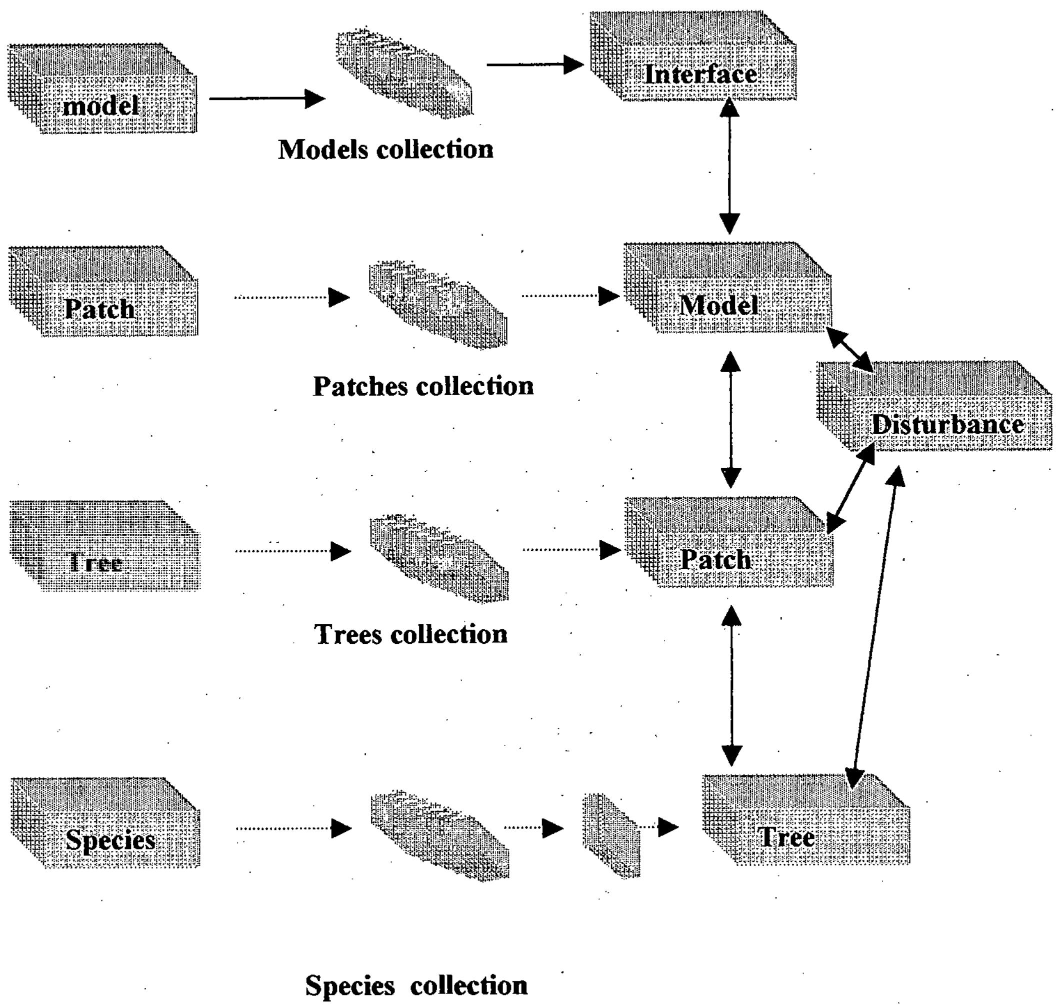
Large models must be divided into manageable parts or modules. A natural way of achieving this is to use divisions that correspond to recognisable entities belonging to the system being modelled. Object oriented programming (OOP) offers a formal structure which enables such modularity (Rumbaugh *et al.* 1991). Until recently OOP was usually implemented using the low level technical programming language C++. C++ is a powerful and versatile language for commercial application development, but development in C++ is slow due to the large number of instructions required to carry out each task. High level languages which permit rapid program development such as Delphi and Visual Basic (VB) have now begun to implement a subset of OOP features. Abstraction and encapsulation are achieved using class modules in VB. VB was principally developed as a tool for programming commercial databases. A feature of the language is its automated linkage with MSAccess databases running under MSWindows. This was used during the development of the model as a natural way of linking the model both to species parameter tables and to data obtained from a forest inventory.

In OOP terminology modules are known as classes. Variables defined within a class are known as properties and the sub routines and functions of a class are known as methods. An object is a specific instance of a class. While it shares the property and method definitions with all other instances, the values its properties take are unique. Objects are held in collections and can communicate with each other through a common interface of "*public*" properties and methods. Under OOP a sequential program structure is largely substituted for a modular design (Mladenoff and He 1999). A few control routines must be used to trigger sequences of methods, such as those involving the yearly changes in a patch. Complex nesting of control loops which makes code hard to follow is greatly reduced. Program design and testing is largely a bottom up process.

The use of OOP leads to a natural and intuitive program structure for patch models as shown in figure 6.1. Each species is an instance of a species class, each tree is an instance of a tree class and each patch an instance of a patch class. All multiple instances of a class are held in collections. A tree object can refer to properties of a unique species object which is incorporated within it when initiated. In C++ this feature could be achieved through class inheritance, but VB, which is still evolving as a language, did not support this OOP feature when programming began. Private properties of trees and patches are altered dynamically as the model runs. Once instantiated a tree object "grows" according to the equations incorporated in its growth method. Some of the information used by the growth method may be passed to the tree by the patch object which holds the collection of trees to which the tree belongs. Properties of the patch object can be calculated using the properties of the trees held in its tree collection. Mortality and establishment are modelled by removing or adding new tree objects to a patch's tree collection. A disturbance object can receive information concerning patch or individual tree properties and trigger mortality when appropriate conditions are met.

VB has some advantages as a language for rapid model implementation for smaller autonomous research projects. Because it is a high level language which incorporates a large number of tools for building graphical user interfaces (GUIs), suitable provisional GUI's can be built very rapidly in order to test and debug objects under development. VB is a flexible language that may be quickly learnt and applied by non specialists. The language has grown rapidly in power over recent years. Some criticisms of VB as a serious development framework (Young 1998) are no longer appropriate. For example, contemporary versions of VB now produce compiled, rather than interpreted code. While not being optimised for speed, VB code compilation is robust. OOP modularity does allow VB code to be easily substituted by C++ within a common GUI if this is desirable for future extension of the model

Figure 6.1 Model structure produces bottom up control of successional change and top down control of allogenic disturbance. Each *model* is based on individual *tree objects* which possess *species* attributes. *Trees collections* are held in *patch* objects. *Trees* receive information from the patch in which they are held, and contribute to the *patch* properties. The *disturbance object* in each model interacts with *trees* and may also receive information from *patches*. The effect of disturbance is thus species specific with local effect on *patches* within the context provided by the *model* scenario.



Linking the model to a database

The link to a database is facilitated by adopting an OOP approach. A recordset corresponds to a collection of objects. Each record in a recordset corresponds to an object. Each field in the record corresponds to a property. Thus movement of data between model and database requires a minimal amount of coding. Values can easily be moved from recordsets which may be tables or queries to initialise model objects.

One advantage of this approach is an increase in flexibility during model development. New properties and their associated methods can be added to modules and their values initialised by adding new fields to an existing table. Data files do not have to be constantly restructured as new features are added to the model.

Implementation of a probabilistic interpretation of parameter variability

All gap models contain stochastic routines for simulating establishment and mortality. However other parameters are treated as possessing no intrinsic variability. This is unrealistic and a potential cause of inaccuracy. If non linear interactions occur in the system the distribution of variation can be expected to alter system behaviour. An important difference between the software designed for this study and other implementations of JABOWA-FORET is the way in which uncertainty and variability of parameter estimates have been incorporated into model structure. Most of the parameters used in the model must be supplied with an associated error term. Error terms in the model have two contrasting interpretations.1)The error term reflects the degree of uncertainty concerning the true value of the parameters used in the model.2)The error term reflects the degree of variability within the system under consideration. These interpretations are fundamentally different. The first assumes that the system is deterministic, but its characteristics are imperfectly known. Thus the incorporation of error terms are required to prevent model output that is more precise than can be justified from available knowledge. The second assumes that the amount of variability in the system must be incorporated in order to produce output similar to that produced by the real system. Thus a model without variability would be not merely overly precise but possibly also inaccurate.

For species specific growth and allometric parameters this error term is the standard deviation estimated from a sample of measured trees which are assumed to be representative of the population of interest. When simulations are run the model uses the Box-Muller transformation to produce pseudo random numbers with a normal distribution around a supplied mean and standard deviation. The VB code used to draw a number from a normal distribution with mean zero is

```
r1 = Rnd

r2 = Rnd

res = sd * (-2 * log(r1)) ^ 0.5 * Cos(2 * pi * r2)
```

When a tree is initialised its parameters are drawn at random from the appropriate distribution. Correlated variability will have a coarse grained effect which may result in greater variability in modelled output than uncorrelated variability. This can be investigated by using the option built into the software to set variability at the patch level rather than the individual level. This results in randomisation at the level of the species objects in each patch.

3. Parameterisation of the individual tree model

Calibrating the fundamental growth equation

Introduction

The method used here for calibrating the classic growth model used in gap models was designed to overcome a challenging site-specific problem without hiding the assumptions made. Only one simple assumption not based on measurements taken from individuals is used. The need for optimisation of the fundamental growth model arose because estimating the values of the parameters in gap model growth equations from direct measurement is not as straightforward as it may initially appear (Schenk 1996; Lindner Sievanen and Pretzsch 1997). Difficulties concern 1) finding measurements which are the true parameters of the optimal growth equation and 2) linking the behaviour of the final model to observed stand behaviour.

Unlike empirical stand level models used in the field of forestry, gross stand productivity predicted from individual based models is not linearly related to the equation used to represent growth (Botkin 1993). Stand level properties emerge as a result of the combined effects of species-specific optimal growth parameters and environmental constraints. Some of these constraints are emergent properties that change dynamically as the model is run. Others are predetermined for each simulation.

Incorporating constraints to tree growth in a model of disturbed forests may be particularly challenging. Disturbance of forests can lead to loss in productive potential due to soil erosion and nutrient loss (Lugo and Brown 1993; Reiners *et al.* 1994; Garcia-Oliva, Sanford and Kelly 1998). Oxidation of soil organic matter and compaction of surface layers occur due to grazing as changes in temperature and soil moisture occur (Jordan 1989; Milchunas and Lauenroth 1993). For the site under consideration there is already some evidence that slash and burn farming has reduced productivity by increasing the variability in edaphic conditions (chapter 1, chapter 3). It also might be argued that the site is naturally marginal for tree growth. Whatever the cause of sub optimum growth may be, it cannot be turned into a basis for process based forest modelling unless a detailed, parameterised soil model is included in the simulation. Though a simulation framework could easily incorporate arbitrary rules, assuming that long term growth potential is constrained without firm empirical support does not seem acceptable. However it is no easier to justify the assumption that a potentially key element should be excluded from a model because data is not available to precisely quantify its effect (Schauber 1999). Here a simplified depiction of soil imposed constraints is added to the model through analysis of available evidence.

While baseline growth rates for the forest in its pre disturbed state are not available, some indication of the extent to which growth has been constrained by edaphic factors can be obtained from tree ring measurements taken from the disturbed forest. A protocol has been designed which is aimed to extract an estimate of optimal growth characteristics from available information and subsequently adjust this estimate downwards in order to appropriately represent observed growth. The data used to fit the model are observations of annual growth rings. The method is therefore only suitable for pines, as oaks do not form legible rings. However it has been found that growth rates of pines and oaks are correlated and the proportional growth of oaks compared with pines has been measured (chapter 1). Thus a complete model parameterisation is possible once growth constraints have been included.

The JABOWA- FORET class of gap models in common with many other individual based stand simulators use a species specific function which predicts the expected diameter increment for a tree of a given diameter under optimal growth conditions. The model follows JABOWA-FORET in using the fundamental growth equation given by Botkin 1993a as;

$$\delta D = \frac{GD(1-(D(137+b_2D-b_3D^2)/D_{max}H_{max}))}{274+3b_2-4b_3D^2} \qquad \text{Equation 6.1}$$

Where D is diameter at a height of 137 cm (breast height), G is a species specific constant, H_{max} is the maximum height in cm the species reaches and D_{max} is its maximum diameter and b_2 and b_3 are allometric constants linking diameter with height. Modelled individuals do not grow at this optimum, due to constraints imposed by shading, temperature, water or nutrient availability. When gap models are used to investigate the factors underlying species distributions at regional to continental scales simulated responses to temperature and water availability are used to reduce growth rates. Because the model developed for this study represents a single stand it does not need to include any climatic information in the model structure. Loss of generality is compensated by simplicity of parameterisation which leads to improved accuracy and reliability of the model at the stand level. However this does mean that an additional simplified consideration of non-light constraints to growth must be included at some point in the model construction process.

It is assumed that any tree growing without appreciable competition will reach the maximum observed diameter increment for its species δD_{max} at some point during its lifetime. The value for the growth parameter G used in the JABOWA- FORET models may be calculated using the approximation

$$G \cong 5H_{max}\left(\frac{\delta D_{max}}{D_{max}}\right) \qquad \text{Equation 6.2}$$

Where H_{max} = the maximum height obtained during the tree's lifetime and D_{max} = the maximum observed diameter and δD_{max} = the width of the widest annual diameter increment if δt is set to one year . On the use of this approximate formula Botkin 1993 comments - "*although preferable because it is linked to observation, this method has not been employed by anyone to my knowledge.*" The failure to exploit this empirically linked parameterisation method is due in part to the detailed process based direction in which forest simulation moved subsequent to the emergence of the JABOWA-FORET paradigm. It offers practical advantages for building forest growth simulators in areas with limited data availability.

A problem with this direct parameterisation method is associated with its underlying rationale. It is assumed that the essential, optimum growth rates and maximum diameters used in the model can be estimated directly for each species. In reality, although these parameters are linked to observation, they cannot always be taken directly from available observations. Gap models assume that the growth of any tree is the result of interactions between the species specific growth rate and limitations acting at the micro-site (patch) scale. Repression through shading is not the only cause of sub-optimal growth, especially when pines are considered which are forming a rather open upper strata of the vegetation. Edaphic and climatic factors are also included as growth modifiers in most gap model formulations. When generalised gap models are used for regional or continental scale modelling the assumption is made that at some point in their range mature trees can be found which have grown at their optimum rates and reached their maximum sizes. The extent to which a given tree's growth could conform to this theoretical optimum is not clear, even for well studied areas. Any given trees' growth is constrained by some environmental factors. If edaphic conditions restrict the potential growth then measures of mean growth rate, even taken from completely open grown trees, will be less than a theoretically estimated optimum.

Each measured estimate of δD_{max} taken on an open grown or dominant tree may be thought of as consisting of

$$\delta D'_{\max} = f(patch).\ \delta D_{\max} \qquad \text{Equation 6.3}$$

Where *f*(patch) is some function representing the combined effects of sub-optimal growth conditions. $\delta D'_{max}$, is a single, (under) estimate of the actual value of δD_{max} for the species. If measurements are made on a sample of trees, the variability of the measurements taken of $\delta D'_{max}$ thus gives some indication of the variability of *f*(patch) provided the trees can be assumed to not have been repressed through shading by other individuals during their period of maximum growth. Note that this argument also assumes that the intrinsic growth rate is species specific and not greatly affected by intra-specific genetic variation. This assumption is used by most gap models.

A patch level parameter, *SoilQ* has been used in both the FORET and JABOWA models (Shugart 1984). It is a feature of most of the FORET-JABOWA descendants, such as FORECE (Kienast 1987) and ForKlim (Bugmann 1996). *SoilQ* is variously interpreted as the maximum basal area or the maximum biomass of all species a patch can support. Basal area is used here under the assumption that basal area is closely correlated with total leaf area and that edaphic limitations place restrictions on patch scale leaf area. In the development of later gap models this single parameter was replaced by process based sub models designed to represent nutrient cycling (Friend, Running and Shugart 1993). However for the purposes of constructing a reliable model of forest growth this simple aggregate measure may still be useful for empirical model calibration. In FORET a dimensionless scalar, *SoilLimit*, which reduces the calculated growth rate as a result of combined, undefined soil quality factors, is assumed to increase in effect as $TotBa_{\text{patch}}$, the total basal area on a patch, increases.

$$SoilLimit = 1 - \frac{TotBA_{patch}}{SoilQ_{patch}} \qquad \text{Equation 6.4}$$

SoilLimit would take the value of *f*(patch) during the phase of maximum radial increment. Clearly the same limiting effect could be achieved through directly adjusting the value of D_{max}. However the basis of the modelling protocol prevents this. In gap models D_{max} is a fixed, species specific parameter and is taken from a single tree. Adjustments to growth of each tree due to site specific constraints must be made after the optimum growth for the species has been defined. A further difference between the effects of directly altering D_{max} and the use of the microsite specific parameter *SoilQ* is that a *SoilLimit* affects all the trees in a modelled patch, and its value is calculated from the total basal area held on the patch. This means that the use of the *SoilQ* parameter will include the negative effects on growth of competition for nutrients and water exerted by smaller trees on larger trees, whereas without the inclusion of this parameter a gap model assumes only one sided competitive effects. In effect the use of *SoilQ* is a simple substitute for the detailed mechanistic representation of a wide range of unmeasured soil processes. The inclusion of *SoilQ* approximates the effects of symmetric scramble competition for water and nutrients that will act in combination with asymmetric competition for light when the model is run. It imposes some top down control on the model. The following study thus aimed to estimate appropriate values for SoilQ and the parameters representing the optimum growth equation.

Method

(a) Calibration protocol for the growth parameters of the three species of pine

As oaks do not form legible growth rings the method developed was only suitable for parameterising the pine growth model. An estimate of the relative growth rate of oaks compared to pines has been possible using data taken from the PSPs (chapter 1). The assumption is made that an estimate of *SoilQ* for pines may also be suitable for constraining oak growth rates. This is supported by the data presented in chapter 3.

The value required in order to use *SoilQ* to constrain growth to within observed limits was estimated as follows. A submodel of individual tree growth used by Jabowa-Foret was constructed using the compartment flow modelling tool ModelMaker, (Cherwell Scientific, 1998). The default continuous Runge Kutta integration method used by Model maker was changed to discrete Euler integration using time steps of one year in order to ensure identical results to the sub-model programmed as a class module in the Visual Basic implementation of the gap model (see Bugmann, Fischlin and Kienast 1996 for a discussion of the correct updating procedures for state variables in IBMs) Numerical verification of the results obtained by the separate implementations was checked by running single instances of the tree class used in the gap model and comparing results with the Model Maker implementation. Calculations of the allometric parameters *b2* and *b3* from *Dmax* and *Hmax* was carried out within the sub-model using the formulas provided by Shugart (1984)

$$b_2 = 2\left(\frac{H_{\max} - 137}{D_{\max}}\right)$$ Equation 6.5

$$b_3 = \left(\frac{H_{\max} - 137}{D^2_{\max}}\right)$$ Equation 6.6

Site quality affects the height-diameter ratio. This is included in the sub-model by multiplying *Hmax* by a hyperbolic function of *SoilQ*. The hyperbolic function was fitted to set the lowest observed value for height variation, ≅ 60% of the asymptotic value (chapter 1), at the lowest expected bound for *SoilQ* of 20 m^2 ha^{-1}

$$H'_{\max} = H_{\max} \frac{SoilQ_{patch}}{SoilQ_{patch} + 13.33}$$ Equation 6.7

This is rather arbitrary, but is based on observation (chapter 1 and chapter 3) and is preferable to completely excluding the well studied effect of low growth rates on height/diameter ratios from the model.

Figure 6.2 Compartment flow implementation of the growth model run using Model Maker. Note that the model is optimised through the lookup table linked to tree ring data.

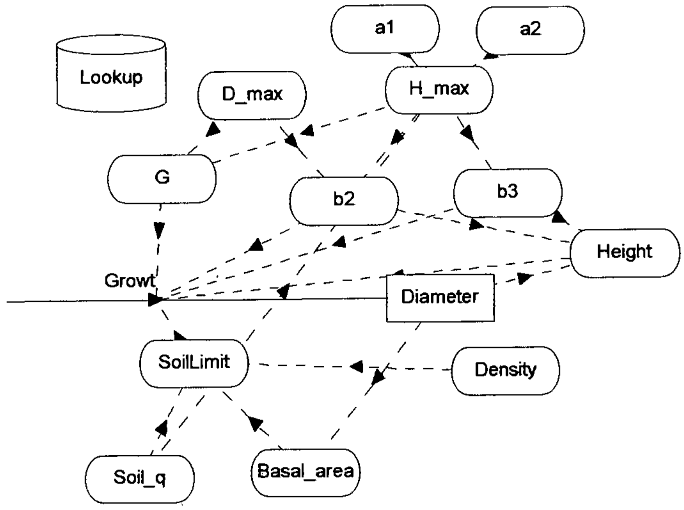


Figure 6.2 shows the model as implemented using Model Maker. Five parameters must be used to run the sub-model. D_{max}, H_{max}, δD_{max}, $SoilQ$ and n (trees ha $^{-1}$). The number of mature trees expected to be found per hectare must be included together with $SoilQ$ in order to adjust growth rates due to the way in which $SoilQ$ acts on diameter increment by setting bounds to the total basal area. If the model were used in forestry this parameter would be easily obtained with reference to stocking levels. However in natural forests its estimation requires making some assumptions. At a level of around 400 mature stems per hectare canopy closure occurs at a mid point in stand development (Oliver and Lawson 1990). Competition for light at this density can be assumed to be low for most of the stand development, yet trees will still interact. Most importantly it does correspond in general terms to the density of pine stems found in semi-mature patches of forest at the field site (chapter 1).

(b) Measurements obtained for calibration

D_{max} and H_{max} were simply estimated by measuring the girth and height (using a clinometer) of the largest trees for each species found at the field site. As other variables in the model are derived from D_{max} and H_{max} this left δD_{max} and $SoilQ$ to be estimated. In order to incorporate $SoilQ$ in the final model an estimate of variability was as important as estimating the central tendency of the parameter, particularly as D_{max} and H_{max} are point estimates. Fifty individuals of each of the three pine species were selected for measurement. Because it was desirable to obtain data that are independent of the data set used for model verification and validation these individuals were not located in the permanent plots. The aim was to include only trees not subjected to competition for light with any neighbouring individuals. Insufficient completely isolated individuals were found, so the initially proposed criteria of only including open grown individuals was relaxed to include clear dominants in open stands. The diameter and height of each tree was recorded together with slope, aspect, soil type and distance to competing trees.

Two orthogonal cores were extracted using an increment borer at breast height from each tree producing a total of 300 cores. Because the model is used to predict growth after sapling establishment has occurred, coring at breast height, rather than ground level produces data that is directly comparable with the model output. The cores were mounted, sanded and varnished. Growth rings were counted under a binocular microscope. Legible patterns of rings were not apparent for all cores. Forty four of the cores could not be read reliably. For each core the total number of rings (age - age at breast height) was recorded. The combined width of the band containing the five widest rings was taken as an estimate of $\delta D'_{max}/2.5$ .The combined width of the band containing the five narrowest rings was taken as an estimate of $\delta D'_{min}/2.5$. Where two legible cores were obtained from a single tree the mean for the two cores was taken to represent the best estimate of the parameter for the tree. Otherwise the data from the core that appeared most reliable were used.

In addition cores from ten trees were selected at random from each species and the distances between each radial ring measured to the nearest millimetre to produce a cumulative growth curve. Ten such growth curves were combined for each species and standard deviation calculated at each point to produce a curve with associated standard deviation.

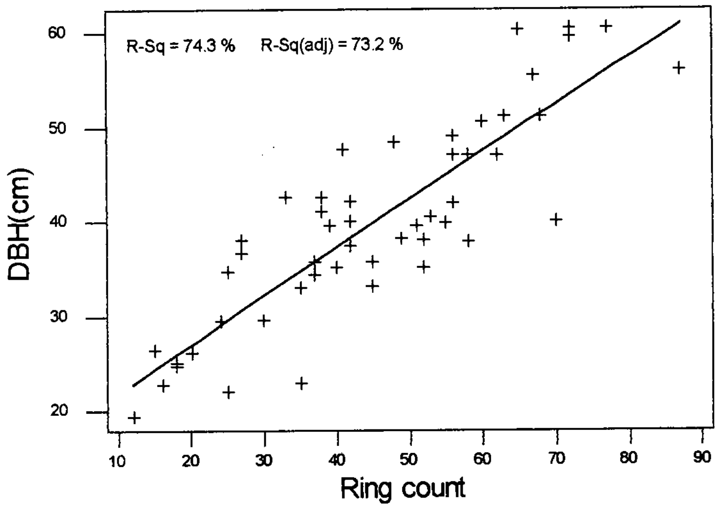
Results

The stand level relationship between age and diameter was analysed by regressing measured diameter on ring counts. As a test of the general shape of the relationship a quadratic equation was fitted to the data. Figure 6.3 shows that a great deal of variability in growth rates around the fitted relationship was found for all three species. The quadratic term used in fitting the regression was significant at the 5% level for *P. oocarpa* but not for *P. maximinoi* or *P. devoniana*. The inclusion of a quadratic term should improve the fit of the statistical model if the age-diameter relationship follows the proposed mechanistic growth model, which is curvilinear. This lack of significance suggests that stand level characteristics do not follow directly from models of individual tree growth. The larger trees included in the data set have apparently grown at above the mean rate for the stand as a whole throughout their lifetime. This is supported by the finding that significant ($p<0.05$) correlation existed between $\delta D'_{max}$ and $\delta D'_{min}$ for all three species. This would be expected in a data set which included repressed individuals, but repression through shading was not the most likely cause as only open grown or dominant trees were chosen for core extraction. If a model for individual tree growth were derived directly from the stand level data a biased estimate would arise. The optimum individual tree growth therefore cannot be directly inferred from stand level properties even when only dominant or open grown trees are included in the data set.

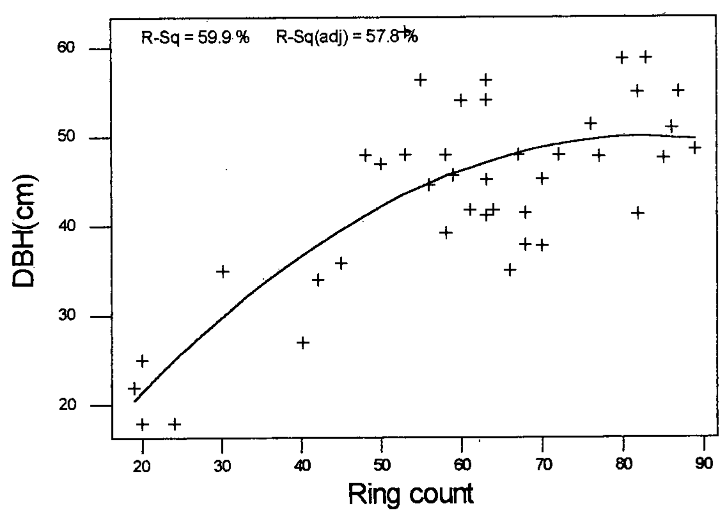
It was assumed that much of the variation in growth rates could be statistically explained by the measured environmental variables. As a test of this slope, aspect, soil depth and distance to nearest trees were standardised (see chapter 1) and a regression of $\delta D'_{max}$ on all independent variables tested. The result was non significant, even when all three pine species were pooled to increase power ($R= 0.2290$ $R^2= 0.0526$ $p=0.426$). This suggests that the measurements taken were uninformative. Stratifying the data by species produced no further insight. One way analysis of variance failed to detect significant variation in either maximum or minimum growth rates between species (table 6.1). However small differences would be masked by the large amount of variability within species and a larger data set may be needed to detect them. Power analysis with beta set at 0.95 and sigma at the pooled estimated standard deviation showed that a sample size of at least 91 trees for each species would be required to establish the significance of the observed difference between the two most extreme means.

Figure 6.3 Estimated age diameter relationships for the three species of pine. Note that although regression equations have been fitted using a second order polynomial in order to show the shape of the relationship, the equations for this model have not been provided as they are inappropriate in the context of the modelling framework being developed.

a) P. maximinoi



b) P. oocarpa



c) P. devoniana

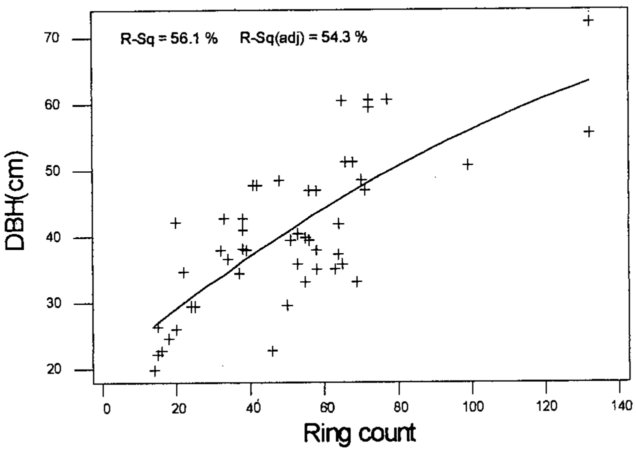


Table 6.1 One way analysis of variance between species in the measured width of the five widest rings

Source	DF	SS	MS	F	P
Species	2	352.6	176.3	2.2	0.111
Error	131	10340.0	78.9		
Total	133	10692.5			

Table 6.2 Maximum and minimum diameter increments calculated from the width of the five widest rings and the widths of the five smallest rings for the three species of pines.

Species	Mean δD'max (cm)	Sd	95% C.I.	Mean δD'min (cm)	S.d	95% C.I.
P. oocarpa	0.98	0.392	+-0.13	0.24	0.07	+-0.025
P. devoniana	1.08	0.344	+-0.09	0.31	0.22	+-0.078
P. maximinoi	1.12	0.356	+-0.11	0.29	0.20	+-0.071

The estimates of the maximum growth rate given in table 6.2 are below the true species specific values as they are biased by the growth conditions experienced by the trees. The standard deviation of each estimate gives some indication of the amount of variation in growth conditions at the site. It can be interpreted as representing the standard deviation of *f(patch)* from equation 6.2

Table 6.3 gives the maximum diameters and heights found for each species at the site. It should be noted that these may be underestimates due to disturbance. The values can be compared with the asymptotic heights estimated in chapter 1.

For each species the readings for each increment measured from the ten cores which had been set aside for model verification were pooled and the mean and standard deviation calculated. The error term was found to increase in absolute value as the number of rings increased. A proportion of the variability arises from errors in reading growth rings, rather than true variation in growth rates. The data provides a guide to the shape of the growth curve of trees at the site. This was used to test the performance of the growth equation for each species and recalibrate it to include limitations to growth.

Table 6.3 Maximum diameter and greatest recorded height for each species at the site.

Species	*Dmax (cm)*	*Hmax (cm)*
P. oocarpa	*77*	*3200*
P. devoniana	*82*	*3200*
P. maximinoi	*102*	*3700*

Figures 6.4, 6.5 and 6.6 show an example of the model calibration process being used to optimise the growth model parameters for *P. maximinoi*. The model was first run with δD_{max} set to take the value of $\delta D'_{max}$ and *SoilQ* set to be effectively not limiting (Figure 6.4). This corresponds to the most direct parameterisation method which includes the fewest additional assumptions. When compared with validation data the model was found to underestimate ring widths for early growth and overestimate later increments. This was expected as using the mean value of $\delta D'_{max}$ should underestimate underlying growth but the lack of sufficient site specific constraints during later stages of growth will lead to an overestimate of the potential actually reached . Adding a single standard deviation of the estimator to $\delta D'_{max}$ led to model output which consistently overestimated measured growth (figure 6.5). This was rectified by using the Marquart method to optimise the value of *SoilQ* in order to produce the best fit to the data. The coefficient of variation of both δD_{max} and *SoilQ*, neither of which could be measured directly, were assumed to be equivalent to the coefficient of variation estimated for *f*(patch) presuming the function reduced to a constant. Confidence intervals were calculated for the model output, based on this assumed variation (Figure 6.6). Figure 6.7 shows the effect that a range of values of *SoilQ* has on individual tree's growth. It shows that asymptotic diameter would be constrained to below 30 cm with *SoilQ* at 20 m^2 ha^{-1}. This corresponds approximately to the estimate obtained less two standard deviations. When the full model is assembled around 5% of plots would have this highly constraining value. However the constraint to an individual trees growth does assume densities of 400 stems ha-1. The level of constraint to growth that low values of *SoilQ* imposes would not be necessarily be so severe when the full model is implemented due to variations in stem densities and mortality implemented by the model when growth falls beneath the measured minimum growth rate.

As the parameter *SoilQ* is not specific to any of the modelled species the model fitting procedure should produce similar estimates of the value of the parameter for each of the species in turn. In fact the point estimates of *SoilQ* varied. However because of the large error associated with the estimation there was no significant differences between them (table 6.4).

Figure 6.4 Optimisation of the growth model *P. maximinoi* using Model Maker step 1. Points with error bars are taken from the measured growth of ten trees. Error bars are +- 1 s.d.. The continuous line is the result of running the growth model. It is run here with δD_{max} set to the measured mean value of 1.12 cm. The x axis represents time after sapling establishment in years, the y axis is tree diameter at breast height in cm.

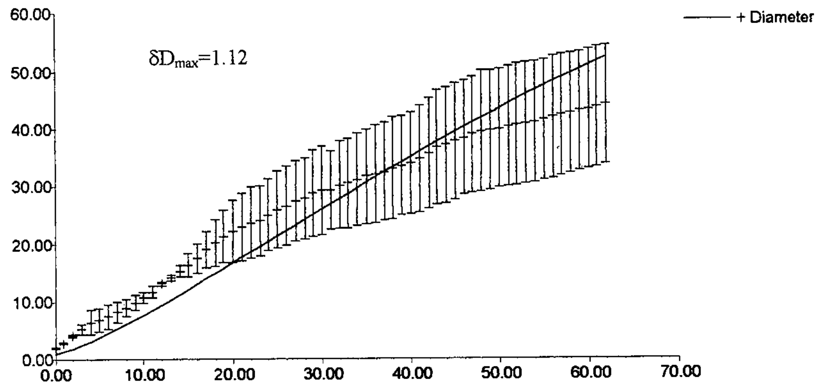


Figure 6.5 Optimisation of the growth model for *P. maximinoi* using Model Maker step 2. Points with error bars are taken from the measured growth of ten trees. Error bars are +- 1 s.d. The continuous line is the result of running the growth model. Here δD_{max} has been set to a higher value obtained from the estimated mean plus 1 s.d. 1.12 + 0.36. = 1.47 cm. The x axis represents time after sapling establishment in years, the y axis is tree diameter at breast height in cm.

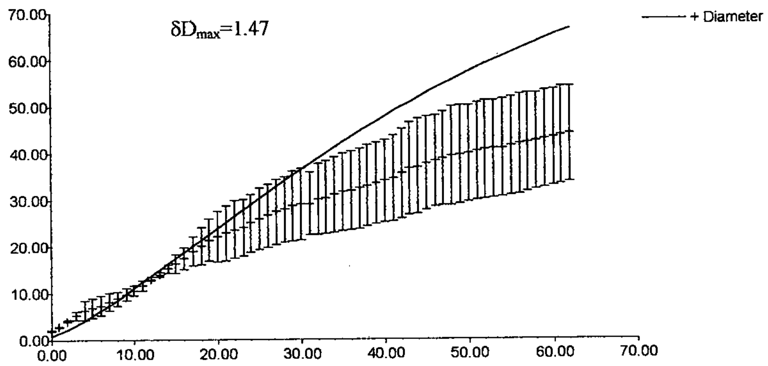


Figure 6.6 Optimisation of the growth model for *P. maximinoi* using Model Maker - step 3. Points with error bars are taken from the measured growth of ten trees. Error bars are +- 1 s.d.. The continuous line is the result of running the growth model and the dashed line is the estimated error contained in the growth model. Here δD_{max} has been set to the higher estimate used in step 2 (1.47 cm), but the error has also been incorporated in the model. The constraining parameter *SoilQ* has then been found through optimisation and set to 55.69+-18.7. The x axis represents time after sapling establishment in years, the y axis is tree diameter at breast height in cm.

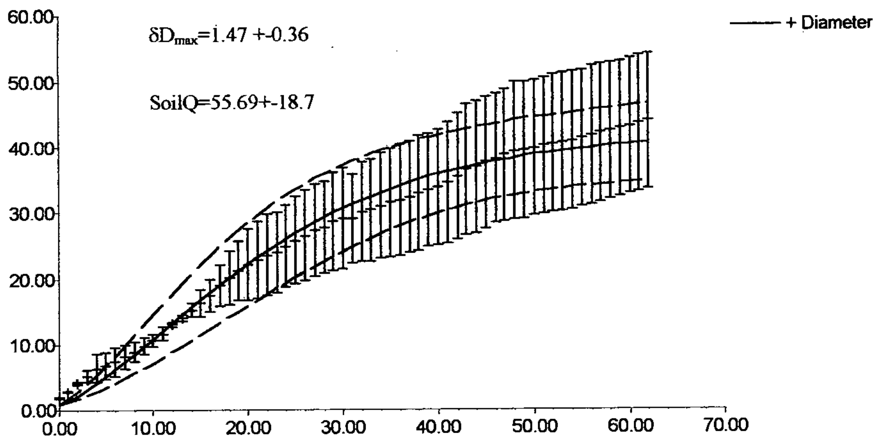


Figure 6.7 Constraining effect on the growth model of *P. maximinoi* of a range of values for the patch level variable *SoilQ*, when densities of 400 stems of equal size are assumed. The x axis represents time after sapling establishment in years, the y axis is tree diameter at breast height in cm.

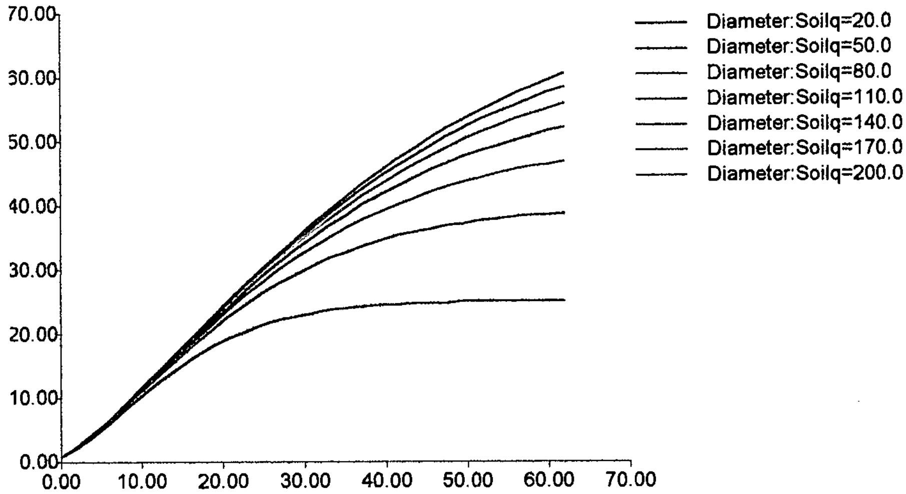


Table 6.4 Estimates of the empirically calibrated constraining parameter SoilQ based on observed growth.

Species	SoilQ	SoilQ sd
P. oocarpa	48.71	23.1
P. devoniana	47.32	21.4
P. maximinoi	55.69	18.7

Discussion

The degree of variation in growth rates found at the site was much greater than expected and the analysis failed to reveal expected patterns. A linear fit of the stand level growth data, which was found for *P. maximinoi* is not predicted by either the growth model used here or the Chapman-Richards model used in applied forestry. This is perhaps an artefact of the data set, but if it is due to a higher average growth rate of the largest trees found at the site it does demonstrate the need for careful interpretation of growth data. Any direct extrapolation from stand characteristics would certainly overestimate forest productivity. Most trees are growing at surprisingly slow rates, which are much lower than the maximum possible. The tree objects in an individual based forest model must incorporate this variability if model output is to reflect stand level patterns of growth or the final growth model will be biased.

It would normally be expected that slope, aspect or soil depth would be useful predictors of growth rate. That these variables were not found to be significantly correlated with measured growth rates was not surprising following previous results from this site. Individual tree growth in these forests seems to be inherently unpredictable. The difficulty is not unique. Monserud and Sterba (1996) found that the best fitting models only explained between 20 % to 63% of the variation in an extremely extensive data set taken from the Austrian national inventory of natural forests.

More detailed information on soil properties might reveal details of the factors underlying the observed growth rate variation. Nevertheless the variability observed in this data set should be considered when planning further studies on disturbed natural forests in the area in order to ensure sufficient power. Every line of evidence from this site has suggested that anthropogenic disturbance is breaking up underlying patterns and confounding the detection of expected effects. This demonstrates both the urgent need for more effective models, and the challenges involved in using currently available field data for their construction

Simulation models of tropical forests have traditionally ignored below ground limitations to growth, despite the fact that tropical soils are extremely vulnerable to nutrient loss, compaction and erosion. For example the model SYMFOR 1 (Young 1998) designed to predict yield in Indonesian forests did not include any non-light limitations to growth. This was largely due to difficulties associated with the measurement of edaphic factors and the difficulty of incorporating available measurements into model structure (Young *pers comm.)*. The field site has already been subject to the type of disturbance currently being imposed on other forests with no previous history of usage. The variability in growth rates found in this study may be more commonly encountered as studies are conducted on previously burnt or clear cut areas in the tropics. This raises some serious concerns. If IBMs of this type are found to have an intrinsic positive bias when applied to predicting tropical forest yields they could lose credibility unless the consequences of the assumptions made in their construction are clearly stated.

The estimates for *SoilQ* produced by this method are close to the measured maximum basal areas found in the region for mature pine-oak forest. The inclusion of this parameter in individual based simulation studies will therefore not greatly alter the successional end point of the model simulations. It will only affect the rate at which forests approach this endpoint. The use of the parameter thus seems justified by these results. Its inclusion produces a closer approximation of the actual trajectory of growth observed than simulations that exclude the parameter. It does not lead to a situation in which the model endpoint is purely tautological.

SoilQ has been included in other gap models, but is usually set to some rather arbitrary value. Bugmann 1996 writes "*For the FORECE simulation it was assumed that SoilQ is constant throughout the temperature precipitation space and this may be unrealistic.*". The difficulty associated with including this parameter at all in a process based model is that it is not clear which limiting processes it models. Though nominally linked to below ground processes, here it is best given a simple empirical interpretation as it also must be adjusting the model for the effects of sub optimal climatic conditions for all species simultaneously. The absence of any water balance or temperature response functions in this model can only be justified if it is assumed that all species respond equally to microsite heterogeneity in such conditions over the range of conditions from which the data has been drawn. If the model is used as a tool for investigating the consequences of anthropogenic disturbance it is not necessary to propose a mechanistic basis for *SoilQ*. Its inclusion does appear to be adjust the fundamental growth equation in such a way that the resulting model is a better emulator of the complex combined of effects of nutrient and water limitation, temperature stress and even physiological senility.

The high variability in growth rates suggests that a sub-model representing below ground processes has the potential to produce additional insight into the underlying causes of forest structure in this region. This suggests many areas for future study. Several hypotheses are available which may provide a basis for this research. For example one intriguing possibility is that patchiness in the availability of mycorrhizal inoculates may be responsible in part for this variability. This would explain the failure to find correlation with easily observed variables. Variability in inoculate availability has been proposed by Alexander *et al.* (1992) and Janos (1980; 1992) as an important mechanism in determining tropical forest productivity and maintaining diversity. Pine species, and most oaks, differ from the species studied by Janos in possessing ecto-mycorrhizae rather than vesicular-arbuscular mycorrhizae. While low intensity fires may have little effect on levels of pine inoculation (Jonsson *et al.* 1999) the effect of slash and burn clearance remains unknown. Loss of organic matter may has an important negative effect both on the probability of inoculation and the effectiveness of nutrient uptake through the mycorrhizal relationship (Amaranthus, Trappe and Molina 1989).

In conclusion, some effect in addition to competition for light is responsible for variation in the growth rate of trees at the site. This has been treated as process error (*sensu* Pascual and Kareiva 1996), in other words variation that is not due to erroneous measurement but which has unknown causes. This variation has been incorporated into the simulation in a simplified form. The principle result of incorporating this variation may be a more accurate representation of growth rates and productivity in a previously disturbed forest, which may have lost part of its productive potential.

Calibration of the light interception equation

Introduction

Successional replacement and stand development in gap models occurs through a model of competition for light. While the use of an accurately parameterised growth equation alone will lead to output which is accurate in the short term, as simulation times increase accurate representation of competitive effects become more important.

Individual based simulation of multi layered multi species canopies use species specific light interception equations, which when combined with allometric calculations of crown areas estimate the proportion of incoming light intercepted by each modelled entity within a patch (Botkin *et al.* 1973; Shugart 1998; Pacala *et al.* 1996). Canopy light interception is an internal model property, rather than a stand level parameter and varies dynamically as the model is run (Botkin 1993). This is an important distinction between IBM's and whole stand models which can be expected to result in a more accurate representation of the stand level productivity of complex natural forests than simpler aggregated models (O'Neill and

Rust1979; Huston, 1994). It contrasts with IBMs in which a distance-based model of competitive interactions is included (Ek and Monserud 1974)

Light interception by forest canopies is measured either at the stand level or at the level of individual trees (Ross 1981). Whole canopy light interception is an informative measure for crops and plantations and is a forcing factor in models in which net productivity is assumed to be proportional to total intercepted radiation (Monteith 1965). Canopy interception is closely related to individual plant light interception for monospecific stands of closely spaced individuals with non-overlapping crowns (Lang, Xiang Yuequin and Norman 1985). Stand canopy light interception can vary as a result of differences in the spacing of individuals, whereas each tree's light interception will have a species-specific component that depends on architecture and leaf arrangement (Charles-Edwards and Thornley 1973; Norman and Jarvis 1975; Mann, Curry and Sharpe 1979). A "big leaf" (Jarvis and McNaughton 1982) approach has been used in some alternative aggregated forms of forest succession models (Bossel and Krieger 1991; Bossel and Krieger 1994; Lischke, Loffler and Fischlin 1998). However for the purposes of parameterising a gap model it is the individual trees' light interception which is of interest. Fundamental growth is calculated from direct observation. Light availability is used to calculate the contextually appropriate reductions in growth rates.

Theoretical basis for parameterisation

Gap models use a simple allometric relationship for estimating the shading effect of individual tree canopies. It is assumed that total leaf area is proportional to the diameter squared of the tree (Shugart 1984)

$$La = c_{leaf} D^2 \qquad \text{Equation 6.8}$$

Where La is total leaf area, C_{leaf} is a constant of proportionality and D is diameter at breast height. C_{leaf} can be estimated from data on crown dimensions and leaf area index (L). If leaf area index is assumed to be a species specific constant equation 1 becomes. 1984)

$$La = c_{canopy} LD^2 \qquad \text{Equation 6.9}$$

Where C_{canopy} is also some constant. These simplifications ignore a great deal of the complexity of tree form, but present a useful framework for simulation. Projected canopy cover has been measured directly (chapter 3). Estimating leaf area index may however require an indirect technique. The Monsi-Saeki equation assumes a homogeneous canopy of randomly placed elements as a convenient simplification. The zenith angle Θ of a probe or solar beam is its angle measured from the vertical. To avoid confusion it should be noted that in an alternative usage the term zenith angle refers to the sun's angle from the horizon. In canopy models Θ takes the value of 0° when the sun is directly overhead rather than 90°. The transmission coefficient Γ for a canopy of randomly placed elements for a given zenith angle Θ is area index is assumed to be a species specific constant

$$\Gamma(\Theta) = \exp(-KL) \qquad \text{Equation 6.10}$$

Where L is the projected leaf area index of the canopy and K is an extinction coefficient. K will vary during the course of a day depending on zenith angle. Leaf angle distribution may be assumed to be relatively constant except in the case of heliotrophic plants.

Canopy light transmission is calculated in a gap model using the Monsi-Saeki equation. However in the model the equation is given a slightly different interpretation to that commonly employed in the field of mensurative ecophysiology. It is used to estimate the integrated light interception at any given height in the canopy over the modelled patch and over a time interval that is commonly one year or one growing season using the equation

$$I_h = I_0 \exp(-kL_h) \qquad \text{Equation 6.11}$$

Where I_h is the light at some height h in the canopy, L_h is the projected leaf area index for all canopy elements above height h and I_0 is the incident light at the top of the canopy. Because this equation uses a slightly different, integrated, interpretation of the canopy light interception coefficient to the K used in equation 3 the extinction coefficient here is given the notation k in order to distinguish it as a model parameter which does not vary with zenith angle. Gap models are sensitive both to the proportion of light intercepted by layers of leaves of individual species and the area of tree canopies. It is clear from equation 4, that an estimate of k is required in order to run such a model. Most gap models make the simplifying assumption that k is constant for all canopies (Shugart 1984; Urban and Shugart 1992). However as Urban and Shugart (1992) point out "*A smaller extinction coefficient makes the canopy leaky and reduces the asymmetry of light competition, while a larger coefficient strengthens this asymmetry. Total stand level productivity is also sensitive to this coefficient.*" Sensitivity analysis conducted during the development of the gap model revealed the influence of this parameter. Allowing k to take values from between 0.1 to 0.8 resulted in equilibrium basal areas of simulation runs varying from around 80 m^2 ha^{-1} to 40 m^2 ha^{-1} when soil limitations are excluded from the model structure. Direct measurement of the canopy transmission coefficient for a mixed forest is challenging, but the implication of making arbitrary assumptions regarding the value of k cannot be ignored. The value for k used in the published code for FORET and JABOWA is 0.4. It is unclear from available descriptions of the model structures how this parameter value was arrived at (Botkin 1993;Shugart 1984; Shugart 1998). It was therefore aimed to measure this parameter directly and investigate the differences in light permeability between the species at the site.

Methods

(a) Calibration of the canopy extinction coefficient

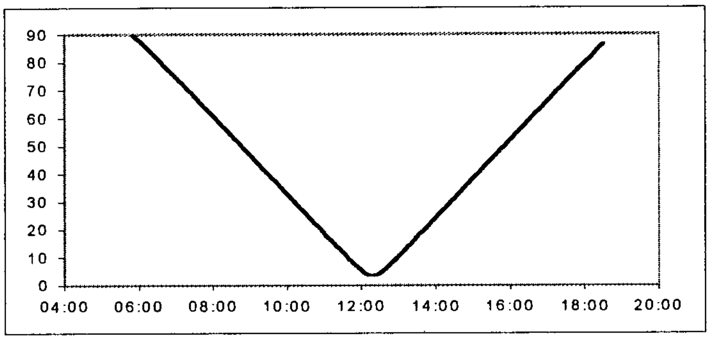
Direct measurement of light absorption by a single canopy at any single time produce estimates of K which are specific to a single zenith angle. Point measurement thus provides a guide to the value of k as an integrated parameter used in the model, but not a direct measurement. Jarvis and Levernez (1983) provide estimates of k ranging from 0.25 to 0.5 for temperate forests. Tropical pines and oaks differ greatly in the geometry and orientation of their canopy elements and it is desirable to make k an explicit species specific parameter included in the set of parameters used to run the gap model. It would appear likely that differences in canopy permeability is a factor in determining patch scale coexistence.

Assuming that a useful first step in finding a value of k for modelling purposes may be taken by estimating K for some appropriate zenith angle, it is necessary to find a suitable protocol. (Campbell 1986) suggests that if an ellipsoidal distribution of leaf angles is assumed K is related to Θ by the equation

$$K = \frac{(x^2 + \tan^2 \Theta)^{1/2}}{x + 1.774(x + 1.182)^{-0.773}}$$ Equation 6.12

Where x is the ratio of the projected area of an average canopy element on a horizontal plane to its projection on a vertical plane. The shape of the curve produced by this equation depends on the value of x. Unless leaves are held horixontally both K and $\delta K/\delta\Theta$ increase with Θ. In tropical regions zenith angles are small (i.e. the sun is overhead) for a large proportion of the day. Zenith angle (in radians) is calculated from the length of a shadow x cast by a vertical object of length y as Θ= tan-1(x/y). Figure 6.8 Shows the zenith angle in degrees for the study site on July 20,the mid point of the period over which data on light interception was collected, using a model from the US Naval Astronomical department Washington DC.

Figure 6.8 Calculated zenith angle Θ for the study site at 17°00' N 91°00' W on July 20, 2000. Source model US Naval Astronomical department Washington DC)



The study thus needed suitable data to provide working estimates of two species specific parameters used in gap model simulations to model light attenuation for three species of pine, two species of oaks. The parameters are:

1. An estimated value for the species specific canopy extinction coefficient K for Θs <30

2. The leaf area index L

(b) Data collection

Photosynthetically active radiation (PAR) in the 400-700 nm wavebands was measured using a portable light meter (Sunfleck Ceptometer model SF 80, Decagon Devices, Pullman, WA, USA). The ceptometer has 80 light sensors placed at 1 cm intervals along a probe. The device measures both PAR and sunfleck fraction. Sunfleck fraction gives the most direct measurement of intercepted radiation as used in the inversion equations. However in tall canopies, or canopies with small leaves, overlapping penumbra make measurements of sunfleck fractions unreliable. (Pierce and Running, 1988). The inversions to estimate K and L were thus performed using measurements of transmitted PAR.

Measurements were made between 11 am and 1 pm (zenith angle < 15)on fifteen separate days with completely clear skies between June 2 and August 20 2000. This period was selected as both pines and oaks have fully developed canopies of recently produced leaves. Measurement during the growing season had to be made on an opportunistic basis as periods with completely clear skies were rare. Zenith and azimuth angles did therefore vary slightly between readings . Transmitted photosynthetically active radiation and sunfleck fraction was measured for 50 sample trees of the six common canopy forming species in the stand. Completely random sampling from the 1,027 hectare stand was impractical so a pseudo random sample of trees was selected by measuring the closest suitable individuals to random points taken along a transect through the stand. Trees with overlapping penumbra or poorly formed crowns were excluded. Only larger trees with a projected canopy area of over 100 m^2 forming a single canopy layer were included. In some cases where trees crowns were touching it was impossible to distinguish precisely the identity of the tree casting the penumbra. This was considered unimportant providing the neighbouring tree was of the same species. The double layered nature of most of the forest could have led to some bias as areas had to be sampled where a monolayer was present. These areas may not have been representative of the forest as a whole.

For each tree 10 random points which fell completely beneath the penumbra of each tree were selected. At each point 36 readings of incident PAR and sunfleck fraction were taken by turning through 360 degrees and taking readings every ten degrees. After each of the readings were taken the ceptometer was inverted to measure reflected diffuse radiation beneath each tree. This was subtracted from the mean for the 36 readings which was then divided by measured incident PAR in open areas taken within a few minutes of the readings in the penumbra in order to give a fraction of the PAR intercepted by the canopy. The 10 readings were pooled for each tree. Statistical analysis thus used samples of size n= 50 for each species. The ceptometer was manually calibrated to avoid erroneous sunfleck readings of 100% in full shade. However due to the problem of overlapping penumbra in tall canopies the measured sun fleck fraction was not used to calculate L.

In addition a single point estimate of x was obtained in order to use the inversion equations. If readings are taken on the penumbra of a single tree at differing zenith angles it is possible to estimate the value of x using an iterative algorithm which searches for the minimal value for F using the Marquart method where

$$F = \sum \ln(\Gamma_i + K_i L)^2 \qquad \text{Equation 6.13}$$

Subject to the constraint x>0 and where Γi are transmission coefficients measured at several zenith angles Θi and the Ki are the extinction coefficients for the corresponding angles. The code of an appropriate algorithm in BASIC is provided by the Decagon Ceptometer User's manual (1989) and by Cambell and Norman 1992. This was rewritten using Microsoft Visual Basic. Readings on a single tree of each species were taken at 8 am, 10 am, 12 am, 2 pm and 4 pm. As weather conditions were changeable the results from several days monitoring were pooled. As logistics prevented more than a single tree being measured in this way an individual which appeared to best represent the form of the species at the site was selected. Unfortunately this method did not allow any estimate of the associated variability. It required moving the point of measurement to ensure that all ceptometer measurements were made in the penumbra which may have introduced measurement error which could not be evaluated using statistical means.

Results

Analysis of variance of the proportions of intercepted light after arc sine square root transformation to improve statistical properties (reduce heteroscedacity) showed a highly significant difference between species ($F(1,4)=130.7$, $P<0.0001$). Table 6.5 shows the p values for the Student Neuman Keuls adjusted pairwise comparisons between means. All pairwise comparisons were significant with the exception of comparisons between the two species of oak and between *P. oocarpa* and *P. devoniana*. *P. oocarpa* and *P. devoniana* have significantly more permeable canopies than *P. maximinoi*. Oaks intercept significantly more light than pines.

Table 6.6 summarises the results of the measurements taken and the results obtained from substituting the values in the appropriate models. The tables show that based on these models leaf area index is not greatly different between the species. The principal difference lies in x, and therefore the arrangement of canopy elements in space and the angles in which canopy elements are held to the zenith.

Table 6.5 P values for pairwise comparisons between light interception measured beneath the penumbra of fifty trees of each of the five species.

	P. oocarpa	*Q. crispipilis*	*Q. segoviensis*	*P. devoniana*
P. maximinoi	**0.003179**	**0.000022**	**0.000009**	**0.000388**
P. oocarpa		**0.000008**	**0.000022**	0.377771
Q. crispipilis			0.919133	**0.000017**
Q. segoviensis				**0.000008**

Table 6.6 Estimated parameters for a light interception model for each of the five principal species. % light is the measured figure at ground level on a clear day with a zenith angle of less than 10 ° Leaf area index is estimated with the inversion equation using K(0)

	% light	s.d.	c.v.	s.e.	x	K(0)	K(15)	K (30)	LAI	LAI sd
P. maximinoi	31.72	8.17	0.25	1.15	0.27	0.234	0.392	0.538	3.16	0.63
P. oocarpa	38.47	14.76	0.38	2.08	0.39	0.167	0.363	0.525	2.43	0.82
Q. crispipilis	15.74	6.48	0.40	0.90	1.21	0.563	0.614	0.678	3.01	0.56
Q. segoviensis	15.97	6.64	0.41	0.94	0.98	0.492	0.558	0.638	3.28	0.61
P. devoniana	40.48	16.86	0.42	2.37	0.13	0.080	0.34	0.516	2.67	1.0

Discussion

The study was necessary in order to provide parameters for the model under development, but there are many potential sources of error associated with the method used. If a detailed understanding of the canopy light environment were the principal motive of the study further detailed work is necessary. The inversion method was not particularly appropriate to the field situation, particularly when pine canopies are considered. All three pine species have apically bunched fascicles of needles. The "clumped" arrangement of canopy elements is particularly accentuated in *P. devoniana.* This violates the assumption of randomly placed canopy elements which is made when using the inversion equation to estimate leaf area and may in part be responsible for the unusually low estimates of x for pine canopies. In order to avoid introducing measurement errors into the model, literature estimates taken from more detailed studies could have been used for model parameterisation. However available literature provided a large range of possible values for k and it was not clear which would have applied at the field site.

Although these measurements may be less accurate than would be ideally required for model parameterisation, it could also be argued that comparatively little would be gained in the context of this single study from further attention to light measurement. Productivity at this site seems largely to be constrained by below ground factors. Monteith (1985) advocates the application of the "*principle of least work*" to estimating canopy parameters on the grounds that the precision of all measurement methods available can always be improved without necessarily increasing the predictive power of the model of interest. The amount of effort that should be expended on measuring light interception parameters will depend largely on modelling objectives. The method employed here gives a first approximation and demonstrates quantitative differences between oak and pine canopies. Precision may well be adequate for these purposes. Using a similar procedure Vose and Swank (1990) found that predicted LAI values using ceptometer readings in a *Pinus strobus* plantation were within 9% of those obtained by destructive sampling, but also reported a linear decline in light with canopy depth rather than the exponential decline predicted by the Monsi Saeki simplification which suggested that the assumptions required for the inversion method to be applied were not met.

A feature of this data is the high permeability of both pine and oak canopies. This may be attributed to three factors. 1) Intrinsic attributes 2) Low site quality 3) The persistent defoliating effects of ground fire at the site.

The marked difference in the light intercepted by each species appears to be mainly due to differences in shape, distribution within the canopy and angle at which canopy elements are held, rather than leaf area index. The same pattern of differences between pines and oaks would be expected in most mixed stands of pine and oak, regardless of species. The precise values for k and LAI will however vary greatly, possibly even within the same species. McCrady and Jokela (1998) found considerable genetically linked variation for LAI and x within a single species (*P. contorta*). Growing conditions also will greatly affect these estimates.

Both water and N availability seem to play an important role in determining pine foliage area (Raison *et al.* 1992). As water becomes a limiting resource inefficiencies in light capture may be of less significance to overall plant performance. In seasonally dry areas water use efficiency may be an important determinant of integrated growth over a season. The growing season can be prolonged by conservative water use and thus low LAI and steeply inclined needles. Nitrogen (N) has been found to be highly concentrated in the sun leaves of conifers (Sternberg *et al.* 1998) . Fertilisation experiments suggest that N availability is linked to LAI in pines (Albaugh 1998). The close correlation between N availability and LAI has also been suggested as useful for regional scale modelling (Pierce, Running and Walker 1994). Thus if either water or N are naturally limiting in the system, or have become limiting as a result of soil erosion, nutrient leaching and oxidation of soil organic matter following slash and burn clearance low LAI's would be expected both at the individual and canopy level.

Leaf longevity of between 3 and 4 years have been reported for *Pinus strobus* and *Pinus resinosa* (Gower, Reich and Son 1993). It is therefore appears highly likely that low LAI reflect some persistent effects of defoliation following the ground fire. Wirth *et al.* (1999) report canopy LAI as low as 0.5 in stands of *Pinus sylvestris* affected by ground fire, but these measurements did not represent the LAI of single trees. Similarly, although oak leaves are shed each season, the persistent effects of the fire may also explain the rather low LAI of the oaks when compared to figures reported for other oak stands of 3.3- 6 (Breda, Granier and Aussenac 1995) 4.3-6.2 (Kull *et al.* 1999) 3.4 – 3.58 (Wang *et al.* 1992). Joffre Rambal and Romane (1996) reported a comparably low LAI of 2.96 for Mediterranean oak canopies.

The extremely low values of x may have been an artefact of the measurement procedure, but were in part confirmed by the observation that needles of all three species are held at very steeply inclined angles to the zenith. Although the two pine species intercept a smaller fraction of light than oaks, their morphology may make them well adapted to make efficient use of the light they intercept in conditions of high water stress. On sunny days the measured PPD varies between 1400 and 1700 μ mol m^{-2} s^{-1}. For many species photosynthesis response curves tend to saturate at around 700 μ mol m^{-2} s^{-1} (Bazzaz 1998). Thus drooping needles at an approximately 70° angle to the zenith may operate efficiently while avoiding the heating effect of exposure to full sunlight. Oaks may be more efficient at using diffuse radiation on overcast days.

The assumption was made that estimates of K at midday can be used as a means to predict k needed for modelling. Diffuse radiation has been found to be centred around the zenith at a higher latitude Mexican site (Ackerley and Bazzaz 1995). However the assumption is an oversimplification. While a large proportion of the incoming photons may arrive at the canopy from low zenith angles it is not clear what proportion of such light is actually used by the photosynthetic process. Stomatal closure and photo inhibition at high light intensities are among the factors which limit light use on clear days. A more accurate routine for estimation could be used. k could be derived by numerical integration of a model in which equation 6.12 is combined with modelled growing season PFD and zenith angles as is used for the analysis of hemispherical photography. However any gain in accuracy for simulation may be obscured or counteracted by the manner in which gap models rely on the measure of comparative light availability to calculate the extent to which optimum growth must be reduced.

Hemispherical photography permits integrated light interception over a complete growing season to be modelled and has an important application in the analysis of microsite conditions and canopy gap size. This has led to an elegant solution for modelling light interception in SORTIE (Pacala *et al.* 1996). In this model the position of individual trees is known, and the light available to each is calculated through an algorithm that effectively simulates the process of analysing the measurements taken from hemispherical photography. There are some advantages to this approach which should be considered if model extension is undertaken, but unless the position of individual trees is held in the model such an approach is inappropriate and adds a great deal of additional time to simulations.

4. Modelling interactions between trees

Introduction

Once fundamental growth rates, leaf areas and allometric parameters are available for each species the next step in the construction of the gap model is to define how modelled individuals interact. As in the previous section this involved some model testing and sensitivity analysis during development. Gap models are designed to be comparatively realistic simulators with an intuitive structure. Thus the model's sensitivity to changes in many of the parameters are also intuitive and rather easily predicted from a consideration of the system the model is based on. However some unexpected effects were found. For reasons of space only the unexpected findings of sensitivity analysis and model verification have been reported here. A more detailed account of the findings regarding the effect of modelled patch size is included due to its importance as a potential source of artefactual behaviour.

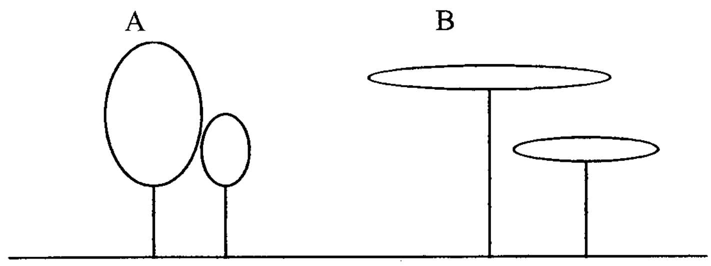
Simulating light interception

Gap models assume that the light environment in a small patch of forest can be treated as horizontally homogeneous. In effect canopy layers are treated as if they were spread out over the whole patch. The area of influence of a large tree is not its projected crown area but is distributed over the total area it can shade during the course of a growing season. Patch size in gap models is typically from 200 m^2 to 600 m^2.

Two ways of simulating the effect of shading of smaller trees by larger trees were tested during the development of the model. In the first a similar algorithm was used to that developed for the model ZELIG (Smith and Urban 1988). The canopy elements were modelled as being distributed between canopy layers. Species specific canopy depth was included in the model. Extensive experimentation during model development led to the conclusion that this algorithm, though intuitively realistic and computationally intensive, could not produce dynamic behaviour such as self thinning (Yoda *et al.* 1963,Westoby 1984; McFadden and Oliver 1988) or the patterns produced by JABOWA-FORET models. The reason for the problem was most easily perceived when monitoring dynamic profile diagrams that were a feature of the GUI used to test the model. Under this model trees of similar heights differed only slightly from each other in the amount of light they received. Consequently their mutual competitive effect were very similar. Canopies developed to the point of closure and then stagnated. It is interesting in this context that ZELIG was designed specifically to model boreal forests with very different patterns of light zenith angles.

A second implementation was therefore used in which canopy elements were modelled using a slightly modified version of the algorithm used in JABOWA-FORET. All canopy shading effects were assumed to be concentrated at the top of each tree. Figure 6.9 shows the conceptual differences between these two models. In both models the implementation divides the canopy into a number of layers and tallies the leaf area in each layer. The more layers that are used, the sharper the competitive hierarchy becomes when trees are modelled as having their leaves concentrated at the top of the canopy. Experimentation with up to 100 layers showed that ten layers provided sufficient contrast providing the width of the layers is adjusted dynamically as the canopy height increases. This is an alteration to the version of FORET given by Shugart 1984 which uses layers of fixed width. The light profile is calculated using the Monsi- Saeki equation (see previous section). All trees were considered to be completely shaded by trees in all the canopy layers above them and by the trees in their own layer. This highly simplified model, reproduces the conventional pattern of self thinning under a competitive hierarchy arising from interference competition as has been reported for FORET and JABOWA (Botkin 1993).

Figure 6.9 Two alternative views of light competition between modelled trees. In scenario A trees are assumed to have a realistic canopy depth. In scenario B all leaf area is assumed ot be concentrated at the top of the tree.



These findings suggest that a greater degree of subjectivity is required when selecting appropriate simplifications for modelling than may be desirable. The assumption that all leaf area is concentrated at the top of a tree is made in most gap models. This is initially surprising. The assumption appears to demand improvement on the grounds of a disconcerting lack of realism. However the gap model's representation of both shading and whole tree's light response are both highly simplified caricatures. When gap models were developed they were found to produce contextually appropriate behaviour when these two simplifications were combined. Changing one element of the model without altering the other appears to disrupt its ability to reproduce the phenomenon of interest. Such observations question the extent to which the term process based can be truly applied to gap models. The use of light measurements to produce a competitive hierarchy gives the impression of a degree of realistic reductionism that is difficult to find when gap models are subjected to closer scrutiny.

Simulating growth and mortality as a function of shading

Throughout the field site oak saplings are found in the penumbra of pines. The converse is rarely observed (chapter 1). This observation alone could be used to project forest succession using the tree replacement model of Horn (1975). The outcome of building such a model would undoubtedly be a prediction of the replacement of pines by oaks. However Horn's model is only effective in predicting successional endpoints in the absence of allogenic disturbance and has limited value for this study. Gap models assume that the underlying explanation for this observation lies in differences in growth responses of species to light.

Detailed studies of light responses have not as yet been undertaken at the site. Parameterisation of this aspect of the model must therefore be undertaken with reference to studies conducted elsewhere.

In the JABOWA model the simplifying assumption was made that two categories of light response can typify all species. These categories are shade tolerant or shade intolerant. The number of classes was extended to include an intermediate response in later versions of JABOWA. Despite progress in measuring leaf level photosynthetic response it is still extremely difficult to typify whole tree light response in natural conditions (Hubbell *et al.* 1999). FORET was parameterised with reference to "*the foresters concept of tolerance*" (Shugart 1984). Species empirical response to light under field conditions are well understood by experienced sylviculturalists (Oliver and Larson 1996). Rules based on natural history observations may allow rapid assessment of tree tolerance. Simple field observations can provide adequate clues to light response when detailed studies are not available. For example Thomas and Bazzaz (1999) found that shade tolerance in Malaysian forests could be predicted quite successfully simply from knowledge of whole tree asymptotic height.

Because differences in shade tolerance are most marked in juvenile trees (Kobe 1996) the presence of advance regeneration under fully formed canopies may be a good indicator of a species tolerance class. The lack of such regeneration for all three pine species suggests they must be assigned to the class of light demanding trees. There is considerable evidence that supports the assertion that pines are generally light demanding (Keeley and Zedler 1998; Bazzaz 1998). In general oak species are not considered to be particularly shade tolerant (Bassow and Bazzaz 1998; Barton and Gleeson 1996) but they were found to support a higher leaf area than pines. Oak saplings can be found under pine canopies (chapter 1). They are therefore placed in a slightly more tolerant class than pines.

Shading not only leads to poor growth but also is assumed to be a cause of mortality in gap models. A rigorous study of comparative rates of sapling mortality under naturally occurring conditions was carried out by Kobe (1996). It appears from these studies that the trade off between fast growth under high light conditions and mortality in shade may be the key factor shaping undisturbed forest dynamics rather than growth rates alone. The response curves given by Botkin (1993) contrast with the curves produced by Kobe 1996 for sapling light response which have a much steeper initial slope.

The work by Kobe showed that few saplings of shade intolerant trees survive over five years if growing at below 20% of their maximum potential. Saplings of shade tolerant trees such as beech do however survive almost indefinitely in deep shade, though without achieving a substantial amount of growth. The rule for density dependent mortality incorporated in this model was

p(mortality | diameter increment<critical increment)=0.15 Equation 6.14

Kobe's results suggests more complex functions are better descriptors of natural mortality. However because saplings have to undergo iterated tests for mortality in a gap model as it runs, the overall model performance was found, when tested, to be insensitive to added detail. Assuming a rule based critical increment model has the advantage of being a simple, easily measured parameter for most species which form annual rings. The critical increment for pines which form clear growth rings was taken to be the lowest measured width of five consecutive rings (see previous section) . The critical increment for oaks, which are assumed to survive well with low rates of growth, is assumed to be 5% of the maximum growth. Extreme shade tolerators would be given a lower critical increment. The use of this parameter also automatically results in a simulation of mortality through senility (see Shugart 1984).

The software programmed for the study models a continuum of whole tree growth response to light availability using the equation

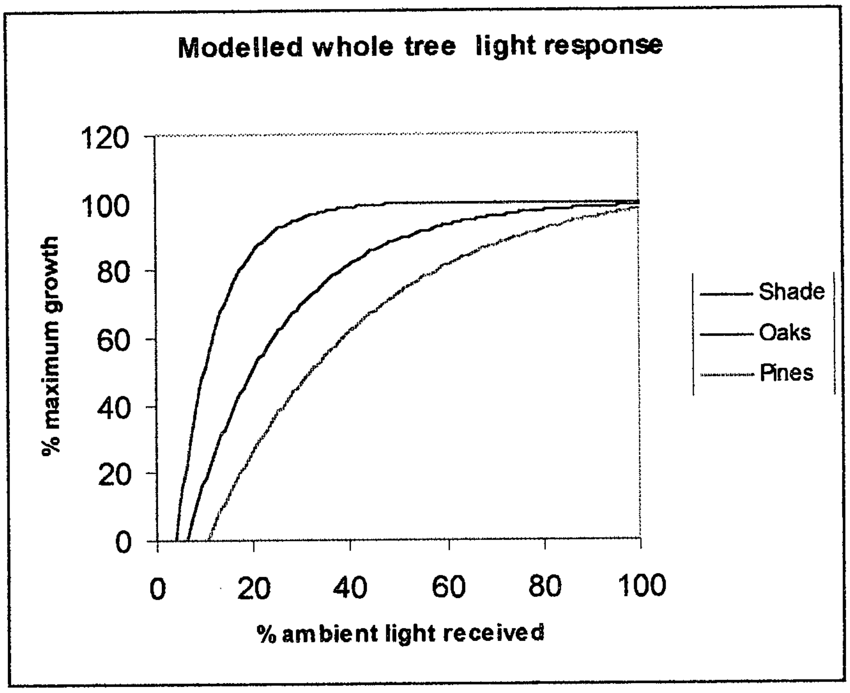
$$f(A) = c_1 \left(1 - e^{-c_2 (A - c_3)}\right) \qquad \text{Equation 6.15}$$

Where f(A) is the light response function, A is the available light and c1,c2 and c3 are constants. Based on the literature three light response classes have been used. These are shown in table 6.7 and figure 6.9 A shade tolerant class has been included in order to allow experiments which include additional species from broad leaf forests.

Table 6.7 Parameters used to model light response for three classes of tree

Class	c1	c2	c3
Shade tolerators	1	0.04	12
Oaks	1	0.06	5
Pines or heliophiles	1.05	0.12	3

Figure 6.9 Modelled whole tree light response for three classes of FG. A shade tolerant class that has not been observed at the field site has been included in order to allow scenario analyses.



The effect of modelled patch size on the simulation

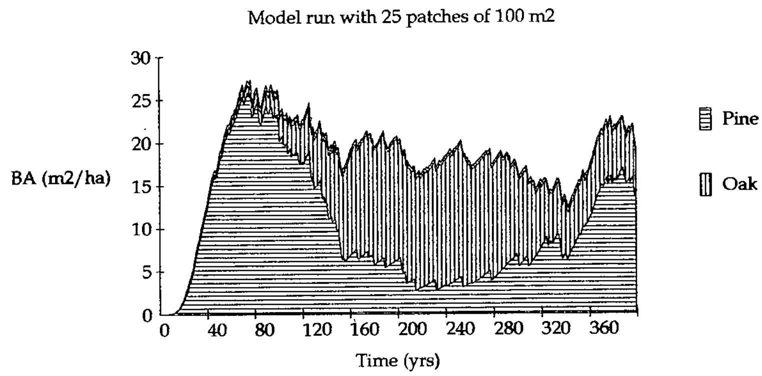
To conclude this treatment of the structure used to link individual trees in the simulation, a consideration of the effect of modelled patch size is necessary. Gap models assume that a suitably small area of forest floor can be treated as having a homogenous light environment. The area of a patch is set to be the "*area of influence of one large tree*" (Botkin 1993). This fundamental premise of all gap models is opposed by work suggesting that sunflecks and within-gap light gradients are critical determinants of successful recruitment and thus successional dynamics (Canham 1988; Chazdon 1988; Pearcy *et al.* 1994). Spatially explicit IBMs attempt to resolve this problem by including fine scale heterogeneity. Because the effect of patch size could be fundamental in determining the behaviour of the model the results of a simple sensitivity analysis are included. It hypothesised that the gap model constructed to predict pine-oak dynamics may be sensitive to modelled patch size.

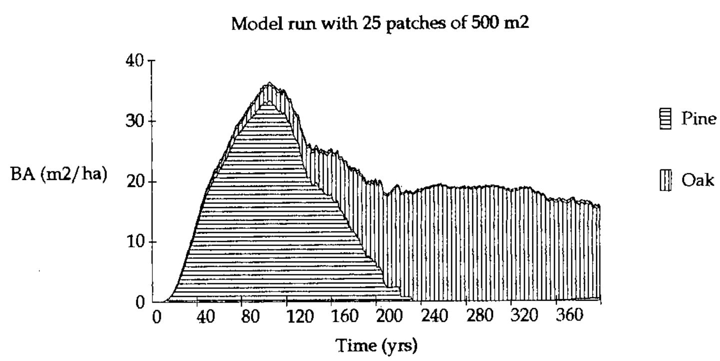
Sensitivity analysis

The species specific parameters measured from the field site were used to initiate the model. To simplify interpretation only *P. maximinoi* and *Q. crispipilis* were included in the model. Modelled patch size was set to 100 m^2, 500 m^2 and 1000 m^2 and the model run for 400 years starting with completely empty patches. Figure 6.10 shows changes in basal area over the 400 years of simulated succession. There is very little difference between runs with patch size set to 1000 m^2 and 500 m^2. Pines are replaced by longer lived and slightly more shade tolerant oaks after around 200 years. However if patch size is reduced to 100 m^2 a marked alteration to the pattern emerges. Pines are not lost from the vegetation when the first wave of mortality of large trees takes place.

When an anthropogenic disturbance regime is simulated which kills all trees in a patch regardless of size, the patch size effect is much less noticeable. Figure 6.11 shows the results of running a model of 25 patches for 400 years which includes a stochastic anthropogenic disturbance regime with three different patch sizes. The pattern produced by each of the models is very similar.

Figure 6.10 Gap model simulations of the dynamics of a pine-oak forest using three contrasting patch sizes. 1) Small patch size 100 m^2, 2) Intermediate patch size 500 m^2 3) large patch size 1000 m^2





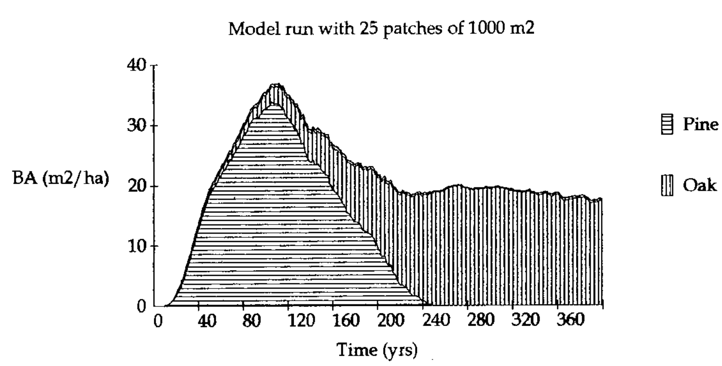
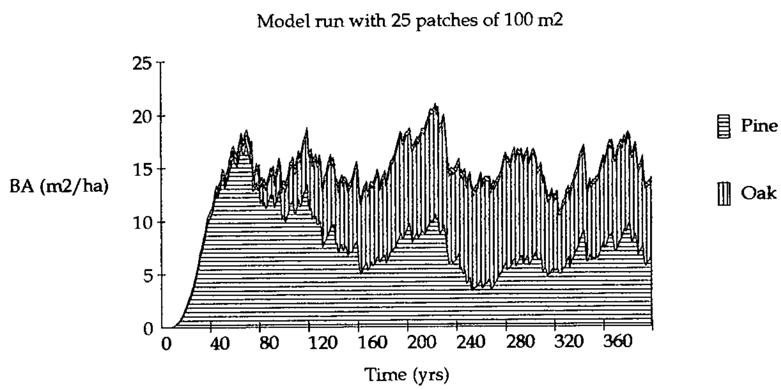
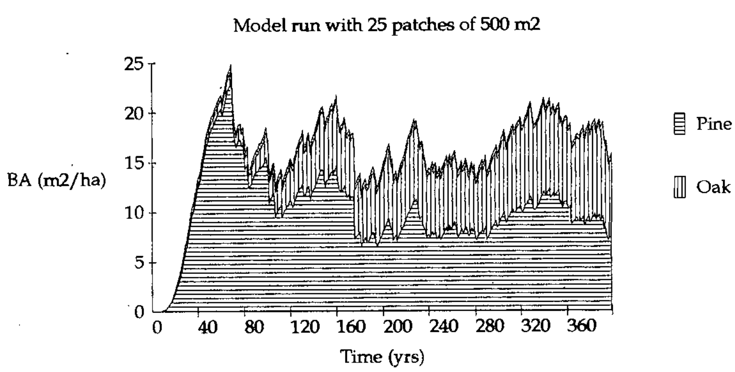
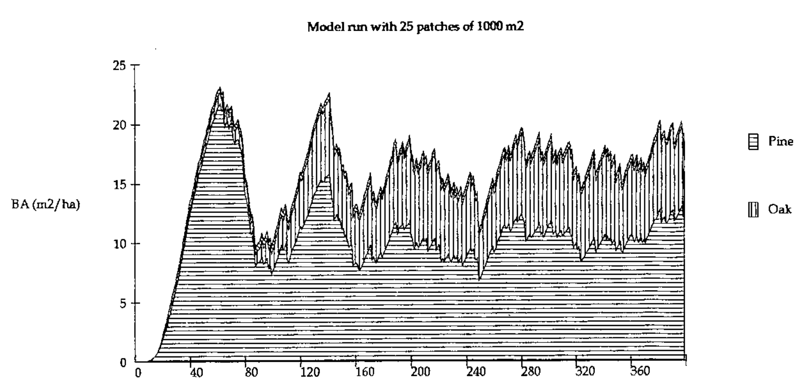


Figure 6.11 Gap model simulations of the dynamics of a pine-oak forest being periodically disturbed by low intensity slash and burn agriculture using three contrasting patch sizes. 1) Small patch size 100 m^2, 2) Intermediate patch size 500 m^2 3) large patch size 1000 m^2







Discussion

This gap model is sensitive to arbitrary decisions regarding the size of the modelled patch. There is no reason to believe that other versions of JABOWA-FORET would be less sensitive, and the effect has been recognised by the originators of the approach (Botkin 1993; Shugart 1984; Shugart 1998). While this is of intrinsic interest to system theorists it is a barrier to model development based only on measurable individual attributes. If a modelled patch is initiated with no trees, the effect arises in mid succession. At some point the patch may become dominated by one or a few large trees. The difference between a patch holding one tree and one with several large trees is important when the tree dies. If the patch holds only one large tree, its death has a large impact on the patch environment. In the most extreme case the light at ground level may change from below 10% of ambient light to 100%. If the patch is large enough to hold several trees the light environment will not alter as much. Therefore, counter to intuition, a small modelled patch size leads to simulations in which autogenic disturbance appear to cause large canopy gaps, while a large patch size leads to autogenic disturbance having small effects. As gaps in forests are not only the result of the death of very large trees setting gap size to the area of influence of the largest possible tree only provides a partial solution.

From a systems theory perspective the gap size problem could be described as a form of edge effect. Information from outwith the models boundaries is needed to fully capture the system properties. If the patch is set to the size of a single large tree the sudden change in light when it dies is not a realistic representation of the system under consideration if the tree is growing within a stand of other trees of similar size. However increasing the patch size too much removes most of the spatial heterogeneity that gap models were designed to capture. The extent of information needed from outwith the patch will depend on many factors and will be specific to the forest type. Tree size, community structure, successional rates and disturbance frequencies all will be important. Furthermore, because the main cause of the effect is the way the model represents light, latitude plays an important role due to its effect on zenith and azimuth angle. On hill slopes aspect may also be important.

The challenges associated with modelling light in IBMs has been extensively discussed (Deutschman 1996; Deutschman *et al.*1997a; Deutschman, Levin and Pacala. 1999) A particularly accessible treatment is provided by Deutschman *et al.* (1997b). In the context of shade induced mortality Pacala *et al.* (1994) concluded that FORET-JABOWA type models "*produce the right results for substantially the wrong reasons*". The assumptions of patch models were also criticised when using mean field approaches to parameterising the model SORTIE (Deutschman *et al.* 1997b). This work in developing a predictive tool for this project supports this assertion that the gap model paradigm could be inappropriate as a framework for purely process based modelling. Simple gap models such as that produced for this study are perhaps best regarded as emulators of forest dynamics rather than truly mechanistic simulators, and are demonstrably unrealistic. However it is not lack of realism which is considered to be the fundamental problem. All ecological models lack realism to a greater or lesser degree yet may be successful. The limiting aspect of gap models for purely bottom up modelling arises from the effect that unmeasurable, or poorly typified parameters and subjective design choices have on model results. Fortunately for the case under consideration, when simulations are conducted in which forests periodically suffer allogenic disturbance the patch size problem is of less concern. Ironically it turns out that despite many of the problems of data interpretation that have arisen as a result of disturbance, highly anthropogenically disturbed forests are easier to model than the undisturbed situations. Under an anthropogenic disturbance regime errors associated with inaccurate light measurements and artefacts arising as a result of modelled gap size become largely irrelevant.

The gap size problem remains as a barrier which prevents precise prediction of the ultimate outcome of some model scenarios. The question of whether pines would completely be displaced by oaks over long time scales or become fugitive species within a forest matrix dominated by oak can not be fully answered. Yet for many purposes the patch model should produce contextually correct behaviour. Despite having gone to considerable lengths to improve the modelling of light interception in IBMs Deutschman, Levin and Pacala (1999), in what may seem a direct contradiction to the conclusions of earlier work state:

"*The FORET class of models use an algorithm in which the landscape is divided into cells and the light is assumed to follow Beer's law as it penetrates the aggregated canopy of all trees in each cell. Our work with a more detailed light routine supports the idea that simplified light regimes are appropriate.*"

This statement was made as it became apparent to the researchers that emulation of forest behaviour does only require comparatively simple models when it is assumed that long term forest dynamics are known before modelling begins. The result that oaks replace pines over long periods without disturbance may be sufficiently uncontroversial to allow a model which successfully predicts this behaviour to be used to investigate novel scenarios.

Additional aspects included in the model

Non density dependent mortality

It has become a convention in gap models to include a parameter (AGEMAX)which represents the maximum expected age of a tree. This is used to estimate non density dependent mortality by assuming a small proportion (1%) of trees reach this age. From Shugart (1998) this gives

$$Pm = 1 - e^{\frac{-4.605}{\mathrm{AGEMAX}}} \qquad \text{Equation 6.16}$$

Modelling establishment

Some form of positive interaction between colonisers is usually assumed to occur during pine-oak succession. The classic pattern of pine-oak dynamics which has been found by studies in the Eastern United States, notably the Piedmont area of Carolina, is that establishment of pines on abandoned fields produces conditions which are attractive to jays and small mammals, leading to the eventual establishment of oak understorey (Peet and Cristenson 1988). Similar patterns have been reported from many other mixed pine hardwood stands (Horn 1974; Peet 1984). Oak regeneration has been found to be facilitated by the presence of shrubs (Rousset and Lepart 1998).The comparative extremity of the microclimate of open tropical establishment microsites when compared with areas with canopy cover is accentuated in montane areas by the localised effects of winter frosts. Alteration in micro-habitat which may influence establishment are commonly found when more arid habitats are considered (Valiente-Banuet *et al.* 1991; Valiente-Banuet, Vite and Zavala-Hurtado 1991). Herbaceous plants may compete with oak seedlings (Gordon *et al.* 1989; Gordon and Rice 1993) but the extent to which this leads to mortality is unclear.

Facilitation (Clements 1928; Connell and Slatyer 1977) has been defined by Glenn-Lewin and van der Maarell (1992) as describing a *situation in which one or more species enable the growth or development of other species.* The avoidance of the term process in this definition recognises that the processes involved may be extremely complex and can not be easily summarised in a single term (Walker and Chapin 1987; Bazzaz 1996). If the situation in which facilitation occurs can be detected by the model during the course of a simulation its effects can be simulated. Clearly a model which adopts this approach is not capable of fully investigating the processes underlying succession. Most gap models to date have in fact used such a set of simple contextual switches to determine establishment. There are few alternatives available for modelling the system under consideration without a great deal of further work.

Consideration of these observations led to the incorporation of a simple establishment rule into the model. The rule is based on the proportion of ambient light at ground level in the model. Species are placed into three classes with minimum and maximum requirements for light at ground level. Light at ground level is considered a surrogate for a range of factors involving canopy development.

Table 6. 8 Minimum and maximum light levels for three establishment classes used in the model

Class	Minimum	Maximum
Extreme heliophile	35 %	100 %
Exposure sensitive	5 %	95 %
Shade tolerator	0 %	35 %

In order to reduce computations involving large numbers of individuals, establishment in all gap models is modelled at the sapling stage. Thus after a major disturbance the model does not permit establishment for five years in order to represent the process of growth to sapling size. Resprouting is incorporated in the model by allowing a proportion of disturbed stems to re establish, regardless of whether the light requirement for facilitated establishment is met. This proportion is species specific and is set at 0.9 for oaks and 0.1 for *P. oocarpa* from a consideration of the results produced at the site.

Rates of establishment for each species were estimated from observations of abandoned milpas (chapter 3). The model was found to be trivially sensitive to these estimates when patch level dynamics are followed over short periods, but sensitivity over longer periods and at larger spatial scales was found to be extremely low unless pathologically low rates of establishment which fall below mortality rates were simulated. Further work into the demography of trees at the site would improve short term model behaviour.

Simulation of disturbance regimes.

A simplified rule based representation of disturbance has been incorporated in the model at this stage. This is intended as a step towards automated linkage of a successional model with Bayesian belief networks (chapter 5)

The rules incorporated for milpa disturbance act only at the patch level, rather than the whole model level, even though over long periods feedback between stand level properties and decision making should be incorporated. Each modelled year the patch basal area is compared with a minimum at which it becomes vulnerable for slash and burn clearance. This matches the most important criteria used by the farmers to evaluate suitability (chapter 5). Each suitable patch is given a random probability of being a selected for clearance. This probability would be some function of population size and could be linked to either a simple or a detailed model of demographic growth if this were desirable for scenario building.

Each species in the model is provided with a parameter for the minimum diameter at which a tree becomes available for logging. For non loggable species this is set to any value above the maximum size for the species. In the disturbance module the number of years between logging regimes can be set, and the proportion of suitable trees extracted. This simple regime does not take into account collateral damage, or stratified systems for logging. Collateral damage caused by falling pines is a rather minor cause of mortality in these forests (pers obs) This contrasts with the observation that up to 75 % of mortality in some tropical forests can be caused by the impact of falling trees (Van Der Meer and Bongers, 1996). Stratified logging regimes could be easily incorporated into the model if a management plan were available on which to base scenarios. Suitable seed sources for regeneration are always assumed to be available by the model, thus changes in the species mix due to disturbance is due mainly to alterations in competitive interactions between species.

Fire is simulated as causing the same pattern of mortality to that observed and reported in chapter 4. This could be altered to take into account fuel accumulation. However fuel does not accumulate to the same extent in this form of forest as it would elsewhere due to fuelwood collection. Thus when fires occur they may well have a similar intensities. There is little evidence of more intense fires at the site in historical times.

In all simulations, suitable seed sources for regeneration are always assumed to be available by the model, thus changes in the species mix due to disturbance is due mainly to alterations in competitive interactions between species.

Conclusion

The detailed analysis of gap model characteristics which was required in order to build a working version only partly supported the initial postulate that large scale patterns at the field site can be predicted from available knowledge of the behaviour at lower scales. Difficulties were encountered in parameterisation. Decisions had to be made regarding measurements based on logistical considerations rather than the needs of the model. While building an internally consistent model may be possible, linking such a model to the natural system of interest was found to be the principal challenge. A process based approach places demands on the level of knowledge that can force over analysis of incomplete data that would otherwise not be attempted. Because the inclusion of speculative assumptions was considered highly undesirable, some of the relationships used in the model were over simplified to allow their linkage with available information. As the model developed it became less complex than initially planned as detailed formulations were substituted for simpler rules. The formulations of the original versions of the gap model were returned to after experimentation with other methods. Subjective choices made concerning the implementations of an IBM were found to have a greater influence on the final results than expected.

Initially unexpectedly technical issues arose and the gap size problem was identified as a fundamental weakness of gap models. Young (1998), reporting the results of an extensive period of model development, refers to unexpected problems of this kind using the informal but revealing expression "*pathological*" behaviour. In other words either an undetected error, or some unexpected property of the structure used to link entities in the model caused behaviour which deviates so greatly from an expected pattern that the model's predictions were considered unsuitable for their purpose. Object oriented programs are comparatively easy to debug and true errors can usually be traced. Model structure itself remains the most likely cause of unexpected behaviour. The term "pathological behaviour" gives an impression of weakness in the general approach It seems preferable to refer to behaviour which arises as a result of decisions regarding model structure as artefactual behaviour.

Recognition of artefactual behaviour will depend on the context of the model's use and the experience the model designer has of the natural system that is being modelled. It may be undesirable to place confidence in the results of mathematical or simulation models alone. For example, a mathematician could find exotic behaviour, such as deterministic chaos, limit cycles or the effect of modelled patch size in gap models a fascinating area for study in itself. Whether any given natural system's behaviour follows directly from that found in mathematical models is unclear (Hastings *et al.* 1993). The question of how a model's behaviour arises may need careful investigation. For example chaotic behaviour can arise in a model as an artefact of the integration method chosen (May 1979). Simple changes in the order in which updating of state variables is carried out can cause artefactual behaviour (Bugmann, Fischlin and Kienast 1996).

Just as uninformative experiments are not documented, model runs which produce artefactual behaviour may often go unreported and are therefore not available for evaluation by those not involved in the model building process. This could lead to a degree of over optimism regarding the potential uses of bottom up process based models. The most appropriate tools for management purposes may well be robust top down expert systems rather than bottom up process based research models.

These considerations apart, designing a model and inspecting model runs improves understanding of the system and reveals areas for further research. More confidence can be placed in the combined conclusions drawn from the model and observations than those drawn from observations alone. The software became a valuable tool not only for research but for didactic purposes. In the context in which the research was conducted visual output in the form of profile diagrams was found to be especially valuable for communicating results to forest users. Bottom up system modelling is challenging and requires a great deal of research effort in order to reach its full potential. However it is not easy to find alternative quantitative methods for addressing questions regarding the dynamics of a system when limited phenomenological information is available. Empirical approaches to predicting forest change require time series data

To some extent the model of pine-oak dynamics presented in this study did become an expert system over the period of development. Field experience does inevitably produce undocumented natural history based understanding of the natural system. While this experience may not be directly incorporated in models, it exercises a degree of "editorial" control over model behaviour (see Dennis 1996 for criticism of statistical models which mix data with beliefs). Behaviour that was believed not to represent the system of interest was observed at several points during development of this model. The problems caused by this were resolved with reference to conceptual models of how the system would behave such as the self thinning rule or the replacement of pines by oaks, even though direct evidence of such processes in operation at the field site was not available.

Applied sylviculture relies mainly on knowledge based on natural history, yet is widely successful. If the work documented here is to be developed, further information derived from phenomenological observation is necessary for validation. This will become available as monitoring of the PSPs continues and further research into processes is conducted. New knowledge should be incorporated into the model framework in a formal manner. A promising new statistical approach that could be used is Bayesian synthesis (Green and Strawderman 1996; Green, MacFarlane and Valentine 2000). Bayesian synthesis can combine information on both underlying processes and the resulting larger scale phenomena into a single formal statistical framework Unfortunately the techniques involved are mathematically involved and many problems involving non linear dynamic models are as yet intractable (Kass and Raftery 1995). The use of Bayesian inference in basic research has been strongly criticised on fundamental grounds (Dennis 1996; Edwards 1996).

In conclusion, individual based gap models are capable of flexibly reproducing successional patterns but may require some higher level information to do so. The exercise in model construction successfully identified areas for attention and produced a model which can be used for making site specific predictions, providing all the assumptions being made are clearly recognised by model users.

Chapter 7. Scenario building using a gap model representation of pine-oak dynamics

Introduction

In the last section the model's sensitivity to decisions regarding a subset of the parameter values and structural considerations were investigated in isolation during software development. Sensitivity analysis was used to critically assess the model's structural basis and the assumptions used. Attention now turns from a study of the model to a study of the connection between the model and the real system it represents. Despite a degree of structural complexity, the model remains very much simpler than the system of interest. Questions which arise are; Can the model's behaviour be related to aspects of the system it represents? Can predictions be made regarding the behaviour of the real system which could not have been derived without the use of the model? These question leads to model validation and scenario building.

The parameter space of even this moderately complex simulation model is too large for comprehensive exploration. Analysis of all aspects of behaviour using formal techniques of sensitivity analysis is not possible. A moderately large model (225 patches) requires over five hours to complete a run of 200 years on a 300 MHz PC. An alternative to complete exploration is to focus on a small set of parameterisation which represent plausible scenarios built from a consideration of the natural system on which the model is based.

Limitations of the model must be considered when it is used. Questions the model can address involve yield of the two FGs, long and short term changes in dominance of the two FGs and changes in the forest's overall structure under different disturbance regimes. Changes in the relative abundance of each species of pine and oak can also be investigated, but unless the model is deliberately adjusted to mimic the site under consideration, all species are assumed to be available to colonise each model patch. Without imposing additional constraints the model does not reproduce a situation in which species are spatially segregated. Dispersal of propagules is not included, thus although the position of patches used to initialise the run may be visualised, the model is non spatial. There is no communication between patches and spatial relationships found in data used for initialisation will tend to break down during each run. No suitable data is available from which to parameterise scenarios involving propagule dispersal, but the consequences of relaxing these constraints in a simplified derivative of this model will be investigated in chapter 8.Additionally, while the model has been optimised in order to reproduce the effect of poor growth conditions through the *SoilQ* parameter it cannot be used to investigate situations in which chronic stress dynamically alters growth potential.

Five scenarios have been used to demonstrate the model's properties. The results of each scenario can be translated from the quantitative output into more general qualitative statements regarding the system of interest.

Validation scenario: Does the model produce results compatible with observations at the site if the assumed pattern of historical disturbance based on milpa farming is simulated?

Conservation scenario. What effect would a complete cessation of disturbance have on the stand at the field site?

Fire scenario. What effect do periodic fires have on future dynamics?

Logging scenario. What effect will selective logging have on the stand?

Archaeological scenario: If shade tolerant broad leafed trees typical of cloud forests dominated the site at some point in the past, would they have been lost under slash and burn?

In some implementations of gap models a single modelled patch has been referred to as the model (Botkin 1993). Because gap models used stochastic representations of mortality and establishment repeated runs are usually necessary to discover the repeatable aspects of the simulation. Additional variability is included in this implementation through the use of stochastically drawn parameters. The term model here refers to this collection of patches. This means that a large amount of independent replication is included in model runs.

The software holds results in memory while a run is progressing. An option also exists to save the results of a run in the form of a database table for further analysis. Time series of basal area, biomass or number of stems per hectare for each species are held both at the patch level and the model level. Stacked area plots of the means of time series at the whole model level have become a convention used in communicating gap model results. However this output does not fully display the distribution of variability within the model. This is revealed by histograms of the frequency distribution of patch basal area at some point in the run. More intuitive investigation of patterns may also be conducted through inspection of modelled profile diagrams for each patch, which display a simple representations of trees, light penetration and a description of the forest type. Inspection of this output has proved useful for initial evaluation of model behaviour. Because the model produces a very large amount of output for any single run, graphs have been chosen to demonstrate only the most relevant points for each scenario.

Variability between patches is a structural feature of the model. Nevertheless when the results are reported no estimate of whole model error is available from a single run. An estimate of the variability for the whole model could be provided by multiple runs using different random number seeds. However experimentation showed that little variation occurs between large models, due to internal averaging of stochastic variation. Model runs can be treated as deterministic when means taken from a sufficiently large model are considered. "*sufficiently large*" may be taken to mean a model containing over 50 patches and over 2000 individual trees.

The modelled patch size is 500 m^2, which corresponds to the area used in the inventory data used for validation. Each patch can also be conceptualised as being representative of a rather larger area. Milpa disturbance affects areas of around 1 hectare. A milpa clearance affects all the trees in a single patch. One representative patch may thus be used to represent a single milpa. Model validation is achieved through comparisons of patch and tree level variability between model results and inventory.

Method

The species specific parameter set that has been used for all the scenarios is given in tables 1 and 2. Where data was not available for parameterisation of standard deviations used in the model they have arbitrarily been set assuming a coefficient of variation of 0.1

Comparisons between the model and the inventory data set could be made using a Kolmogorov- Smirnof test or the chi squared statistic. However statistical significance testing can be inappropriate in this context for two reasons. 1) The null hypothesis is intrinsically more likely than its alternative 2)The power to detect a difference is under the control of the modeller. For attributes such as diameter distributions a comparison of the distribution of variation in the model and data is a more important test of the model's validity as is a test of differences between measures of central tendency. This may be particularly important if distributions in the model or data become bimodal. As the model almost certainly differs from the data in some respects failure to find a significant difference would be due to type two error (Johnson 1999).

A easily interpreted goodness of fit statistic is reported instead of a hypothesis test. This statistic is designed to complement visual inspection of histograms and gives a simple guide to the extent of difference between model and data. It is a similarity index calculated as the mean difference between model and data for any N model attributes expressed as a percentage. The attributes could be proportions of trees in each diameter class, or proportions of patches in a basal area class.

$$s = 100\left(1 - \left(\frac{\sum_{i=1}^{N} \left|\text{mod}el_i - data_i\right|}{\sum_{i=1}^{N} (\text{mod}el_i + data_i)}\right)\right) \qquad \text{Equation 7.1}$$

This equation is after Cormack (1971) and Wolda (1981) and has been used in a simulation modelling context by Lischke Loffler and Fischlin (1998) and Bugman (1994).

The regime of milpa clearance used for model validation is based on the knowledge incorporated in the Bayesian networks produced in chapter 5 and studies of regeneration in milpa patches. An automated linkage between the forest model and Bayesian networks has not been used to date. Because the contemporary forest formed when the population of the village was considerably smaller than present and very long rotation slash and burn was still practised the validation scenario has included a low rate of slash and burn clearance. Patches become available for clearance when they reach a basal area of 25 m^2 ha^{-1} . In any single year 5% of the patches which are suitable for use are cleared. This model thus ignores some of the contemporary changes in the milpa regime investigated in chapter 5, but is expected to approximate to the historical disturbance regime which a large part of the extant stand has experienced.

The conservation scenario assumes no disturbance affects any of the modelled patches and begins with the model in the current forest state. The immediate effects of the fire induced mortality are subtracted from the model by assuming all measured trees are alive. The model is then run for 200 years with only naturally occurring mortality simulated.

The fire scenario uses the measurements presented on fire induced mortality in chapter 3. The results presented are for a scenario in which it is assumed that fires of this intensity affect the forest every twenty years. This is a deliberately short fire return interval and the sensitivity of the model to increasing the fire return interval is also discussed. Changes in fire intensity are not modelled due to insufficient information.

A logging scenario is used in which 25% of the available pine timber (trees over 35 cm DBH) is extracted from all plots every 40 years. As in all other scenarios limitations to post logging recruitment are not included. Other logging scenarios could be built. This is included for illustration. Short term production of pine timber should be more accurately predicted by the model than by most alternative methods due to the avoidance of aggregation error in the IBM under the assumption that the method used to optimise the growth model produced an accurate representation of individual based pine growth.

In the archaeological scenario a fictitious shade tolerant broad leafed tree typical of cloud forests is included in the model. One candidate for inclusion in this functional group is *Olmediella bestchleriana* (Goepp.) Loes (Flacourtiaceae). This is an infrequent but widespread member of the flora of the field site. This species like many broadleaved shade tolerant members of the cloud forest flora of the region may be restricted in its distribution not only by the lack of micro sites for establishment but by its dispersal mechanism. In this scenario it is first assumed that no barriers to seed dispersal are found. The model is run for six hundred years from the starting conditions with no disturbance. This allows the shade tolerant species to come to dominate the canopy. This simulated mature forest is then saved and the model is run again with the same disturbance regime which was used in the initial validation scenario.

Table 7.1 Description of the species specific parameters required to run the model.

Parameter	Description	Units	Source
Species code	Integer. Used to link data to inventory table		
Name	Scientific binomial or name of FG		
Dmax	Maximum diameter. Asymptote of growth curve	cm	Ch. 6
Dmaxsd	Standard deviation of maximum diameter	cm	Ch. 6
Hmax	Asymptotic height reached by species	cm	Ch 1.
Hmaxsd	Standard deviation of asymptotic height reached by species	cm	Ch. 1
AgeMax	Maximum age reached by species	yrs	Estimate
Agemaxsd	Standard deviation of maximum age	yrs	Estimate
IncMax	Maximum diameter increment attainable in ideal conditions.	cm	Ch. 6
IncMaxsd	Standard deviation of the maximum diameter increment.	cm	Ch. 6
LAI	Leaf area index		Ch. 6
LAI	Leaf area index standard deviation		Ch. 6
CanopyConstant	Constant of proportionality between squared diameter and projected crown area		Ch. 1
CanopyConstantSD	Standard deviation of canopy constant		Ch. 1
ExtinctionCoefficient	Species specific estimate of canopy extinction coeficient		Ch. 6
c1	Constant in light response curve		Ch. 6
c2	Constant in light response curve		Ch. 6
c3	Constant in light response curve		Ch. 6
CritIncrement	Critical diameter increment below which mortality occurs	cm	Ch. 6
CritIncrementSd	Standard deviation of critical increment	cm	Ch. 6
Resprouts	Proportion of cut stems which survive through resprouting	proportion	Ch. 5

Colonisation	Mean number of stems establishing over time when conditions are suitable	ha^{-1} yr^{-1}	Ch. 3
Colonisationsd	Standard deviation of the colonisation rate	ha^{-1} yr^{-1}	Ch. 3
Biomass1	Allometric constant for converting diameter into biomass in tonnes		Lit.
Biomass2	Allometric constant for converting diameter into biomass in tonnes		Lit.
FormFactor	Form factor used in forestry		Lit.
LoggableMin	Minimum diameter at which a tree becomes suitable for logging	cm	Pers obs.
Fire1	First constant of logistic regression constant of mortality probability on diameter		Ch.2
Fire2	Second constant of logistic regression constant of mortality probability on diameter		Ch.2
Establishment	Shading requirement class for establishment to take place	3 classes	Ch. 6
MatureDiameter	Diameter at which seeds are produced (not used if empirical establishment rate given)	cm	Lit.
Clonal	Can a species reproduce clonally (not used if empirical establishment rate given)	Binary	Pers obs.
Bark	Proportion of diameter occupied by bark	Proportion	Pers obs.
Value	Monetary value in US dollars of 1 cubic metre of timber	US $	Local info.
HardWood	Is the tree likely to be left standing if large when a milpa is cut due to hard wood?*	Binary	Pers obs.

Notes: In the absence of any local measurements, form factor for the three pine species has been set at a conservative level of 0.4 which has been obtained from unpublished data for the area. Many pines at the site have poor form and may be unsuitable for timber. In the absence of precise information it has been assumed that 20% of trees are unsuitable for logging. Form factor has no relevance to oaks which do not produce timber but an arbitrary figure may be included for completeness. The parameter "*Hardwood*" has been included in order to enable the observed effect of isolated large trees being left in milpas when cleared. If a tree is above 50 cm in diameter and the species has hardwood the probability of being spared when milpa clearance occurs is set to 0.2. This is somewhat arbitrary, but is closer to the real situation than assuming complete clearance. In most runs the use of this parameter has had a negligible influence on overall forest structure, but may be useful if the model were used in a conservation context as remnant trees have a special significance as islands of biodiversity, especially when epiphytic plants are considered.

Table 7.2 Parameter values used as the baseline for all simulations.

Name	Dmax	Dmaxsd	Hmax	Hmaxsd	AgeMax	AgeMaxsd	IncMax	IncMaxsd
Pinus oocarpa	77	5	3200	320	110	11	1.37	0.392
Pinus devoniana	82	5	2700	270	120	12	1.42	0.344
Pinus maximinoi	102	7	3700	370	110	11	1.47	0.356
Rapanea juergensenii	20	2	1000	100	20	2	0.7	0.3
Cleyera theoides	30	3	1000	100	50	5	0.7	0.3
Quercus segoviensis	80	8	2200	220	200	20	0.597	0.298
Quercus crispipilis	110	11	3500	350	220	20	0.74	0.262
Shade tolerrant BL	120	12	3000	220	220	20	0.597	0.298
Shrubs	5	1	500	50	5	2	1	0.2

Name	LAI	LAIsd	CanopyConstant	CanopyConstantsd	ExtinctionCoefficient	c1	c2	c3
Pinus oocarpa	2.43	0.82	0.038	0.0027	0.167	1	0.12	3
Pinus devoniana	2.67	1	0.038	0.0062	0.08	1	0.12	3
Pinus maximinoi	3.16	0.63	0.039	0.0022	0.234	1	0.12	3
Rapanea juergensenii	3	0.6	0.04	0.002	0.4	1	0.06	5
Cleyera theoides	3	0.6	0.04	0.002	0.4	1	0.06	5
Quercus segoviensis	3.28	0.61	0.053	0.0013	0.492	1	0.06	5
Quercus crispipilis	3.01	0.56	0.063	0.0021	0.563	1	0.06	5
Shade tolerant BL	4	0.4	0.063	0.0021	0.563	1	0.04	12
Shrubs	2	0.5	0.02	0.002	0.27	1	0.16	3

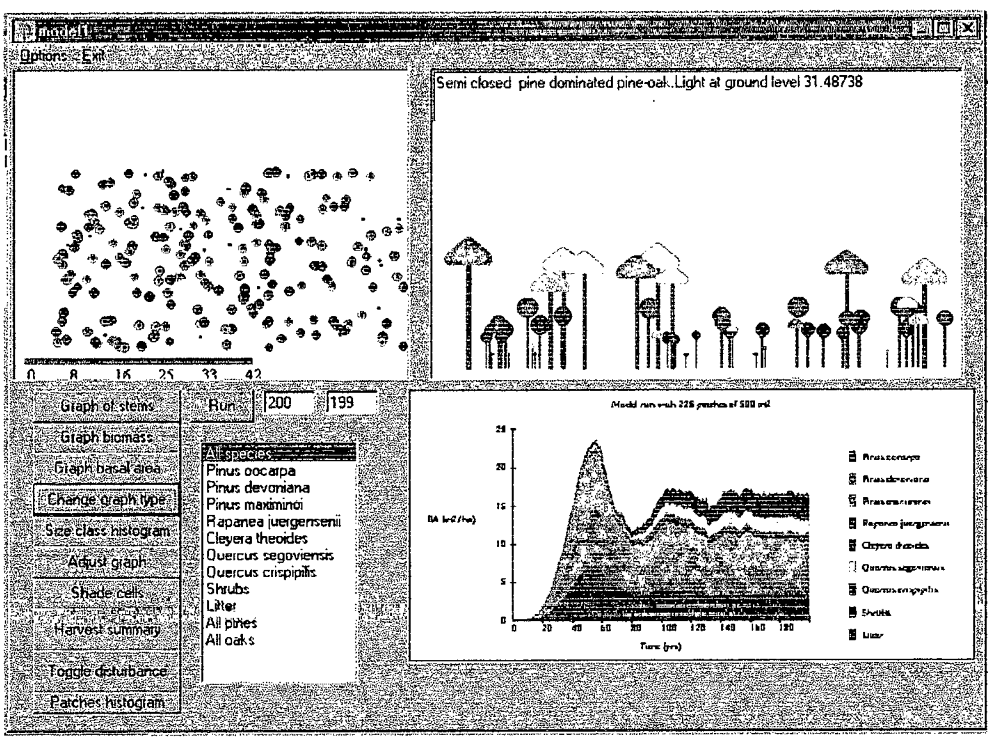
Name	CritIncre	CritIncrementsd	Resprouts	Colonization	Colonizationsd	Biomass1	Biomass2	MatureDiam	Clonal	Bark
Pinus oocarpa	0.24	0.20	0.1	15	3	0.0615	2.1338	15	No	0.1
Pinus devoniana	0.31	0.22	0	7	2	0.084	2.475	15	No	0.2
Pinus maximinoi	0.29	0.07	0	18	4	0.0615	2.14	20	No	0.1
Rapanea	0.1	0.01	0.9	3.2	1	0.113	2.36	5	Yes	0.1
Cleyera theoides	0.1	0.01	0.1	4.2	1	0.113	2.36	5	Yes	0.1
Quercus segoviensis	0.05	0.005	0.9	2.3	1	0.113	2.36	20	Yes	0.2
Quercus crispipilis	0.05	0.005	0.9	5.6	2	0.109	0.109	20	Yes	0.1
Shade tolerant BL	0.05	0.005	0.1	2	2	0.109	0.109	20	No	0.1
Shrubs	0.1	0.01	0.8	30	10	0.113	2.36	2	Yes	0.1

Name	Value	HardWood	FormFactor	LogableMin	Fire1	Fire2	Establishment
Pinus oocarpa	20	No	0.4	35	-1.84	0.03	1
Pinus devoniana	20	No	0.4	35	-2.307	0.342	1
Pinus maximinoi	0	No	0.4	35	-1.84	0.03	1
Rapanea juergensenii	0	No	0.4	100	-1.84	0.03	2
Cleyera theoides	0	No	0.4	100	-2.4	0.1	2
Quercus segoviensis	10	Yes	0.4	100	-2.155	0.367	2
Quercus crispipilis	10	Yes	0.4	100	-2.155	0.367	2
Shade tolerant BL	10	Yes	0.4	200	-2.155	0.367	3
Shrubs	0	No	0.4	0	-1.6	0.1	1

Results

Figure 7.1 shows an example of the GUI written for the model. When the model is run the interface produces "caricature" profile diagrams that provide a convenient means of following the model's behaviour. Profile diagrams are interpreted as showing all the trees in a modelled patch dispersed along a single linear profile. Horizontal distances between trees are not shown in a realistic manner. Tree positions within the patch are not known by the model, and the drawing method used exaggerates distances between them by a factor of 3.14 for circular patches. However the diagrams provide a useful intuitive guide to the structure of the patch.

Figure 7.1 An example of the model interface. Note that in this run patch positions have been randomly assigned in order to give a visual impression of the variability generated as the model is run. As the mouse pointer is moved over the map a profile diagrams is produced for each patch permitting a rapid visual impression of the model characteristics.



Validation scenario

In the validation scenario the model begins with empty patches. The dynamics can be followed with reference to figures 7.2 and 7.3. The initial 100 years of stand development are dominated by pine. Maximum basal area occurs in this phase. The first pines to establish begin to senesce after 100 years in undisturbed plots. Oaks increase their dominance of undisturbed patches as they are released from weak suppression beneath pines. As patches are disturbed by milpa they now begin each regeneration phase with some oak saplings that have been derived from resprouting of already established individuals. This begins to stabilise the model's behaviour. The total basal area as averaged over the whole area falls slightly due to the lower overall rates of diameter increment as oaks increase at the expense of pines. The low levels of disturbance by milpa clearance included in this scenario continue to open the canopy and provide sufficient opportunities for pine species to re-establish. Initially milpa clearances show a degree of synchronicity which leads to damped oscillations. This is due to the way in which the rule used to model decisions regarding clearance combines with the initial low level of heterogeneity in patch basal areas. This breaks down over time. After 200 years the model is beginning to reach an equilibrium at the stand level, although each patch is constantly changing both in its total basal area and in the relative proportion of pine and oak. In this scenario as in others it is assumed that no barrier to oak dispersal into the patches at the beginning of the simulation exists. The overall number of stems and proportions of stems per species in the model stabilises under this scenario before the basal area.

Figure 7.2 Change in basal area over the course of a simulation initialised with no trees and run for 200 years with milpa disturbance. Note that the software produces stacked area plots. The order in which species are listed in the caption is the reverse to the order in which they appear in the stacked graph.

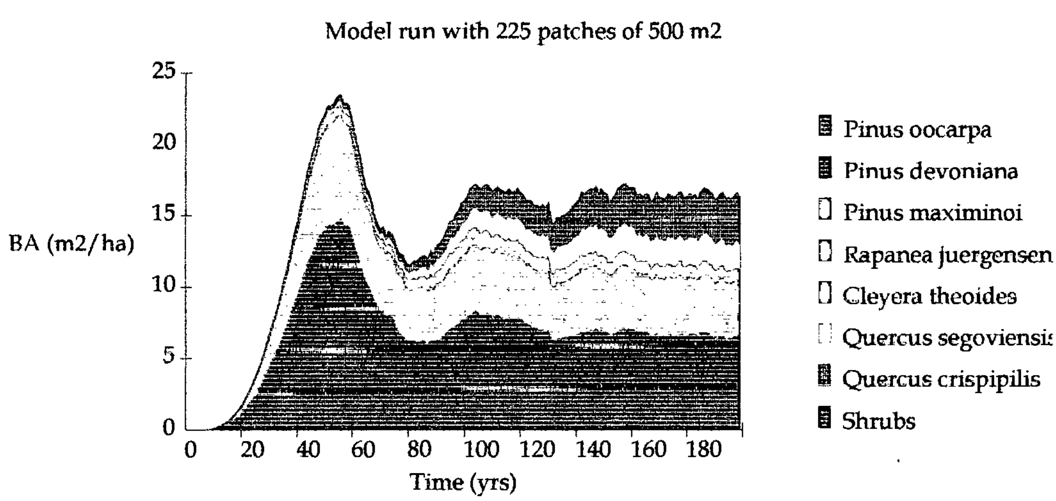
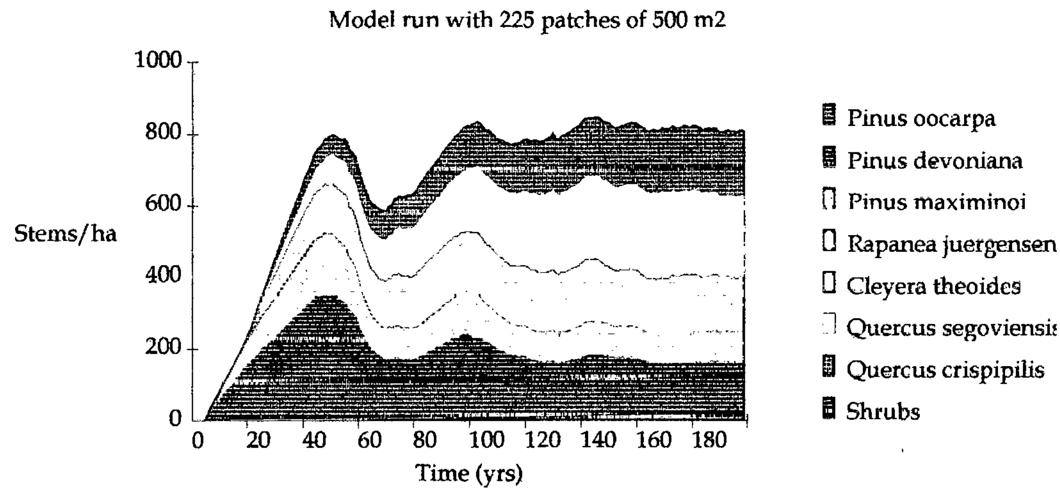


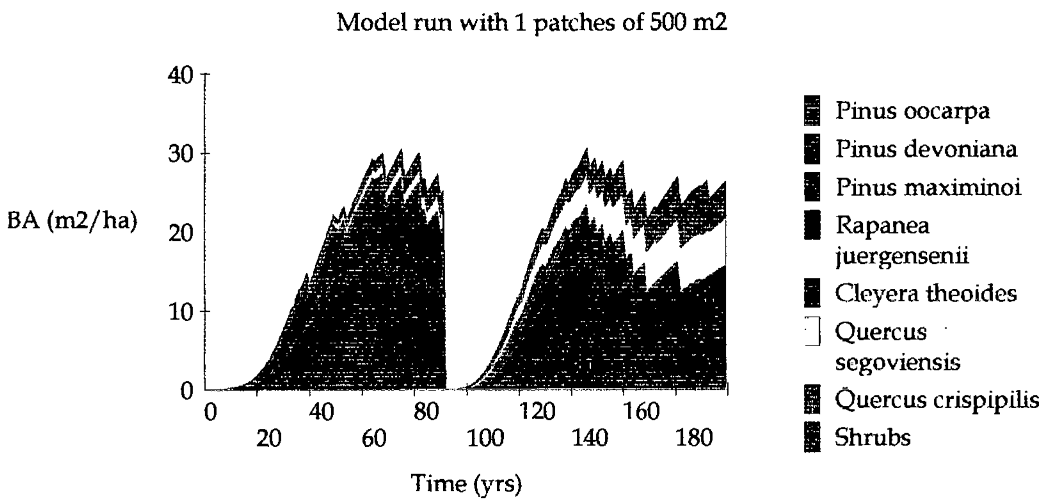
Figure 7.3 Change in stem densities over the course of a simulation initialised with no trees and run for 200 years with milpa disturbance.



This is probably not an accurate representation of how the stand actually formed as it assumes a point at which all patches begin with no vegetation. However it demonstrates the underlying model behaviour. Other runs including some reported here have shown that the model moves towards a similar dynamic equilibria from a very different starting configuration. It may become a more realistic simulation of the current system as the model approaches its dynamic equilibrium.

The dynamics of the system at a smaller scale can be understood by following the development of single patches. Figure 7.4 shows changes in one patch run for 200 years. Following each milpa disturbance full forest cover is re-established within sixty years. During most of the period the patch contains trees or shrubs with only very short periods as agricultural land. This scenario assumes levels of regeneration that were observed at the site and no long term degradation beyond the level which has been incorporated in the model through measurements of the current stand at Sonora. Note also that total basal area thirty years after each clearance is below 5 m^2 ha^{-1} but progression from this rather open and obviously disturbed incipient forest to an area of semi mature woodland that might be superficially indistinguishable from undisturbed areas then proceeds rapidly. The model suggests that superficial visual impressions of forest maturity can be deceptive and that a great deal of spatial pattern may be imperceptible without careful inspection of the age structure of the forest. The common practice of leaving remnant trees in milpas would further hide traces of this sort of disturbance as areas of disturbed forest may be found with some very old trees despite several cycles of canopy opening.

Figure 7.4 Patch level fluctuations in basal area under the milpa model run for a period of 200 years in which two clearances occur. The smaller fluctuations in basal area are due to natural mortality.



After the model has been running for 200 years it begins to reproduce much of the structure found in the forest inventory (Figures 7.5, 7.6, 7.7 and 7.8). The similarity in the distribution of patch basal areas is only 58% (Figure 7.5). However the overall similarity in the diameter distribution of all trees in the model is 72% (figure 7.8). The structure of the pine population is acceptably close to that observed with a similarity index of 79%. (Figure 7.6)This match to the site data might be improved further if disturbance is reduced for the last twenty years of the run to allow some of the smaller pines to move into larger size classes. This has been confirmed, but the run is not reported here. The 63%. similarity between the modelled oak population and the inventory data was less than found for the pines. In particular too few small stems were produced in the simulated data.

Some further support for the model as a realistic representation of the system is provided by figure 7.9 which shows the relationship between above-ground biomass production and basal area in the model. This can be compared with the relationship reported from the PSPs in chapter 1. Although a parabola has been fitted to the data here rather than a hyperbola the match seems acceptable. It shows that yearly net above-ground biomass accumulation reaches a peak when patch basal area is around 25 m^2 ha^{-1}. Biomass production is very variable due to the variability in growth rates built into the model and stochastic mortality but never exceeds 4 tonnes ha^{-1} yr^1.

Figure 7.5 Comparison of the distribution of patch basal areas after the model has run for 200 years with milpa disturbance with the distribution measured in the forest inventory of the bienes comunales at Sonora.

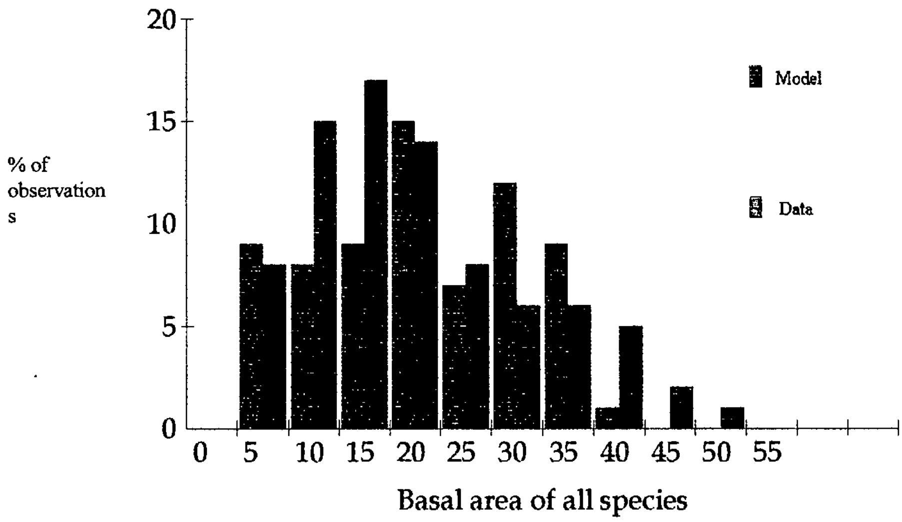


Figure 7.6 Comparison of the distribution of diameter distribution of pines after the model has run for 200 years with milpa disturbance with the distribution measured in the forest inventory of the bienes comunales at Sonora.

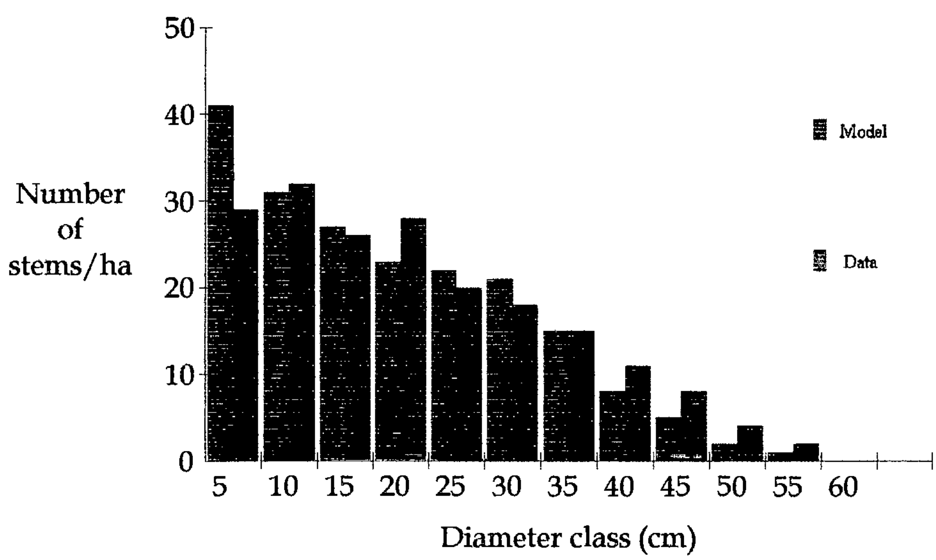


Figure 7.7 Comparison of the distribution of diameter distribution of oaks after the model has run for 200 years with milpa disturbance with the distribution measured in the forest inventory of the bienes comunales at Sonora.

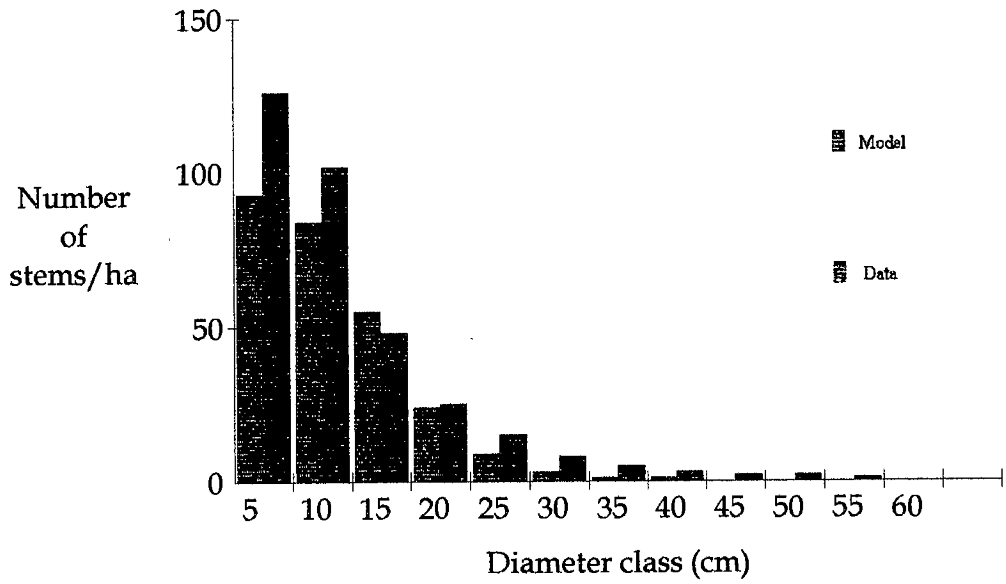


Figure 7.8 Comparison of the distribution of diameter distribution of all species after the model has run for 200 years with milpa disturbance with the distribution measured in the forest inventory of the bienes comunales at Sonora.

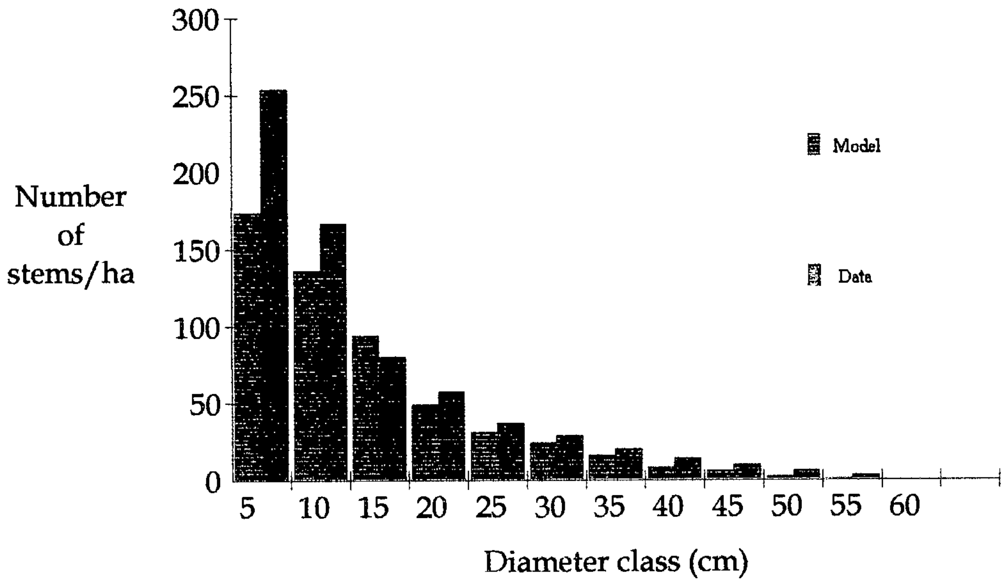
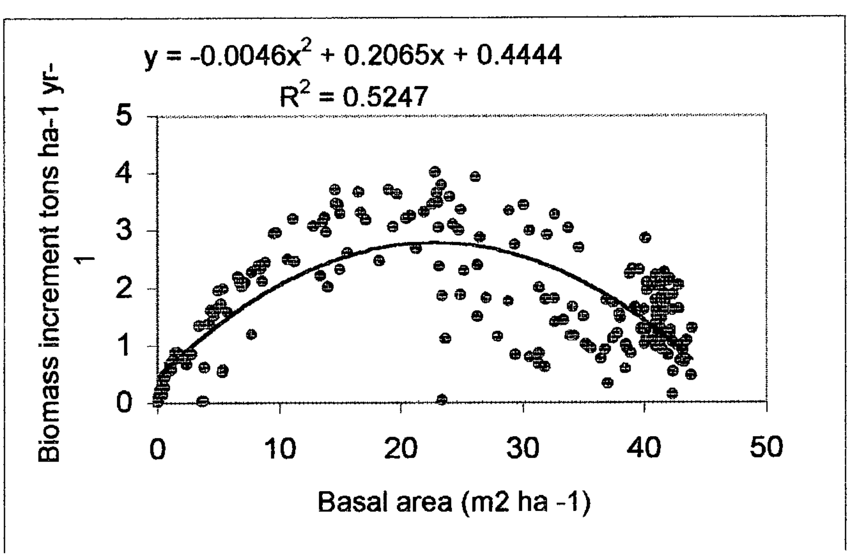


Figure 7.9 Net biomass production in the model as a function of basal area. Dead trees have not been subtracted from the total.



A further test of the model was conducted for validation purposes. The model was initialised using the inventory data. The effect of the recent fire induced mortality was ignored under the assumption that low intensity milpa disturbance rather than fires had played the major role in past stand development and the model was run for a further 200 years. Some changes in the relative species composition occur, most notably an increase in the basal area of *Q. crispipilis* and *P. devoniana* (Figure 7.10). This is largely due to the lack of spatial segregation between the species in the model which allows the spread of rarer species. However the overall pattern of relative dominance of pines and oaks only undergoes minor change over this long period. This does suggest that the disturbance regime included in the model could be a realistic representation of the natural system in dynamic equilibrim

Figure 7.10 Change in basal area over the course of a 200 year simulation initialised with the inventory data and run for 200 years with low levels of milpa disturbance.

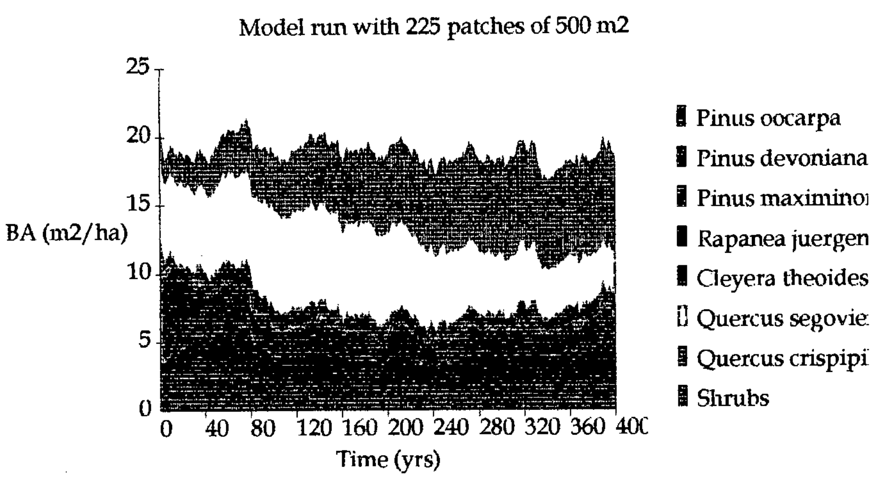
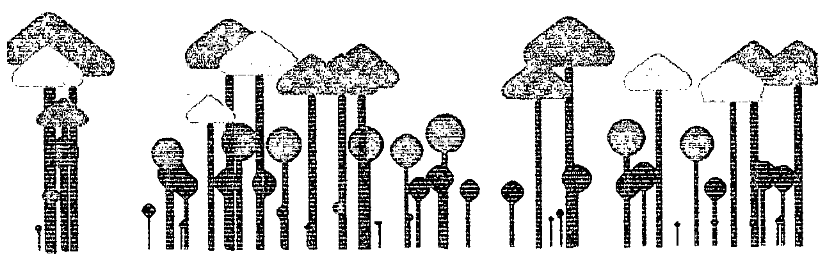


Figure 7.11 Example caricature profile diagram of a typical patch of 500 m^2 after a 200 year simulation initialised with the inventory data and run for 200 years with low levesl of milpa disturbance. The patch has a mixed overstorey of pines with an understorey of *Q. segoviensis*, *Q. crispipilis* , *Cleyera theoides* and *Rapanea juergensenii*.



Conservation scenario.

The results of a model initiated with the inventory data and run for two hundred years with no disturbance other than autogenic treefalls are shown in figures 7.12 and 7.13. The slight decline in basal area and stems at the start of the run is an artefact. It occurs due to shade induced mortality when overstocked inventory patches with many large trees are included. This may have been due to sampling artefacts arising as a result of relatively small quadrats being used rather than a failing of the model itself. The model suggests that with no disturbance basal area should rise to a maximum of around 30 m^2 ha^{-1} at fifty years followed by a slight decline to a stable level of around 25 m^2 ha^{-1}. Following the peak in basal area, pines slowly decline and after two hundred years the forest is dominated by oak as shown in the caricature profile diagram (figure 7.14)

Figure 7.12 Change in basal area over the course of a 200 year simulation initialised with the inventory data and run for 200 years with no disturbance

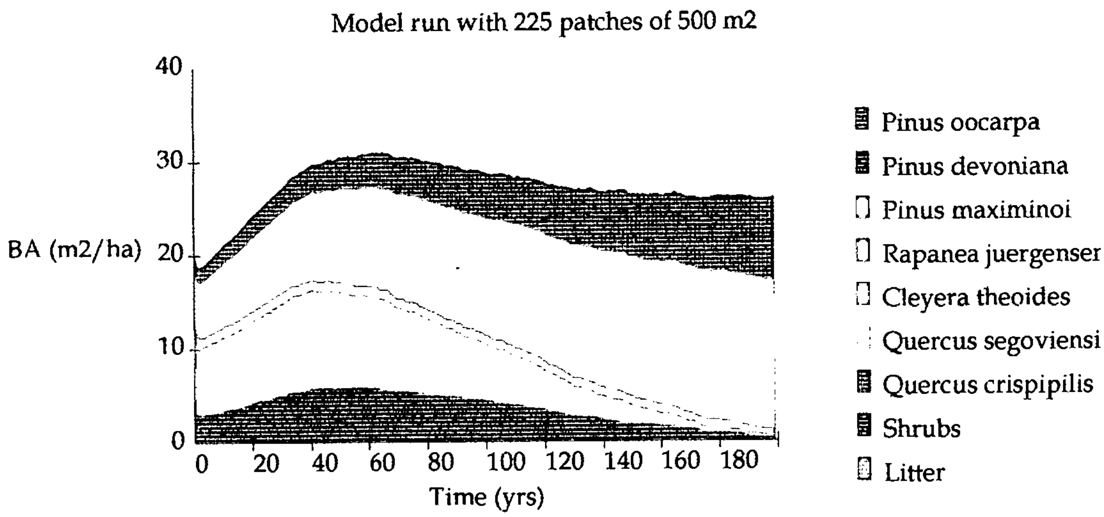


Figure 7.13 Change in stem density over the course of a 200 year simulation initialised with the inventory data and run for 200 years with no disturbance. The slight fall at the beginning of the run is due to a known artefact which has no other consequences.

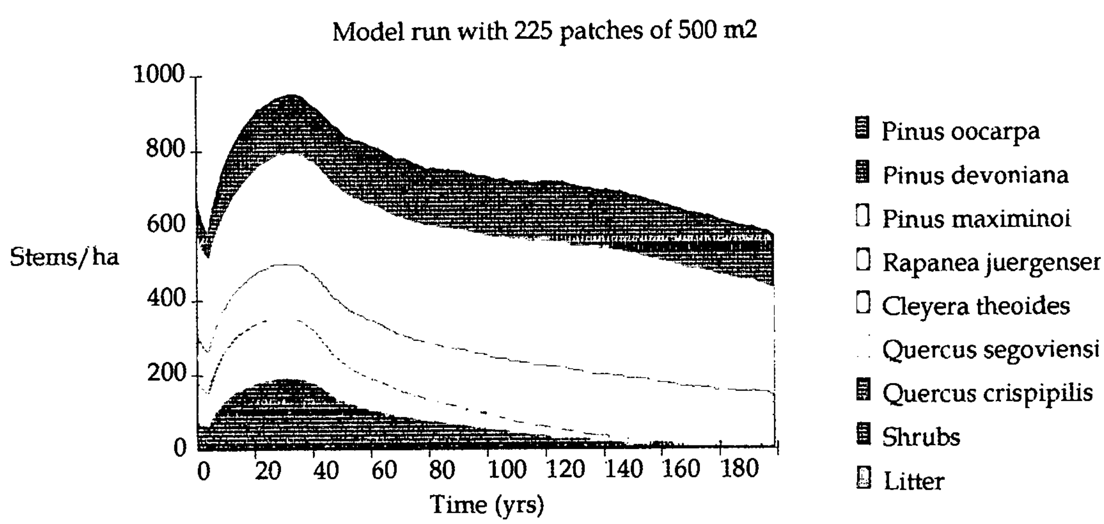
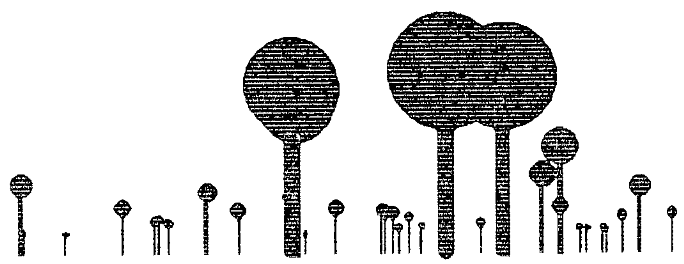


Figure 7.14 Example of a caricature profile diagram of a typical patch of 500 m^2 after a 200 year simulation initialised with the inventory data and run for 200 years with no disturbance. Each patch is dominated by several large *Q. crispipilis* with an understorey of *Q. segoviensis* and *Cleyera theoides*



Fire scenario

Figures 7.15show a scenario in which the only cause of disturbance is ground fire of a comparable intensity to that observed at the site. Mortality is modelled using the logistic regression equations derived in chapter 2. Uniform fire damage is modelled as occurring every twenty years. In this simulation *P. devoniana* becomes the dominant species of pine. The model does not include the potential effects of increased establishment of the serotinous-coned *P. oocarpa* and assumes the potential establishment of all three species. *P. devoniana* increases in relative importance initially as it is better able to survive mild fire. However one of the most interesting features of this simulation is the eventual reduction in pine importance at the site. This occurs due to resprouting of juvenile oaks and a high level of survival of mature oaks. Shade from mature oaks which are unaffected by the fire prevent pine regeneration.

Figure 7.18 shows the cumulative production of fuel wood available for harvesting (trees which suffer natural mortality in the model) over the 200 year period. Fuelwood supplies increase following each fire if it is assumed that top killed trees are not consumed by the fire, an assumption which did match observation of the effects of fire of this intensity. The mean production of fuelwood is 1.39 tonnes ha^{-1} yr^{-1} of dry biomass which translates into a total production of 1,427 tonnes yr^{-1} over the entire forested area.

Figure 7.15 Change in basal area over the course of a 200 year simulation initialised with the inventory data and run for 200 years with fire every twenty years

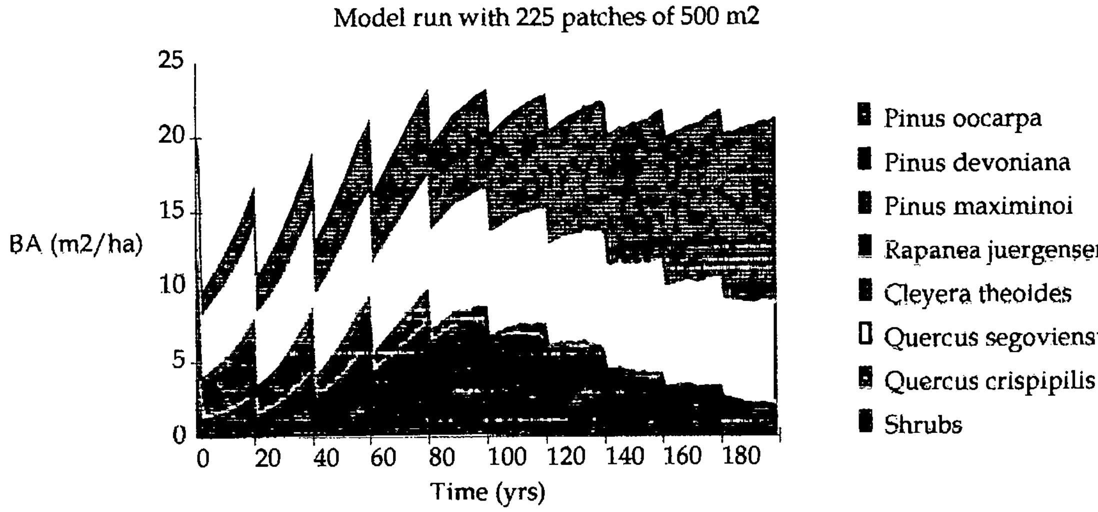


Figure 7.16 Population structure of oaks after the model has run for 200 years with simulated ground fire and no other disturbance.

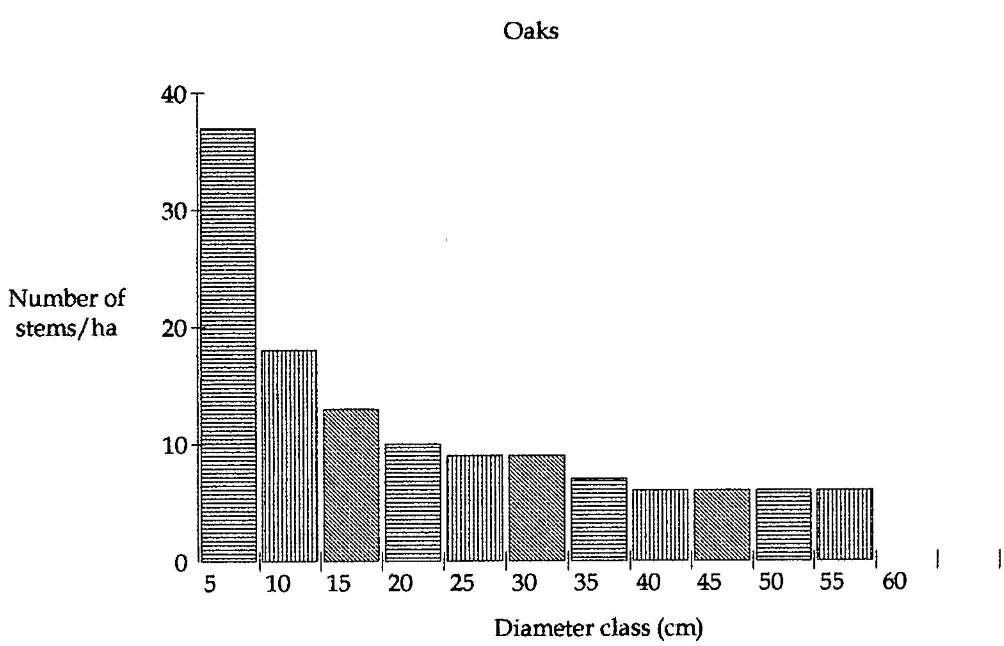


Figure 7.17 Population structure of pines after 200 years of simulated ground fire, with no other disturbance.

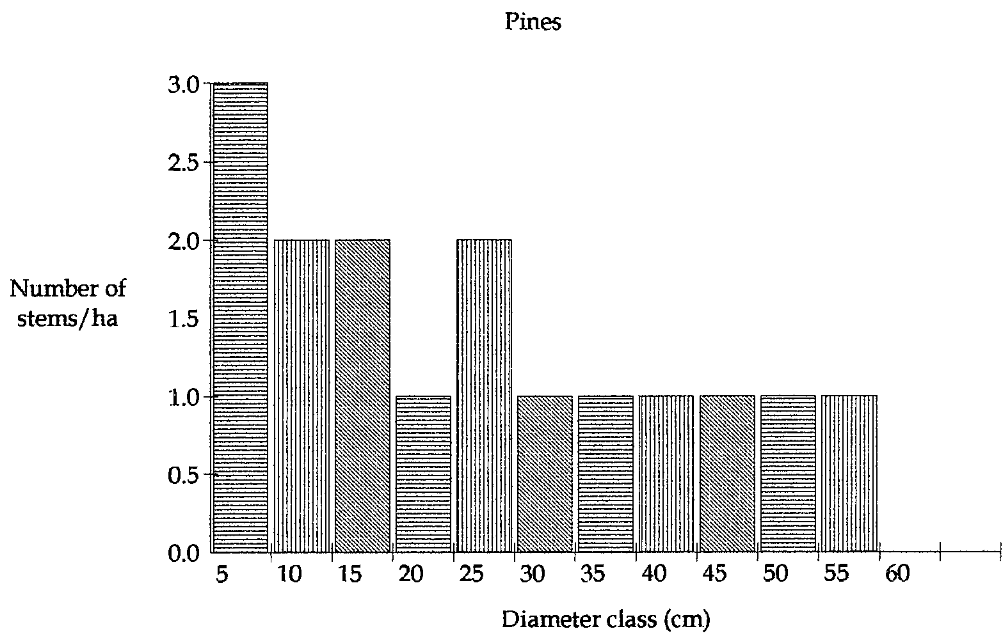


Figure 7.18 Cumulative production of fuelwood under a scenario with frequent ground fire.

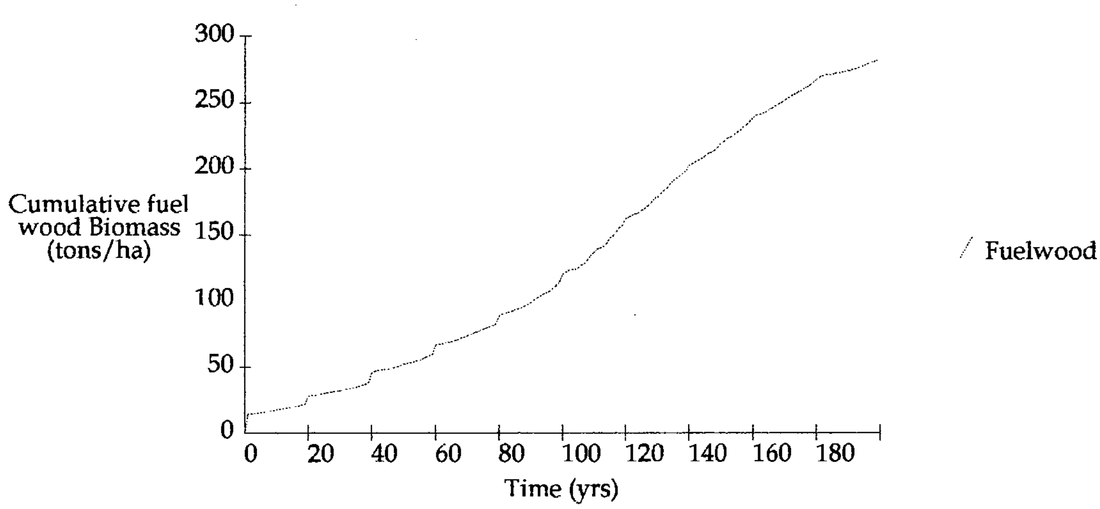
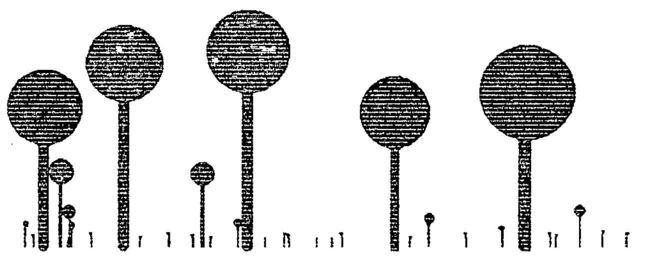


Figure 7.19 Caricature profile of the forest structure after 200 years of ground fire. The patches contain moderately sized oaks with a comparatively open understorey of small oaks and shrubs.



Logging scenario

Under this model although only a very modest harvest of pine is taken in the first cutting cycle as very few of the pines at the site are of commercial size (figure 7.20). However a cumulative harvest of over 50 m^3 per hectare is taken after 40 years (figure 7.21). This quite acceptable figure for commercial production occurs despite rather low growth and establishment rates because the currently established medium sized pines would become available for harvest at this time. The harvest is effectively drawing on pre-existing growth. Only a slight reduction in timber production is apparent for the third cutting cycle and after 120 years of use there is a suggestion that timber production may be sustainable. However under this rather conservative extraction regime for a coniferous forest canopy opening does not take place as pines are removed. Regeneration of pines is prevented by the high basal area of oak and the overall dynamic of the forest follows the pattern expected for no disturbance. After 200 years of use pine timber production effectively ceases and the forest structure would be similar to that found with no disturbance

Figure 7.20 Change in basal area over the course of a 200 year simulation initialised with the inventory data and run for 200 years with 25% of commercially valuable pines extracted every forty years.

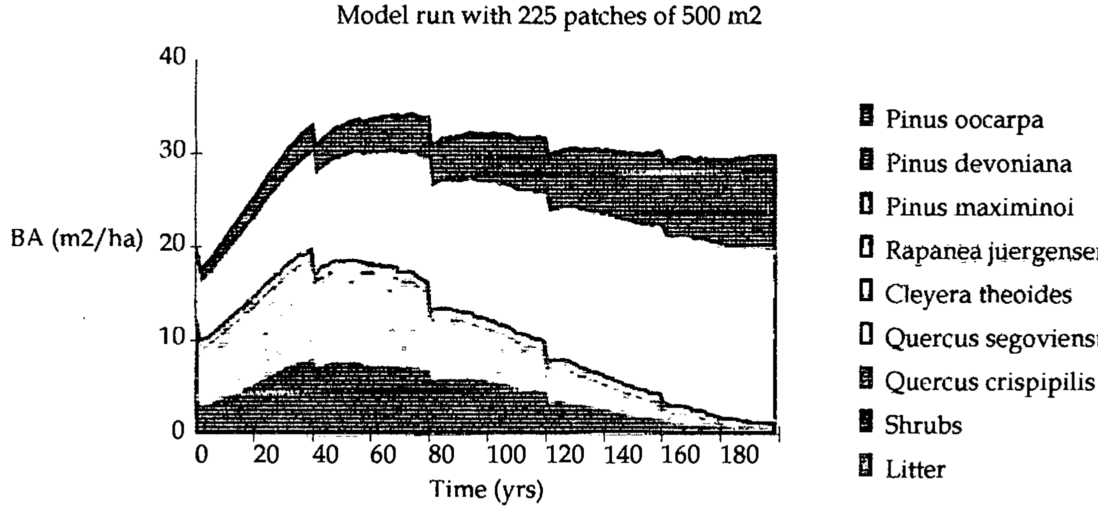
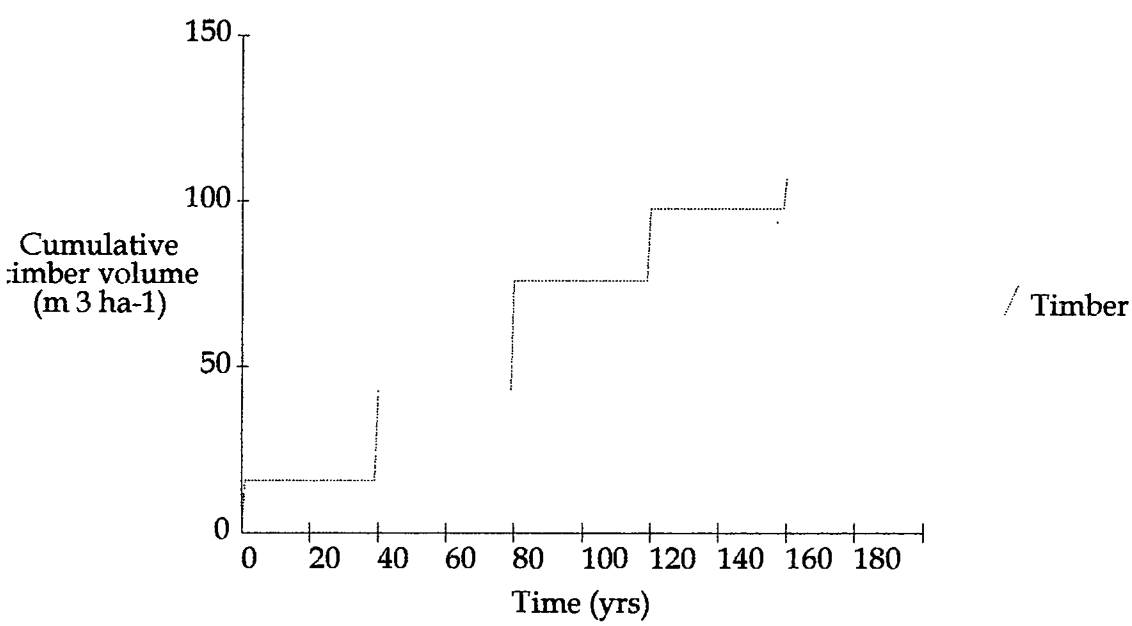


Figure 7.21 Cumulative harvest of commercial pine timber over a 200 year simulation initialised with the inventory data and run for 200 years with 25% of commercially valuable pines extracted every forty years.



Archeological scenario

The archeological scenario is in two parts. In the first the model is run sufficient time for shade tolerant broadleaves such as would be found in a montane cloud forest to dominate the forest. In the second part the simulated cloud forest is subjected to milpa clearance. Longer runs are used in both these scenarios in order to investigate a more complete process of forest succession. In the first run shown in figure 7.22 the fictitious species requires around 400 years to become co-dominant with *Q. crispipilis*. An interesting feature of this run is that although *Q. segoviensis* and *Cleyera theoides* become extinct around the time that the broad leaf begins to close the canopy, they reappear as minor components of the forest as the mature forest begins gap phase regeneration. Pines however do not survive within this matrix of shade tolerant trees. When the scenario is initialised with the broad leafed species and run with milpa disturbance, the broad leafed shade toleratant species is reduced to a residual population after 200 years (figure 7.23)

Figure 7.22 Change in basal area over the course of a 600 year simulation including a fictitious shade tolerant broadleaf species.

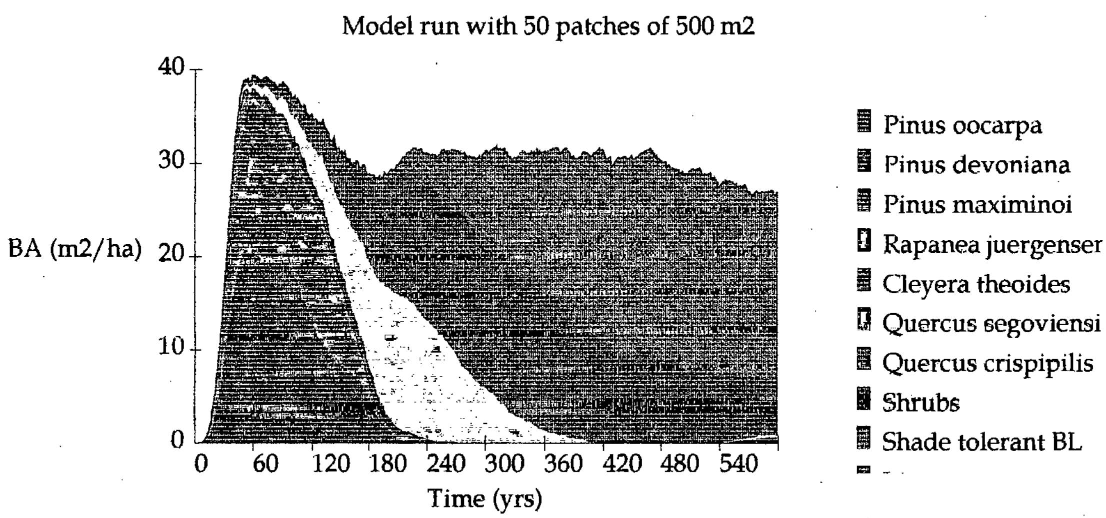
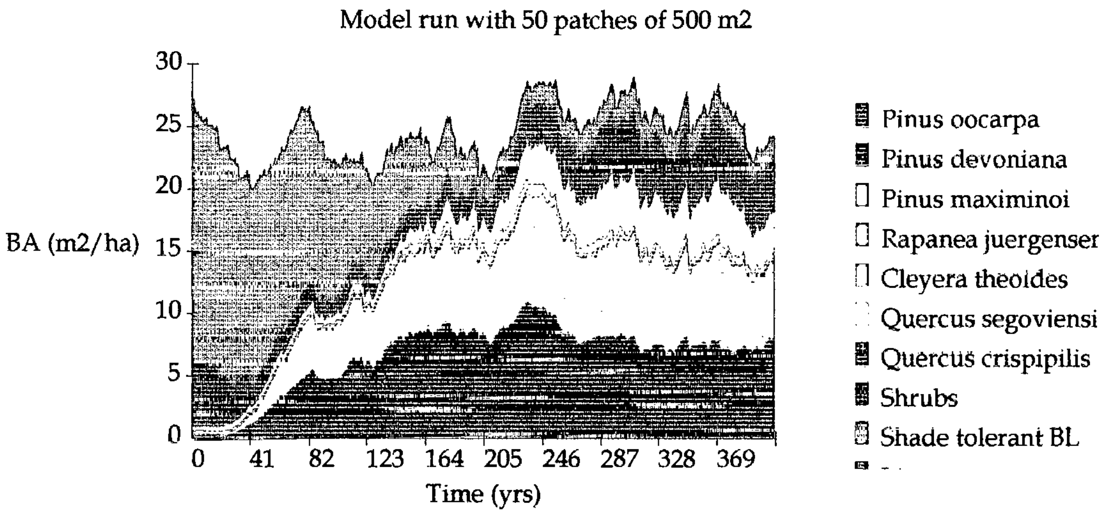


Figure 7.22 Change in basal area over the course of a 400 year simulation beginning with a forest dominated by a fictitious shade tolerant broadleaf species. Milpa clearance takes place as in the validation scenario.



Discussion

Under the verification scenario the oak population were less accurately modelled than the pine population. In particular too few small stems were found. This may be due to the fact that the model does not simulate multiple stems arising from resprouting which were measured as separate trees in the data used for validation. The weak performance of the model in predicting the number of small oak stems is not translated into overall failure to predict oak basal area. Localised self thinning of the smallest stems may lead to dynamics which are insensitive to absolute numbers of juvenile trees. Alternatively it may be that the modelled disturbance regime is rather too conservative, and patches in the forest may be generally younger than assumed in this model. The match between modelled biomass production and the results obtained from a single years monitoring of growth might be taken as a mutual confirmation of the validity of model and data, given that the data was thought to have been rather unrepresentative of the longer term situation at the site due to the previous years' fire. It does appear from this evidence that higher productivity is not to be expected.

The validation scenario produces an example of a dynamic equilibrium under a shifting mosaic. In this case the shifting mosaic is not at the scale of the individual tree as in Watt's (1947) classic example. Each tile in the mosaic would be around one hectare, the size of a milpa patch. It might be expected that a mosaic at this scale would be apparent from superficial visual inspection of the vegetation or from aerial photographs. However under the model patches are forested for most of the time. Forest cover under the model scenario would appear continuous with only a few openings, although considerable structural heterogeneity is found within the forested areas. Any obvious pattern would be obscured by the degree of stochastic variation in establishment and growth rates apparent in the data obtained from the recently abandoned milpas (chapter 3). Patchiness within each cleared area further complicates the picture. Pines establishing at the same time differ in diameter by up to 20 cm after only 40 years growth. Forest patches forming on richer soil can appear superficially more mature than older neighbouring patches with poorer growth conditions. Thus the mosaic nature of the forest would not be perceptible from aerial photographs, particularly if milpa clearances have affected small areas. The mosaic nature of the internal forest structure can only can be discovered when a more detailed inspection is made. A key to identifying this situation may lie in analysis of the pine and oak size distribution histograms. Under model scenarios which include milpa disturbance a typical pattern emerges in which the population of oak stems follows a classic reverse j pattern while pine diameter distribution is either comparatively flat over a wider range of diameters, or may be unimodal with a peak in the mid range of diameters found. Although this pattern could arise in a number of ways, this result may be very useful in supporting theories concerning the origin of other stands.

The predictability of the model behaviour despite a large amount of local variability suggests both areas for future research and unproductive areas which should be avoided. The problem of type two error in middle order number systems arises in the model as in reality. Although the model behaves in an effectively deterministic manner when large simulations are considered, model runs with less than fifty patches become increasingly unpredictable. Thus there are levels of observation at which all interpretation becomes speculative due to insufficient statistical power. This problem arose at several points in the empirical section of this work and may be a general difficulty in forest research. The model suggests that despite extremely clear differences in the behaviour of pines and oaks, when patterns are looked for at an inappropriate scale they might not be perceived. Invocation of a lottery hypothesis (Hubbell and Foster 1986) to explain species co-existence and the failure to find clearly defined gap partitioning in tropical forests may be examples of this problem (Hubbell 1999). If type two error easily arises in a simple species poor situation it would be impossible to avoid in species rich forests.

Although the validation scenario does not accurately reproduce all aspects of the present forest structure , sufficient similarity exists to support the generalised qualitative view of the forest's dynamics that it suggests. Many of the differences may be due to the way in which the model uses extremely simplified rules regarding the past disturbance regime. If a historical recreation were attempted it may well show a closer match. However the ability to precisely mimic the situation at the site is not considered a necessary or correct criteria for evaluating the general characteristics of model behaviour. Fine tuning of this type could easily become a tautological exercise.

In the absence of disturbance the model suggests that the vegetation reverts to a pure oak forest. However the dynamics of a gap model which has no allogenic disturbance built in is sensitive to modelled patch size (chapter 6). It is therefore not clear whether complete extinction of pines would occur in reality. The model results could exaggerate the extent of pine decline. Occasional naturally occurring large scale disturbances are also likely to provide an opportunity for pines. Thus rather than complete extinction a more realistic scenario may be to assume that pines become "fugitive" species within an oak matrix when anthropogenic disturbance is removed.

The eventual dominance of oaks under a scenario of frequent fires was initially the most surprising result of the model. It seemed to directly contradict well documented patterns found elsewhere (Williamson and Black 1981; Rebertus *et al.* 1989 Barrett, Arno and Key 1991; Barrett 1994; Barton 1999). However it is consistent with observations at the site which showed that mild fire kills very few large oaks. More severe fire would be required to open the canopy and provide opportunities for pines to persist in the face of competition for light with oaks. The commonly assumed association of pines with fire thus seems rather more complex than at first sight. Perhaps under the normal climatic regime in the highlands of Chiapas, sites that are already likely to be dominated by pine due to their edaphic nature are maintained as pine dominated by fire. Such stands might be more likely to occur on well drained sandy soils rather than the clay based soils and calcareous karst of the bienes comunales. Ground fire is not effective at this site as a means of increasing pine domination due to the already well formed layer of immature oaks, a high proportion of which survive to subsequently cast shade which reduces post fire pine regeneration. If fire were proposed as a sylvicultural treatment designed to improve timber production it may be found to be counterproductive in this type of forest unless combined with understorey thinning. It should also be noted that fire has been proposed as a management tool for maintaining some forms of North American oak forest (Agee 1996; Arthur, Paratley and Blankenship 1998).

The contrast between the simulation including natural fire and that including slash and burn may have more general implications. Evidence of charcoal in tropical forests has led to a growing awareness of the widespread nature of fire in tropical forests , often being found in what seem to be unlikely settings (e.g. Charles-Dominique *et al.* 1998). However fires may be widespread without being large scale phenomena. In this forest natural fire did not reset forest succession. Fire severity was linked to the presence of inflammable species and fire spread might not have occurred without prior human intervention. There is now considerable evidence that the pre Columbian population of the Neotropics was considerably higher than was once thought. Thus the suggestion is that charcoal, especially if associated with secondary forest is usually likely to be the result of slash and burn agriculture rather than natural fire in most broadleaved forests. This may have implications for understanding not only the montane forests studied here, but also lowland forest in the region.

There is a further, contradictory element involved in the linkage between human use and forest dynamics. From chapter 4 the domestic fuelwood needs of the population of Sonora was found to be between 200 and 400 tonnes yr^{-1}. Fuelwood collection may thus be removing up to a third of all large woody debris from the site, but this will be concentrated on accessible areas, leaving a greater build up in areas distant from the village. Thus it might be speculated that the almost pure pine stands found in the more distant less accessible areas of the *bienes comunales* may have arisen, or be maintained, through more severe fire owing to fuel accumulation.

The timber yield from the area may be well below commercial plantation levels but this must be seen in the local context. A cubic metre of pine timber currently commands around US $30 in stumpage fees. Thus a harvest of 50,000 m^3 from the total area of the *bienes comunales* over forty years represents a source of income for the community which is worth twice as much as the current maize harvest. However if land were more limiting, forestry would not be an attractive option on land which could be permanently cultivated, even if very low yields of maize were produced. If the model prediction of unsustainability of timeber production due to competition with oaks is correct the long term consequences would be extremely serious. However as extraction methods that lead to greater canopy opening through collateral damage to oaks would help to prevent long term competition the model predictions may be overly pessimistic. Also a range of comparatively simple sylvicultural prescriptions could be considered which would help to ensure the maintenance of mixed woodland. These might be designed to mimic the positive effects of milpa clearance on pine regeneration while minimising negative impacts such as soil erosion.

The results of the archaeological scenario may be among the most interesting findings of the model, although they are clearly also the most speculative. While the broad leafed species included in the model was fictional it did have a realistic set of parameters. Model parameterisation could be extended in the future to include such cloud forest species. The model showed how quickly a low level of milpa disturbance, even when followed by rapid regrowth, can remove shade tolerant species from the forest canopy. This does suggest that the forest at Sonora may have been dominated by a very different set of species at some stage in the past. This could account for the continued existence of such typical cloud forest species as *Olmediella betschleriana* and *Juglans mexicana* as scattered individuals within the forest matrix.

Another very interesting result of this scenario is that the tall, light demanding *Q. crispipilis* survives within a community of shade tolerant broadleaves but the shorter, otherwise functionally similar *Q. segoviensis* does not. This suggests that the two oaks will tend to have differing distributions, perhaps determined by changes in moisture availability along an altitudinal gradient. Thus the broad scale patterns presented in chapter 1 do appear to represent the remaining traces of an underlying relationship between the vegetation and environment, rather than a superimposed pattern caused by land use. The model predicts that *Q. crispipilis* should be closely associated with remnant cloud forest broad leaves trees such as *Olmediella betschleriana* and this was indeed found. Because of its shorter stature, *Q. segoviensis* would naturally be associated with more xeric environments where it would suffer less competition with *Q. crispipilis* for light. In such areas co-existence of pines and oaks may well occur without anthropogenic disturbance. This area of forest may well eventually be shown to have a different origin to that proposed for the area dominated by *Q. crispipilis*.

The problem of the model's gap size and lack of a detailed soil description for the site still prevents a more complete investigation of this postulate. A detailed comparison of the ground flora associated with each type of oak would be revealing. This observation also shows that while pooling the two species of oaks for convenience, which was used extensively in this study, may have been useful for finding patterns under a highly disturbed scenario, such a simplification would be highly inappropriate for addressing questions involving undisturbed scenarios over longer time frames. Again, it is suggested that underlying landscape scale pattern will be found when intra-generic distribution patterns are studied. A regional vegetation classification based on floristics rather than physiognomy would not be incompatible with a dynamic view of vegetation processes. The model stresses the need to use a shifting scale perspective to view vegetation that allows patterns to emerge from apparent stochastic noise.

Conclusion

The model confirms the view of the forest as a shifting mosaic, with a low, but potentially sustainable productive potential. When integrating external sources of information into hypothesis forming in this region, some analogies may be drawn with the European, rather than the North American landscape. Unlike most of North America, the highlands of Southern Mexico have supported a population of agriculturists for over a millennium. The population level has fluctuated but a very low level of slash and burn impact can be shown to be sufficient to shape forest structure. It may be useful to perceive this landscape as an ancient "countryside", comparable in some respects to a European landscape. Thus it may be necessary to begin to use historical methods to reconstruct past landscapes in order to understand the contemporary ecology of the area (E.g. Rackham 1976; Verheven *et al.* 1999). Forests in the highlands of Chiapas are rarely pristine, yet they have usually never been fully converted to any other land use. Thus as is the case for ancient English woodland that has been used for many centuries, members of a flora that once was more widespread can still be found within a matrix of disturbed forest. This perception of forests might suggest that contemporary disturbance is less of a threat to the regions diversity than initially thought. However the model's archaeological scenario shows a very clear danger. When disturbed, species rich montane broad leaved forests cannot return to their original state within a time frame which would be considered acceptable under any planned form of land management, even if seed sources are available from relic trees. Restoration of degraded cloud forest will be extremely difficult, even if suitable forms of intervention can be found. The model results strongly emphasise the need to conserve the remaining undisturbed forest fragments in the highlands in an intact state. Any contemporary slash and burn clearance of such areas will almost certainly erode the regional floristic diversity.

Chapter 8: A cellular automaton rule based model of pine-oak dynamics under slash and burn.

Introduction

In chapter 7 it was concluded that IBMs can produce a number of useful insights into the details of forest development. It has often been found that once a complex forest model has been derived, its behaviour can be reproduced with much simpler models (Lischke, Loffler and Fischlin 1996; Bugmann 1996; Acevedo, Urban and Ablan 1995; Urban, Acevedo and Garman 1999). The comparative simplicity of the pine-oak system could facilitate such an approach. In this section a simplified model is derived from the gap model and used to extend the model's application. Simplified models have the advantage of being computationally less intensive. They can either be recombined within larger structures or can be used alone to identify more general qualitative patterns within complex systems. An example was shown earlier in this work when node absorption was used to simplify Bayesian networks which helped both to summarise the model and to produce a simple kernel which could have been combined with a GIS or a dynamic model. In this section the method is used to address a remaining question concerning forest dynamics. In the introduction to this work a process of increased pine domination of forests was proposed as a general phenomenon occurring in the highlands of Chiapas. This leads to a question that was not addressed by the gap model; Could pines spread into an oak woodland being disturbed by a low level of milpa clearance at a fast enough rate to produce mixed pine-oak woodlands over wider landscapes? The alternative is that increased pine domination is a more subtle change in a pre existing pine-oak community.

In order to answer this question a model which includes communication between patches is necessary. Interactive landscape models are becoming increasingly detailed, allowing many aspects of the complex system they represent to be incorporated (He *et al.* 1999; Bugmann and Fischlin 1996; DeAngelis *et al.* 1998; Liu and Ashton 1998; Shao *et al.* 1994). Complex models of this type combine dynamic models with spatially explicit parameterised representations of underlying environmental variability. This can lead to models with a very high degree of realism. However the complex interactions which occur when spatially explicit processes are superimposed on a detailed landscape inevitably reduce generality (Mladenoff and Baker 1999). Conclusions drawn from detailed simulations are limited to scenarios imposed by their parameterisation. Because of the uniqueness of landscapes and the time scales involved, model testing is restricted to verifying their ability to produce patterns which have already been observed (Mladenoff and He 1999). Because general validation of predictions of landscape pattern requires replicated observations, relatively simple simulation models which are designed to provide insight into repeatable qualitative pattern formation using a comparatively small sets of measurable parameters may still have an important heuristic role These models complement both more detailed simulations (Urban *et al.* 1991) and case studies as they allow the investigation of artificial systems with more general implications than more detailed depiction of case study situations (Milne 1992). For example, exploratory models have produced considerable insight into fire behaviour on dynamic landscapes (Gardner *et al,* 1999) and spatial interactions within plant communities (Czaran and Bartha 1992).

In the case represented by the study site dispersal of propagules between patches disturbed by slash and burn is likely to play a role in determining the dynamic of a landscape as it undergoes iterated slash and burn disturbance. This might produce a clear spatial pattern if disturbance patterns were predictable in space. However the position of any milpa clearance is inherently unpredictable. The likelihood of occasional disturbance through long rotation traditional slash and burn clearance is not apparently related to distance from settlement, although more recent deforestation and degradation may be. Thus the historical disturbance through milpa clearance which formed the stand can only be modelled by some rather simple non spatial rules. The spread of propagules across a disturbed landscape could give rise to a large number of alternative scenarios within a single stand. A spatially explicit landscape model with communication between sub models can be used to simulate this situation. The example presented is a simplified model designed to investigate the potential of the approach.

In a spatially interactive landscape simulation the behaviour of an individual unit cannot be predicted without knowing its position with regard to other units. Conceptually the simplest form of spatial simulation is the cellular automaton. In a cellular automaton the interacting units are cells, which use rules regarding the state of neighbouring cells to determine their state. In landscape models the interactions usually concern the movement of determining factors of landscape level attributes such as dispersal of plant propagules or the spread of fire. If within cell behaviour is incorporated into a cellular automaton, models can be built which have some connections with the analytically tractable reaction diffusion models first introduced in a biological setting by Fisher (1937) and extended to a demographic context by (Skellam 1951). While the degree of realistic detail which may be captured by mathematical models is limited by the complexity of finding analytical solutions (Holmes 1993), cellular automata type simulation has fewer constraints. Furthermore, while analytical solutions focus inevitably on equilibrium properties of the model, simulation allows dynamics to be followed. Complex dynamics have been found to arise even from extremely simple rule based spatially explicit cellular automata (Wolfram 1984).

While some of the patterns formed by simple cellular models may be artefacts of mainly theoretical interest (Hansen 1993), constraints imposed by adding more realistic detail to cellular models should be expected to produce greater realism in output (Olson and Sequeira 1995). Cellular automata are particularly useful for making qualitative predictions regarding spatial pattern formation and have found uses in the study of tropical rain forests (Sole and Manrubia, 1995), interspecific competition for space among grass species (Silvertown *et al.* 1992), spatial patterns in savannah systems (Jeltsch *et al.* 1996), banding patterns in arid shrubland (Dunkerley 1997) and the consequences of differing strategies of resource use by competing plants (Colasanti and Grime 1993). Nevertheless to date cellular automata have rarely been used to study the mosaic landscapes produced by shifting agriculture. Spatially defined models of slash and burn agricultural systems usually concentrate on the forces driving disturbance patterns, rather than emergent system patterns.

The model thus investigates of the pattern which may arise as a result of the interactions between the processes of seed dispersal, succession and anthropogenic disturbance. The questions addressed are:

1.Could pine oak forest have formed through the invasion of oak forest by pine under a plausible historical slash and burn regime?

2. What could the consequences of intensification of land use be for forest composition if propagule dispersal is limiting?

The model addresses these questions through an idealised yet realistically parameterised model of a landscape undergoing iterated slash and burn disturbance. It is designed to produce generalised semi quantitative predictions based on a consideration of the entire landscape as single system. Such a model aims to acts as a framework for generalised theorising rather than predicting the behaviour of any single real system.

Method

The model was programmed using a hierarchical object oriented framework with three levels. The landscape level is simulated as a grid of interacting cells. Each cell contains interacting objects which represent cohorts of trees classified by broad functional groups. The model time step is a year. Updating of all cells takes place simultaneously following the determination of interactions between them. Each gridcell in the model can contain up to three functional group cohorts. The approach could easily be extended to include greater complexity, but this was considered unnecessary for addressing the specific question under consideration. The FGs used are *Heliophilic shrubs*, *Pines* and *Oaks*. These comprise the canopy forming elements which may replace each other over the course of succession. Heliophilic shrubs represent a diverse, but rather transient component of the vegetation canopy. Shade tolerant sub canopy species are excluded from explicit consideration in the model, although investigation of the consequences of changes in canopy structure for the interconnectedness of populations of shade tolerant species would represent a natural application for interpretation of the models results.

A cell in the model represents a landscape unit of one hectare, which is the approximate size of a single slash and burn site (chapter 3). The model can thus be used to simulate an idealised mosaic landscape composed of many patches of differing successional age. The model assumes that rotational slash and burn agriculture can affect the vegetation in each cell when a certain threshold basal area is reached. This assumption is a first approximation of the criteria found to drive traditional slash and burn clearance (chapter 5). Differing intensities of usage can be reproduced by altering the threshold basal area at which a cell becomes suitable for clearance and by altering the proportion of cells cleared during any single time step. Recolonisation of a disturbed cell proceeds according to rules based on the state of neighbouring cells and the vegetation of each cell prior to clearance. Thus both spread of pines through seed dispersal and resprouting of oaks present on the site before clearance can be simulated. The interacting objects in each cell represent cohorts of functional groupings of species which establish and increase in total basal area on each grid cell. Co-occurring cohorts interact with each other by querying the state of the grid cell.

Interactions between the species populations during the growth of recolonising cohorts following disturbance are reproduced using a meta modelling approach (Urban Acevedo and Garman 1999). Linkage between the patch dynamics and measured properties of interacting species is achieved through the use of a gap model simulator of the interactions between individual trees. In order to reduce computational time and increase analytical efficiency a simpler successional model based on the Lotka Voltera equations is fitted to the results of the gap model simulation.

The Lotka Volterra competition equations must be interpreted here as non mechanistic emulators of the growth phase reproduced by the gap model. While the Lotka-Volterra predator prey model may have become discredited as a predictive tool (Hall 1988), the Lotka Volterra competition model continues to have some utility, especially when interpreted as representing plant biomass (Huston 1994). The pattern of successional change produced by some of the successional scenarios reproduced by the gap model bears a resemblance to the non linear dynamics produced by this classic set of equations. This similarity is only observed for a subset of gap model scenarios, the richness of the gap model's behaviour and its sensitivity to changes in the parameters is thus ignored. The effects of fire or logging which change the internal dynamics of a patch could not be investigated with such a model. However the emulator is designed simply to reproduce a contextually adequate scenario of interaction between cohorts of FG's growing on the same grid square under a scenario of periodic slash and burn clearance. The interest in the models behaviour lies in observing how the stand level consequences of these interactions can be altered by spatial effects.

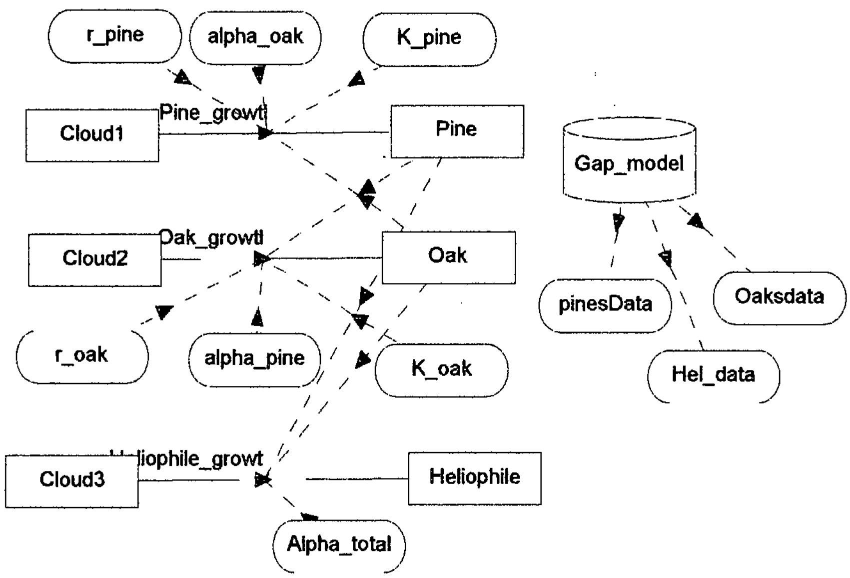
The equations used to calculate basal area (BA) increment for each of the three FGs were derived from a representative simulation of stand development of a single patch using the model described in the previous chapter. It was assumed that all three FGs were present at the start of the simulation. The Lotka Volterra competition equations were optimised using the Marquart method implemented by the program Model Maker as shown in figure 8.1. This produced three equations which were used to model yearly increase in basal area for each of the cohorts, based on their basal area and the basal area of the other cohorts in the patch .

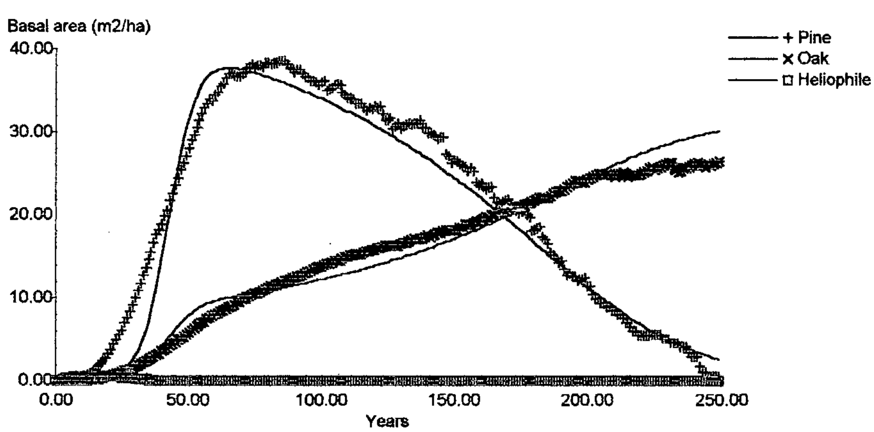
$$\frac{\delta BA_{oak}}{\delta t} = 0.1665\, BA_{oak}\left(1-\left(\frac{BA_{oak} + 0.543\, BA_{pine}}{32}\right)\right) \qquad \text{Equation 8.1}$$

$$\frac{\delta BA_{pine}}{\delta t} = 0.203\, BA_{pine}\left(1-\left(\frac{BA_{pine} + 2.270\, BA_{oak}}{60.2}\right)\right) \qquad \text{Equation 8.2}$$

$$\frac{\delta BA_{shrubs}}{\delta t} = 0.300\, BA_{shrubs}\left(1-\left(\frac{BA_{pine} + 0.020\,(BA_{oak} + BA_{pine})}{8.1}\right)\right) \qquad \text{Equation 8.3}$$

Figure 8.1 A compartment flow model representation of the Lotka Volterra equations used to derive a simple emulator of gap model behaviour. Simultaneous optimisation of model parameters is achieved using the Marquart method implemented by the program Model Maker in order to find the best fit for the parameters of three linked logistic equations.





Prediction of seed dispersal over a landscape has to overcome the challenge represented by the extreme temporal and spatial variability inherent in the process. The number of propagules arriving on a site is some function of its proximity to sources of propagules, the number of propagules produced at the source and the dispersal mechanism. All these factors can be shown to be important empirically. However because of the nature of the combined sources of variability extremely large data sets are needed if systematic patterns are to be incorporated in the model empirically. Observations made at a reduced temporal and spatial scale provide point estimates which provide rather little guidance for modelling processes acting at larger spatial and temporal scales. This difficulty leads to a simplified rule based model of seed dispersal being adopted under the assumption that it could be replaced as new information becomes available.

Propagules of the FG heliophilic shrubs are assumed to be present , or to arrive almost immediately at any disturbed patch. All three pine species produce wind dispersed seeds. A mechanistic model of wind dispersion of winged seeds is provided by Greene and Johnson (1989). Higgins *et al.*(1996) used this model together with a consideration of empirical data provided by (Okubo and Levin 1989) to predict seed dispersal of invasive pine species in South Africa. They modelled dispersal as a negative exponential distribution with a mean dispersal distance of 20 m for heavy seeded pines, and 70 m for light seeded species. While long distance dispersal is an important determinant of rates of species invasion (Portnoy and Willson 1993) rare colonisation events are of rather less consequence when modelling rapid, major structural changes in the vegetation over a comparatively small spatial scale. The assumption is therefore made that colonisation of a disturbed patch requires a pine seed source within a maximum distance of between 100 m and 200 m. This corresponds to the area represented by the width of two cells around the disturbed cell.

Oak seeds may be dispersed over a range of up to 50 m through caching by rodents (Hubbard and McPherson 1999) or over longer distances if dispersed by jays. Nevertheless it is assumed that most oak recruitment from seed in any abandoned milpa is dependent on the presence of oaks in the immediate vicinity. The model therefore permits oak colonisation of a disturbed cell if mature trees are present in one of the six neighbouring cells.

Two additional rule based limitations to colonisation are built into the code in order to take into account well known ecological attributes of the FGs. Oaks are known to be rather slow colonisers of open areas due to the behaviour of their seed dispersers and low seedling survival . Colonisation is assumed to be facilitated by the presence of shrubs or small pines (Rousset & Lepart 1999). On the other hand, light demanding pines cannot colonise areas with an already completely closed canopy of shrubs or small trees.

Resprouting of oaks following clearance is an important mode of regeneration. However resprouting would not occur if more intensive methods of farming are adopted and the process is sensitive to the type of disturbance regime. One of the aims of the model is to enable an analysis the importance of resprouting in determing landscape pattern. Oak resprouting can therefore be either assumed to not occur in any circumstances, or can be modelled as producing a new cohort of oak trees on a previously colonised site providing the basal area of the previous cohort is over 2 m^2 ha^{-1}. and under 50 m^2 ha^{-1} This rule is designed as a first order approximation of the observed process and is supported by data from the study site (see chapter 3). These rules, together with the form of the Lotka Volterra equation used to emulate successional dynamics form the main simplifying assumptions of the model. The results of the simulation should be considered with reference to the restrictions and degree of realism that these assumptions imply.

Figure 8.2 Order in which procedures are carried out in the model. The model holds a copy of the grid in memory in order to enable simultaneous state variable update and to avoid changing the values of cells during the querying operation.

Cell objects query grid object to ascertain state of neighbouring

↓

Cell objects run establishment routine

↓

Cohort objects query cell object in which they are held

↓

Cohort objects calculate their basal area

↓

Disturbance module run over grid

↓

All cells affected by disturbance are reset

↓

Cells updated simultaneously to new state

↓

Results calulated and output

Scenarios

A scenario based analysis (chapter 8) was used to present some of the principal characteristics of the model. Four scenarios were considered in order to address the questions of interest.

Validation scenario. The model was run with the same disturbance regime as used for the patch model validation in the previous chapter. Milpa clearance can occur when a patch has a basal area of 25 m^2 ha^{-1} and the probability of a patch being cleared is 0.05. Resprouting of oaks is enabled. Does this simple model match gap model behaviour?

Segregated scenario. The same scenario as used for validation is run for 200 years. However in this case oaks and pines are initially segregated in two contiguous blocks. How fast do pines and oaks mix to form the two layered intimate mix of pines and oaks found in the forest at the field site?

Intensification scenario 1. Scenario 2. is repeated. However it is now assumed that oaks cannot resprout. This may occur if milpa plots are used for longer periods or if intense grazing or repeated fires kills trees forcing complete re-colonization. Can oaks remain in the forest under such a scenario?

Intensification scenario 2. The model is initiated without spatial segregation of oaks. Intense disturbance such as would occur under a "roza-quema" regime is simulated. Plots are allowed to regenerate only to a basal area of 5 m^2 ha^{-1} . Probability of clearance is set at 0.3. However oak resprouting is assumed to occur. Can pines persist under such a highly disturbed landscape?

Two starting configurations were used in model runs as shown in figure 3. Both configurations represented a simplified landscape of around 33 x 33 grid cells which might be thought of as 1,089 ha of forest. In configuration A the model is initiated as a mix of pines and oaks. In configuration B the two FGs are segregated into two blocks.

Results

Although longer runs can be used to check the eventual equilibrium reached by the model, the behaviour after 200 years has been presented here for comparative purposes and to show the dynamic behaviour of the simulation. The vegetation in each patch has been classified according to basal area and species mix.

An interesting feature of the model was the way in which behaviour at the stand level differed from the simple Lotka – Volterra models running at a patch level In the first scenario which was similar to that used to validate the more complex IBM the two FGs were found to reach a dynamic equilibrium which was very similar to that described as the overall behaviour of the gap model from which this model has been derived. In a few older patches pines began to displace oaks, but the rate of disturbance was high enough to prevent the process producing contiguous blocks of oak which would prevent the spread of pine propagules across the landscape.

When the same scenario was run, but with the landscape divided into two contiguous blocks, pines spread into the area of oak forest. After 200 years pines had penetrated around 1 km into the oak forest. Oaks had not been able to spread into the pine dominated area . Because the model was initiated with each block of forest in a mature state, the overall basal area of pines remained very similar to the starting value. However oaks had declined slightly and continue to do so until a dynamic equilibrium is reached in the upper half of the simulation.

A more dramatic form of pine invasion occurs if oaks are assumed to be unable to resprout in cleared patches. In this case pine invasion occurs more rapidly with the front reaching 1.4 km from the starting position. Oaks are clearly being displaced from the forest and would eventually become extinct if the process continues.

If however a scenario of intensification is assumed in which oaks can resprout but clearance occurs very quickly following abandonment, such as may occur under the *roza-quema* short (< 15 years) rotation slash and burn system pines disappear from the landscape leaving the vegetation dominated by resprouting oaks and heliophilic shrubs. The intensification of use over the whole landscape leads to synchronised cycles of clearance.

Figure 8.3 Starting configurations of the cellular model. Each model represents a block of 1,089 hectares. The model is initialised either as a mixture of pine and oak (configuration A) or as two contiguous blocks of pine and oak forest (configuration B). The total basal area of each FG is identical in each scenario.

Configuration A

Configuration B

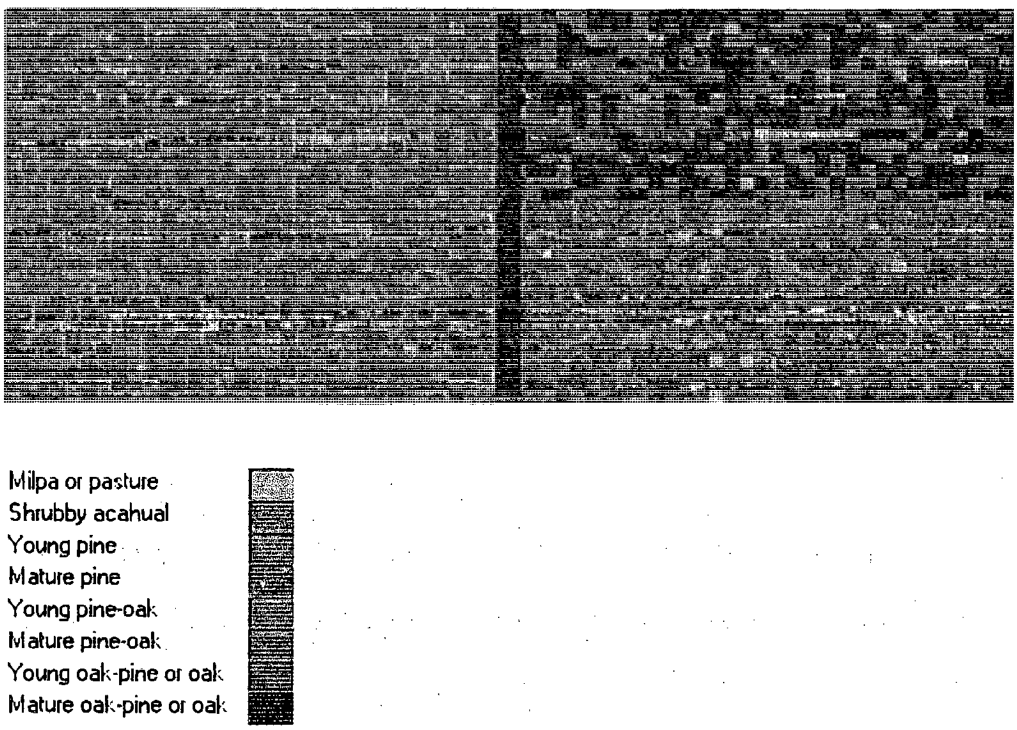


Figure 8.4 Results of running the model for 200 years with starting configuration A. Milpa clearance can take place after canopy closure (basal area = 25 m^2 ha^{-1}) with a probability of 0.05. Seed dispersal is assumed to take place over the entire area and oaks are assumed to resprout readily following clearance.

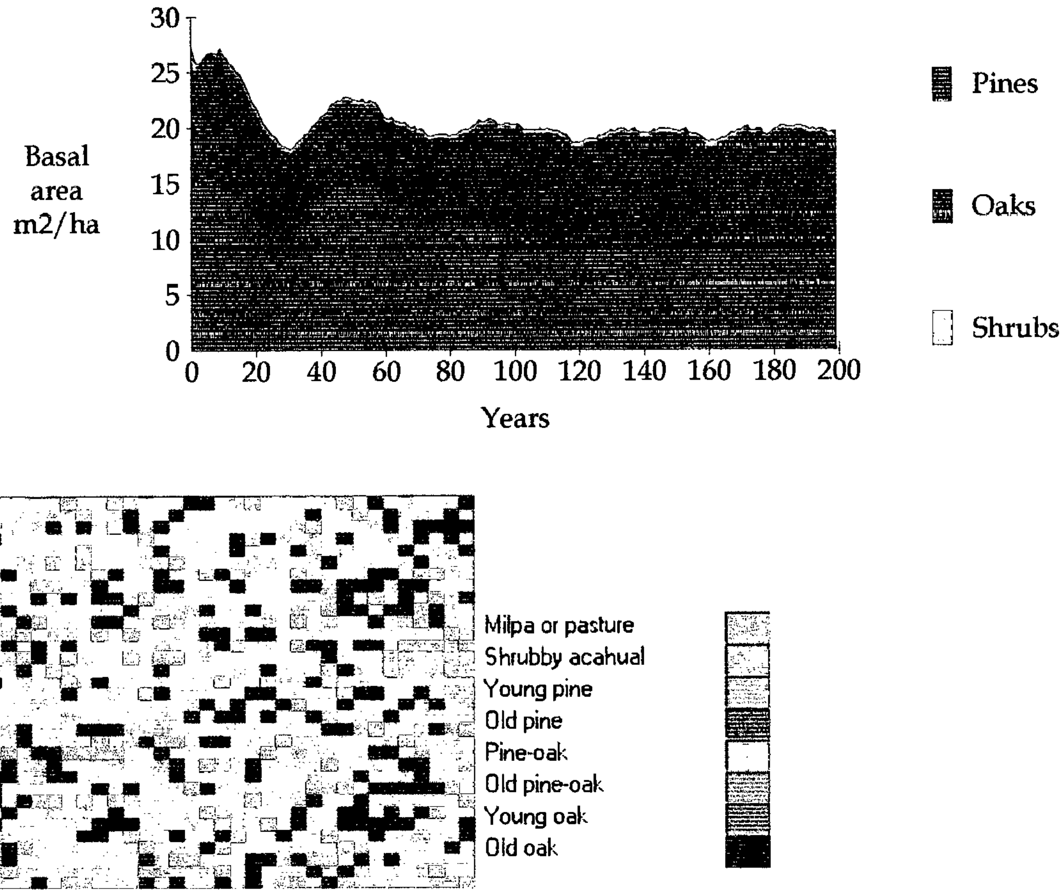
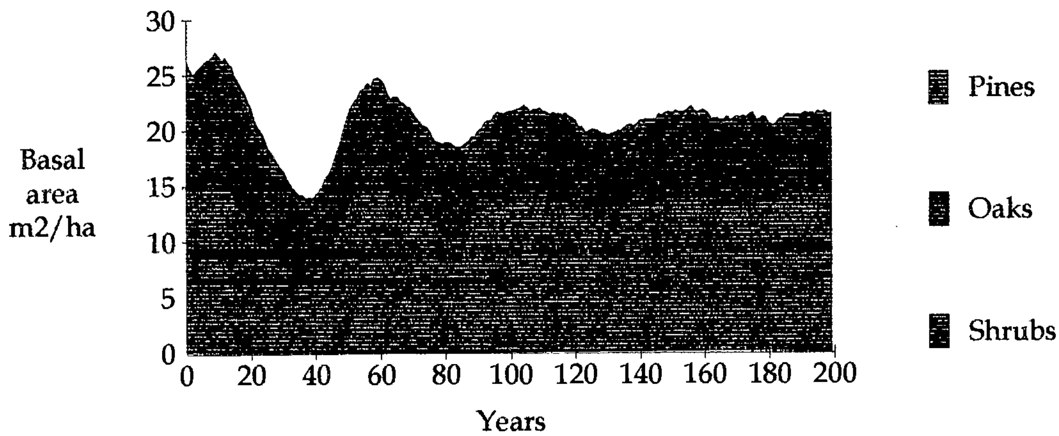


Figure 8.5 Results of running the model for 200 years with starting configuration B. Milpa clearance can take place after canopy closure (basal area = 25 m^2 ha^{-1}) with a probability of 0.05. Seed dispersal rules are incorporated, but oaks are assumed to resprout.



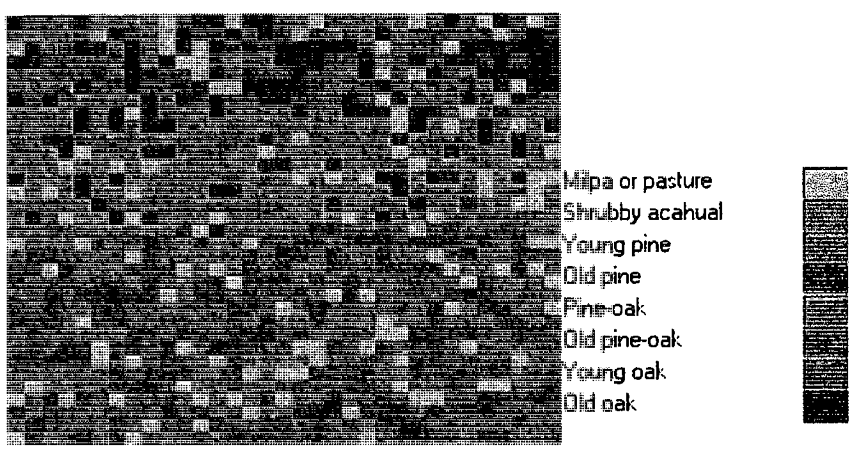
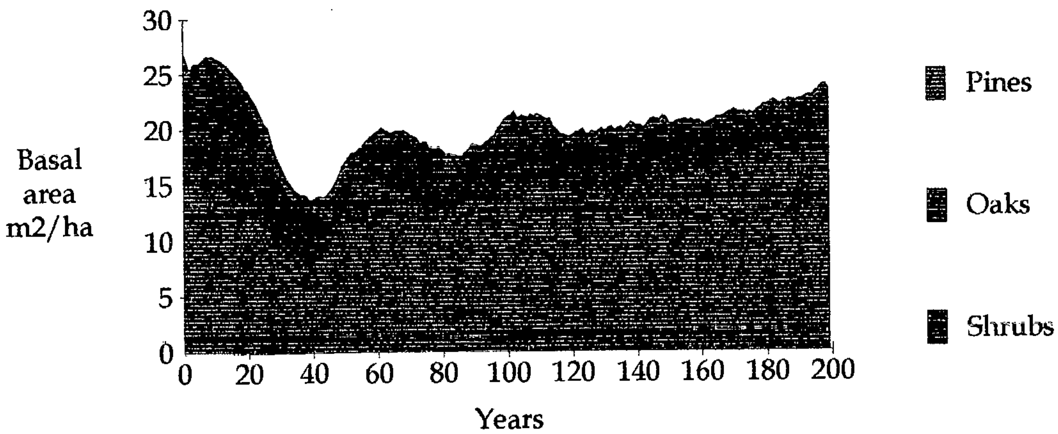


Figure 8.6 Results of running the model for 200 years with starting configuration B. Milpa clearance can take place after canopy closure (basal area = 25 m^2 ha^{-1}) with a probability of 0.05. Seed dispersal rules are incorporated. Oaks are assumed not to resprout following clearance.



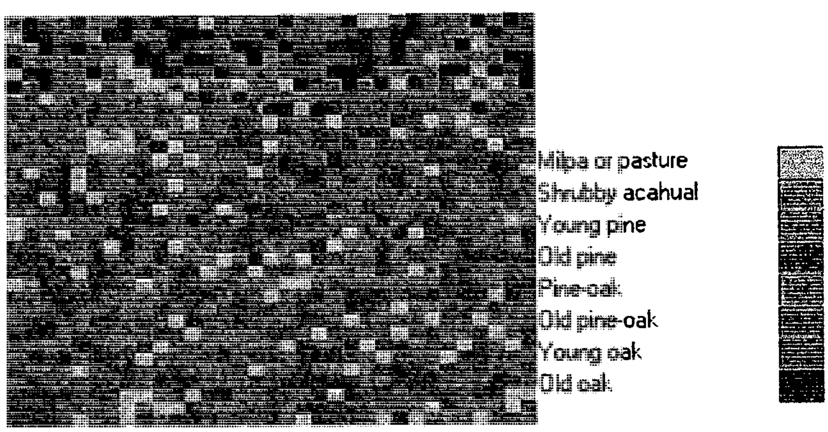
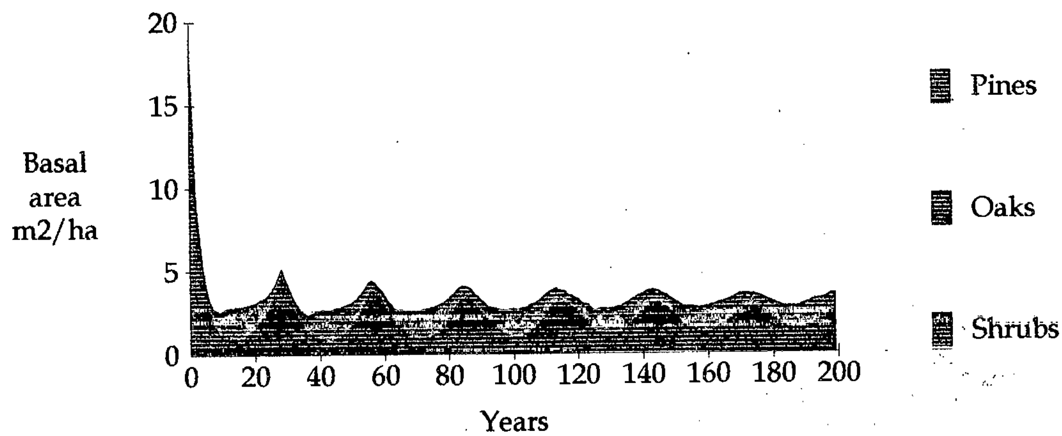
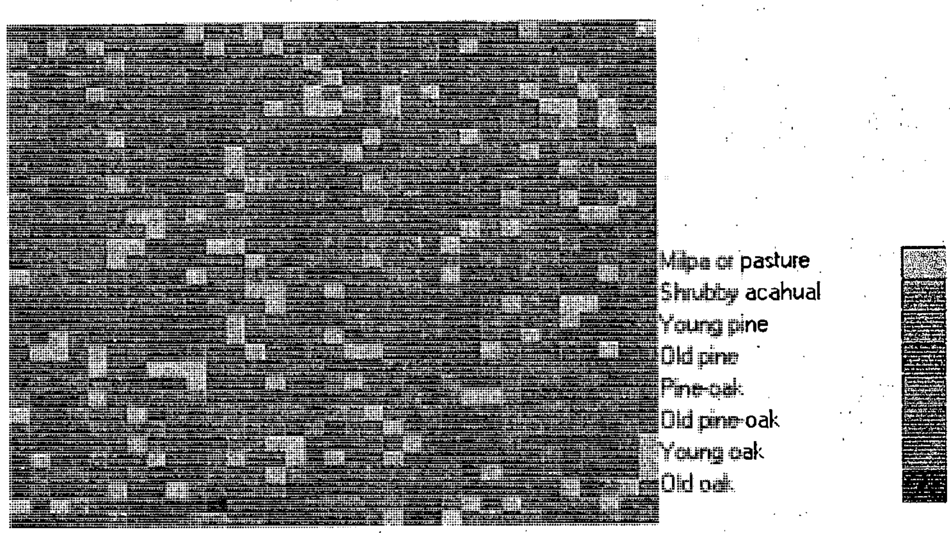


Figure 8.7 Results of running the model for 200 years with starting configuration A. Milpa clearance can takes place with a very short rotation (basal area = 5 m^2 ha^{-1}) with a high probability of 0.3. Seed dispersal rules are incorporated, and oaks are assumed to resprout following clearance.





Discussion

Small models of this type reveal both the strengths and weakness of computer simulation for analysing the logical consequences of conceptual models. Although straightforward to implement, the model produces a rich variety of dynamic behaviour. Solving simpler reaction-diffusion models analytically is a far from trivial task. Because this model includes some rules in addition to differential equations this model as it stands cannot be written as a set of equations and a closed form solution is impossible. However a formal mathematical model of comparable complexity to this simulator would also be intractable. The simple model produces complex behaviour that differs markedly from the Lotka Volterra equations that are used to emulate patch level stand development. It does this without using any top down constraints. Huston (1994) demonstrated a similar result with a non-spatial implementation of disturbed Lotka-Voltera equations. It could be argued that greater complexity is unnecessary if no more than a contextually realistic emulator that can reproduce qualitative and semi-quantitative elements of the real system behaviour is required. Huston (1994) argues that similar processes to those occurring in this model provide a general explanation for species co-existence on disturbed landscapes. The model also shows similarity to analytically tractable models that suggest stable co-existence of plants can occur through trade offs between competitive and colonisation abilities (Hastings 1980; Tilman and Pacala 1993; Tilman 1994). These theoretical arguments gain relevance when a clear example of a situation in which they might occur has been identified.

Despite this, like other simplified theoretical models, the model is inappropriate as a tool for making quantitative prediction. The model is impossible to validate directly and its main support comes from the rather informal observation that predicted patterns appear compatible both with patterns at the site and a large number of undocumented personal observations of pattern made at other sites in the highlands of Chiapas. The visual presentation of the results as a grid of cells may imply the model has aimed to produce a greater level of realism than was intended. Reaction diffusion models, despite generating a body of complex mathematics, have been criticised as being too simple to apply to real situations (Holmes1993). This model is likely to have similar weaknesses. Discussing the use of simple models of this type for theory generation Ford (2000) warns that "*the projection of an ecological system onto a simple model makes simplifications that overrule interactions essential to considerations of stability. In this sense the metaphysics produced in using these models has been* *counterproductive*". It would be unwise to ignore this comment when considering models of this type.

The model is probably most useful as a framework for further research, either in order to confirm predicted patterns, or to investigate underlying process. For example, although the model has obtained a degree of realism from the linkage of the sub model of patch level stand development to field data through the individual based gap model, the rule based model of seed dispersal has no empirical support beyond the field observation that pine establishment takes place very readily in abandoned milpas, providing a seed supply can be found within a distance of around 200 metres. Without further work the model remains an extreme caricature. There is therefore now a clearer context for future work on seed dispersal and the spread of pines. It could be used to provide a substitute for the simple rule-based model included here.

The principal conclusion drawn from model exploration is a confirmation of a simple rule that has been expressed in a more speculative form without the use of the simulator. Pines and oaks can combine to form intimately mixed pine-oak forests over a relatively short space of time under a realistic regime of long rotation slash and burn farming. The movement is in one direction. Oak forests may become pine-oak woodland, but the converse is unlikely to occur. The model suggests that much of the mixed pine-oak forest of the highlands could be a form of disturbed oak woodland. This may only partially match the real system and attention must be drawn to limitations in the domain of applicability of this model which should be apparent from the assumptions on which the model is based. Naturally occurring pine communities can be found with an oak understorey, although the oak species involved is often a shrubby species, such as *Q. sebifera*. However, observations also suggest that the smaller canopy tree *Q. segoviensis* can also occur within a fundamentally pine dominated community as an intrinsically non dominant tree which remains beneath pine canopies. This was also shown by gap model simulations which took into account species-specific differences in height growth. Gap model simulations showed that *Q crispipilis*, rather than *Q. segoviensis* would be the natural dominant of completely undisturbed areas (chapter 7).Thus the conclusions drawn from this model may best represent the situation which arises when a tall, canopy dominating oak species such as *Q. crispipilis* come into contact with a pine dominated community. As in many situations when models are interpreted in real life situations, disparities between model predictions and observations can improve hypothesis forming. In this case more evidence seems to be accumulating that a full picture of the forest dynamics of the region requires that the two species of oaks be treated as functionally distinct.

An undocumented personal observation that provides a counter example which helps to support the general conclusions of the model is that in the areas of the highlands of Chiapas with richer soil and a denser human population than the study site pines and oaks tend to occur as discrete monogeneric fragments. On this landscape of richer deeper soils pines grow in valleys and oaks on hillslopes. This is consistent with the model's predictions. Valley bottoms are often ploughed and heavily grazed which removes resprouting oaks, while hill slopes in highly populated areas are subjected to short rotation slash and burn and timber extraction that removes pines.

The model suggests that clearly visible patterns in relative dominance of pine based on distance from villages are not likely to be found unless disturbance that removes oaks occurs. This also seems to match general experience, and is supported by the observations reported in chapter 1. Again this must be combined with the finding that large scale pattern within forests is still likely to be the result of underlying edaphic or climatic factors rather than any pattern of anthropogenic disturbance found in the region, unless disturbance is extremely intense or combined with chronic stress.

Conclusion

Mixed forest of pines and oaks can arise as a result of iterated slash and burn disturbance followed by regeneration from what would be naturally pure oak stands, or mixed broadleaf forests. There are important implications for vegetation classification. Landscape scale analyses which classify vegetation based on relative proportions of pine and oak will tend to fail to identify the underlying environmentally constrained pattern and will emphasise only superimposed anthropogenic pattern. Pure pine stands are very different systems from mixed stands, but within a mixed pine-oak stand gradations of relative dominance have rather little underlying significance. A particular difficulty arises when aerial photographs are used to trace patterns. Because pines form a layer above oaks, when aerial photographs are analysed stands of pine-oak woodland that have been derived from oak woodland may look identical to stands of pure pine which have a very different origin. The traditional forester's method of using understorey plants as indicators of soil characteristics may be necessary to trace large scale pattern. Intriguingly, slight variations in climate over an altitudinal gradient might be best identified through studies of vascular epiphyte distribution patterns.

When seeking to produce large scale vegetation classification the relative dominance of pine and oak is therefore probably not a suitable criteria unless the intention is to closely follow the contemporary fine scale dynamic. The underlying patterns of species distribution imposed by edaphic or climatic patterns are not completely over written by rotational slash and burn disturbance, but intra generic patterns could provide a better guide to underlying pattern than the more striking structural characteristics of the vegetation. Classifications of edaphic and climatic zones in the region should therefore be based on species identity and not on relative pine-oak mix. Pure stands of pine will still provide an indication of edaphic conditions, providing they have not arisen following abandonment of intensively used agricultural land.

Chapter 9. Conclusions

The most important outcome of this work has been the construction of a series of predictive tools that can be re-used at different sites to predict forest dynamics. Because forest change is so dependent on the nature of the local disturbance regime, forming generalised statements must be approached with care. Nevertheless modelling was able to identify some of the patterns that might be expected to be generally applicable. The conclusions that may be drawn can extend beyond the bounds of the field site at Santa Rita Sonora and could help to predict regional forest change. They also have implications for other areas where pines and oaks form intimately mixed forests.

A contextually appropriate theory of pine-oak dynamics

An operational theory that provided the foundation for this work was first proposed for the dynamics of disturbed montane forest in Chiapas by Gonzalez-Espinosa *et al.* (1991). It was stated that human disturbance led to increased dominance of forests by pines. This work built on this theory and extended it through the heuristics provided by case study description of natural history and modelling. A more complete theory emerged, but it still requires considerable further testing and validation against time series and regional scale data. The extended theory itself is expected to be only partially successful in explaining any single observation. Evaluation should be made of its usefulness in predicting a proportion of the total variability, in other words, it may reduce residual variation to an acceptable level (Peters 1991). The original postulate that pine invasion is occurring has been refined into a series of statements derived from this particular study that taken together are proposed to have some general validity for interacting systems of forests and people in the highlands of Chiapas. The statements below may be comparatively robust generalisations.

1. In the absence of anthropogenic disturbance pines are only abundant where edaphic conditions are unsuitable for oaks. Autogenic gap phase disturbance is insufficient to permit pine populations to develop within an oak dominated matrix.

2. Rotational slash and burn cultivation transforms oak dominated forest to pine-oak.

3. Pure pine stands have not been derived from former oak woodland through rotational slash and burn. Either permanent land conversion followed by abandonment,

catastrophic stand destruction or chronic degradation through grazing must occur in order to convert oak woodland into a pure pine stand.

4. Pine-oak forests are in dynamic equilibrium only if a degree of anthropogenic disturbance continues.

5. Removal of disturbance from pine-oak systems leads to a reversion to oak domination.

6. Ground fire cannot convert pine-oak forest into a pure pine stand. Under some circumstances low intensity ground fires can increase oak dominance.

7. Logging in pine-oak stands will cause a greater reduction in recruitment of pines than logging in pure pine stands. Intense logging and cutting for fuelwood leads to the conversion of pine-oak stands to stands of pure coppicing oak.

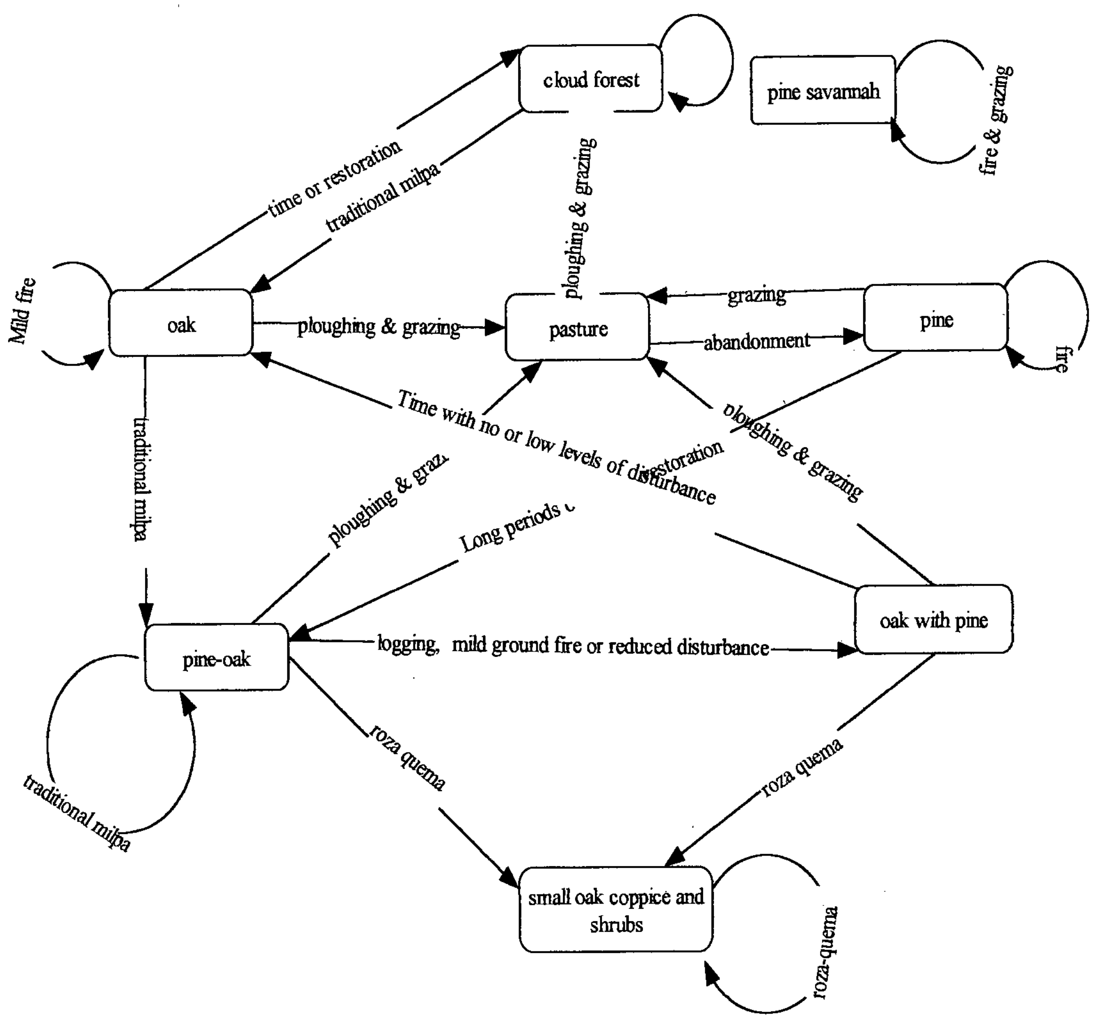
8. Mature mixed broadleaf forest is highly vulnerable to long term change through disturbance by slash and burn farming.

9. The presence of pine provides locally acting incentives for conservation of the forest as a productive system and can allow forests to develop a more mature physiognomy. than would occur in the absence of pine.

10. Chronic stress caused by grazing is likely to lead to permanent deforestation especially when combined with fire, rotational slash and burn farming or logging.

These rules are summarised in figure 9.1. Although expressed in terms of single outcomes, a probabilistic interpretation would be much more appropriate. The pathways shown thus represent the most likely directions of change.

Figure 9.1 Simplified schematic model of the most likely pathways of change in pine-oak systems in the highlands of Chiapas. Note that *roza-quema* is a short rotation slash and burn system in which fallow is not left for more than ten years. Traditional long rotation slash and burn is now restricted to a few areas with low population densities.



The typical pine-oak woodland in the highlands of Chiapas is thus fundamentally an oak woodland with pines, rather than a pine woodland with oaks. It is constantly moving back towards oak domination. One of the most important extensions to the original postulate is that pure pine stands lie completely outwith the pine-oak systems which have been arisen as a result of the most ancient form of indigenous land use. Pure pine stands can only be derived if edaphic conditions are completely unsuited to oak growth, if land has been completely cleared at some point for permanent cultivation, as a result of serious chronic degradation through grazing or possibly as a result of catastrophic stand replacing fire of an intensity not observed in contemporary forests. The theory of pine invasion produces inaccurate predictions without these refinements. Milpa disturbance causes a partial rather than a complete conversion to pine dominated woodland. Fuelwood usage by subsistence farmers does not normally increase pine dominance. By reducing the amount of combustible material in forests, fuelwood collection may even prevent the type of intense crown fires which have been found elsewhere to favour pine over oak. The increase in pure pine stands is a contemporary phenomenon associated with fundamental changes in land usage as populations increase and new farming methods become available. The formation of mixed pine-oak forests is a result of an ancient historical disturbance.

Nevertheless observations can be found which cannot be explained. Some directly contradict this theory and demand new hypotheses. For example the almost pure pine stand found in the most remote inaccessible area of the field site is not predicted. It may have been initiated by stand replacing fire of an intensity that has not been observed recently. In could be speculated that such fires were more common several centuries ago when population levels were lower and less dead wood was gathered from the forest. Investigation using archaeological and palynological methods could cast fascinating insight into the pre historical dynamics of pine-oak woodland. Future investigation will test theories of forest change and undoubtedly produce more surprising results.

Details of the effects of chronic stress on forests, rather than temporally discrete disturbance events, have not been predicted. These may be more important than disturbance for predicting contemporary change. Stress can overcome the fundamental inertia of oak populations and result in irreversible change. There is also an urgent need for more detailed studies designed to trace changes in soil properties. Some important questions that were overlooked in this work must be addressed. Completely new areas for research might need to be developed before a sufficiently accurate picture emerges. Can compaction and oxidation of soil organic matter through grazing lead to permanent collapse of pine-oak systems? To what extent does soil nutrient availability become heterogeneous in disturbed areas? Could variability in the availability of mycorrhizal inoculates be responsible for variability in growth rates or diversity patterns?

Suggestions for management

Can this theory help in the search for sustainable management? Successful management requires consideration of factors outwith the forest system. However knowledge of long term forest dynamics does help to provide guidelines for sustainable use. Old growth oak stands and mixed broadleaf forest are vulnerable to permanent change through any form of disturbance. Prevention of human impact on representative areas of old growth forest is necessary if the regional diversity of woody species is to be conserved. However these stands are now a rare and unique resource which are quite unlike most of the remaining forest in the region. Their conservation raises quite different concerns than those which generalised regional forest management must address. Management designed to reduce levels of disturbance is not required for conservation of the most abundant form of mixed pine-oak forests. The focus should instead be placed on reducing the chronic stress which may be imposed by intensification of grazing and on the prevention of catastrophic disturbance events.

Pine-oak woodland has a relatively low productive potential when compared to plantation systems, but it does effectively meet local needs for timber and fuelwood. While an increase in the productive potential of the system might be desirable to meet rural development objectives, management strategies may have to accept ecological constraints. Pine-oak systems are demonstrably resilient to normal levels of anthropogenic disturbance but they are also constantly changing, are vulnerable to chronic stress and can easily move towards undesirable states.

Oaks compete with pines for resources and pines do not recruit well under oak canopies. The consequence is a reduction in timber production in mixed forests when compared to pure pine stands. It may be very difficult to remove oaks from the system and such action is unlikely to be generally desirable. A reduction in the relative importance of oak through direct intervention could perhaps increase short to mid term timber production. In the right conditions prescribed burning could be used as a sylvicultural tool. However in the present circumstances such action could often be counter productive. Strategies designed to reduce risk seem more appropriate than strategies designed to maximise yield.

Destructive fire is an ever present threat to this type of forest. Nevertheless the current fire regime in disturbed pine-oak woodland is not stand replacing. Sufficient fuel build up must occur in order for fire to cause widespread mortality of mature trees. Where fuelwood is constantly gathered from heterogeneous mixed stands such conditions do not arise. The presence of oaks not only encourages fuelwood collection, but seems to reduce the impact of fires by forming a relatively non inflammable matrix around pines. In most pine-oak forest mild ground fires are much more likely than stand destroying crown fires. If the stocking level of inflammable pine species were increased the risk of crown fire would also increase.

The challenge when planning for sustainable management lies in finding effective ways of recreating the positive effects of slash and burn clearance while avoiding the long term degradation associated with intensification of usage. The alternative is to concentrate timber production on areas of pure pine and allow pine-oak stands to slowly return to their original condition of oak domination.

Can case studies find generality?

Work on single case studies in which natural history observations are made could automatically lead to a mistrust of generalised theory. Conversely modelling alone could propose generality where non exists. It was argued in the introduction to this work that a prior interpretation of generalised ecological theory might not form an effective operational basis for field research. This decision has been supported by observations that suggest that variability at one field site could only be explained with reference to specific historical factors. Forcing observations to fit general conceptual models would have reduced predictive power when such situations are considered. Concepts drawn from classical succession theory appeared to be poor predictive tools. Classifying pine-oak woodland according to a single scheme representing a linear successional sequence would have produced too restrictive a model. This conclusion extended to the elements of the systems. Even though very clear functional differences were found between pines and oaks it was not easy to unequivocally classify the species using linear successional concepts alone. It became apparent that disturbance, even when narrowly defined, can be too broad a term to use as a single predictor variable. There was a marked difference between the effects of disturbance through fire and disturbance through slash and burn. These conclusions were reached in a modelling context when only five species were concentrated on, but data on the more diverse understorey provided little support for a view of succession as a linear process. Situations that arise in more diverse forests must inevitably challenge the ability of simple models to incorporate the necessary realism to provide predictive power.

Successional concepts do have an important role to play in the study of pine-oak woodland, but a perspective that recognises the importance of defining temporal and spatial scale are required in order to identify the appropriate model. If successional change is of interest as a process for study it could be productive to concentrate the attention on longer temporal gradients as perceived by the individual plants that compose the system. Thus studies that include herbaceous species would be interesting as they cover shorter chronosequences. Comparisons between pine-oak systems and the old growth stands from which they have probably been derived represent a long temporal gradient and may be extremely informative. Attempts to describe a linear successional dynamic for canopy trees on disturbed sites have less relevance because once a pine-oak system has been formed through initial disturbance its structure represents a comparatively short section of any pattern arising as result of species replacement over time.

Broad scale patterns are not completely destroyed by slash and burn disturbance. Many species are probably lost during an initial cycle of clearance, but patterns linked to underlying edaphic and climatic variability seem to be still perceptible. Studies that base vegetation classification on intrageneric distribution, rather than more visible physiognomic and structural characteristics can follow underlying patterns in the relationship between species and their environment. Models based on functional classifications of response to disturbance will allow the overlying dynamic to be tracked, quantified and predicted, but classifications based on relative pine-oak dominance should be interpreted using a knowledge of the rate at which change can take place.

Throughout this work use of the multiply defined term *secondary* was avoided to describe pine-oak woodland. However the evidence points to the conclusion that most pine-oak woodland is indeed secondary under almost any working definition, often being derived from the collapse of a more complex system. There is a clear difficulty here for the interpretation of the role of the associated flora. Where the forest is secondary in origin some relic species which are no longer an integral part of the derived system with its shifted point of attraction will be found. However where pine, oak or pine-oak forest is indeed a climatically or edaphically defined system, these species would not be present. The choice of terms used to describe the habitat will influence the perception of the threat to these species and the value of the forest. There may also be a natural tendency to base the use of the term secondary on the maturity of the vegetation rather than its composition. One conclusion from this work is therefore that very complete descriptions of vegetation are needed in order to allow accurate assessment of threats to the local flora. Habitat classifications based on a few dominant species will not provide an effective basis for evaluating the true importance of areas of vegetation. In the long term there may also be a need to consider how the traditional vegetation classifications of the area might be revised in order to better reflect changed theoretical views, altered realities of contemporary patterns of land use and improved knowledge of the historical processes which have shaped the landscape of the highlands of Chiapas.

This progress in understanding forest change was made by linking observations through quantitative modelling. Yet it was found that while process based models provided a framework for investigation, operational prediction still required consideration of site-specific factors. Ecological investigation, as often seems to be the case, was caught between a natural desire to test or apply general theory, and the need for specific, operational statements regarding the real world. This has been expressed as a deep rooted division between essentialist and instrumentalist views of the science. "*Essentialism is the view that science addresses true and palpable realities behind phenomena of nature. Instrumentalism is the view that scientific theories and hypotheses are merely tools to deal with the world around us.*" Peters (1991). Because the world is changing in ways that threaten natural resources and biological diversity there is a need for more powerful and accurate tools to predict change. The contemporary focus on the applied aspects of ecology has forced a positive reevaluation of the sciences' theoretical base. Ecology is strengthening its predictive power through continual refinement and criticism of theory (Ford 2000). At the same time some critics have suggested that ecology should move away from attempts to confirm essentialist constructs (Hall 1988). A tool can only be retained if it has been found to be suitable for at least one purpose. It can then be extended in order to carry out specific tasks. There is a clear divide between the essentialist activity of using data to test models and the strictly empirical intrumentalist approach advocated by critics such as Peters, which fits models to data. The two can be reconciled through an appreciation of the suitability of any model for its purpose. Mistakes that can arise from fitting data to inappropriate models might then be avoided. Where phenomena are approached which can be viewed at multiple scales, multiple models may be required. The simultaneous use of linked models may help to ensure that changing scales only alters the precision of predictions, rather than their accuracy. It may be as important to know how models behave when they are scaled down as how they behave when scaled up.

Forcing a forest succession model to make predictions regarding forest yield proved to be a powerful means of testing its fundamental base. Demanding testable predictive power from ecological models may be an effective means of using the science of ecology to confront issues of societal relevance. The conflict in Chiapas against which this research was conducted brought this into very sharp relief.

Conclusion

It emerges that when a whole system perspective that includes forest users is taken, pine-oak forest have an inherently complex dynamic. Pines increase in dominance as a result of milpa farming, but forests dominated by pines are less likely to be affected by such disturbance. Logging reduces pine dominance which can encourage either a return to rotational slash and burn, or more realistically under contemporary conditions deforestation and land conversion. In a very different context from the natural systems for which the general ecological theory was proposed, the system supports the view that diversity increases stability.

Pine-oak forest is the most widespread forest type in the highlands. This is largely because it has a degree of long term dynamic stability that other types of forest do not possess. This stability arose under a disturbance regime which is now undergoing change. Whether pine-oak forests can retain their place as useful, attractive and biologically diverse features of the landscape of highland Chiapas.may depend on the extent to which research can begin to provide operational models of these forest as interactive systems.

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Appendix: Provisional list of species of vascular plants recorded from Santa Rita Sonora

Name	ID	Family	Local name	Abundance.	Habit.
Ruellia lactea Cav.	375	ACANTHACEAE		common	small herb
Dyschoriste sp1.	291	ACANTHACEAE		common	small herb
Dyschoriste capitata (Oerst.) O. Kuntze	281	ACANTHACEAE		very common	small herb
Saurauia scabrida Hemsl.	28	ACTINIDACEAE	ja ash te	uncommon	small tree
Adiantum capillus-veneris L.	144	ADIANTACEAE		uncommon	herb
Iresine celosia L.	170	AMARANTHACEAE		uncommon	herb
Hypoxis decumbens L.	322	AMARYLLIDACEAE		very common	geophyte
Mosquitoxylum jamaicense Krug & Urban	33	ANACARDIACEAE	po'osh um te	uncommon	small tree
Rhus terebinthifolia Schl. & Cham.	8	ANACARDIACEAE	a'k pajulul	locally common	low shrub
Rhus schiedeana Schldl. var. schiedeana	1	ANACARDIACEAE	pajulul	very common	low shrub
Ilex vomitoria Ait.	77	AQUIFOLIACEAE		local	tall shrub
Ilex macfadyenii spp. pringlei (Standl.) Edwin	95	AQUIFOLIACEAE		rare	small tree
Oreopanax peltatus Linden	61	ARALIACEAE	ka'ab chun te	rare	low shrub
Oreopanax xalapensis (H.B.K.) Decne. &	182	ARALIACEAE		rare	low shrub
Asclepias auriculata H.B.K.	140	ASCLEPIADACEAE		local	tall robust herb
Asclepias curassavica L.	40	ASCLEPIADACEAE	cha kal nich	local	herb
Gonolobus stenocepalus (Donn.-Sm.) Woodson	105	ASCLEPIADACEAE		rare	low shrub
Asclepias curassavica L.	211	ASCLEPIADACEAE		locally common	herb
Eupatorium ligustrinum D.C.	57	ASTERACEAE		common	tall robust herb
Eupatorium macrophyllum L.	71	ASTERACEAE		common	tall robust herb
Senecio cobanensis Coulter	27	ASTERACEAE	xa te	locally common	low shrub
Eupatorium odoratum L.	39	ASTERACEAE		common	tall robust herb
Pinaropappus spathulatus Brand.	361	ASTERACEAE		locally common	herb
Perymenium grande Hemsl. var. nelsonni	54	ASTERACEAE	b'il il	locally common	low shrub
Eupatorium mairetianum DC.	70	ASTERACEAE		common	tall robust herb
Eupatorium pycnocephalum Less.	109	ASTERACEAE	t'on ka te	common	tall robust herb
Eupatorium sp.	58	ASTERACEAE		uncommon	tall robust herb
Fleischmanniopsis leucocephala King & H. Rob.	51	ASTERACEAE	sa kal nichim	very common	tall robust herb

Gnaphalium semiamplexicaule DC.	98	ASTERACEAE		common	herb
Hymenostephium microcephalum (Less.) Blake	87	ASTERACEAE		rare	low shrub
Eupatorium aschenbornianum Schaver	68	ASTERACEAE		locally common	tall robust herb
Ageratum rugosum Coulter	187	ASTERACEAE		locally common	small herb
Melampodium divaricatum (Rich.) DC.	133	ASTERACEAE		very common	tall robust herb
Melampodium montanum Benth.	332	ASTERACEAE		very common	tall robust herb
Salmea scandens (L.) DC.	35	ASTERACEAE	sus ak	locally common	low shrub
Stevia lucida Cav.	119	ASTERACEAE		uncommon	low shrub
Alliospermum integrifolium (DC.) H. Rob.	194	ASTERACEAE		locally common	small herb
Alomia echioides (Less) Rob.	198	ASTERACEAE		locally common	herb
Aster moranensis H.B.K.	212	ASTERACEAE		common	small herb
Vernonia patens H.B.K.	29	ASTERACEAE	ka osh te	uncommon	small tree
Vernonia leiocarpa DC.	12	ASTERACEAE	b'ak te	common	tall shrub
Vernonia canescens H.B.K.	10	ASTERACEAE	y'och yom	common	tall shrub
Verbesina turbacensis Kunth	154	ASTERACEAE		uncommon	low shrub
Baccharis serraefolia DC.	84	ASTERACEAE	meste (hojas serradas)	uncommon	low shrub
Baccharis trinervis (Lam.) Pers.	168	ASTERACEAE		rare	low shrub
Baccharis vaccinioides H.B.K.	24	ASTERACEAE	meste	local	low shrub
Bidens bicolor Greenman	221	ASTERACEAE		local	herb
Senecio deppeanus Hemsl.	5	ASTERACEAE	t'an po'or	locally common	low shrub
Bidens pilosa L.	222	ASTERACEAE		common	small herb
Chaptalia dentata (L.) Cass.	242	ASTERACEAE		locally common	rosette forming herb
Piqueria trinervia Cav.	102	ASTERACEAE		uncommon	tall robust herb
Senecio doratophyllus Benth.	386	ASTERACEAE		local	rosette forming herb
Elephantopus angustifolius Sw.	297	ASTERACEAE		locally common	rosette forming herb
Ageratum rugosum Coulter	131	ASTERACEAE		rare	tall robust herb
Dalea leporina (Ait.) Bullock	146	ASTERACEAE		rare	tall robust herb
Dahlia australis (Sherff) Sorensen	273	ASTERACEAE		uncommon	tall robust herb
Tagetes lucida Cav.	401	ASTERACEAE		locally common	small herb

Cirsium mexicanum DC.	245	ASTERACEAE		local	tall robust herb
Senecio cristobalensis Greem. ex Loes.	25	ASTERACEAE	tza men po'o	uncommon	low shrub
Calea zachatechichi Schlecht.	67	ASTERACEAE		local	tall robust herb
Solidago stricta Ait.	395	ASTERACEAE		uncommon	tall robust herb
Spilanthes oppositifolia (Lam.) D'Arcy	396	ASTERACEAE		uncommon	tall robust herb
Calea ternifolia Kunth.	92	ASTERACEAE		rare	tall robust herb
Stevia caracasana DC.	398	ASTERACEAE		uncommon	herb
Conyza coronopifolia H.B.K.	259	ASTERACEAE		rare	herb
Lithospermum calycosum (McBride) I.M.	328	BORAGINACEAE		local	herb
Lobelia cardinalis L.	329	CAMPANULACEAE		locally common	tall robust herb
Viburnum lautum Morton	143	CAPRIFOLIACEAE		rare	small tree
Viburnum jucundum Morton	59	CAPRIFOLIACEAE		rare	small tree
Clethra suaveolens Turcz.	56	CLETHRACEAE	kumil te	rare	small tree
Clusia flava Jacq.	15	CLUSIACEAE	niwan memelita	local	small tree
Tradescantia commelinioides R. & S.	402	COMMELINACEAE		rare	herb
Cymbispatha commelinoides (Roem & Schult.)	268	COMMELINACEAE		rare	herb
Dichondra sericea Sw.	280	CONVOLVULACEAE		locally common	prostrate herb
Ipomaea sp1.	325	CONVOLVULACEAE		uncommon	herbaceous vine
Evolvulus sericeus Sw..	311	CONVOLVULACEAE		locally common	prostrate herb
Cornus excelsa H.B.K.	152	CORNACEAE	tze men te hoja chica	rare	small tree
Cornus disciflora DC.	7	CORNACEAE	tze m'en te	locally common	small tree
Cyperacea sp2.	271	CYPERACEAE		common	upright narrow leaved herb
Rhyncospora radicans (Schlecht. & Cham.)	368	CYPERACEAE		common	upright narrow leaved herb
Cyperus manimae H.B.K.	272	CYPERACEAE		common	upright narrow leaved herb
Scleria bourgeavia Boekler	383	CYPERACEAE		uncommon	upright narrow leaved herb
Bulbostylis juncoides (Vahl.) Kük.	233	CYPERACEAE		locally common	upright narrow leaved herb
Carex sp2.	238	CYPERACEAE		common	upright narrow leaved herb
Carex polystachya Sw. ex Wahlenb.	236	CYPERACEAE		common	upright narrow leaved herb
Acalypha phleoides Cav.	186	EUPHORBIACEAE		local	small herb

Euphorbia amourii Millsp.	303	EUPHORBIACEAE		rare	small herb
Euphorbia graminea Jacq.	304	EUPHORBIACEAE		rare	small herb
Euphorbia macropus (Klotz. & Garcke) Boiss.	305	EUPHORBIACEAE		rare	small herb
Tragia mexicana Muell. Arg.	403	EUPHORBIACEAE		locally common	small herb
Euphorbia sp1.	306	EUPHORBIACEAE		locally common	small herb
Chamaesyce hyssopifolia (L.) Small	241	EUPHORBIACEAE		locally common	small herb
Euphorbiaceae sp2.	310	EUPHORBIACEAE		locally common	small herb
Euphorbia villifera Scheele	307	EUPHORBIACEAE		locally common	small herb
Phyllantus acuminatus VAHL.	357	EUPHORBIACEAE		locally common	small herb
Phyllanthus glaucescens H.B.K.	55	EUPHORBIACEAE	k'ol k'osh	common	low shrub
Desmodium palmeri Hemsley.	277	FABACEAE		common	herbaceous vine
Astragalus guatemalensis Hemsl.	141	FABACEAE		rare	herb
Acacia angustissima (Mill.) Kuntze	50	FABACEAE	wax, xa k'al	locally common	small tree
Rhynchosia longeracemosa (Martens & Galeotti)	106	FABACEAE		common	herbaceous vine
Rhynchosia longeracemosa (Martens & Galeotti)	367	FABACEAE		common	herb
Mimosa albida Humb. & Bonpl. ex Willd var	78	FABACEAE		common	low shrub
Senna sp.	181	FABACEAE		locally common	small tree
Erythrina chiapasana Krukoff	74	FABACEAE	uj kum	locally common	small tree
Desmodium amplifolium Hemsl.	274	FABACEAE		common	herbaceous vine
Eriosema diffusum (H.B.K) G. Don	299	FABACEAE		rare	herb
Desmodium sp2.	278	FABACEAE		common	herbaceous vine
Acacia pennatula (Cham.& Schlechtendal)	16	FABACEAE	ki jib	locally common	small tree
Calliandra grandiflora (L' Her) Benth.	49	FABACEAE	xa kal puku	locally common	low shrub
Chamaecrista glandulosa (L.) Greene	239	FABACEAE		locally common	small herb
Chamaecrista nictitans Moench.	240	FABACEAE		locally common	small herb
Phaseolus coccineus L.	93	FABACEAE		rare	herb
Phaseolus coccineus L.	354	FABACEAE		local	herb
Cologania procumbens Kunth	249	FABACEAE		common	herbaceous vine
Crotalaria pumila (Rose) Lavin	260	FABACEAE		common	herbaceous vine

Crotalaria pumila (Rose) Lavin	97	FABACEAE		locally common	tall robust herb
Crotalaria pumila Ortega	261	FABACEAE		common	herbaceous vine
Harpalyce formosa DC. var. goldmanii (Rose)	101	FABACEAE		common	low shrub
Desmodium grahamii A. Gray	275	FABACEAE		locally common	herbaceous vine
Cologania broussanettii (Balb.) DC	247	FABACEAE		common	herbaceous vine
Desmodium amplifolium Hemsl.	96	FABACEAE		locally common	tall robust herb
Pachyrrhizus vernalis Clausen	345	FABACEAE		locally common	herb
Quercus benthamii A. DC.	423	FAGACEAE	roble	rare	large tree
Quercus sebifera Trel.	118	FAGACEAE	pixk'olol	locally common	small tree
Quercus crispipilis Trel	18	FAGACEAE	chikinib	very common	large tree
Quercus rugosa Née	98	FAGACEAE	roble	rare	large tree
Quercus segoviensis Liebm.	45	FAGACEAE	roble, yax te	very common	large tree
Xylosma flexuosum (H. B & K) Hemsley.	75	FLACOURTIACEAE	espina	common	small tree
Xylosma chiapensis Lundell	148	FLACOURTIACEAE		rare	small tree
Olmediella bestchleriana (Goepp.) Loes.	43	FLACOURTIACEAE	ur ma ax	locally common	large tree
Gesneriaceae des1	318	GESNERIACEAE		locally common	small herb
Hypericum uliginosum H.B.K.	321	GUTTIFERAE		rare	small herb
Neomarica gracilis (Herb.) Sprague	337	IRIDACEAE		local	geophyte
Sysyrinchium dimorphum R. Oliver	399	IRIDACEAE		uncommon	geophyte
Iridaceae unidentifiable	326	IRIDACEAE		rare	geophyte
Scutellaria caerulea Moc. & Sessé	384	LABIACEAE		locally common	small herb
Satureja brownei (Sw.) Briq.	380	LABIACEAE		locally common	small herb
Salvia lavanduloides H. B. K.	103	LABIACEAE		local	tall robust herb
Salvia holwayi Blake	377	LABIACEAE		local	herb
Salvia cinnabarina M. & Gal.	38	LABIACEAE	sa ben su nul	locally common	tall robust herb
Salvia chiapensis Fern.	82	LABIACEAE		uncommon	tall robust herb
Salvia microphylla var. neurepia (Fern.) Epl.	379	LABIACEAE		locally common	herb
Hyptis verticillata H.B.K.	323	LABIACEAE		rare	herb
Salvia rubiginosa Benth	113	LABIACEAE		local	tall robust herb

Hedeoma costatum Hemsl.	320 LABIACEAE		locally common	small herb
Prunella vulgaris L.	364 LABIATEA		locally common	small herb
Litsea neesiana (Schauer) Hemsl.	127 LAURACEAE	laurel	uncommon	small tree
Ocotea mollifolia Mez. & Pittier	60 LAURACEAE	o'on te	local	small tree
Persea americana Miller	19 LAURACEAE	tsitz	rare	large tree
Allium glandulosum Link	196 LILIACEAE		local	geophyte
Echeandia macrocarpa Greenm.	293 LILIACEAE		locally common	geophyte
Cuphea aequipetala Cav.	156 LYTHRACEAE		common	small herb
Bunchosia lindeniana A. Juss.	178 MALPIGHIACEAE		uncommon	low shrub
Hibiscus uncinellus DC.	175 MALVACEAE		uncommon	low shrub
Sida barclayi E.G. Baker	389 MALVACEAE		common	herb
Miconia mexicana (Bonpl.) Naud.	32 MELASTOMATACEAE	tzab ak	locally common	tall shrub
Parathesis belizensis Lundell	13 MYRSINACEAE	tilish te	very common	small tree
Rapanea juergensenii Mez	6 MYRSINACEAE	memelita	common	small tree
Rapanea myricoides (Schlecht.) Lundell.	2 MYRSINACEAE	a tzam te	common	small tree
Eugenia acapulcensis Steud	179 MYRTACEAE	grandes	locally common	tall shrub
Calyptanthres schlechtendaliana O. Berg	235 MYRTACEAE		uncommon	tall shrub
Psidium sartorianum (Berg) Niedenzu	41 MYRTACEAE	Pajal pata, guayaba	locally common	tall shrub
Eugenia sp.	180 MYRTACEAE	(huele a limon)	locally common	tall shrub
Psidium guajava L.	17 MYRTACEAE	Guayaba	locally common	tall shrub
Ximenia americana L.	11 OLACACEAE	m'oj k'ol	locally common	small tree
Fuchsia microphylla H.B.K.	145 ONAGRACEAE		locally common	low shrub
Oenothera pubescens Willd. ex Spreng.	339 ONAGRACEAE		locally common	small herb
Botrychium decomposiitum Martens & Gal.	158 OPHIOGLOSSACEAE		uncommon	herb
Culcita coniifolia (Hook.) Maxon	265 OPHIOGLOSSACEAE		uncommon	herb
Oxalis latifolia H.B.K.	344 OXALIDACEAE		locally common	prostrate herb
Oxalis alpina (Rose) Kunth	341 OXALIDACEAE		locally common	small herb
Oxalis corniculata L.	343 OXALIDACEAE		locally common	prostrate herb
Passiflora adenopoda DC.	352 PASSIFLORACEAE		local	herbaceous vine

Passiflora membranacea Benth.	111	PASSIFLORACEAE		local	herbaceous vine
Passiflora foetida L.	162	PASSIFLORACEAE		local	herbaceous vine
Phytolacca rivinoides Kunth & Bouche	360	PHYTOLACCACEAE		uncommon	low shrub
Phytolacca icosandra L.	151	PHYTOLACCACEAE		locally common	low shrub
Pinus devoniana Lindl.	21	PINACEAE	cantaj	very common	large tree
Pinus oocarpa Schiede	22	PINACEAE	ixtaj	very common	large tree
Pinus maximinoi H. E. Moore	23	PINACEAE	ixtaj	very common	large tree
Pinus pseudostrobus Lindley	125	PINACEAE		rare	
Piper aequale Vahl	172	PIPERACEAE		rare	low shrub
Plantago australis Lam.	362	PLANTAGINACEAE		common	rosette forming herb
Agrostis perennans (Walt.) Tuckerm.	189	POACEAE		common	upright narrow leaved herb
Paspalum minus Fourn.	350	POACEAE		very common	upright narrow leaved herb
Agrostis sp2.	192	POACEAE		common	upright narrow leaved herb
Androphogon bicornis L.	199	POACEAE		locally common	upright narrow leaved herb
Arthraxon quartinianus (A. Rich.) Nash	204	POACEAE		common	prostrate herb
Briza subaristata Lam.	232	POACEAE		locally common	upright narrow leaved herb
Axonopus compressus (Sw.)Beauu.	216	POACEAE		locally common	upright narrow leaved herb
Sporobolus indicus (L.) R. Br.	397	POACEAE		very common	upright narrow leaved herb
Brachiaria fasciculata (Sw.) Parodi	224	POACEAE		locally common	upright narrow leaved herb
pasto des4	353	POACEAE		common	upright narrow leaved herb
Brachypodium mexicanum (Roem. et Schult.)	226	POACEAE		locally common	upright narrow leaved herb
Paspalum conjugatum Bergius	348	POACEAE		very common	upright narrow leaved herb
Calamagrostis sp1.	234	POACEAE		locally common	upright narrow leaved herb
Arundinella deppeana Nees	208	POACEAE		locally common	upright narrow leaved herb
Muhlenbergia macroura (H.B.K.) A. Hitchc.	334	POACEAE		common	upright narrow leaved herb
Panicum sp1.	346	POACEAE		locally common	upright narrow leaved herb
Cynodon dactylon (L.) Pers.	270	POACEAE		locally common	upright narrow leaved herb
Gram 1....	319	POACEAE		common	upright narrow leaved herb
Ichnanthus nemorosus (Swartz) Doell	324	POACEAE		rare	upright narrow leaved herb

Agrostis hiemalis (Walt.) B. S. P.	188	POACEAE		local	upright narrow leaved herb
Muhlenbergia montana (Nutt.) Hitchc.	335	POACEAE		common	upright narrow leaved herb
Setaria geniculata (Lam.) Beauv.	388	POACEAE		common	upright narrow leaved herb
Dichanthelium laxiflorum (Lam.) Gould	279	POACEAE		common	upright narrow leaved herb
Olmeca reflexa Soderstrom	340	POACEAE		uncommon	upright narrow leaved herb
Polygala floribunda Benth.	363	POLYGALACEAE		locally common	low shrub
Polygala adenophora DC.	44	POLYGALACEAE		locally common	low shrub
Monnima xalapensis H.B.K.	184	POLYGALACEAE	pitzo'tz (tallos rojos)	locally common	low shrub
Polypodium sp.	169	POLYPODIACEAE		uncommon	herb
Pteridium aquilinum (L.) Kuhn	365	PTERIDACEAE		locally common	tall robust herb
Ranunculus petiolaris H. B. K. ex DC. var.	366	RANUNCULACEAE		common	small herb
Clematis dioica L	108	RANUNCULACEAE		locally common	woody climber
Sageretia elegans (H.B.K.) Brongn.	3	RHAMNACEAE	shulub chan	locally common	tall shrub
Rhamnus mucronata Schlecht.	155	RHAMNACEAE		rare	small tree
Rubus hadrocarpus Standley & Steyerm.	176	ROSACEAE	morash grande	locally common	woody climber
Rubus adenotrichus Schlecht.	4	ROSACEAE	morash	locally common	woody climber
Prunus lundelliana Standley	34	ROSACEAE	capulin	uncommon	small tree
Crataegus pubescens (H.B.K.) Steudel	20	ROSACEAE	manzana	locally common	tall shrub
Randia aculeata L.	177	RUBIACEAE		common	low shrub
Psychotria galeottiana Taylor & Lorence	30	RUBIACEAE	kol co te	local	low shrub
Galium uncinulatum DC.	317	RUBIACEAE		locally common	small herb
Galium aschenbornii Schauer	316	RUBIACEAE		locally common	small herb
Richardia scabra L.	371	RUBIACEAE		locally common	small herb
Psychotria costivenia Griseb.	185	RUBIACEAE	kol co te grande	uncommon	low shrub
Chicocca alba (L.) A. Hitchc.	14	RUBIACEAE	chi ik	local	small tree
Crusea laevis (Lam.) Griseb.	263	RUBIACEAE		common	small herb
Bouvardia longiflora (Cav.) H.B.K.	223	RUBIACEAE		local	tall robust herb
Zanthoxyllum foliolosum J. D. Smith	42	RUTACEAE	Yash xa kish	locally common	low shrub
Dodonaea viscosa (L.) Jacq.	26	SAPINDACEAE	Tzal te	locally common	tall shrub

Silvia serpyfollia Benth.	391	SCROPHULARIACEA		common	prostrate herb
Smilax mollis Humb. & Bonpl.	142	SMILACACEAE		locally common	woody climber
Smilax jalapensis Schld.	53	SMILACACEAE	Yas ax	locally common	woody climber
Smilax lanceolata L.	123	SMILACACEAE		locally common	woody climber
Solanum hispidum Pers.	36	SOLANACEAE	pajal blanco	common	low shrub
Physalis phidadelphica Lam.	359	SOLANACEAE		common	low shrub
Cestrum aurantiacum Lindl.	122	SOLANACEAE		common	low shrub
Lysianthes ciliolata (M. &. G.)Bitter.	330	SOLANACEAE		uncommon	herb
Solanum torvum Swartz.	130	SOLANACEAE		uncommon	tall shrub
Solanum myriacanthum Dunal	128	SOLANACEAE		uncommon	low shrub
Physalis gracilis Miller	358	SOLANACEAE		uncommon	herb
Anoda cristata (L.) Schlecht.	203	SOLANACEAE		locally common	small herb
Solanum lanceolatum Cav.	129	SOLANACEAE	Pajal morado	local	tall shrub
Ternstroemia oocarpa (Rose) Melchior	183	THEACEAE		locally common	small tree
Cleyera theaeoides (Sw.) Choisy	9	THEACEAE	cosh ush te	common	small tree
Daphnopsis americana (Miller) Johnston	31	THYMELAEACEAE	Cham pat	local	tall shrub
Triumfetta columnaris Hochr.	165	TILIACEAE		local	tall shrub
Eryngium gracile Delar	302	UMBELLIFERAE		common	small herb
Micropleura renifolia Lag.	333	UMBELLIFERAE		very common	prostrate herb
Eryngium foetidum L.	300	UMBELLIFERAE		common	herb
Lantana hispida H.B.K.	120	VERBENACEAE	Kilwet kawu	common	low shrub
Duranta repens L.	125	VERBENACEAE		rare	small tree
Lantana camara L.	327	VERBENACEAE		locally common	tall robust herb
Lippia substrigosa Trucz.	159	VERBENACEAE		common	low shrub
Verbena carolina L.	406	VERBENACEAE		locally common	small herb
Vitis tiliifolia H.& B. ex R. & S.	110	VITACEAE		uncommon	woody climber