Simulation of Forest Ecosystem Dynamics, with Respect to the Problem of Hierarchy

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A thesis submitted in fulfilment of the requirements for the degree of
Doctor of Philosophy to the University of Edinburgh

1994

Declaration

This thesis has been composed by myself and it has not been submitted in any my previous application for a degree. The work report within was executed by myself, unless otherwise stated.

Jingsheng Luan

October 1994

Dedication

To
my grandmother and
my parents
for all their love

and
to nature
which is the source of both science and art, and our life

Acknowledgements

I wish to express my profound gratitude to my supervisors Professor John Grace and Dr Robert I Muetzelfeldt for their meticulous supervision, continuous help, and inspiration throughout this work. I am most grateful to John for guiding me to the front end of ecological modelling, and for many heuristic discussions and criticisms of my work and thesis, for his general support at all times, and providing me with data to test my forest model against. I will remember Robert for his unending constructive criticisms, and his instilling into me the constant need to pay attention to detail. Thanks to him I have learnt a lot about how to achieve the high standards required by scientists today. Most of all I will remember John and Robert for all their everlasting enthusiasm and patient introduction to my work and science in general, which undoubtedly provided inspiration to help me throughout my work.

In addition I would like to acknowledge the help and constructive comment given by Dr John Blyth regarding my field work in Glentress, and from him I have learnt much forestry knowledge which is useful to my modelling work. I would also like to thank the many colleagues in my group who helped me in many aspects during my study, especially, I thank Gail Jackson and Jennifer McConnell for their help in correcting the English of my thesis. Thanks go to the staff at the computer support group of the Life Sciences in JCMB who gave me a lot of help in computing and programming.

I am grateful to my family and relatives at home in Beijing, who have given me so much love, encouragement and comfort throughout these years. I give my heartfelt thanks to Shiu-Wan and Jane, for their huge mental support.

Finally, this work was carried out with aid of the Overseas Research Student Award Scheme (ORS) from the British Council, and the Postgraduate Studentship of Edinburgh University, to whom I wish to express my sincere gratitude.

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Abstract

As knowledge about forest ecosystems accumulates, it becomes important to develop an explicit description of the functional relationships between processes. These relationships include processes ranging from cell to leaf, tree and forest. Knowledge obtained at any one of these levels cannot provide much understanding or predictive power, because the overall behaviour is influenced by positive and negative feedback between levels. A hierarchical approach is applied for coupling processes at these levels. In this study, a hierarchical forest model FORDYN is developed, which can integrate knowledge at a biochemical or physiological level to make statements on tree growth and forest succession levels. This procedure is referred to as 'scaling up'.

The model FORDYN consists of four levels of process characterised by the time step or behaviour frequency. In level 1, a forest succession process is described by accounting for the fate of spatially distributed individual trees in an annual time step. In level 2, growth of each tree is represented by a 'process-based' approach, whereby assimilation, assimilate allocation, nitrogen dynamics and water balance are accounted for in a daily time step during tree growth. In level 3, daily photosynthesis is accumulated by hourly values by a 3-point Gaussian scheme. In level 4, instantaneous CO_2 assimilation rate is calculated by a biochemical (mechanistic) photosynthesis model.

To exploit fully the hierarchical feature of the model structure, FORDYN is designed to be used in different simulation modes to meet the demand of different purposes of users.

FORDYN was tested against the common data set provided by the European Pine Modelling group, and sensitivity analysis of this model was compared with other published and validated European pine models. It was shown that FORDYN is robust and responsive. FORDYN has been used to analyse current problem of global change, such as the impact of CO_2 increase. It was shown that this model can provide new insights into ecosystem dynamics and environmental problems of wide concern.

This is probably the first model that can simulate long term forest development by scaling up biochemical processes, physiological processes, and tree growth processes. It is a contribution to the modelling methodology in forest modelling, also it provides a good example of unification of ecosystem science and population biology.

Chapter 1 Introduction

1.1 Background

Many current ecological questions concern ecosystem processes at regional to global scales. It has become necessary to predict the consequences of large-scale changes, like CO_2 increase, and regional air pollution from previous knowledge obtained at leaf, individual and community scales (Norman, 1980). Forests play a determining role in soil conservation, watershed management and climate change, at local, regional and global scales. Hence, there has been a new impetus in the study of ecological system dynamics of forests in recent years.

Traditional ecological models are limited in their predictive power for the simulation of current ecological problems because of their empirical representation of plant-environment processes. Ecophysiology concerns plant physiological processes in relation to environmental variables. It is an experimentally based field of inquiry that operates at the level of individual plants and organs. It is at these levels that much of our knowledge of plant response to the environment exists. Therefore an important recent objective is to use this knowledge to predict the responses of vegetation to environmental changes and management influences. This requires *scaling up* from small to large scale.

1.2 Objectives of Forest Modelling

To understand the pattern and process of forest ecosystems, and to deal with problems related to disturbance, one can acquire predictive power through theories and simulation models of forest dynamics. Scientists first began to use the computer to design mathematical models of changes in forest composition in the 1960s (Odum, 1960; Olson, 1963; Hool, 1966).

There are fundamentally two types of objectives in forest modelling: one is *application*, where the models are built as a tool to deliver technology, knowledge, an expert system, or designed to simulate growth of a species. Such models usually need local parameters and optimisation. The other type is *research*, where the models are built for integrating knowledge for a deeper understanding of general behaviour and mechanisms. e.g. to extend knowledge of physiological and biochemical processes to understand the forest as a whole such as the need for current ecological predictions about climate change. The models for these two types of objectives may or may not be similar. Sometimes, there is also a need for developing compact models (e.g. forest growth models) which use a minimum number of state variables, and provide a valid behavioural spectrum for the range of site, climate, management and pollution conditions found in reality (Bossel, 1991).

There was a transition of forest modelling objectives as time went by, e.g. in the 1960s, models were built for the prediction of forest yield, element cycling etc. in plant-soil systems, or trophic-level dynamics (Olson & Christofolini, 1966).

By the 1970s, there was an increasing emphasis on quantitative ecology and systems ecology due to the utilisation of engineering science and the exploration of mathematics in ecological studies, as well as the development of ecological theory and availability of computers (Garfinkel, 1962; Davidson & Clymer, 1966; Watt, 1966). The International Biological Programme (IBP) used ecosystem models as a central theme. All these developments provided a suitable climate for the evolution of ecosystem models.

In the 1980s, discussion about global change provided another stimulus for developing ecological models. Many 'process-based' forest growth models (whereby most of them are 'stand models') were built then (Dixon *et al.*, 1990). These models are sensitive to environmental change, can describe physiologically-based tree growth processes, but cannot yet predict long term forest development.

Currently, *scaling* physiological processes to ecosystem and higher scales of processes is becoming a new focus in studying global change (Ehleringer and Field, 1993), e.g. a simulation that describes both biogeochemical processes and individual species distributions and dominance patterns. Norman (1980) noted that scaling-up from leaf physiology to ecosystem dynamics level or beyond is one of the fundamental challenges in predicting effects of global change.

Motivated by the above considerations, I decided to develop a simulation system that is capable of predicting the effects of environmental changes in CO_2 increase, temperature, and radiation on the long term forest development (succession).

To do this, a proper modelling approach is crucial. In the following, I will firstly review the range of existing forest models in the search for the possible candidates, then present the modelling approach to be used in this study.

1.3 Review of Forest Models

1.3.1 Historical Development of Forest Modelling

During the last three decades there has been a remarkable proliferation of computer models designed to simulate ecological dynamics. Many of these focus on forests. Reviews of forest models are found in Munro (1974), Shugart & West (1980), Dale *et al.* (1985), Shugart (1984), Shugart *et al.* (1988), and Ågren *et al.* (1991).

For historical reasons, each of these reviews has its own categories, which marked the development of ecological theory and ecological modelling methodology over time (Fig 1.1).

In the early stage of forest modelling, from the 1960's till early 1970's, as indicated by Munro (1974) (Fig 1.1) 'modelling philosophies' were on the basis of two features: inter-tree dependency status (distance dependent or independent between trees) and primary unit parameter requirement (need parameters about trees (location or no location) or stand). These models are concerned with forest yield or production, and the growth of trees or stands are represented in empirical ways.

- Single tree/distance dependent models: these assume that the unit of stand modelling is a single tree and that inter-tree distance is a necessary parameter. Therefore, the locations of each tree in the site must be represented.
- Single tree/distance independent models: these also consider that the unit of stand modelling is a single tree, but the inter-tree distance is not a necessary parameter. These models do not require locations of trees to be represented.
- Whole stand/distance independent models: these consider the unit to be the whole stand and hence it is not necessary to take individual trees into account. Forestry yield tables belong to this subset.

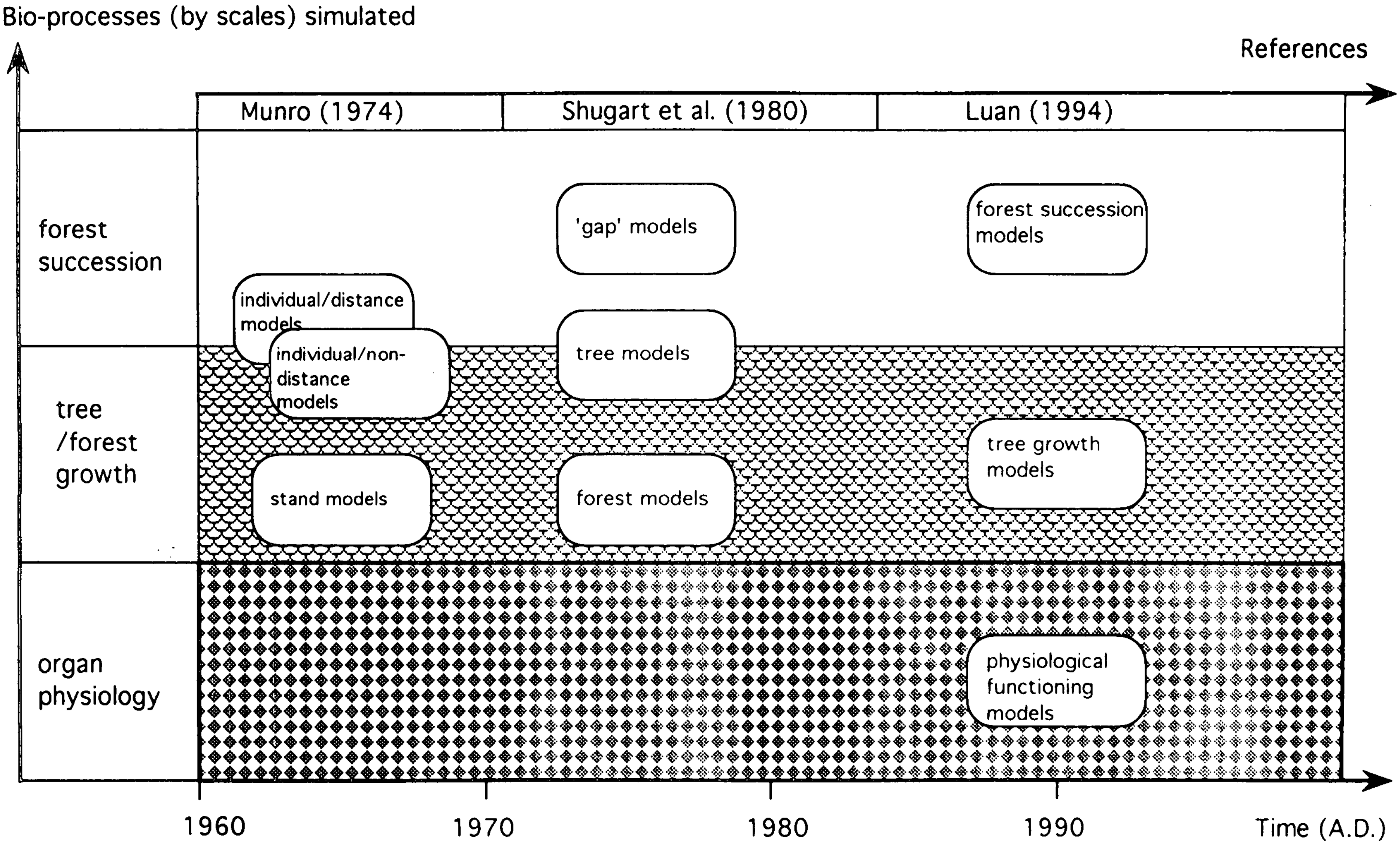


Fig. 1.1 Evolving classification of forest models

Development of classification of forest models according to the scales of biological processes of each model's objective.

Among these forest models, the most obvious use of growth models is to provide an estimation of the yield of wood from forested land. Munro (1974) insisted that 'This indeed may be the final objective of the application'. Therefore, we can see that most of these classical forest models originate from the demand of traditional forest management for a forecast of the timber output.

Simulation of forest succession was not given enough concern until the 1970's (although a small number of succession models were developed before then, such as Hool's (1966) Markov model for forest succession), as ecologists began to re-consider the underlying mechanisms involved in ecological succession (Odum, 1969; Drury & Nesbit, 1973). Forest succession models are proposed to simulate long term forest development in term of species composition change (e.g. tree number or total biomass by species) over time. Most of these models permit a simulation time of more than one life cycle of trees, say 200 years or longer.

In Shugart & West's (1980) review (Fig 1.1), there were three categories of forest models namely, tree, forest, and gap models. Tree and forest model correspond to tree and stand models in Munro's categories, while some tree models are capable of simulating forest succession. They considered gap models (which in fact are a subset of individual tree models) as a category developed exclusively for use in simulating forest succession. Shugart (1984) gave more ecological implication of this type of forest succession model.

In a later stage, there was an emerging interest in spatial and temporal variability in biospheric and geospheric processes (Rosswall *et al.*, 1988), whereby the scale problems relevant to global change became an important concern in the IGBP (International Geosphere-Biosphere Programme). Then Shugart *et al.* (1988) further classified forest succession models into four categories according to the representation of spatial and temporal dimensions among the simulated plants:

- Markov models: these simulate the change of an ecosystem in the time dimension. These models are built by first determining from observation the probability of the conversion of an ecosystem's status at a certain time to another status after a certain time interval. It is most important to define the status of units which are used as elements in the Markov chain. Horn's (1975a, b; 1976) famous Markov model was developed for simulating the species dynamics of forest canopy trees. The same method can be found in other models (Hool, 1966; Waggoner & Stephens, 1971).

- Gap models: this group of models simulates community dynamics by considering the vertical profile of light that develops over time as trees grow and attenuate the light. Such models simulate the life history of constituent plants (birth, growth and death). Gap models belong to the class of individual tree models. The first model of this type was JABOWA developed by Botkin *et al.* (1972). Another gap model that has been used in a larger number of applications in mixed-forest is FORET (Shugart *et al.*, 1977) derived from JABOWA. The JABOWA/FORET class of models is the most widely used type of forest succession model. Gap models calculate birth, growth and death of individual trees on a small plot (0.01 ha), and forest succession is estimated by sampling 50 to 100 plots.
- Transect models: these simulate vegetation structure in the horizontal dimension. A transect model can be a conceptually straight-forward extension of the approaches used in gap models which involves a reformation of the competition function so as to have only one horizontal dimension of competition. Shugart *et al.* (1988) proposed a transect model that maintains the computational efficiency of a Markov model but also incorporates both a mechanistic formulation of the important population processes and the realism of spatial heterogeneity. These transect models are most suitable for situations where the community is apparently zoned over an environment gradient.
- Spatial models: these simulate community dynamics by two or three dimensional competition between plants. Most single tree models belong to this group. They also simulate dynamics of recruitment, growth, competition and mortality as gap models. The spatial models differ from gap models mostly in their explicit consideration of horizontal competition between trees. An example is the model FOREST (Ek & Monserud, 1974).

These models simulate forest succession by describing the population dynamics of each species, although they may vary with spatial or temporal dimensions of relations between plants emphasised. However, the processes such as tree growth and mortality involved in these models are still mostly represented in empirical ways.

In the last few years, ecological modelling has evolved to place more emphasis on biologically process-based modelling, and dozens of process models have been developed (Dixon *et al.*, 1990).

In this context, 'process' refers to underlying mechanistic phenomena, both physical, biological and chemical. Examples of biological phenomena that models try to capture are such processes such as assimilation, assimilate allocation, photosynthesis, and respiration. One advantage of using process modelling is that very often the component processes are relatively well understood from laboratory or field studies. The challenge for the modeller is to put them together in the right way.

To date, as noted above, *scaling up* physiological processes from leaf to ecosystem and larger scales becomes an important challenge in current ecological study and modelling.

One reason for this emphasis is that advances in ecophysiology need to be incorporated into the ecosystem level of studies in order to contribute to ideas about the impact of global change. e.g. much experimental work on the influence of elevated CO_2 and temperature has been carried out at the leaf scale, but it is not usually practical to do long-term CO_2 fumigation experiments at the ecosystem scale. Therefore there is a need for scaling up.

A recent book, *Scaling Physiological Processes, leaf to globe,* edited by Ehleringer and Field (1993), is an effort in this direction. It intends to fill an important gap by summarising the state of knowledge concerning strategies and techniques available for transferring information from one scale to the next.

1.3.2 Classification of Forest Models by This Study

The current demand for explicitly incorporating scaling in considering the effects of global environmental change calls for a new view towards the classification of forest models.

All forest dynamic processes are shaped by the characteristic time-scales of their components, e.g. forest succession is in centuries, tree growth is in years, etc.

The modeller needs to determine which level will be emphasised, since the description of the forest will vary with the choice of scales (Levin, 1992). However, it is suggested that the descriptions of scales, or the recognition of the scales should rely on both the precision of aggregated *processes with different time and spatial scales* (Levin, 1992), and the *behavioural validity of the phenomenon* being concerned (Allen *et al.*, 1987).

Therefore, in this study, three categories of existing forest models are arranged along a spectrum according to the hierarchical level of biological process (phenomenon characterised by time scales) corresponding to the modelling objective (Fig 1.1). They are *physiological functioning models, tree growth models,* and *forest succession models.* In *physiological functioning models*, bio-processes are described (explicitly or implicitly) to various depths of physiological information down to biochemistry. *Tree growth models* integrate (explicitly or implicitly) the physiological processes to the whole individual tree and describe the tree's growth, by either size or biomass, within its life cycle. *Forest succession models* intend to describe forest dynamics by representing the population dynamics of species in the stand. The processes such as competition, growth, regeneration, and mortality are usually represented, hence these models can be run for more than one life cycle of trees in the stand (Shugart, 1984; Shugart *et al.*, 1988).

In the present classification, the 'forest models' and some 'tree models' (those without succession processes involved) in Shugart and West's (1980) categories will belong to the category *tree growth models* in that they aim to represent the growth of either a single tree or the whole stand (also based on a single tree's growth), and no tree death and birth processes are described. These models can only run in less than one life cycle of trees in the stand. 'Gap models' and 'tree models' that can simulate forest succession would be in the category *forest succession models*. These models can be run for more than one life cycle of trees in the stand. As for *physiological functioning models*, they were not included in forest models in previous reviews, although there already some models were developed only for simulation of specific physiological functioning processes of forest, e.g. MAESTRO (Wang & Jarvis, 1990) was designed to simulate crown (then canopy) photosynthesis and transpiration. It is time to recognise the importance of these models, as they are the very processes we want to incorporate into our current study for scaling up to ecosystem and higher scale of processes.

From a hierarchical point of view, the processes in one type of model can sometimes be included in another type of model (next higher level of evolving hierarchy), e.g. the processes in tree growth models are often be included in some forest succession models. The idea of this classification is that each type of forest models can contribute to identifying and describing the forest dynamic processes in certain time scales.

Physiological functioning models

Advances in plant physiology have made a great contribution to the explanation and prediction of plant responses to the environment. Our knowledge of processes such as leaf energy balance, carbon uptake through photosynthesis, transpiration and respiration have been improved through the development of concepts and instrumentation, but most importantly through the application of experimental method in ecophysiology. Such knowledge enables us to describe the response of tree physiological processes to environmental changes from seconds to days.

The objective of physiological functioning models is to understand how the plant exchanges energy and material (carbon, nitrogen, water, etc.) with its environment. Many physiological functioning models focus on the canopy by integrating leaf responses to microclimate. Some physiological processes are often addressed separately such as photosynthesis, respiration and transpiration of the canopy. Others such as assimilate allocation, phenology, and growth regulation are usually described together with tree growth process in process-based tree growth models. As this is a classification based on *modelling objectives* rather than the *processes* involved, so the later part will be discussed in tree growth models.

Many traditional models utilise empirical responses of the leaf. For example, photosynthesis is described as a light response curve in the form of a rectangular hyperbola (Michaelis-Menten equation), negative exponential, or non-rectangular hyperbola (Thornley, 1976). However, some physiological processes have been intensively studied in a mechanistic way.

Farquhar and von Caemmerer's (1980) biochemical model of leaf photosynthesis is an example of a physiological model with resolution at the cell biochemical level. Based on the C_3 pathway of photosynthesis, the model describes the biochemical mechanism of leaf photosynthesis, and calculates CO_2 assimilation rate by considering the limitation of the activity of the photosynthetic enzyme Rubisco (ribulose-1, 5-bisphosphate carboxylase-oxyenase), or regeneration of RuBP (ribulose-1, 5-bisphosphate), and electron transport. Intermediate related processes are accounted for by incorporating sensitive environmental responses. These processes include the kinetic properties of Rubisco; the requirements of the photosynthetic carbon reduction and photorespiratory carbon oxidation cycles for reduced pyridine nucleotides; the dependence of electron transport on photon flux and the presence of a temperature dependent upper limit to electron transport, etc. To estimate rate of CO_2 assimilation by the leaves, a statistical approach is used to account for the carboxylation rate under both RuBP saturated and electron transport-limited processes.

The discipline of micrometeorology has provided an important insight into the controlling influences of climate on the exchange of energy, mass and momentum. For example, the Penman-Monteith combination equation is a rigorous method for combining energy, heat, and water transfer, and has been widely accepted to give good estimates of the transpiration rate of a leaf or a forest. MAESTRO (Wang & Jarvis, 1990) was developed to predict radiation absorption, photosynthesis and transpiration by the individual crowns of trees in a stand as a whole. The fluxes of radiation are treated in the photosynthetic (PAR), near infrared (NIR) and thermal wavebands; direct beam and diffuse radiation are considered separately. The spatial heterogeneity of the leaf area density distribution within the tree crown has been incorporated into MAESTRO, and can be used to study the spatial distribution of the radiation regime, and of the water vapour and carbon dioxide exchange of leaves within the tree crown, in relation to the stand structure. Within MAESTRO, various photosynthesis models may be implemented to estimate CO_2 uptake from a knowledge of absorbed PAR. MAESTRO is not a tree growth model (according to the present system of classification) in that it can not represent tree growth processes either by size or by biomass, and nor can it represent phenological development. Moreover, the run duration is limited to days, or less than one year.

Respiration is another aspect which has been studied at quite fundamental levels during the past two decades. To estimate dry matter production it is necessary to also know the respiration rate involved in the synthesis and maintenance of biomass. McCree (1970) proposed that respiration had effectively two components, one being proportional to the gross supply of substrate and independent of the plant dry weight, and the other being proportional to the plant dry weight and independent of the substrate supply under the conditions used. Thus respiration is calculated by a summation of growth respiration and maintenance respiration, with growth respiration assumed to be in constant proportion to gross photosynthesis (McCree, 1970) or growth rate (Thornley, 1976), or calculated from biochemical data on the 'costs' of synthesis (Penning de Vries, 1975).

Since a physiological functioning model is designed to simulate tree or forest physiological functioning process, the run duration of this type of model is usually less than one year.

Tree growth models

The growth of a tree by size or by biomass is dependent on genetically controlled physiological processes and influenced by the environment. It can be represented by either fitting an equation to describe the empirical size increment (Dale *et al.*, 1985), or by process modelling (Dixon *et al.*, 1990). Most classical or empirical tree growth models, use tree diameter as the unit of measured growth; others use tree height, bole diameter at different heights, and crown size. Individual tree characteristics are aggregated to describe the stand. The time step for these tree growth models is mostly days or years, or longer, and run duration is within one life cycle of trees in the stand (Dale *et al.*, 1985). As noted above, these models include stand models and some tree models (those without succession processes involved) in Shugart *et al.*'s (1980) categories, e.g. Solomon's (1974) even-aged mixed-species nonspatial tree model is related to the present category. It uses a typical tree at different ages in a system of dynamic equations and solves for forest attributes of northern hardwood forest stands. But it is not able to simulate forest dynamics over a time scale exceeding the life spans of the species considered.

Tree growth is the result of interacting physiological processes influenced by both the inherited genetic constitution and the ambient environment. Some physiological phenomena are recognised to be particularly useful in modelling tree growth, such as, mineral metabolism, carbon assimilation and allocation, absorption and accumulation (intake of water, minerals, gas), translocation, and growth regulation (Dixon *et al.*, 1990). In order to analyse, simulate, and predict tree growth in response to environmental stress, it is necessary to acknowledge, understand, and link these phenomena in a proper way, e.g. Thornley's (1991) transport-resistance forest growth model. It is designed for a monoculture of identical trees of the same age, which is directly relevant to plantations. A transport-resistance approach of dry-matter partitioning is introduced, and the growth of the tree is represented by means of the size and activity of the meristem. Various tree growth models differ in aspects of the plant physiological processes emphasised. The following are some processes that are most generally modelled in a process-based tree growth model besides those usually described in *physiological functioning models*:

- assimilate allocation:

Trees acquire both energy and carbon by photosynthesis, and convert the energy to chemical energy (ATP) required for the maintenance of existing cells (maintenance respiration) and production of new cells (growth respiration), and allocate the photosynthate production (source) to growing organs (sink) for tree growth. Tree factors that influence this assimilation process include age, phenology, leaf morphology, crown architecture, and branch growth patterns (Isebrands *et al.*, 1990).

Assimilation partitioning is a major factor in tree growth. It includes loading of assimilates into phloem, vascular transport, and unloading at the sink. Modelling dry matter partitioning is a difficult but important part of tree growth modelling. Models developed for this may be described according to Thornley (1991) as: empirical

(McMurtrie, 1985); teleonomic or goal-seeking (Valentine, 1985); and quasi-mechanistic (Thornley & Johnson, 1990). There is a growing body of literature to suggest that environmental stress significantly influences tree growth by altering carbon partitioning between organs (Reich & Amundsen, 1985; Little, 1980). A recent transport-resistance approach (Thornley, 1991) represents nitrogen uptake and partitioning by defining a concentration gradient between organ compartments (root, stem, branch, and leaf). The matter in each compartment is further subdivided into meristem, structure, carbon substrate, and nitrogen substrate. The meristems use the substrates to generate new structure, hence maintaining the concentration gradient. Dewar (1993) further coupled nitrogen, carbon, and water cycles together in a simplified way. In this scheme the activity of meristems was a linear function of water content. However, the approach still needs more experimental work.

There is a well-developed conceptual framework for water transport but this has rarely been applied in modelling carbon assimilation. Water transport has been described in a soil-vegetation-atmosphere transfer scheme or model (SVATS or SVAT models) (Geyer & Jarvis, unpublished). For example, Forest-BGC (Running & Coughlan, 1988) can simulate water (and carbon) balance of forests with time scales of days to years. Daily canopy averaged physiological processes such as leaf water potential, leaf temperature, evaporation, transpiration and water use efficiency are calculated.

- mineral metabolism:

Mineral nutrition is critical to tree growth. Minerals have many functions in trees, serving as constituents of cells and tissues, biochemical catalysts, and osmotic regulators (Clarkson and Hanson, 1980).

Nitrogen is an essential component of amino acids, the building blocks of proteins (including enzymes), chlorophyll, and growth regulators. Emphasis has been placed on nitrogen uptake by roots and reduction in leaves, and on the influence of leaf-N on photosynthesis and respiration. The processes of mineral metabolism are described from the ecosystem (Goldstein *et al*, 1984) to the subcellular level (Oaks and Hirel, 1985). Models linking nitrogen supply with water and carbon flux between tree parts are now required.

- morphology and phenology:

Tree morphology influences growth in many respects. Crown shape, total leaf area, and spatial distribution, leaf inclination, and leaf-root ratio (Bossel *et al.*, 1989) all affect radiation absorption, photosynthesis, transpiration, respiration (Wang, 1989), and assimilate allocation (Bossel *et al.*, 1989). Phenology is not frequently modelled in tree growth models partly because it is not well understood. Sometimes it is considered as an empirical curve of temperature effect on assimilation (Mohren *et al.*, 1990). In reality, a plant perceive cues from the environment, such as photoperiod and chilling, and uses these cues to regulate development. One aim in modelling the response of forest to climate change is to use this sort of information as it becomes available for particular species.

- translocation:

Tree metabolism and growth depend on the efficient movement of organic compounds, minerals, and water. Acropetal transport of water and dissolved nutrients from the root system to aerial portions of the tree occurs in the xylem. In contrast, the phloem carries metabolic products from leaves to other organs. The direction and rate of intra-tree transport are influenced by source-sink relationships. e.g. carbon metabolite transport between leaves. Developing leaves with significant metabolic activity firstly import from mature leaves until full expansion is achieved. Then, after full expansion, leaves become net exporters of carbon metabolites. The ageing and senescence of leaves is accompanied by a decline in photosynthesis and carbon metabolite export. These complex transport patterns have yet to be fully incorporated into process-based tree growth models.

- growth regulation:

There is an interactive control of metabolic source and sink relationships by genes and growth-regulating substances, termed plant growth regulators or hormones (Wareing, 1980). Experimental evidence suggests that growth-regulating substances play a pivotal role in intra-tree communication, as well as in the regulation of physiological processes in response to environmental stress (Kossuth and Ross, 1987; Zeevart and Creedman, 1988).

There is competition for growth resources (water, minerals, light, and CO_2, etc.) between organs during their growth phases, as well as allocation of resources (e.g. carbon metabolites) to various organs (Ho, 1988). This resource allocation among tree organs may be considered as a function of differential sensitivity to growth-regulating substances (Wareing, 1980). It is suggested that future modelling in this respect should consider membrane transport processes, growth regulators, and enzymatic regulation of rate-limiting processes of developing organs (Dixon *et al.*, 1990).

A proposed tree growth model should incorporate carbon, nitrogen, and water cycling processes into assimilation and assimilate allocation. A recent approach, introduced by Thornley (1991) and modified by Dewar (1993), represents efforts towards this direction. Nevertheless, there still seems to be a lack of knowledge, e.g. the effect of water availability on growth rate (Dewar, 1993) is yet to be understood well and needs more experimental support.

In short, empirical and analytical (process-based) tree growth models differ in the underlying physiological processes that are being described, and in levels of simulation resolution, while various process-based tree growth models differ in aspects of plant physiology, or in the range of complexities emphasised (Ågren *et al.*, 1991).

Forest succession models

Various models and approaches that are available for the simulation of forest succession are based on representing competition and population dynamics. Individual tree growth may be either explicitly or implicitly simulated. Besides approaches reviewed by Shugart and West (1980), Shugart (1984), and Shugart *et al.* (1988), Bossel and Krieger (1990) also listed some possible approaches for tropical forest successional modelling, such as life cycle models, age class models, height class models, and development stage growth models (canopy layer models).

Some forest succession models take a group of trees as the basic unit. Forest dynamics are projected by simulating the interrelation between these tree groups. The pattern and processes of the stand are therefore the aggregated result of individual tree behaviour. For example, the Markov model is a mathematically and conceptually straight-forward succession model with implicit individual trees, constructed by determining the probability that the current stand will be in some other vegetation type after a given time interval as mentioned above.

The developmental stage model (canopy layer model) (Bossel and Krieger, 1990) considers trees in a stand according to their development stage: seedling, sapling, pole, main canopy, and emergent. These classes or canopy layers can reflect different light environments: saplings are growing in the shade of poles, which is in the shade of the main canopy. Therefore, different layers have different conditions. The regeneration in the seedling layer is defined by seed survival from that mature tree's seed production in the main canopy and emergent layers. This approach offers a simplified level of structure, behaviour, and computation efficiency. However, the model does not describe the response of the forest to environmental factors such as temperature, soil nitrogen, and soil water in a 'process-based' or analytical way.

Other approaches such as age class (Luenberger, 1979), and life cycle modelling (Wissel, 1990) are in the same spectrum. In the age class models, population structures (diameter and height distribution) are based on age distribution, but age is a poor indicator of tree structure such as height, diameter, biomass etc. The life cycle models represent the current development stage of a particular forest gap by its present location on its life cycle from regeneration by seeds through sapling pole, mature stage, and finally death (Wissel, 1990). This approach provides a crude image of forest mosaic dynamics, but lacks all detail of stand structure, its components and dynamics.

Some forest succession models are designed to simulate forest dynamics on the basis of single tree processes of birth, growth, and death, such as the 'gap' models, and some 'individual tree models' (e.g. mixed-age) in Shugart and West's (1980) review. For example, the FOREST model (Ek & Monserud, 1974) is recognised as one of most complex classical forest models (Shugart and West, 1980). It considers the explicit spatial and horizontal distribution of each tree, whereby competition is calculated as a function of crown overlap. Tree growth depends on species-specific regressions of the relations: height-diameter, tree-height-age, open-grown crown-width, and diameter-height curves. The model can simulate a forest of any size, but it requires considerable data for validation.

To look back at all the existing forest models, it seems none meets the demand of current ecological modelling for predicting the effects of global change. Existing forest succession models do simulate long term forest development, but fail to represent any sensible response to environmental change. On the other hand, existing physiological functioning models and process-based tree growth models can describe plant-environment relations in a more mechanistic way, but are limited in predicting long term forest development. Therefore a new modelling approach is needed, and this will be the focus of the present study.

1.4 The Aims of This Study

One important current challenge is to make models of long term forest dynamics more responsive to local scale climate change (Shugart *et al.*, 1988). In developing such a modelling approach, one has to deal with various aspects of the problem of scale or hierarchy. Therefore, the objectives of present study are as follows:

- to predict long-term forest dynamics (e.g. forest succession) from existing knowledge through modelling;
- to utilise our extensive knowledge at leaf-scale process to scale up to the forest ecosystem level.

The structure of this research project is as follows:

1. As already shown in this Chapter 1, to review existing forest models for selection of candidate modelling approaches, learning useful knowledge and experience from those existing models.
2. To apply hierarchy theory in identifying scales of forest dynamic processes, and to demonstrate how different levels of processes can be integrated or linked in a proposed forest dynamic simulation system. These are discussed in Chapter 2.
3. To develop a model of forest dynamics in a hierarchical context. There is a need to link the fine scale of physiological processes and the coarse scale of ecological

processes, to explore the proper structure or scaling pathway in the model. The detail model structure of FORDYN developed in this study is described in Chapter 3.

4. To validate and to test the sensitivity of the model, FORDYN is used to simulate real forest ecosystems (based on a boreal mixed European forest and an European pine ecosystem). Simulation results are compared with other validated forest models run on the same data. These results of the simulation are presented in Chapter 4.
5. To apply the model FORDYN in simulation of an environmental problem, so as to show what kind of insight one can get from this hierarchical modelling approach. The model is used to assess the forest responses (by scales) to the environmental change of atmospheric CO_2 increase. These are shown in Chapter 5.
6. Lastly, in Chapter 6, discussion is focused on the experience of this scaling study on both theoretical and practical aspects, such as the perspective of scaling issue, how to link levels through phenomena, scaling rules, how to avoid errors in scaling, and finally to indicate remaining problems, future challenge and applications.

Chapter 2 Hierarchical Approach To Forest Ecosystem Simulation

2.1 Introduction

As knowledge about forest ecosystem accumulates, it becomes important to develop an explicit description of the functional relationships between processes. These relationships are essentially hierarchical, with levels of processes ranging from cell to leaf, tree and forest. Knowledge obtained at any one of these levels cannot provide much understanding or predictive power, because the overall behaviour is influenced by positive and negative feedback between levels.

The problem of scale is a central one in ecology. As Levin stated, this problem is challenging, and crucial in unifying population biology and ecosystem science, marrying basic and applied ecology (Levin, 1992). By addressing this challenge, and using the insights gained from similar studies in other sciences together with approaches that must be developed for ecological systems, we can enhance greatly our understanding of the dynamics of ecosystems and develop the theoretical basis necessary to manage them (Levin, 1992).

As noted before, many of the current ecological questions address ecosystem processes at regional to global scales, and there is a need to *scale up* knowledge gained from studies at a smaller scale (sometimes physiological scale).

Scaling up requires an understanding of the hierarchical structure of ecosystems. Many authors have pointed out the relevance of a general hierarchy theory to the study of complex systems (Simon, 1962, 1973; Mesarevic & Macko, 1969), showing how it simplifies description and assists analysis. The application of hierarchy theory to biology including ecology is not new (Shultz, 1969; Overton 1972,1975; Allen & Starr, 1982; O'Neil *et al.* 1986). O'Neil *et al.* (1986) provided a 'dual hierarchy' concept of ecosystems: *functional component*, *ecosystem*, *biosphere*; and *organism, population, community*. They also indicated the general difficulty of developing a more unified perspective of ecosystems by listing some specific problems that seemed particularly complex and intractable. The discussion still continues on integration of the two main subdisciplines of population biology and ecosystem science (Carney, 1989,1990; Rowe, 1992; Allen & Hoekstra, 1989, 1992).

The present study is concerned with hierarchical structure in forest ecosystem modelling, both from a theoretical point of view and as a general paradigm. In this chapter I will demonstrate how forest ecosystem modelling can be realised in the context of hierarchy theory. The hierarchical model FORDYN developed in this study can simulate the forest ecosystem in scales ranging from forest succession, tree growth, leaf physiology, to cell biochemical processes. It embodies the view that each level above finds its processes in the next lower level, and its phenomena in the next higher level. Furthermore, an appreciation of hierarchical organization of these scales is a precondition of understanding causes and effects, or disturbance and response in different scales.

2.2 Hierarchy Theory

Simon (1962, 1973) noted that hierarchical structure has a vertical separation that isolates each level from levels above and below, and a horizontal separation that segregates the components of any level into groups, thus defining the level above. Vertical separation is based on behavioural frequencies (Fig. 2.1). A single process operating at any level is the outcome of several lower level processes operating relatively frequently.

It is essential to recognise the functions of organisational hierarchy. First, behaviour at one level cannot be explained directly in terms of lower level behaviour. The higher level of behaviour is always a result of interactions at lower levels. Also the higher level places constraints or sets boundary conditions upon the lower level. Therefore, there is feedback between related higher and lower levels. Second, from an evolutionary point of view, a multilevel system cannot form instantly (Gerard, 1969): the lower level of organisation must have existed before the higher level. The higher level organisation then evolved to include those lower level systems which through their interaction obtained the greatest stability (Levins, 1973).

2.3 Hierarchies of Ecosystems

An ecosystem is an example of a hierarchical system, which can be viewed as consisting of levels corresponding to: population, individual, organ, cell, etc. The higher level of population dynamics is defined by individual development (growth) and fate by species, while individual growth can be explained in terms of organ physiological processes, which are integration of cell biochemical processes, and so on. Each of these levels has a greater interaction among its subsystems than interaction with other elements in the same levels. In other words, each level of the

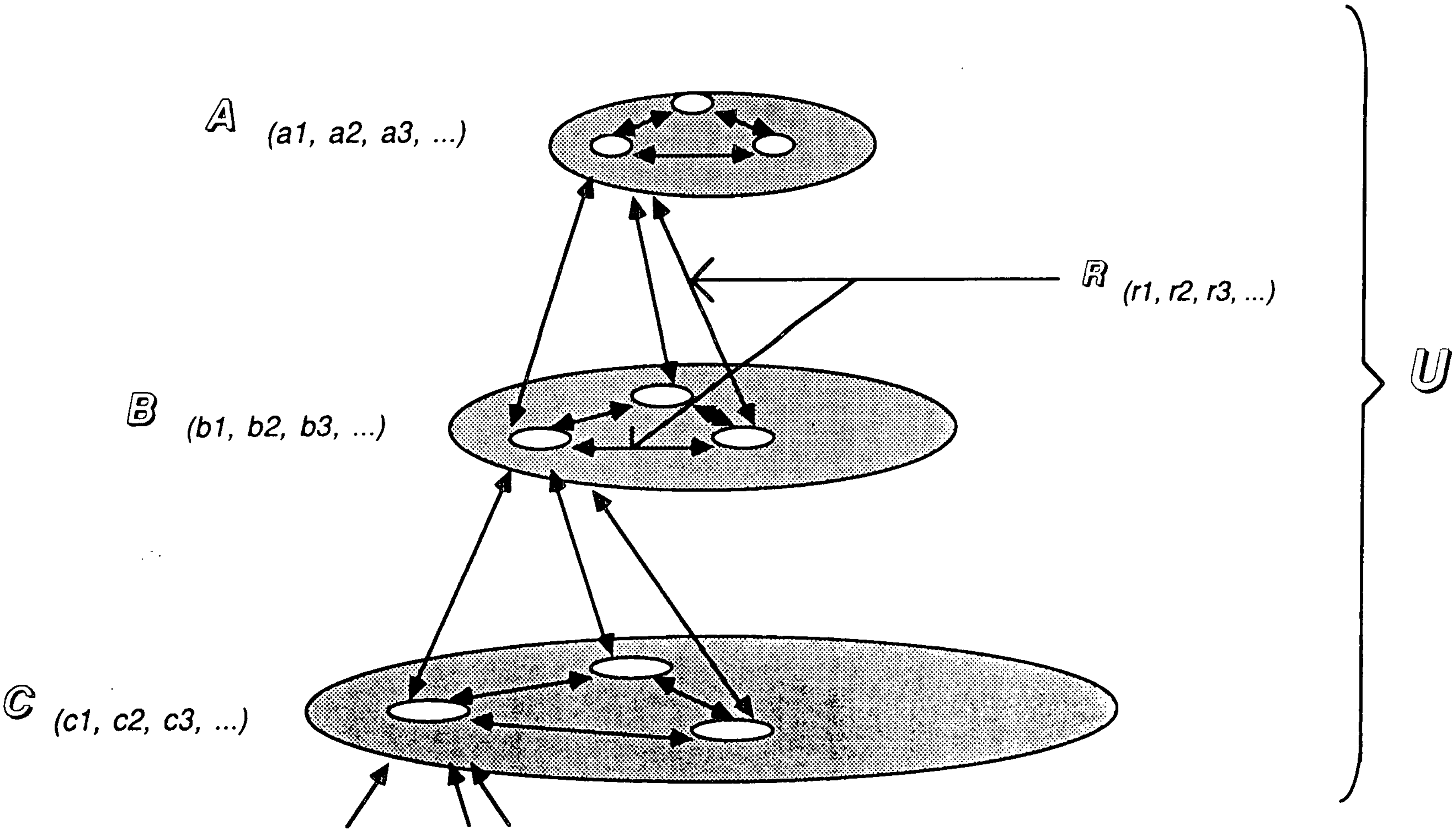


Fig. 2.1 Structure of a hierarchical system

A hierarchical system, with subsets A, B, C, ..., is formed by ordering the subsets by a relation R (r1, r2, r3, ...), which specifies that the elements of A (a1, a2, a3, ...) are higher than that of the elements of B (b1, b2, b3, ...), which are in turn higher than that of the elements of C (c1, c2, c3, ...). Therefore a subset, say B, can be defined by its next lower level of subset such as C, and constrained by its next higher level of subset such as A. There are more lower level of subsets (or information) than that in higher level, but each lower level of a subset has a smaller time scale (or higher frequency) than higher level of subsets.

system, e.g. individual, organ, ..., is defined by strong internal interaction and weak external interaction. For instance, the organs of one tree certainly have much stronger links among themselves than with those in other trees.

Advances in ecosystem ecology must proceed first from an understanding of ecosystem level behaviours and laws. Next comes specification of individual-level dynamics and finally identification of the statistical formalism connecting the two (Webster, 1979). However, in ecology nowadays, most studies have focused on levels corresponding to population biology and ecosystem science. There is still a big gap between these two for historical reasons. My intention is to link these two main streams in a modelling context so as to draw benefit from both subdisciplines. Furthermore, the responses of plants to environmental change (as the needs of current interest in global change dictate) may be best addressed on an organ physiological (e.g. leaf) or a cell biochemical process. Therefore, forest ecosystem models should represent these different levels of processes. Some models may be only concerned with a certain level of processes as noted above. However, in this study, these different processes are integrated into one model in a hierarchical context, so as to explore the hierarchical relationships or linking relationships between the different levesl of processes.

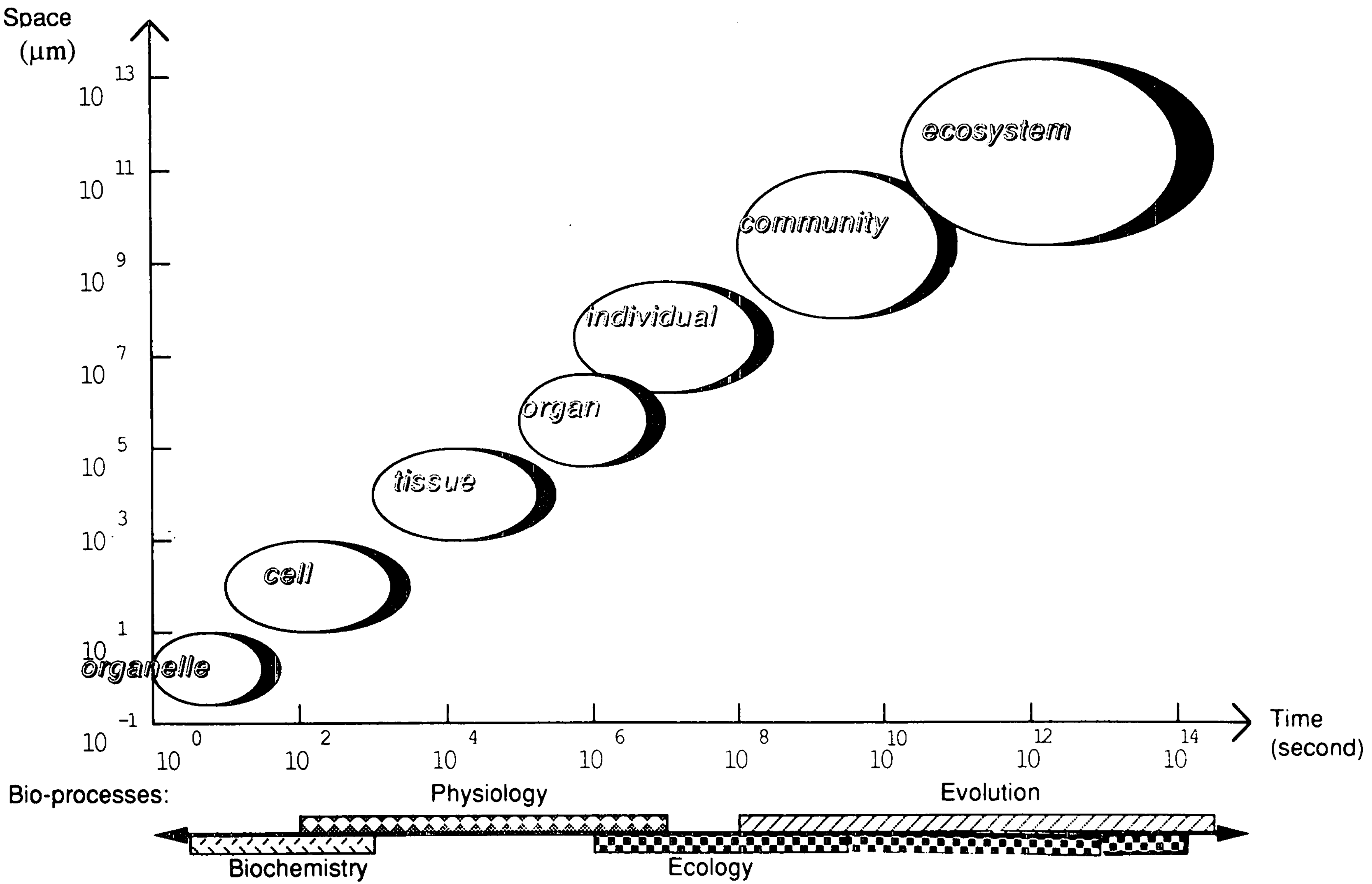
2.4 The Integration of Ecological Studies

Our knowledge about the natural world has been separated by different disciplines of science for the convenience of study, and the feature of each scale of natural process has been emphasised (Fig. 2.2).

For historical reasons, two main groups of ecologists have emerged. Population and community ecologists are concerned primarily with the diversity, description and integration of species. Ecosystem (process-functional) scientists, on the other hand, are concerned primarily with energy flow, material flux and nutrient cycling (Carney, 1989).

There is a recognised need to integrate the approaches of the above two groups (Macfadyen, 1975; Smith, 1975). However, as discussed by O'Neil *et al.* (1986), there is a general difficulty in developing a more unified perspective and some specific problems arise, which seem complex or intractable.

Fig. 2.2 Scales of ecosystem (Based on Osmond *et al.*, 1980)



O'Neil *et al* (1986) explored some of the implications of hierarchy theory for the study of population-community, and process-functional aspects of ecosystems, and provided a 'dual hierarchy' concept to clarify some confusion on hierarchical organisation of ecosystems. Allen and Hoekstra (1989, 1992) contributed by identifying scales as a source of confusion in the conventional hierarchies of cell, organism, population, community, ecosystem, landscape, biome and biosphere. Levin (1992) also demonstrated that the problem of scale is a central one in ecology.

In many cases, an approach which is both more mechanistic and comprehensive will prove quite challenging (Carney, 1989). Many ecosystem processes are still not measured and the underlying forcing functions are not even identified (MacFadyen, 1975; Mitchell *et al.*, 1976). Moreover descriptive studies are still more numerous than process-oriented in modelling studies (Mitchell *et al.*, 1976). Nevertheless, in some cases, the correspondence and links between the population/community and process/function can be clearer and stronger than a 'dual hierarchy' framework would suggest. An exploration of these links has been undertaken in this study and will be demonstrated in the following discussion.

Besides the need to discover the links between the levels for a more unified perspective in ecology, there is also a need to clarify the subject matter of ecology and ecology's specific point of view (Rowe, 1992). Based on the original scientific viewpoint, *ecologists* would study the external relationships of organisms (subject) by attending to the levels above, while *physiologists* would more focus on studying the internal relationships of the organisms (subject) by attending to the levels below. Therefore, ecologist would be concerned with roles, niches, purpose (such as the concepts of competition and succession). Physiologist would be more concerned with mechanisms which the interaction of lower levels (parts) reveal (Feibleman, 1954). There is already a trend of integration between these two subdisciplines, such as the emerging of 'process-based' models (Dixon *et al.*, 1990), which include more physiological knowledge in forest ecosystem processes (e.g. carbon balance of forest ecosystem). However, the attributes of these physiological processes to more forest ecological phenomenon such as competition and succession are still not given enough attention, thus less addressed.

The distinction between looking in towards mechanism (physiology) and outwards towards role (ecology) has also caused knowledge to be dissected out of the hierarchies imposed on a unified world. However, for some purposes, an ecological process will eventually need to be addressed by either an implicit or explicit representation of physiological processes of mechanism; and a physiological process to be addressed by either an implicit or explicit representation of ecological processes of constraints or boundaries.

Nevertheless, insofar as science seeks a unifying and complete vision, a key question is what kind of conceptual hierarchical scheme can provide the most powerful insight into the problems we study. In this study, a hierarchical model FORDYN is developed, with intention to scale up physiological and biochemical knowledge to stand and ecosystem levels. As it will be shown in the following, this modelling approach also provides an example of unifying population and ecosystem processes, as well as ecological and physiological processes.

2.5 Scales of Organisation in Forest Ecosystem Modelling: A Hierarchical Approach

Most classical forest models (Munro, 1974; Shugart *et al.*, 1980) focus on the process of forest dynamics and tree growth, with just two structural levels and one time scale of behaviour (Allen & Starr, 1982). While, it is demonstrated by Allen (1982) that particularly powerful models (e.g. FORET) are commonly hierarchical, since the hierarchical model structure may provide the richness of model behaviour.

The current scientific goal of understanding forest dynamics and the many goals of being able to forecast stand dynamics and timber output, require a model that can not only simulate stand structure and development, but also the responses of forest ecosystems to environmental change. Therefore a hierarchical forest model (named FORDYN) is proposed to integrate data at lower scales (physiological and biochemical processes) to generate responses at the stand and ecosystem levels.

In this section, I will demonstrate how a hierarchical approach is applied in organising different levels of processes in a forest model FORDYN which is developed in this study.

By applying hierarchy theory to ecosystem modelling, two stages are found to be important:

2.5.1 Recognition of levels

This includes two aspects. One is the identification of scale. The description of a system will vary with our choice of scales or levels. Disciplines or subdisciplines of biology have different focus on spatial and temporal scales, and it may be not easy to distinguish when spatial or temporal scales are overlapping. Identifying natural scales or patterns in different modelling programmes remains a tough and challenging task, which needs to be explored through multidisciplinary co-operation. The second aspect is the implementation in models of an explicit hierarchical structure. For most classical forest models, assumptions arise as direct consequences of the simplifications that are necessary in practice to construct any single abstract explanation of phenomena. Actually, when efforts are made to understand the mechanism of ecosystem dynamics, the internal and external factors that influence ecosystem behaviour should be considered. Then redundant spatial and temporal scales will be avoided. There can be some significant advantages of an explicit or implicit hierarchical model structure (Allen *et al.* 1982; O'Neil *et al.*, 1986).

To identify the levels or scales of the problem, in the model FORDYN, forest ecosystem dynamics is represented on the basis of four levels of process (Fig. 2.3), which are characterised by four different time steps (Table 2.1). These four levels of process are the phenomena we are interested in. As indicated before, we want to incorporate the knowledge at lower levels of physiological and biochemical processes, to scale up to high levels of tree growth and forest succession processes. Therefore as shown in Fig. 2.3, in level 1, *forest succession* can be represented by tree number changes by species, which is an integration of the fate of individual trees in the stand. In level 2, physiologically-based *tree growth processes* are described such as assimilate allocation, phenology, etc. In level 3, *leaf physiological functioning* such as photosynthesis, respiration and transpiration are represented. In level 4, cell biochemical or *mechanistic processes of photosynthesis* are described.

TABLE 2.1

Hierarchies of the model FORDYN

Bio-processes	Time step (resolution) t of processes in each level
level 1	$t \geq 1$ year
level 2	1 day $< t <$ 1 year
level 3	1 hour $< t \leq$1 day
level 4	1 second $\leq t \leq$1 hour

2.5.2 Linking levels

The second step in applying the hierarchical approach is to link the levels of processes or phenomenon we study. It was demonstrated by Allen *et al.* (1987) that it is phenomena that form the links between levels. For example, in a hierarchy of *cell, individual,* and *population*, the phenomena 'death' (individual death changes death rate of population) can be chosen as the link between *individual* and *population*, the phenomena 'growth' (increase in cell number, thus change in individual size) as the link between *cell* and *individual*. In another words, a phenomena can either be treated in an empirical way, or an analytical way. For example, in the model FORDYN as it is shown in Fig. 2.3, tree growth can in one way be described as tree size (DBH) increment in level 1, in another way as total assimilate allocation in the stem of the tree in level 2 (link 1).

The linking between differently paced behaving parts of the model FORDYN, is shown as lines across the levels in Fig. 2.3.

All of these integrations or linking between levels are based on phenomena. As shown in Fig. 2.3, annual assimilate production is an accumulation of daily net photosynthetic production by leaves throughout a year (link 4). Soil water content, consumed by all the trees in the plot (link 6) and recruited by precipitation, constrains the leaf stomatal conductance (link 7) (Khalil & Grace, 1993), and thus the photosynthetic rate (link 10).

In addition to the linkage from the lower levels to the higher ones, FORDYN also incorporates linkages in the reverse direction. These take the form of constraints by state at the higher level on rates at the lower level. In FORDYN, examples of this are seen: i) tree growth in level 2 is constrained by resource availability at level 1 (e.g. nitrogen availability in the soil is constrained by nitrogen uptake by individual trees); ii) leaf photosynthesis production in level 3 depends on total leaf area of the tree in level 2; iii) and cell photosynthetic CO_2 assimilation rate at level 4 is limited by leaf stomatal conductance in level 3. However, the mechanism for doing this is simple and standard: variables associated with the higher level simply appear on the right-hand side of the lower-level rate equations.

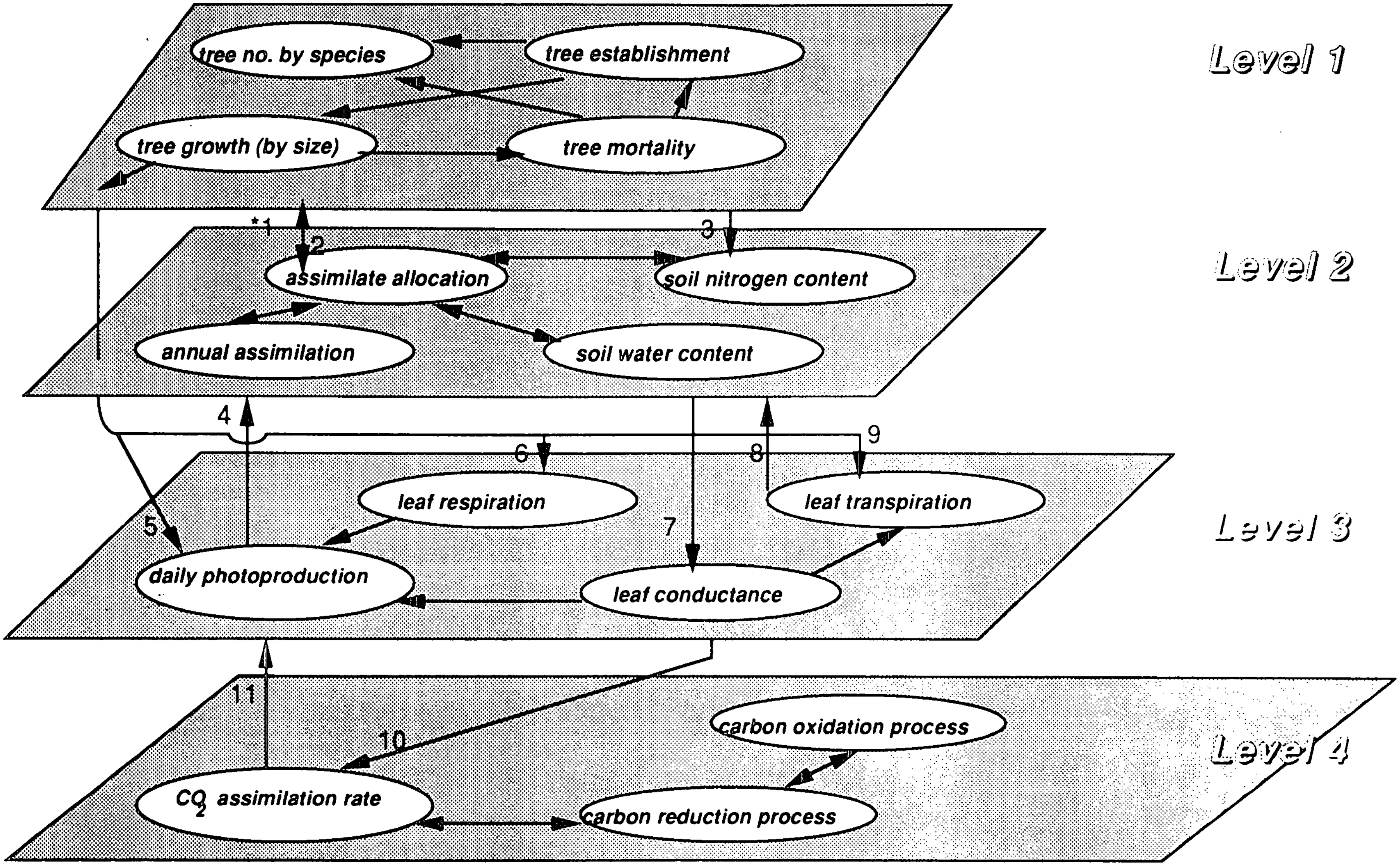


Fig. 2.3 Hierarchical organisation of the model FORDYN

There are four levels of processes are described in the modelFORDYN (level 1 = forest succession, level 2 = tree growth, level 3 = leaf physiology, and level 4 = cell biochemistry), whereby each level of process is identified on the basis of time scale or time step (Table 2.1), the linking between each levels are discussed in the test.

2.6 Discussion and Conclusions

It is importance to address the problem of scale for both theoretical and application reasons. Theoretically, it is useful in unifying population biology and ecosystem science, ecology and physiology, and marrying basic and applied ecology. See also Levin (1992).

The practical advantage of this hierarchical approach is in providing a flexible framework to integrate and utilise knowledge obtained at small scales of time and space, such as physiological and biochemical processes, enabling such knowledge to be *scaled up* to ecosystem scales so as to be useful to resource managers and environmental scientists. And with simulation control design, it can also provide some useful features that enable the user to select different simulation modes (see more in simulation control in next chapter). Therefore, by addressing and meeting the scaling challenge we gain more insight and understanding of ecosystem dynamics.

Chapter 3 A Scale-Based & Process-Based Forest Ecosystem Simulation Model

3.1 Introduction

Many current ecological questions address ecosystem processes at regional to global scales. There is therefore a challenge to ecologists of how to predict these global changes, such as the impacts of the CO_2 increase, the consequences of regional air pollution, and the rate of any regional vegetation decline etc. from knowledge of the ecosystem at the individual or smaller scales. These questions can be answered from an understanding of fundamental processes such as the rates and control of energy, carbon, water and nutrient exchange by vegetation surfaces.

As discussed in previous chapters, there is a need to link levels of processes. Ecophysiology is concerned with plant physiological process in relation to environmental variations. The integration between ecological and physiological process models should not merely describe the processes involved in the exchange of carbon, water and nutrients between the plant and its environment, but should also predict the response of vegetation to environmental change and management effects.

The model FORDYN is designed to represent forest ecosystem dynamics at four levels which are characterised by four time steps and corresponding phenomena (Table 2.1, Fig. 2.3).

FORDYN is different from other ecological models in that not only can it simulate long term ecosystem dynamics with individual and species attributes of physiological functioning processes, but also it can be used for different simulation objectives (see more in section 3.4 of this chapter).

3.2 Model Structure

Integration between physiological process and ecological processes in the simulation model seems highly desirable. The model FORDYN is a hierarchical forest ecosystem simulator which can simulate long-term forest ecosystem changes using hourly data in responses to critical variables like radiation, temperature and CO_2 etc. In chapter 2, discussion is focused on how FORDYN can be implemented in a hierarchical context. In this chapter, discussion is on the detailed structure of FORDYN.

The main influence relations in the model FORDYN are shown in Fig. 2.3 in Chapter 2. There are four level of processes are described on the basis of typical time step of the phenomenon involved (Table 2.2),. where, at level 1, forest succession is accounted for by calculation of recruitment, growth, competition (merged into the growth submodel) and mortality processes of every individual tree in an annual time step. At level 2, physiologically-based growth processes of each tree in the stand are described by calculation of assimilation, assimilate allocation, nitrogen dynamics and water balance processes in a daily time step. At level 3, leaf physiological functioning processes of stomatal conductance, mesophyll conductance, boundary layer conductance, transpiration, respiration and photosynthesis are incorporated in an hourly time step. At level 4, a mechanistic model of leaf biochemistry based on Farquhar *et al.* (1980) is incorporated to represent instantaneously leaf photosynthesis rate.

The model FORDYN is written in FORTRAN 77, and has been run on the mainframe computer Sequent 2000 in the University of Edinburgh.

Fig. 3.1 is the main flow chart of the computer program FORDYN where nested time loops correspond to different simulation time scales (based on time steps, see Table 2.1), and boxes represent subroutines. Simulation is controlled by setting a switch, noted as MODE, to select simulation modes and choosing the run duration by subroutine *CONTROL*. When a simulation mode is selected, different input data are needed correspondingly:

For the simulation mode 1, forest succession is described in an annual time step (within year-loop) by accounting for the progress of every single tree in the stand, such as growth (subroutine *GROWTH1*), mortality (*MORTAY1*, *MORTAY2*), and regeneration (*RECRUT1*, *RECRUT2*) (A seed dispersal model is used following Levin et al (1984)).

For simulation mode 2, the calculation of annual tree growth is refined by accounting for the processes of assimilation and assimilate allocation to tree parts in a time step of days. Assimilate allocation is based on a transport-resistance approach following Thornley (1991). Therefore, instead of using *PHOSYN1* to derive the input for annual tree growth as that in mode 1, the day-loop is introduced, and daily climate parameters (subroutines *ASTROL*, *METEO*), development stage of tree (subroutines *PHENO*, *FOLIAGE*) are calculated. Daily light climate is calculated in subroutine *RADIAT*. Daily net photosynthetic production is derived from the daily photosynthetic production (subroutine *PHOSYN2*), and respiration (subroutine *RESPN*), and it is used for calculation of assimilate allocation (subroutine *ALLOC*). Nitrogen uptake by trees from soil is accounted for in a time step of days (subroutine *NCYCL1*).

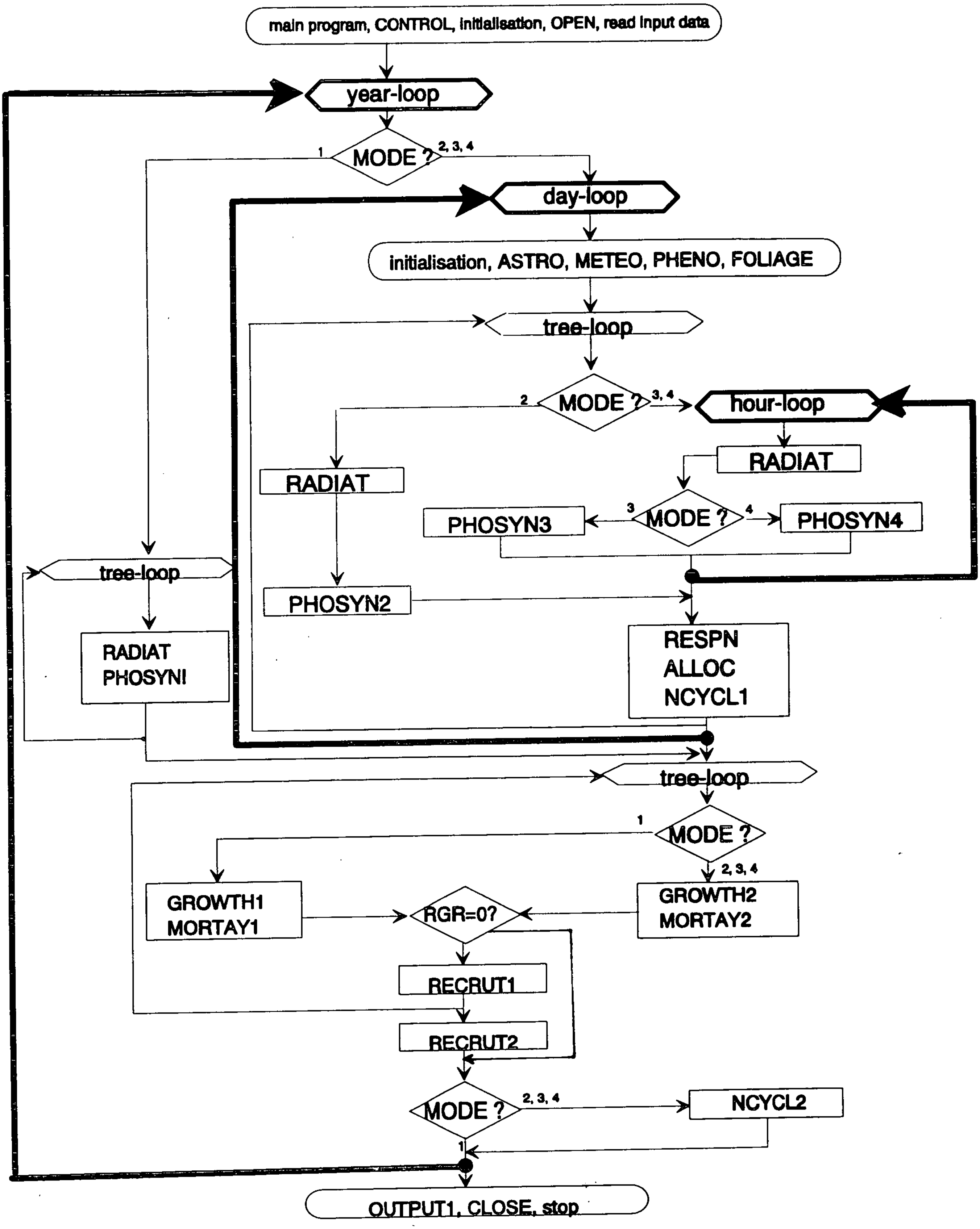


Fig. 3.1 Main flow chart of the FORDYN program

▭ : represents subroutine, ⬭ : represents process, ◇ : represents decision point number 1— 4 represent modes. The heavy and faint lines represent the pathway of execution, the heavy lines emphasise the main loops over the time intervals: hours, days, and years. Decision points are selected according to mode, except for RGR=0?, which depends on the sign of tree's mortality.

For simulation mode 3, the calculation of daily photosynthetic production is calculated by hourly data (within hour-loop) to get daily total accumulation through a 3-point Gaussian integration approach (Goudriaan, 1986) (subroutine *PHOSYN3*), rather than just using a daily average value as in mode 2 (subroutine *PHOSYN2*).

For simulation mode 4, the hourly photosynthetic rate is derived from the instantaneous CO_2 assimilation rate by a mechanistic biochemical model based on Farquhar *et al.* (1980) (subroutine *PHOSYN4*).

The names of parameters and variables used in the following discussion are based on the names used in the FORTRAN program of the model FORDYN, and are listed in Appendix III.

Summary Table: the model FORDYN

Aims:

To simulate forest ecosystem dynamics on the scales of cell biochemistry, leaf physiology, tree growth processes, and forest development (succession), and their response to environmental change and management effect.

Main assumptions:

The forest ecosystem is a hierarchical system, with progressive processes in different scales (O'Neil *et al.*, 1986), and thus different scales of forest ecosystem processes can be viewed and integrated in a hierarchical context (Allen & Starr, 1982). There are four levels of processes represented in the FORDYN:

level 1: forest succession is represented by a spatial, individual-based model, with regeneration processes based on Levin et al (1984), time step is annual;

level 2: tree growth processes are described by a transport-resistance approach for assimilate allocation (Thornley, 1991), time step is days;

level 3: daily leaf photosynthetic production is accumulated by a 3-point Gaussian integration scheme (Goudriaan, 1986), time step is hours;

level 4: instantaneous photosynthetic rate is calculated by a biochemical model modified from Farquhar et al (1980), time step is seconds.

Main inputs:

mode 1: Annual climate data, initial stand and tree structure (spatial location and size of every individual tree), tree morphological data.

mode 2: Daily climate data, initial stand and tree structure (spatial location and size of every individual tree), tree physiological parameters.

mode 3: Hourly climate data, initial stand and tree structure (spatial location and size of every individual tree), tree physiological parameters.

mode 4: Hourly climate data, initial stand and tree structure (spatial location and size of every individual tree), tree physiological parameters, leaf biochemical parameters.

Main outputs:

Forest succession processes such as biomass and population development by species in more than one life cycle of trees, tree growth processes such as biomass and size increment by tree parts in a time steps by days, physiological functioning of tree and stand such as transpiration rate of single crown or whole canopy, and forest ecosystem dynamic processes such as nitrogen cycling and water balance in the plant-soil system.

3.2.1 Level 1

In level 1, FORDYN can simulate forest succession by describing the birth, growth and death processes of every individual tree in the stand. It is designed as a 3-dimensional 'spatial model' (Shugart *et al.*, 1988). The simulation time step for this level of processes is years (Table 2.1).

3.2.1.1 Establishment

The regeneration of a species is described by a seed dispersal model based on Levin *et al.* (1984), whereby the appearance of a newly established seedling in a 'gap', produced by a dead tree in the stand, mainly depends on seed dispersal (from all source trees in the stand) and seed germination processes (of the seeds received in the gap). A previous treatment of this process was the model FOREST (Ek & Monserud, 1974).

Establishment in the stand is simulated by the subroutine *RECRUT1* and *RECRUT2*.

A tree is considered as dead in the stand when it no longer has the vigour to grow (see 3.2.3 Mortality). As a result, a gap is produced in the stand. As every tree in the stand is identified by spatial position, so the gap can potentially receive the randomly distributed seeds from every mature tree of every species in the stand. Fig. 3.2 shows a dispersal process in the model FORDYN.

When a tree is dead, a gap is produced in the stand. This gap can potentially receive seeds from all the mature trees in the stand. This seed dispersal process is described by an exponential dispersal process in subroutine *RECRUT1*, and calculated for each tree in the stand:

$$\mathrm{BANK(NG)=BANK(NG)+INT(SDDF(J)*G(J)*EXP(-D2(J)*DTT(K)))} \quad (3.1)$$

$$\mathrm{SDDF(J)=SDDF(J)+INT(SSY(J)*EXP(-D1(J)*DEN*TDF(K)))} \quad (3.2)$$

(K=1,...SNTREE, J=1,...NSPEC)

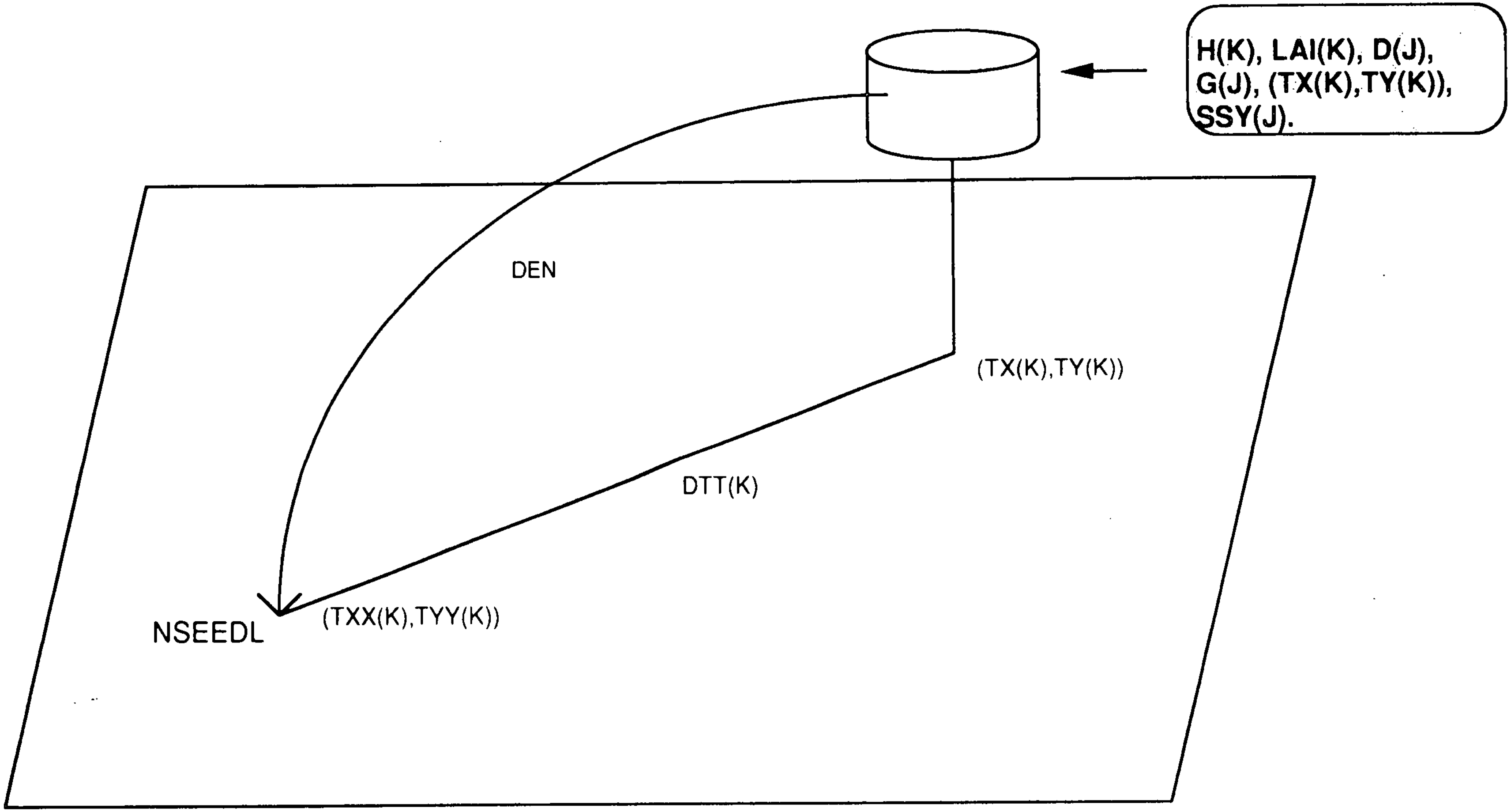


Fig. 3.2 Dispersal process of seed in the model FORDYN

The seedling production in the gap (TXX(K), TYY(K)), NSEEDL, is decided by the number of seed received from dispersal processes of all trees in the stand (where dispersal is an exponential function of all mature trees, decided by the dispersal distance DTT from tree K at location (TX(K), TY(K)), potential seed production SSY(J), which is modified by crown size LAI (K), tree height H(K), dispersal parameter D(J), and stand density DEN), and seed germination ability G(J).

where,
BANK(NG) is the seedling production in the gap NG,
J is species of received seed K,
NG is the number of gap,
G(J) is germination parameter,
SDDF(J) is the density-dependent seed production by species J,
SSY(J) is the potential seed production of species J,
TDF(K) is the tree-size-dependent seed production parameter for tree K,
DTT(K) is the dispersal distance between source tree K and the gap,
DEN is the density of the stand,
D1(J), D2(J) are parameters for density dependent and distance-dependent dispersal parameters of species J,
INT is a function in FORTRAN to turn a real into an integer,
NSPEC is total number of species in the stand, and
SNTREE is the total number of trees in the stand.

When a gap receives many seeds from source trees in the stand, there is competition for germination. For the whole stand, there is also a constraint on the maximum number of trees in the stand, and this represents competition for stand resources (or the resource limit of the site).

Establishment of young trees in the site is calculated in the subroutine *RECRUT2*, and calculated for total seeds received in the gap. The survival of seedlings is a random process, whereby the species, and numbers of seedlings are randomly selected. The number of newly established young trees is constrained by the maximum tree number of the stand.

Summary Table: subroutines *RECRUT1, RECRUT2*

Aims:

To calculate seed production and number of seedlings entering into a plot in a gap caused by tree death. This is done in a time step of years.

Main assumptions:

The seedling production in a gap of stand, depends on:

i) the number of seeds received from dispersal processes of all mature trees in the stand, which is a function of potential seed production of source tree, and affected by stand density, dispersal distant, source tree size;

ii) the germination ability of seeds (Levin *et al.*, 1984).

Main inputs:

RECRUT1: location of gap, location of source tree, tree size of source tree (DBH, height, and LAI), potential seed production of mature source tree, germination parameter of seed, distance dependent and density dependent dispersal parameters of seed, and stand density.

RECRUT2: total seed production (from all source trees in the stand) in the gap.

Main outputs:

RECRUT1: total seed production (from all source trees in the stand) in the gap.

RECRUT2: location, and initial tree size (DBH, height, etc.) of new established young tree, number of newly established young trees in all gaps.

3.2.1.2 Growth

On the level 1, every tree in the stand is represented by its diameter at 1.3 m 'breast height' DBH, height H, crown length, crown radius, and total leaf area. As shown in Fig. 3.1, when simulation mode 1 is chosen, subroutine *GROWTH1* is used to calculate tree growth by size, when simulation mode is set as 2, 3, or 4, then subroutine *GROWTH2* will be used to replace *GROWTH1*.

In subroutine *GROWTH2*, tree growth is calculated as tree stem growth by size, known as $\Delta(H \times DBH^2)$, which is driven by annual stem biomass increment STEMI(K). By rearrangement of $\Delta(H \times DBH^2) = STEMI(K)/(SL \times BW))$, the DBH increment, DBHG, is then calculated as:

DBHG(K)=STEMI(K)/(SL(J)*BW(J)*M) (3.3)
H(K)=b1(J)+b2(J)*DBH(K)+b3(J)*DBH(K)**2 (3.4)
with,
M=2*b1(J)*DBH(K)+3*b2(J)*DBH(K)**2+4*b3(J)*DBH(K)*DBH(K)*DBH(K)

where,
DBH(K) is the diameter at breast height of each tree K (m),
DBHG is DBH increment of tree K (m),
STEMI is annual average net assimilate production per tree (kg CH_2O stem^{-1} y^{-1}),
H is the height of each tree K (m),
BW is the wood mass per volume of tree by species (Mg CH_2O m^{-3}),
SL is a specific coefficient (dimensionless), and
M is an intermediate function, and
b1(J), b2(J), and b3(J) are species-based coefficients (m, dimensionless, m^{-1}).

In subroutine *GROWTH1*, equation (3.3) is represented by a more empirical approach, with DBH increment driven by net annual assimilate production instead of stem biomass increment.

Leaf area index LAI can be calculated in two ways. One way is an empirical approach based on Shugart *et al.* (1977), that used in subroutine *GROWTH1*:

LAI(K)=C(J)*DBH(K)**2/CP(K) (3.5)

where,
LAI(K) is leaf area index of tree K (stem^{-1}),
CP(K) is crown profile of tree K (m^2 stem^{-1}), and
C(J) is a species-based coefficient (dimensionless).

The other way for calculating LAI is in subroutine *GROWTH2*. Leaf area is obtained by conversion from the leaf biomass (see also equation 2.3) which is derived from process-based tree growth:

LAI(K)=LEAF(K)/(CP(K)*LEAFWA(J)) (3.6)

where,
LEAF(K) is the leaf biomass of tree K (kg $stem^{-1}$), and
LEAFWA(J) is the mass per leaf area of species J (kg m^{-2}).

subroutine *PHOSYN1*

When simulation mode 1 is selected, subroutine *PHOSYN1* is used to calculate annual average assimilate production (Fig 3.1), by using an empirical light response curve, in fact a rectangular hyperbola model (Thornley, 1976):

$$PHOPL(K)=FLUX*PMAX(J)*ELL(J)/(FLUX*ELL(J) + PMAX(J)) \qquad (3.7)$$

where,
PHOPL(K) is the photosynthetic rate (μmol CO_2 m^{-2} s^{-1}),
PMAX(J) is maximum photosynthetic rate of species J (μmol CO_2 m^{-2} s^{-1}),
FLUX is the incident photon irradiance (μmol photons m^{-2} s^{-1}), and
ELL(J) is the initial slope of the light response curve by species J (or the apparent quantum efficiency) (μmol CO_2 μmol $photon^{-1}$).

This submodel is used with an input of average annual total radiation, and an output of annual total photoproduction.

Summary Table: subroutines *GROWTH1, GROWTH2*

Aims:

To calculate the size increment of each tree by years.

Main assumptions:

Tree size growth can be described as driven by assimilate production (for mode 1, using subroutine *GROWTH1*), or by tree biomass increment (for modes 2, 3, and 4, using subroutine *GROWTH2*).

Main inputs:

GROWTH1: annual net photosynthetic production, tree height and DBH.

GROWTH2: stem biomass increment, tree height, DBH, and leaf biomass.

Main outputs:

GROWTH1, GROWTH2: DBH, height, LAI, crown length, and crown profile of each tree in the stand.

Summary Table: subroutine *PHOSYN1*

Aims:

To calculate annual photosynthetic production of a tree.

Main assumptions:

Leaf photosynthesis response to light can be described as a rectangular hyperbola curve (Thornley, 1976).

Main inputs:

Annual average radiation received above canopy, maximum photosynthetic rate by species, light extinction parameter of leaves by species, apparent quantum efficiency of leaves by species, spatial location and size of all trees in the stand, and total leaf area of the source tree.

Main outputs:

Annual photosynthetic production of a tree.

3.2.1.3 Mortality

The growth of a tree is constrained by its age, optimal size and resource limitation of the site etc. Eventually, a tree's growth will slow down, and it will die.

FORDYN uses two ways to represent tree mortality by subroutines *MORTAY1* for simulation mode 1, and *MORTAY2* for simulation mode 2, 3, and 4 (Fig. 3.1). In subroutine *MORTAY1*, the criteria for killing a tree is set as:

$$RGR1(K)=DBHG(K)/DBH(K) \tag{3.8}$$

where,

RGR1(K) is the growth rate of tree K that is used for mode 1 (y^{-1}), and

DBHG(K) is DBH increments per year ($m\ y^{-1}$).

It is assumed that the increment rate of tree size can be a measure of the tree's vigour. Thus, when RGR1(K) is less than a certain value, say 0.01, tree K is killed.

Another way used in simulation mode 2, 3, and 4 for tree mortality, is on the basis of tree physiological activity:

$$RGR2(K)=BIOMI(K)/BIOM(K) \qquad (3.9)$$

where,
RGR2(K) is the growth rate of tree K that is used for mode 2, 3, 4 (d^{-1}),
BIOMI(K) is the biomass increment of tree K (kg $stem^{-1}$ d^{-1}), and
BIOM(K) is the biomass of tree K (kg $stem^{-1}$).

When BIOMI(K) is equal to zero, tree K is killed. BIOMI(K) is derived from underlying physiological processes (see 3.3 for more) and calculated from the sum of interacted growth processes of tree parts such as leaves, stems and roots. This is therefore a more accurate way of representation of tree vigour.

Summary Table: subroutines *MORTAY1, MORTAY2*

Aims:

To assess the tree's vigour, and kill the tree when it is 'dead'.

Main assumptions:

For mode 1, a tree is killed when there is no size increment (DBH increase) (*MORTAY1*). For modes 2, 3, and 4, a tree is killed when there is no biomass increment (*MORTAY2*).

Main inputs:

MORTAY1: DBH, DBH increment.

MORTAY2: tree biomass increment, tree biomass.

Main outputs:

MORTAY1, MORTAY2: number of dead trees, updated biomass by species.

3.2.2 Level 2

In FORDYN, a tree's growth can be described in two ways, either as annual assimilate production in an empirical way (simulation mode 1, when only level 1 processes are involved), or by physiologically based tree growth processes in simulation mode 2, 3, 4 (Fig. 3.1), so that assimilate allocation, plant-soil water relations, and plant-soil nitrogen dynamics are represented to calculate tree biomass growth by parts. The time step in this level is by days. As it will be shown in following section (Fig. 3.7), processes on level 2 will be used for simulation modes 2, 3, and 4.

3.2.2.1 Light Climate and Competition

Light is a driving factor in tree growth. The derivative of the relationship between light extinction and leaf area gives the amount of photosynthetic active radiation (PAR) absorbed per unit of leaf area, from which total crown assimilation is calculated.

As shown in Fig. 3.1, for simulation modes 2, 3, and 4, light climate and competition within stand are described in a time step of days, whereby light climate above canopy is calculated by subroutine *RADIAT*, and light competition between crowns is described in each subroutine of photosynthesis (subroutines *PHOSYN2* for mode 2, *PHOSYN3* for mode 3, *PHOSYN4* for mode 4).

The light climate is considered both above the canopy and inside the canopy (or between crowns). Fig. 3.3 shows the light competition relationship between crowns and leaves inside the crown in the model FORDYN. The radiation climate above the canopy is accounted for as the vertical fraction of radiation, which is affected by the solar constant, daylength and atmospheric transmission (Spitters *et al.*, 1986), while the light interception of each crown in the stand is determined by light extinction from the outer boundary of the canopy and competition for this light between crowns and leaves. The leaves are homogeneously and randomly distributed within crowns.

For the light climate on the surface of the canopy, daily changes throughout a year can be calculated if no daily or monthly radiation data are available. Thus in subroutine *RADIAT*, daily radiation is calculated based on daylength and solar elevation (Spitters *et al.*, 1986). Daylength is calculated from the day of year and latitude (Goudriaan, 1977) in subroutine *ASTROL*.

For the light environment inside the canopy, competition for light between every individual tree is accounted for by considering a competition relationship for the vertical fraction of incoming light (from above the canopy) between each crown. There is a geometrically calculated light shading relationship between target tree crown and its neighbouring competitors (Fig. 3.3). Therefore every crown can be divided into sunlit and shaded fractions. For light competition inside the crown, there is a self-

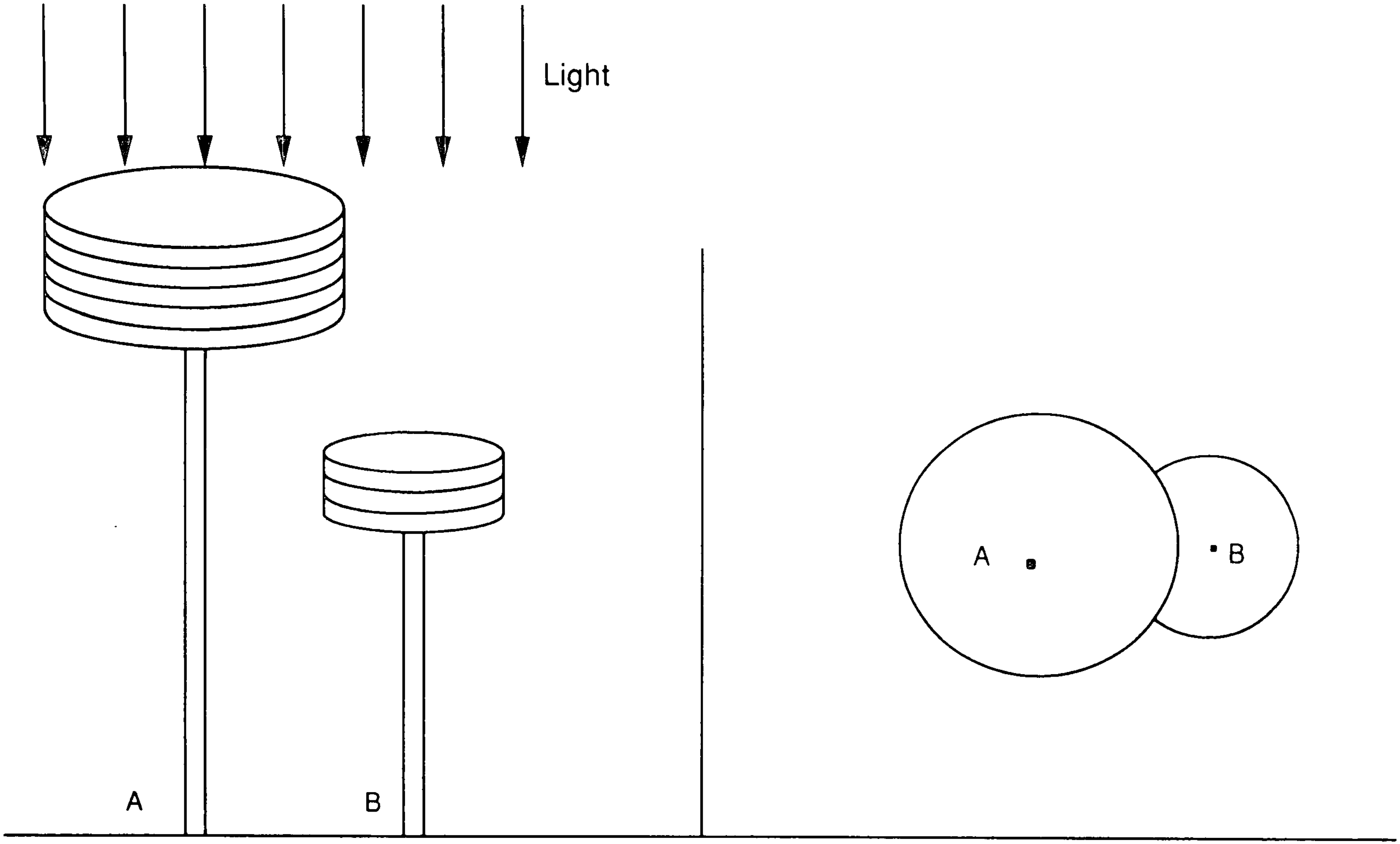


Fig. 3.3 Light competition between trees and leaves

The light is assumed from above canopy in a vertical direction, so the competition for light between crowns can be described as a overlap or shading effect, and the competition for light between leaves within a crown ('self-thinning effect') is described by setting different homogeneously distributed 0.5 m layers of leaves.

shading effect achieved by dividing each crown into 0.5 m layers of leaves. The calculation of the shaded and sunlit fraction of the leaves within each crown layer is as follows (Mohren *et al.*, 1990):

$$\mathrm{FLSHA(K)=1\text{-}CLUSTF(J)*EXP(\text{-}KDIRBL(J)*FZ)} \tag{3.10}$$
$$\mathrm{FLSUN(K)=1.0\text{-}FLSHA(K)} \tag{3.11}$$

where,

FLSHA(K) is the shaded fraction of the crown of the tree K (dimensionless),

FLSUN(K) is the sunlit fraction of the crown of the tree K (dimensionless),

CLUSTF(J) is a clustering factor of foliage (of species J) for diffuse light (dimensionless),

KDIFBL(J) is a light extinction coefficient for direct flux of species J (m^{-2}), and

FZ is accumulated leaf area above the crown depth (m^2), which includes leaves both from upper crown layers (same tree), and those from shading crowns (neighbouring trees).

So, the fraction of shaded leaves in a crown (source tree) is proportional to the total leaf area from all crowns of neighbouring competitors that are above the overlapped target tree's profile area. Thus, the influence of neighbouring trees is mainly from a vertical shading effect. The total shading leaf area from different neighbouring crowns is not distributed homogeneously resulting from separation of individual trees. Therefore a clustering factor CLUSTF is introduced as an adjustment, on the basis of the ratio between the actual extinction coefficient and the theoretical value for a homogeneous crown (normally the actual extinction coefficient is smaller than the theoretical value). This clustering factor is a function of diffuse and scattering light coefficients (Goudriaan, 1977; Mohren *et al.*, 1990). Therefore, the total assimilation of a crown can be obtained by accumulation of every layer's leaf photosynthetic production, which is the sum of both sunlit and shaded leaf fractions based on total leaf area of a crown layer.

Summary Table: subroutines *ASTROL, RADIAT*

Aims:

ASTROL: to calculate the daylength for a day of a year;

RADIAT: to calculate light climate in a day of a year.

Main assumptions:

The flux of radiation above the canopy is treated as vertical fraction.

ASTROL: daylength is a function of the day of the year and latitude;

RADIAT: light climate within a day is a function of daylength.

Main inputs:

ASTROL: day of a year, latitude;

RADIAT: daylength, solar constant, atmospheric transmission, diffuse light coefficient, and scattering light coefficient.

Main outputs:

ASTROL: daylength;

RADIAT: daily PAR absorbed, clustering factor.

3.2.2.2 Assimilate Allocation

The CO_2 assimilation is a measure of the photosynthetic productivity of the tree, and is mainly driven by the amount of radiation received by a leaf, and affected by leaf age, leaf temperature, nitrogen content, air humidity, saturation deficit, soil water content etc.

In FORDYN, the increment of tree size can either be driven by annual total assimilate production (when only level 1 (see page 34) is involved in the simulation (see section 3.4)), which is calculated as a function of average annual PAR based on an empirical rectangular hyperbola light response curve (Thornley, 1976); or, it is calculated by considering assimilate production and its allocation in a time step of days or a fraction-of-a-year in level 2 (see page 41). Tree size increment is therefore derived analytically by biomass increment of the tree parts based on physiologically process-based tree growth (Thornley, 1991).

In level 2, a process-based tree growth submodel (Thornley, 1991) (subroutine *ALLOC* in Fig. 3.1) is used to calculate assimilate allocation or dry-matter partitioning during each tree's growth. It is used for simulation modes 2, 3, and 4 (see more in following section 3.4).

As shown in Fig 3.4, each tree is described as consisting of different tree compartments: shoot (foliage, branch), stem, and root (coarse, fine roots). The growth or biomass (noted as X) increment of each compartment is driven by meristem activity, which is contributed by carbon substrate C, and nitrogen substrate N. Tree growth is driven by carbon assimilation through leaf photosynthesis (assimilate CO_2 from the air), and the uptake of nitrogen by the root from the soil. The assimilated carbon is allocated to other tree parts from foliage, and the nitrogen uptaken by fine root is transferred to other tree parts. Both these processes are driven by the substrate concentration gradient, and on the basis of a transport-resistance mechanism.

The approach was first used to construct a forest growth model for a monoculture of identical trees of the same age, and it is directly relevant to plantations (Thornley, 1991). The approach used in the model FORDYN in this study is to describe individual tree growth in a mixed-species and mixed-age forest stand, and therefore it can be applied to a natural forest.

However, it still remains unclear whether this approach actually describes the mechanism of assimilate allocation. This transport-resistance approach for assimilate allocation can provide more potential in describing the behaviour of plant growth than other existing approaches such as empirical, and goal-seeking approaches (Thornley, 1991). Also, some parameters (such as meristem size and meristem activity constant) are difficult to get, and thus currently (without more experimental support) we have to guess.

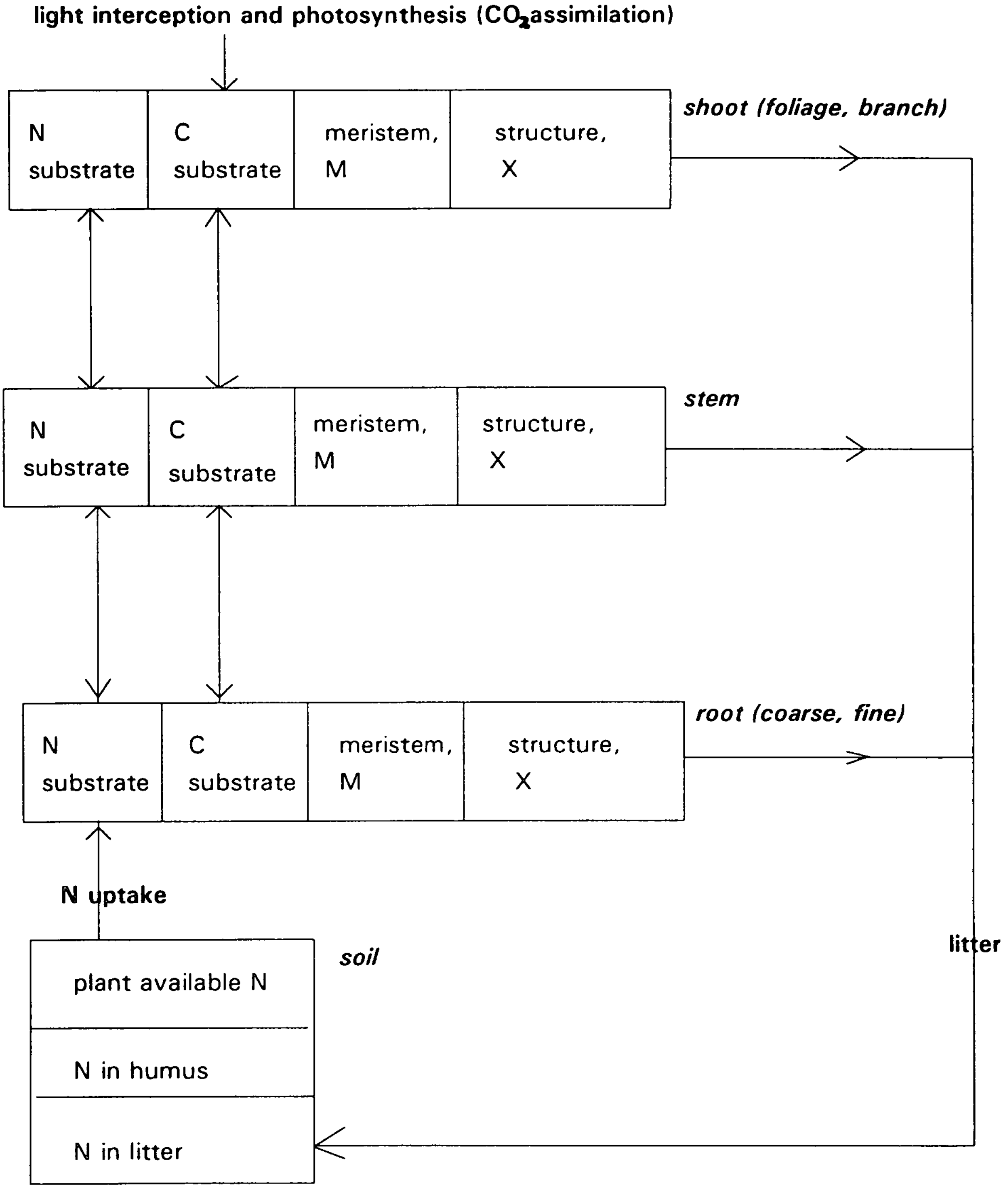


Fig. 3.4 Tree growth process, with a transport-resistance approach (Thornley, 1991) to assimilate allocation

Summary Table: subroutine *ALLOC*

Aims:

To calculate tree biomass growth by parts in a time step of days.

Main assumptions:

The growth of tree parts is driven by local carbon and nitrogen substrate concentration rate. The transport of carbon from leaf to root, and nitrogen from root to leaf are represented in a transport-resistance manner (Thornley, 1991).

Main inputs:

Initial biomass, carbon substrate, nitrogen substrate and meristem size of tree parts (leaf, branch, stem, coarse root, and fine root), meristem constant, nitrogen uptake rate of fine roots, photosynthetic rate of leaves.

Main outputs:

Biomass of tree parts (leaf, branch, stem, coarse root, and fine root).

3.2.2.3 Nitrogen Dynamics

Nitrogen cycling and nitrogen supply are two of the most important environmental processes affecting tree growth. Nitrogen dynamics between trees and soil are described in subroutines *NCYCL1* and *NCYCL2* (Fig. 3.1).

In FORDYN, nitrogen dynamics in the soil are based on the processes of decomposition and mineralization of nitrogen, and nitrogen fixation following Bossel & Schäfer (1989). These processes include decomposition of litter, humification of litter, mineralization of litter, decomposition and mineralization of humus, biological nitrogen fixation, atmospheric nitrogen deposition, and nitrogen leaching.

The total plant-available nitrogen pool in the soil, NAV, is calculated in subroutine *NCYCL2* as follows, and is calculated in a time step of years (normally annually) and plot area of the stand is 0.1 ha:

$$NAV = NAV + (NAVR - NUP) * YSTEP \qquad (3.12)$$

$$NAVR = NPREC + NOMNP + NLINP - NLEACH \qquad (3.13)$$

where,

NAV is plant available nitrogen in the soil (kg N),
NAVR is recruiting rate of plant available nitrogen in the soil (kg N y^{-1}),
YSTEP is simulation time step for level 1 (y),
NPREC is nitrogen input by deposition (kg N y^{-1}),
NOMNP is nitrogen mineralization from humus (kg N y^{-1}),
NLINP is nitrogen mineralization rate of litter (kg N y^{-1}),
NLEACH is nitrogen leaching rate (kg N y^{-1}), and
NUP is nitrogen uptake rate by all trees in the stand, which is calculated as:

$$NUP=NDTOT-NRTOT \quad (3.14)$$

$$NDTOT=NDTOT+(Nu(K)*ROOTF(K))*DT \quad (3.15)$$

$$(K=1, 2, \ldots, SNTREE)$$

where,
NUP is nitrogen uptake rate (kg N y^{-1}),
NDTOT is total nitrogen demand from tree growth (kg N y^{-1}),
NRTOT is total nitrogen relocation of tree parts for all trees (kg N y^{-1}),
ROOTF(K) is fine root biomass of tree K (kg),
Nu(K) is nitrogen uptake rate by fine roots of tree K (kg N kg^{-1} d^{-1}),
YSTEP is simulation time step for level 1 (y),
DT is simulation time step for level 2 (d), and
SNTREE is total number of trees in the stand (stem).

The total nitrogen uptake by all trees in the stand, NUP, is a sum of every individual tree's nitrogen uptake demand NDTOT, and total nitrogen relocation of all the trees (sum of tree parts), NDTOT. The total nitrogen uptake rate by trees NDTOT is a function of fine root amount ROOTF(K), and the nitrogen uptake rate Nu(K).

For the nitrogen cycling in the plant-soil system, there is a feedback process during stand development following Bossel & Schäfer (1989). As in Fig. 3.4, the litter from all tree parts can go back to the soil (as well as dead trees in the stand), be turned into humus through humification, then into plant available nitrogen by mineralization (or mineralized into plant available nitrogen directly from decomposed litter).

Summary Table: subroutines *NCYCL1, NCYCL2*

Aims:

To calculate tree nitrogen uptake from soil in a time step of days, and to calculate soil nitrogen dynamics in an annual time step.

Main assumptions:

The nitrogen dynamics in the soil are based on the processes of decomposition and mineralization of nitrogen, and nitrogen fixation. All these processes are affected by soil temperature (Bossel & Schäfer, 1989).

Main inputs:

NCYCL1: Turnover rates of leaf, root, maximum nitrogen fixation rate of tree, soil temperature, reference temperature for soil temperature effect, temperature for zero soil activity.

NCYCL2: Topsoil depth, weight of soil, plant available nitrogen rate, plant-available nitrogen turn-over rate, decomposition rate, humification rate, carbon in litter, organic matter content of soil, C/N ratio in litter, and C/N in soil organic matter.

Main outputs:

NCYCL1: Total amount of nitrogen for relocation, total nitrogen loss of trees (to litter), nitrogen fixing rate of trees, parameter for temperature dependence of soil processes.

NCYCL2: Total amount of plant-available nitrogen in the soil.

3.2.2.4 Water Balance

Water is another important factor to tree growth. In FORDYN, water relations between plant and soil are represented as in Fig. 3.5. There is a dynamic water pool in the soil, noted as SOILw, which is consumed by transpiration from each tree, and recruited by precipitation. The time step is days:

$$\mathrm{SOILw}=\mathrm{SOILw}+(\mathrm{WPREC1}-\mathrm{WTRAN})*\mathrm{DT} \qquad (3.16)$$

where,

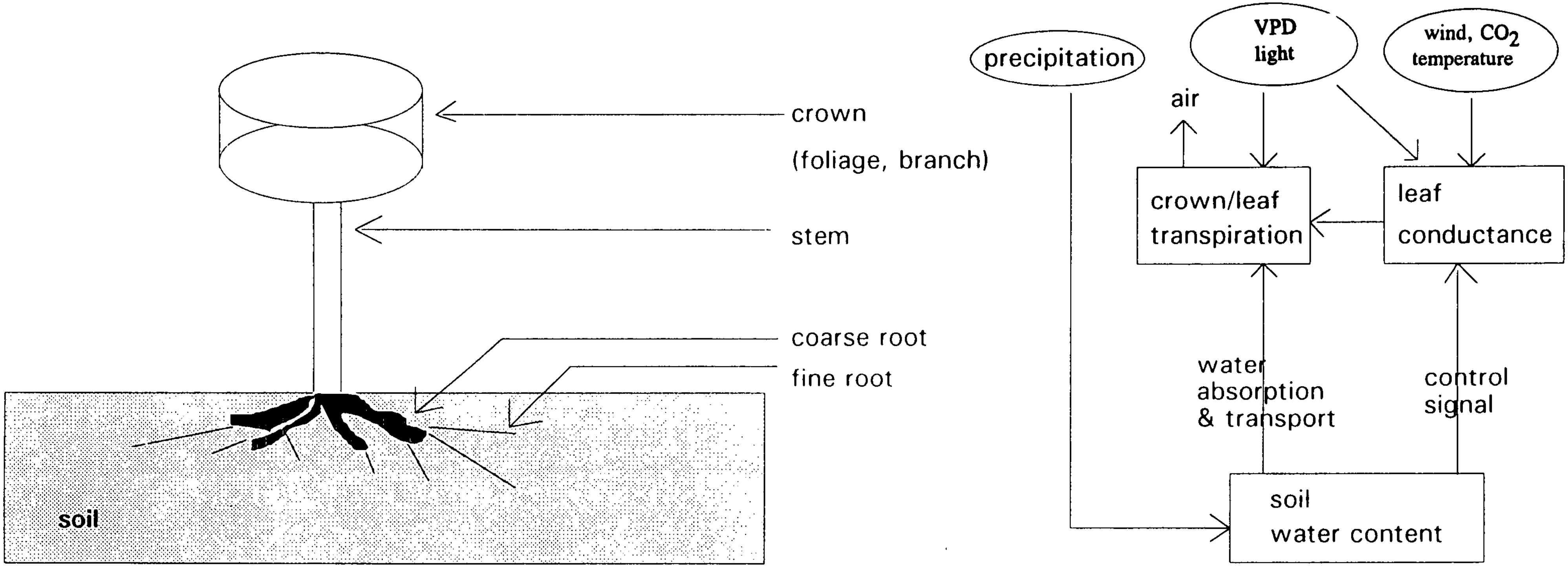


Fig. 3.5 Tree growth process, with plant-soil water relations.

There is a dynamic soil water pool which is consumed by root uptake and recruited from precipitation on a time step by days.

SOILw is total volume of soil water in the stand (m^3 H_2O),
WPREC1 is average daily precipitation (Mg H_2O d^{-1}),
WTRAN is water absorption (from soil) by trees through transpiration (m^3 H_2O $stem^{-1}$ d^{-1}), and
DT is the same as that in equation 3.15.

There is experimental evidence (Khalil & Grace, 1992) that soil water content can have a direct control over stomatal conductance (subroutine *PHO31*), which further affects transpiration rate (subroutine *TRANSPN*).

subroutine *PHOSYN2*

When simulation mode 2 is selected, subroutine *PHOSYN2* is used for calculation of daily average photosynthetic rate with an input of daily average radiation (Fig. 3.1). In subroutine *PHOSYN2*, a negative exponential model (empirical light response curve) of photosynthesis is used (Thornley, 1986):

PHOPL(K)=PMAX(J)*(1-EXP(-ELL(J)*FLUX/PMAX(J))) (3.17)

where,
PMAX(J), ELL(J), and FLUX are the same as in the rectangular hyperbola model in subroutine *PHOSYN1*, as shown in equation (3.7).

Summary Table: subroutine *PHOSYN2*

Aims:

To calculate daily average photosynthetic production.

Main assumptions:

Leaf photosynthesis response to light can be described as a negative exponential curve (Thornley, 1986).

Main inputs:

Daily average radiation received above canopy, maximum photosynthetic rate by species, light extinction parameter of leaves by species, apparent quantum efficiency of leaves by species, spatial location and size of all trees in the stand, and total leaf area of the source tree.

Main outputs:

Daily photosynthetic rate.

3.2.3 Level 3

When simulation mode 3 is selected, processes in level 3 are incorporated (Fig. 3.1). Then the daily total daytime photoproduction is calculated by the integral of hourly average photosynthetic rate PHOPH(K):

$$\mathrm{PHOPD(K)=PHOPD(K)+PHOPH(K)*DAYL*WGAUS3(IN)} \qquad (3.18)$$

where,

PHOPD(K) is daily total day-time photoproduction (g CO_2 stem^{-1} d^{-1}),

PHOPH(K) is hourly average photosynthetic rate (g CO_2 stem^{-1} h^{-1}) ,

DAYL is day length (h), and

WGAUS3(IN) is the weight of each time point (IN) in using the three-point Gaussian integration method (Goudriaan, 1986) to calculate daily total photoproduction based on a photosynthetic production curve within one day.

3.2.3.1 Photosynthesis

In FORDYN, leaf photosynthesis can be calculated by different submodels depending on the simulation mode being selected (Fig. 3.1).

For simulation mode 3, a physiologically-based leaf-scale photosynthesis model (empirical photosynthesis model) is introduced in subroutine *PHOSYN3* to derive hourly photosynthetic rate PHOPH(K) for use in equation 3.18, using a non-rectangular hyperbola model (Miranda, 1981). The reason to employ this submodel is that more physiological parameters are involved, and they are best described in a time step of hours (such as leaf stomatal conductance and mesophyll conductance):

$$\text{PHOPL(K)**2*VEX(J)-PHOPL(K)*(ELL(J)*FLUX+PMAX(J))+} \\ \text{ELL(J)*FLUX*PMAX(J)=0} \qquad (3.19)$$

where,

PHOPL(K) is photosynthetic rate by leaf of tree K (μmol m^{-2} s^{-1}),

VEX(J) is the convexity of the light response curve for species J (dimensionless),

ELL(J), FLUX(K) and PMAX(J) are the same as that in the rectangular hyperbola model in subroutine *PHOSYN1* as shown in equation (3.7).

The interesting part in the above equation is that these parameters can be incorporated with some useful physiological parameters, such as leaf stomatal conductance and leaf boundary layer conductance, for representing a more sensitive environmental response, e.g. atmospheric CO_2 concentration, leaf stomatal conductance, mesophyll conductance and leaf boundary layer conductance etc. are calculated in subroutine *PHO31*, and then used in subroutine *PHO32* to calculate hourly photosynthetic rate. See more in Miranda (1981).

The subroutine *PHO31* is taken from MAESTRO (Wang, 1988), and thus no feedbacks between stomatal conductance and the local atmospheric environment are considered. Stomatal conductance is calculated by using the inputs of temperature, PAR flux density to the leaf surface, and water vapour saturation deficit. Boundary layer conductance of leaves within a crown in the canopy is calculated based on the air temperature, and wind speed at that height (which depends on the wind speed above the canopy, crown dimensions of all trees within the plot and shoot structure).

Summary Table: subroutine *PHOSYN3 (=PHO31 + PHO32)*

Aims:

PHO31: To calculate the conductances (stomatal, boundary layer, and mesophyll conductance of leaves in a crown layer) for water vapour and carbon dioxide between ambient air and the intercellular spaces of leaves in an hour of a day.

PHO32: To calculate hourly photosynthetic rate.

Main assumptions:

Leaves are homogeneously distributed within the crown, The inputs of air temperature and water vapour saturation deficit, radiation fluxes and wind speed on a horizontal surface at the height of the leaves are appropriate for calculating the stomatal and boundary layer conductances (Wang, 1988), and the photosynthesis of leaves (Miranda, 1981).

Stomatal conductance and mesophyll conductances are calculated by a boundary-layer approach (Jarvis, 1976).

Boundary layer conductance is assumed to be depent on the wind speed above the canopy, aerodynamics properties of the tree crowns in the plot and the shoot structure (Wang, 1988).

Main inputs:

PHO31: Reference height, wind speed, air temperature and water vapour saturation deficit at the height, crown dimensions of all trees in the stand, and PAR flux density incident normal to the leaf surface.

PHO32: Leaf temperature, PAR flux density incident normal to the leaf surface, the leaf boundary, stomatal and mesophyll conductances.

Main outputs:

PHO31: Hourly stomatal, boundary layer, and mesophyll conductances of the leaves in the crown.

PHO32: Hourly photosynthetic rates of the leaves in the crown of the target tree.

3.2.3.2 Respiration

In level 3, daily net photosynthetic production is derived from daily daytime photosynthetic production and daily total respiration. The calculation of daily respiration is calculated as a sum of maintenance and growth respiration (McCree, 1970) in subroutine *RESPN*:

NPPD(K)=PHOPD(K)-RESP(K) (3.20)
RESP(K)=RESPM(K)+RESPG(K) (3.21)
with that,
RESPM(K)=MRLEAF(K)+MRWOOD(K)+MRROOT(K)
RESPG(K)=BIOMG(K)*GB(J)*TRES(J)

where,
NPPD(K) is daily total net photosynthetic production (kg CH_2O stem^{-1} d^{-1}),
PHOPD(K) is daily total gross photosynthetic production (kg CH_2O stem^{-1} d^{-1}),
RESP(K) is daily total respiration of tree K (kg CH_2O stem^{-1} d^{-1}),
RESPM(K) is maintenance respiration of tree K (kg CH_2O stem^{-1} d^{-1}),
RESPG(K) is growth respiration of tree K (kg CH_2O stem^{-1} d^{-1}),
MRLEAF(K) is leaf respiration during night-time of tree K (kg CH_2O stem^{-1} d^{-1}),
MRWOOD(K) is wood maintenance respiration of tree K (kg CH_2O stem^{-1} d^{-1}),
MRROOT(K) root maintenance respiration of tree K (kg CH_2O stem^{-1} d^{-1}),
BIOMG(K) is daily biomass increment of tree K (kg CH_2O stem^{-1} d^{-1}),
GB(J) is growth respiration parameter (dimensionless), and
TRES(J) is temperature effect on respiration (dimensionless).

As shown above, the total maintenance respiration of a tree RESPM(K) includes leaf, wood, and root maintenance. Each of these maintenance respiration rates is assumed to be proportional to temperature, roughly doubling for each temperature increase of 10 ^{0}C in the normal temperature range (Luxmoore *et al.*, 1986). e.g. wood maintenance respiration (root and leaf maintenance respiration are calculated in a similar way) is calculated as:

MRWOOD(K)=WOOD(K)*SPREWD(J)*TRES(J) (3.22)
with,
TRES(J)=Q10**((DATMP-THORM(J))/10.) (3.23)

where,

WOOD(K) is biomass of woody part of tree K (kg CH_2O stem^{-1}),
SPREWD(J) is specific respiration rate of wood (d^{-1}),
DATMP is daily average temperature (^{0}C),
THORN(J) is reference temperature for temperature effect of species J (^{0}C), and
Q10 is a coefficient of the temperature effect, set to 2.0 (dimensionless).

Summary Table: subroutine *RESPN*

Aims:

To calculate daily respiration rate.

Main assumptions:

The respiration of a tree can be treated as maintenance and growth respiration (McCree, 1970). They are strongly affected by temperature, and double for each temperature increase of 10 ^{0}C in the normal range (Luxmoore *et al.*, 1986).

Main inputs:

Biomass of leaf, wood, and root of a tree, daily biomass increment of a tree, specific respiration rate of leaf, wood and root, night length, specific growth respiration parameter, reference temperature for temperature effect, and temperature for zero activity.

Main outputs:

Daily respiration of a tree.

3.2.3.3 Transpiration

Transpiration of leaves of each tree is calculated in a daily time step (Fig. 3.1). The process is represented by the Penman-Monteith equation following the form that is used in MAESTRO (Wang, 1988), and represented in subroutine *TRANSPN*.

The input of this subroutine includes leaf temperature, net radiation absorbed of leaves, water vapour saturation deficit, and the output calculated from subroutine *PHO31* such as wind speed at the height of leaves, stomatal conductance and boundary layer conductance.

Summary Table: subroutine *TRANSPN*

Aims:

To calculate transpiration rate of leaves in a crown layer within a day.

Main assumptions:

Transpiration of a leaf is calculated based on the Penman-Monteith equation in the form expressed by Wang (1988).

Main inputs:

Net radiation flux density absorbed by the leaf surface, *VPD*, atmospheric pressure, leaf boundary and stomatal conductances.

Main outputs:

Hourly transpiration rate of leaves within a crown.

3.2.4 Level 4

3.2.4.1 C_3 Photosynthesis

One of the most important characteristics of plants is their ability to harness energy from the sun to 'fix' atmospheric carbon dioxide into a range of more complex organic molecules. This process of photosynthesis provides the free energy plants need by storing it in photosynthetic assimilates. This will further be transferred in the processes of respiration to high energy compounds that can be used for synthetic and maintenance processes (Jones, 1992).

Plants can be classified into at least three major groups, C_3, C_4 and CAM, on the basis of the biochemical pathway by which they fix CO_2. Trees and the majority of crop plants use the C_3 pathway. So, discussion in the following will focus on the C_3 pathway.

Photosynthesis can be conveniently treated as three related components: i) light reactions, in which radiation energy is absorbed and used to generate the high energy compounds ATP and NADPH; ii) dark reactions, which include the biochemical reduction of CO_2 to sugar using the high energy compounds generated in the light reactions; and iii) supply of CO_2 from the ambient air to the site of reduction in the chloroplast.

The overall reactions can be represented in a simplified diagram as follows in

Fig. 3.6. It is shown that, a C_3 photosynthetic pathway consists of a carbon reduction cycle (PCR) and a photorespiration cycle (PCO). There is a competition between CO_2 and O_2 for the enzyme Rubisco, and depending on the outcome the carbon is directed to one of two different cycles. For the PCO cycle, O_2 is consumed and CO_2 released, while in the PCR cycle, CO_2 is utilised to fix carbon into sugar, and to regenerate RuBP.

The combined photorespiratory (PCO) and Calvin (PCR) cycles show the stoichiometry in which ϕ molecules of RuBP are oxygenated to every one carboxylated (Based on Farquhar *et al.* (1980)).

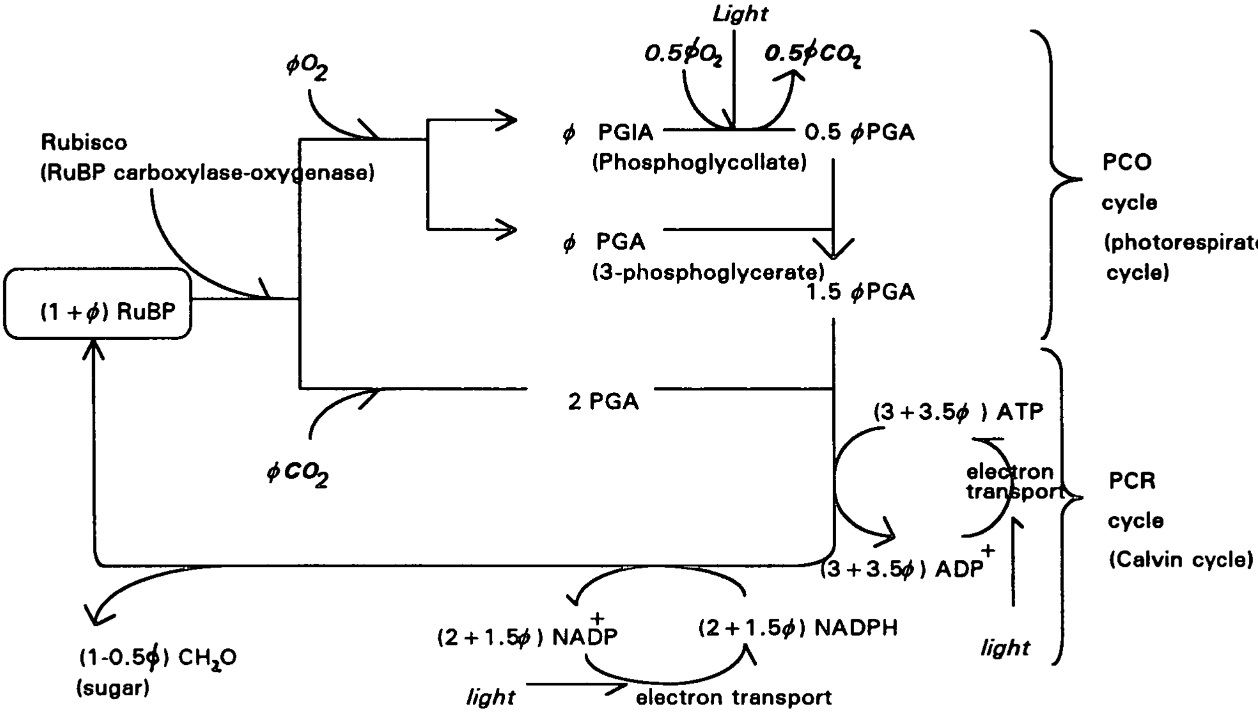


Fig 3.6 Schematic representation of C_3 pathway of photosynthesis

3.2.4.2 Calculation of CO_2 Assimilation Rate

When simulation mode 4 is selected, subroutine *PHOSYN4* is used to calculate instantaneous photosynthetic rate by a mechanistic model of leaf photosynthesis based on cell biochemical processes.

My objective here is to derive a physiologically explicit model of photosynthesis that is capable of predicting the responses of tree leaves to important environmental factors, but requires only a few parameters, and thus is easy to use.

Most previous descriptions of various biochemical aspects of photosynthetic carbon assimilation in the C_3 plant were brought together in a quantitative way by Farquhar *et al.* (1980), and later on modified by Friend (1991), Gross *et al.* (1991).

In subroutine *PHOSYN4* (Fig. 3.1), the photosynthesis is represented in a mechanistic way, and on the basis of cell biochemical processes. It represents the photosynthesis process (with mechanistic base) under a changing environment, or in response to environmental factors such as radiation, ambient CO_2 partial pressure, leaf temperature, atmospheric pressure, leaf nitrogen content, water use efficiency, wind and leaf-air vapour pressure deficit

The basis of the model structure follows so-called 'mechanistic' models of photosynthesis at the biochemical level, such as Farquhar *et al.* (1980), Farquhar & von Caemmerer (1982), Gross *et al.* (1991) and Friend (1991). A key variable in the model is intercellular partial pressure of CO_2, Pi, which is obtained from the co-limitation of a detailed biochemical model and stomatal conductance (Friend, 1991).

It is assumed that under certain environmental conditions, biochemical processes or components should be in dynamic equilibrium states. There are three main biochemical components described in the submodel *PHOSYN4*. They are RuBP pool (also includes intermediate components leading to RuBP), glycolate and glycerate pathway components pool, and equilibrium (under certain PFD levels) carboxylation rate (which marks the activity of Rubisco and other enzymes involved in oxygenation/carboxylation) (see Gross *et al.* (1991)).

When the submodel is called, firstly, under certain environmental conditions, biochemical processes or components should be in dynamic equilibrium states (include the processes of photorespiratory (PCO) and Calvin (PCR) cycles as in Fig. 3.6), and thus the equilibrium RuBP production, noted as RuBP pool size and the equilibrium production of components of the glycolate and glycerate pathway, noted as pool size are calculated from derived equations based on Gross *et al.* (1991):

R = (-BB+SQRT(BB**2-4*AA*CC))/2*AA (3.24)

G = 2*Gamma(J)*Wc*(R/(R+Kr(J)))/(Psi(J)*Pi) (3.25) with,

AA = -Vj/Rmax(J)

BB = Vj-Kr(J)*Vj/Rmax(J)-(1+2*Gamma(J)/Pi)*Wc

CC = Kr(J)*Vj

where,

R is pool size of RuBP and reduced intermediates leading to RuBP (μmol m^{-2}),
G is production of components of the glycolate and glycerate pathway (μmol m^{-2}),
Vj is electron transport-limited carboxylation rate (μmol m^{-2} s^{-1}),
Wc is RuBP-saturated carboxylation rate (μmol m^{-2} s^{-1}),
Rmax(J) is maximum size of R pool (μmol m^{-2}),
Gamma(J) is CO_2 compensation point when there is no non-photorespiratory respiration (μmol m^{-2} s^{-1}),
Psi(J) is rate of breakdown of G pool (s^{-1}),
Kr(J) is effective Michaelis-Menten constant for activation of Rubisco by CO_2 (Pa), and
Pi is intercelluar CO_2 partial pressure (Pa).

Secondly, the equilibrium carboxylation rate is calculated based on an extended Michaelis-Menten form of the radiation dependent process (Equation (7) as in Gross *et al.* (1991).

Thirdly, to estimate Pi by a Newton's iteration approach. This is because there is no existing equation to calculate Pi. Thus it is obtained by a co-limitation between biochemical processes with leaf conductance processes (Friend, 1991).

To do this, it starts from an initial dummy value of Pi, which is expected to meet the demand of the equilibrium R and G pools. By co-limitation of both biochemical and leaf level processes. It is thus estimated by setting the following two equations which are based on equation 11 in Gross *et al.* (1991), and equation 6 in Farquhar & Sharkey (1982), equal to each other:

PHOPL(K)=Wc*R/(R+Kr(J))-0.5*Psi*G -Rd(K) (3.26)

and

PHOPL(K) =(Pa-Pi)*Glc0-((Pa+Pi)*TRANSP(K))/2 (3.27)

where,
PHOPL is carboxylation rate (μmol m^{-2} s^{-1}),
Rd(K) is dark respiration rate (μmol m^{-2} s^{-1}),
Kr(J) is Michaelis-Menten constant for the production of the R pool (Pa),
Pa is ambient partial pressure of CO_2 (Pa),
TRANSP(K) is transpiration rate (μmol m^{-2} s^{-1}),
Glc0 is leaf conductance to diffusion of CO_2 (μmol m^{-2} s^{-1}), which is converted to the corresponding value for water vapour, by division by the ratio of the binary diffusivities of water vapour/air and CO_2/air (Farquhar & Sharkey, 1982), and
Wc, R, Kr, Psi, are the same as that defined in previous equations.

The newly estimated Pi is compared with the initial dummy Pi. If there is a difference, then Pi is updated. This Newtonian iteration is carried on for Pi, to determine that new Pi should meet the demand of the co-limitation of biochemical and leaf levels as in equations 3.26 and 3.27, or in other words, it is estimated by either of above two equations.

Pi is estimated through iteration, until there is no difference by using two measures. The resulting Pi is used to calculate instantaneous CO_2 assimilation rate PHOPL(K) by either of the above two equations, 3.26 or 3.27.

It needs to be noted that, when this iteration operates, leaf conductance Glc0 is optimised together with Pi.

Furthermore, the response of this CO_2 assimilation process to the crucial environmental changes has been integrated in the model and is represented as follows:

Radiation

The radiation dependence process of photosynthesis can be represented as the photon flux density dependence of electron transport rate, and this relationship can be described in a non-rectangular hyperbola Michaelis-Menten form (Gross *et al.*, 1991):

$$Vj = ((aj*FLUX+Vjmax) - sqrt((aj*FLUX+Vjmax)^2 - 4*aj*FLUX*Vjmax*q))/2*q \qquad (3.28)$$

where,

Vj is electron transport rate (μmol m^{-2} s^{-1}),
aj is quantum yield (dimensionless),
FLUX is photon flux density (μmol m^{-2} s^{-1}),
Vjmax is maximum electron transport rate (μmol m^{-2} s^{-1}), and
q is the curvature of the light dependence of electron transport (dimensionless).

Leaf nitrogen

The leaf nitrogen content and its partitioning between Rubisco and chlorophyll are assumed to constrain the maximum velocity of carboxylation, and maximum electron transport rate (Friend, 1991):

$$Vcmax = Vck*kc(J)*Nrub*Ln \tag{3.29}$$

and

$$Vjmax = Vjk*Jmax(J)*Nchl*Ln \tag{3.30}$$

where,
Vcmax is maximum rate of carboxylation at full activation of Rubisco (mol m^{-2} s^{-1}),
Vjmax is maximum electron transport rate (m^{-2} s^{-1}),
kc(J) is turnover number of RuBP carboxylase (s^{-1}),
Jmax(J) is irradiance-saturated potential electron transport rate per mol of chlorophyll (mol^{-1} s^{-1}),
Vck is a constant to convert mols of nitrogen in Rubisco to moles of reaction sites of Rubisco molecules (mol mol^{-1}) (= 7/5500),
Vjk is a constant to convert mols of nitrogen to moles of chlorophyll (mol mol^{-1}) (=0.25),
Nrub is leaf nitrogen proportion in Rubisco (dimensionless),
Nchl is leaf nitrogen proportion in chloropyll (dimensionless), and
Ln is leaf nitrogen content (mol m^{-2}).

Temperature

The dependence of the assimilation process upon temperature affects the upper limit of electron transport rate. Because of the misprint of equation 36 in Farquhar *et al.*

(1980), I here use the modified equation by Jon Lloyd, which has shown a reasonable behaviour (personal communication) :

$$Jmax(J)=(467*\exp((TLEAF/298.15-1)*E/Rgc*TLEAF))*(1+\exp((S*298.15-H4/Rgc*298.15)))/(1+\exp((S*TLEAF-H4)/(Rgc*TLEAF))) \quad (3.31)$$

where,

Jmax(J) is the same as defined in equation 3.30 above,

TLEAF is the Kelvin temperature of the leaf,

E, S, H4, Rgc are the parameters equivalent to E, S, H, R in equation 36 in Farquhar *et al.* (1980).

Soil water

It was found that soil water content can affect leaf conductance (Khalil & Grace, 1993), which further influences CO_2 assimilation rate (equation 3.27):

$$GS(K)=GS1*GS2 \quad (3.32)$$

$$GS1=Rgs1(J)*SOILh+Rgs2(J) \quad (3.33)$$

where,

GS(K) is stomatal conductance to water vapour (umol $m^{-2}s^{-1}$), which can be converted to stomatal conductace to CO_2 when divided by the ratio of the binary diffusivity of water vapour/air and CO_2/air as 1.6 (Farquhar & Sharkey, 1982),

GS1 is the soil water effect on leaf conductance (dimensionless),

GS2 is the effect of other factors on leaf stomatal conductance such as light, temperature, water vapour, and predawn xylem water potential as described in Wang (1988) (dimensionless).

SOILh is soil water content (m^3 m^{-3}), and

Rgs1(J) (m^{-3} m^3) and Rgs2(J) (dimensionless) are coefficients which relate stomatal conductance to soil water content.

Ambient CO_2 partial pressure

The function of CO_2 is as the substrate and activator for photosynthetic carbon assimilation. Therefore, a change in ambient CO_2 partial pressure can affect the supply of substrate by diffusion into the leaf. This CO_2 dependence of CO_2 assimilation is expressed in equation 3.27. Simulated results have shown that changes in ambient CO_2 partial pressure cause assimilation rate to increase, and leaf conductance to decrease (see more in Chapter 5).

Simulation also shows that there is a constant Pi/Pa as ambient CO_2 partial pressure (Pa) changes, which is maintained by stomata action. This result is supported by experiment (Farquhar & Wong, 1984).

Air humidity & wind

These two environmental factors mainly affect leaf conductance and boundary layer conductance, which are described in subroutine *PHO31*, following Wang (1988).

The leaf boundary layer is treated according to whether the tree is a conifer or broad leaf, as in Jarvis *et al.* (1976), and is mainly affected by wind speed and temperature. Water vapour dependence of leaf conductance follows an empirical relationship as in Jarvis *et al.* (1976).

Summary Table: subroutine *PHO4 (within PHOSYN4)*

Aims:

To calculate leaf photosynthetic rate in a mechanistic way.

Main assumptions:

Leaf photosynthetic rate can be calculated by co-limitation of both biochemical processes (Farquhar *et al.*, 1980) and leaf conductance limited processes (Farquhar & Sharkey, 1982) following Friend (1991).

Main inputs:

Environmental parameters: irradiance, atmospheric pressure, atmospheric CO_2 and O_2 pressure, dummy intercellular CO_2 partial pressure;

Physiological and biochemical parameters: stomatal and boundary layer conductances to water vapour, leaf nitrogen content, leaf temperature, maximum pool size of RuBP concentration, Michaelis-Menten constants for CO_2 and O_2, Michaelis-Menten constant for activation of Rubisco by CO_2, CO_2 compensation point;

Constants: gas constant, constant that converts mols of nitrogen in Rubisco to moles of reaction sites of Rubisco molecules, and constant that converts moles of nitrogen to moles of chlorophyll.

Main outputs:

Instantaneous photosynthetic rate of leaf.

3.3 Simulation Input

3.3.1 Biotic Parameters

It has been shown that FORDYN has four basic levels of process (Fig. 2.3). When a simulation mode is selected (Fig. 2.4 in Chapter 2), appropriate input files are called (Appendix V). Names and units of each parameters are found in Appendix IV.

3.3.1.1 Stand Structure and Properties

In FORDYN, the level 1 process is designed to simulate a mixed-age, mixed-species forest, and an individual tree-based model is represented (section 3.2.1).

To describe stand structure, input file STANDINT is provided (to be used in all four simulation modes), to specify the total number of trees, SNTREE, and the maximum stand biomass, SBIOMX. Then each individual tree, with tree number TREENO and crown radius CR, is located in the stand by its coordinate on the X and Y axis, (TX, TY) to represent stand spatial (horizontal) structure. The following is an example of input file STANDINT:

```
            *** STAND.INT ***
--------- Stand structure data for the model fordyn.f
            ====> mode 1, 2, 3, 4  (site size: 10*100m^2)
*********************************************************

-------------------------------
SNTREE        SBIOMX
163             113462
----------------------------------------------------------
TREENO     SPECNO        TX       TY      CR
1             1           1.0      2.5     1.4
2             1           1.0      5.0     1.4
...
163           1           98.5     10.0    1.4
```

3.3.1.2 Tree Structure and Properties

A tree can be described in terms of morphology, phenology and physiology. While in FORDYN, the input of these different aspects depends on the simulation mode selected.

In the input file TREE0INT, which is used for all four simulation modes, the morphology of each tree is described by DBH (m) and height H (m). The radius of crown profile CR (m) is input from STANDINT as above.

Some other morphological properties of species including maximum tree height H (m), height-DBH ratio HD (dimensionless), mature tree height HMH (m), and wood weight per volume BW (Mg CH_2O m^{-3}) are provided in TREE1INT (for simulation mode 1) and TREE2INT (for simulation mode 2, 3, 4).

The dispersal and germination factors, like G (dimensionless), D1 (dimensionless), SSY (stem) etc. are provided in TREE1INT. They are also used for all four simulation modes.

The following is an example of input file TREE1INT:

```
                    ***  TREE1INT  ***
----- Tree morphology, physiology data file for the model fordyn.f
     ====> mode 1
*******************************************************************

-------------------------------------------------------------------------------
SPECNO  HMAX   DBHX   HD   C     HMH   BW   SL   CD   CLR
1       30     .30    100  165   20   0.4   500  10   1
-------------------------------------------------------------------------------
SPECNO  b2      b3     b1     BRK    GB     LEAFWA
1       116.84  -98.79 -1.25  0.08   0.08   4.04
-------------------------------------------------------------------------------
SPECNO   SSY  G  D1  D2
1        2000 1  1   1
```

3.3.1.3 Leaf Physiological Properties

For the use in simulation modes 2, 3, 4, physiological parameters of the tree are mainly provided from the input file TREE2INT, where species-based photosynthesis, respiration, nitrogen content and assimilate allocation parameters are provided. e.g. maximum photosynthesis rate per tree PMAX0 (μmol CO_2 m^2 s^{-1}), specific respiration rate of leaf SPRERT (dimensionless), nitrogen content of green leaves NLF (kg N kg^{-1} C^{-1}), and assimilate relocation rate ASRLOC (dimensionless).

For simulation modes 3 and 4, the input file needs some extra leaf physiological parameters which are provided by TREE3INT and TREE4INT, e.g. in TREE3INT, the maximum value of stomatal conductance MAXGS (mol m^{-2} s^{-1}), maximum and optimal leaf temperatures for leaf mesophyll, THGM (^{0}C) and TLGM (^{0}C), and the slope of the response curve of leaf stomatal conductance to vapour pressure deficit are provided to describe the response to the environment of all the relevant leaf physiological processes that are mainly used in mode 3.

The following is an example of the input file TREE2INT:

```
                 ***   TREE2INT   ***
------- Tree physiological parameters data file for the model fordyn.f
            = ===> mode 2, 3, 4
*****************************************************************
-----------------------------------------------------------------
SPECNO HMAX  HD  ...
...
---------------------------------------------------------------------
SPECNO   SPRELF   SPRERT   SPREWD   GB   TNORM   RELOC
1          1.        1.        0.3        1.2   15        0.1
----------------------------------------------------------------------
SEPCNO   LFTUR    RTTUR     WDLSR    BRANSR    TO     ASSUR
1          0.000002 0.00007  0.0        0.1       -5.0   0.12
...
```

3.3.1.4 Cell Biochemical Properties

The biochemical processes of photosynthetic carbon assimilation are represented in subroutine *PHOSYN4* and are used for simulation mode 4 (Fig. 3.1). This is an improved and simplified version as described before (see section 3.2.4). Most parameters used in *PHOSYN4* are from the input file TREE4INT.

The following is an example of the input file TREE4INT:

```
                    ***   TREE4INT   ***
-------  Tree physiological parameters data file for the model fordyn.f
              ====> mode 4
*****************************************************************
--------------------------------------------------------------------------------
...
SPECNO    Patm        Pa     Pi      Po2
1          1000000  35.0  30.0   21000
----------------------------------------------------------------------------------
SPECNO    Rmax   Kr      Ka    Gamma    Vo     Psi     Nlk
1           47.3     2.75   1.0    4.44       0.16  0.04    0.399E-3
...
```

3.3.2 Abiotic Parameters

3.3.2.1 Geographical Parameters

To represent the spatial distribution of trees (for all four simulation modes), a rectangular sample site is located. The size is usually 0.1 to 1 ha, and varies depending on the diversity of stand. So, in the input file GEOGRINT, a retangular sample site is described by the length of two adjacent sides (XML, YML), thereby each tree's position can be fixed to represent stand structure.

The following is an example of the input sile GEOGRINT:

```
                   ***   GEOGRINT   ***
-------  Geographical parameters data file for the model fordyn.f
              ====> mode 1, 2, 3, 4
*****************************************************************
--------------------------------------------------------------------------------
XML    YML
100      10
```

3.3.2.2 Astronomical Parameters

The light climate of a day in a year can be calculated from the day of a year DAY, and latitude LATIN as provided in the input file ASTROINT.

The following is an example of the input data file ASTROINT:

```
                    ***   ASTROINT   ***
-------  Astronomical parameters data file for the model fordyn.f
           ====> mode 1, 2, 3, 4
*****************************************************************************************

------------------------------------------------------------------------------------
LATIN   DAY
53        1
```

3.3.3 Meterological Parameters

The meteorological data input file METEO1INT is used for mode 1, while, METEO2INT is used in modes 2, 3, and 4.

In METEO2INT, meteorological parameters are requested to calculate the effect of daily temperature, radiation, and humidity on photosynthesis. Maximum and minimum daily temperature, TMAX and TMIN, are requested to calculate daily average temperature DATMP (^{0}C), which is used for calculating daily respiration, leaf temperature and phenological development. The base temperature for phenological development BATMP (^{0}C), together with the phenological-temperature table DVSTB (dimensionless), temperature-photosynthesis table PMTMPT (dimensionless) and leaf age-photosynthesis table PMAGTB (dimensionless), are used to describe the phenology throughout a year (Mohren *et al.* ,1990).

In addition, the light scattering coefficient, maximum photosynthetic rate, apparent quantum efficiency are provided to describe the light climate in the stand. Vapour pressure and the respiration-temperature coefficient are also provided in this input file.

The following is an example of input file METEO2INT:

```
             ***  METEO2INT  ***
------- Meteorological parameters data file for the model fordyn.f
          ====> mode 2, 3, 4
********************************************************

------------------------------------------------------------------------------

ELL  BATMP  KDIF  PMAX0  KL  Rgs1  Rgs2   GSsw  Rd  EL
0.45  5        0.07   3.79    0.01  5.13  -0.4527  10     0.3  0.0073
------------------------------------------------------------------------------------

ATMTR  AVRAD  SCV  VAP  TMAX  TMIN  Q10  LPAR  PARV  APAR  ATEMP
0          9000000  0.2   1.0   25      -5     2.0   106      5000     200     9
----------------------------------------------------------------------------

DVSTB
            0.0    1222.0    2538.0    3500.0   9000.0
            0.0    1.0          2.0          3.0        3.0
----------------------------------------------------------------------------

 PMDVST
            0.0    1.0          2.0          3.0
            1.0    1.0          1.0          1.0
----------------------------------------------------------------------------

PMTMPT
            -30.0    -5.0    0.0    5.0    20.0    35.0    50.0
            0.0       0.0     0.2    0.5    1.0      0.6      0.0
----------------------------------------------------------------------------

...
```

3.3.4 Soil Parameters

Soil parameters are used to calculate nitrogen and water dynamices of the soil in the plant-soil system (section 3.2.3). These are provided in the input file SOILINT, and used mainly for modes 2, 3, and 4 (Appendix IV).

Soil physical properties are described by topsoil depth TOPSL (m), the weight of soil SPWSL (Mg m^{-3}), and plant-available nitrogen leaching rate RLEACH (y^{-1}). Some parameters for decomposition are also needed to derive the available nitrogen and minerals in the soil, such as normal decomposition rate DECR (y^{-1}), humus mineralization rate HUMINR (y^{-1}), temperature for zero activity TSO (^0C) etc. In addition, some initial values are also required, such as the organic matter content of the soil HUMC (Mg C Mg^{-1} soil), and the C/N ratio in the litter CNLIT (dimensionless).

The parameters needed to represent water relations in the plant-soil system are also provided from SOILINTl. They are soil water volume SOILw (m^3), and soil water capacity SOILc (m^3).

The following is an example of input file SOILINT:

```
              ***  SOILINT  ***
-------    Soil parameters data file for the model fordyn.f
              ====> mode 2, 3, 4
**************************************************************

---------------------------------------------------------------------------------
DECR   HR   HUMINR   TNORS   TSO   NPREC   NAV
0.3     0.1   0.01       20.0      -5      2          10
---------------------------------------------------------------------------
RLEACH    NUR    CLITR   HUMC   CNLIT    CNSOM
0.2          0.5     2000    0.02      45        14
---------------------------------------------------------------------------
NITC    NFIXM    TOPSL    SPWSL
 0.083   0.00015   0.3       1500
---------------------------------------------------------------------------
SPOILw   SOILc   WPREC   PSIc
45         100      63       -1500
...
```

3.4 Simulation Control

In FORDYN, there are four basic simulation modes depending on the level of process involved, or the resolution required (Fig. 3.7). When a simulation mode is selected, the process and its time step is fixed appropriately (Fig. 3.7). Simulation control can be obtained by combination of simulation mode and run duration.

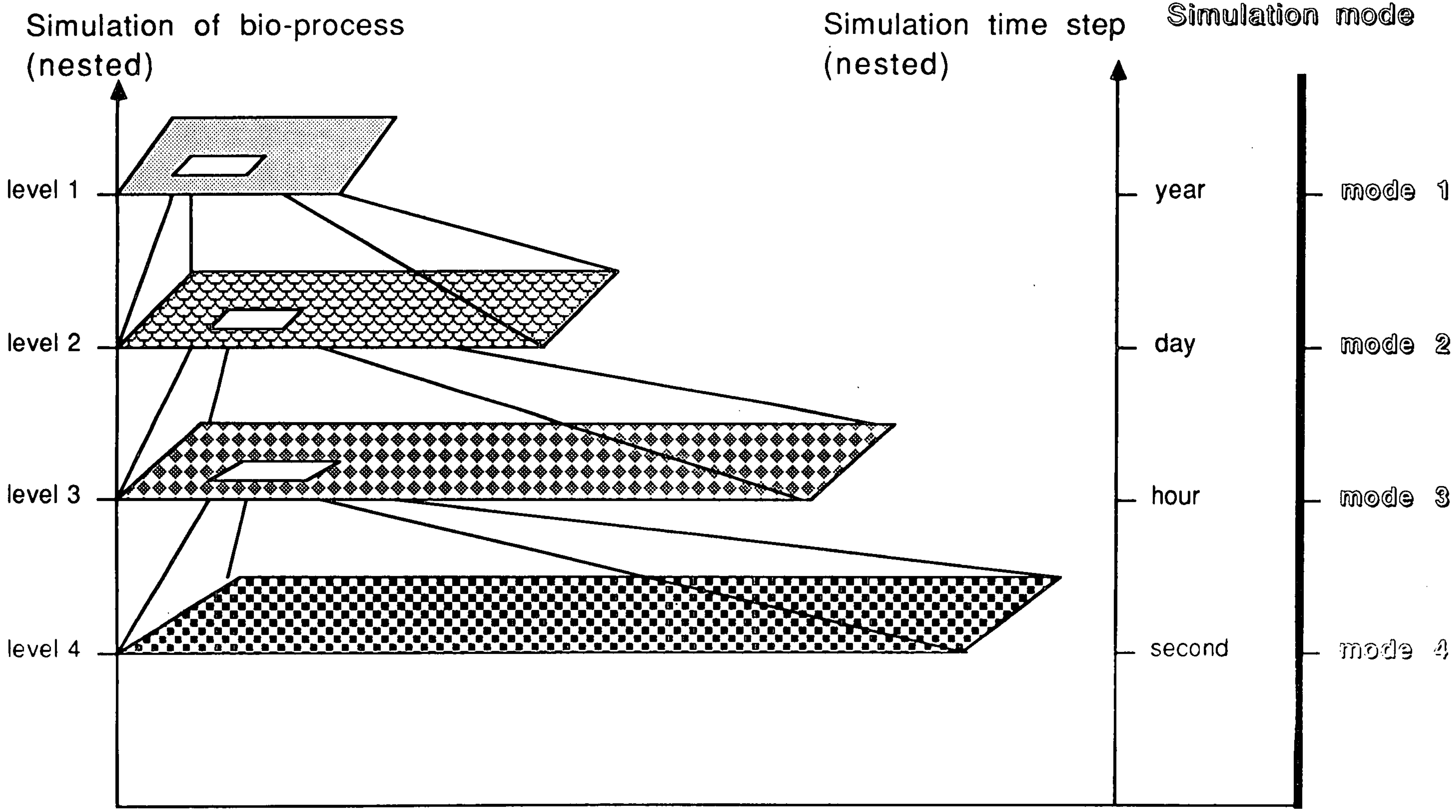


Fig. 3.7 Simulation control of the model FORDYN

Simulation control of FORDYN is achieved by setting simulation modes as 1, 2, 3 and 4, and each mode corresponds to different time step (year, day, hour and second), and thus involving different levels of processes. So, mode 1 includes level 1, mode 2 includes levels 1 & 2, mode 3 includes levels 1, 2, & 3, and mode 4 includes levels 1 , 2, 3, and 4.

If the user is interested in forest development over (say) 200 years, four simulation modes can be chosen depending on the resolution required (cell **A**, **B**, **C**, **D** in Table 3.1; Fig 3.7):

TABLE 3.1

Simulation control of the model FORDYN,
each simulation can be controlled by selecting one of four simulation modes (mode 1 to 4) and simulation time needed, and thus there will be 11 characteristic run (cell A to K) for different simulation purposes.

	Characteristic run duration (t) of simulation objectives		
Simulation mode	$t \geq 200$ years	1 year $\leq$ $t < 200$ years	1 day $\leq$ $t < 1$ year
mode 1	**A**	**E**	▨
mode 2	**B**	**F**	**I**
mode 3	**C**	**G**	**J**
mode 4	**D**	**H**	**K**

- Mode 1 (cell A in Table 3.1): when the user selects mode 1, temporal resolution is in years, and an empirical tree growth model is employed, where tree size increment measured as diameter at breast height (DBH) is a function of annual average assimilation, and leaf area increment is derived from an empirical relationship. Thus FORDYN is quite similar to a classical forest succession model in this simulation mode.
- Mode 2 (cell B in Table 3.1): when the user selects mode 2, the time step is in days or fractions-of-a-year. Annual tree size increment is then derived by physiologically 'process-based' tree growth rather than empirically by annual average assimilation in mode 1 (see following discussion). Daily photosynthetic production is driven by a daily averaged photon flux, and it is affected by phenology. Daily respiration is a function of day length and daily temperature.
- Mode 3 (cell C in Table 3.1): when the user selects mode 3, the time step is in hours or fractions-of-a-day. Daily photoproduction of each tree is calculated by

accumulating the hourly average photoproduction over 3-points in time based on a daily light distribution curve. The hourly photosynthetic rate is calculated by a semi-analytical model of an empirical light response curve (Miranda, 1981).

- Mode 4 (cell D in Table 3.1): when the user selects mode 4, the time step is in seconds or fractions-of-an-hour. The hourly photosynthesis rate is represented by biochemical processes of CO_2 assimilation by the leaf.

If the user is interested in stand growth over less than 200 years, e.g. for simulation growth of a plantation or a mixed natural forest, four simulation modes can be chosen depending on the resolution required (cell E, F, G, H in Table 3.1). In this situation, when mode 1 (cell E in Table 3.1) is selected, the time step is set by years, and each tree's growth, birth and death can be examined on the same time scale. When mode 2, 3, and 4 (cell F, G, and F in Table 3.1) are selected, tree growth processes are described in more detailed ways as noted above, the model then is similar to those process-based forest growth models (Dixon *et al.*, 1990).

If the user is interested only in forest dynamics at a temporal resolution of less than one year, e.g. forest growth response to climate change such as precipitation and radiation distribution within one year, mode 2, 3, 4 (cell I, J, and K in Table 3.1) can be chosen.

When one starts running FORDYN (Fig. 3.1, Appendix IV), subroutine CONTRO is called. The model will then ask a series of questions about simulation control so that the user can define the simulation to specify some purpose, e.g. start and end year of simulation, time step of simulation, and the simulation mode. Depending on the simulation mode defined, the program calls for input data files, and subroutine OPEN calls for corresponding output files.

For instance, when simulation mode 1 is chosen, the subroutine INPUT1 is used to call the input files needed: TREEOINT, TREEINT, STANDINT and GEOGRINT. After this, subroutine READAT1 is called to read the data from these four input files, and then OPEN is called to open the output files COMMUT1.OUT, COMMUT2.OUT, POPL.OUT, and PLANT.OUT. Finally, FORDYN runs the simulation then closes all the output files by the subroutine CLOSE.

3.5 Implementation of the Model FORDYN

FORDYN is programmed by FORTRAN 77 in about 6000 lines of code. It has been run on the mainframe computer Sequent s2000, operated by the Edinburgh University computing service.

FORDYN is very time consuming to run when all four level of processes are involved, e.g. for a 500-year-simulation in simulation mode 4, it will take up to four days to run on a Sequent s2000 mainframe computer. However, one can make 'shortcuts' to save simulation time, such as changing the simulation time step, and selecting simulation modes according to the aims of the work, e.g. a simulation for forest management can be made without involving leaf physiology and cell biochemistry by assuming a constant environment, e.g. by selecting simulation mode 1.

3.6 Simulation Examples

In this section, I will show the general behaviour of FORDYN, with some simulation examples at each level of process.

Table 3.2 illustrates the type of information required when running FORDYN at each level. Much of this information is available in the literature, at least for temperate species. Where species-specific data are lacking, as in tropical species, we are obliged to guess intelligently, taking the values from the existing literature on related species and life forms.

For large-scale studies of forest succession (setting the run duration to more than 200 years as in Table 3.1), the model operates with a plot size of 0.1 to 1.0 ha, because the size and number of plots are usually limited by the available human resources. As concluded by Levin (1992), this plot can then provide the information about forest patterns that we need for dozens of plots as used in the 0.01 ha plots of a 'gap model' (Shugart *et al.*, 1977). Moreover, since each individual tree in the plot is identified, the effect of density and spatial variety of source trees for dispersal and competition can then be described in a more realistic way, especially the influences of gap size on regeneration that most 'gap models' fail to represent satisfactorily.

TABLE 3.2

Example of inputs used in each level in FORDYN

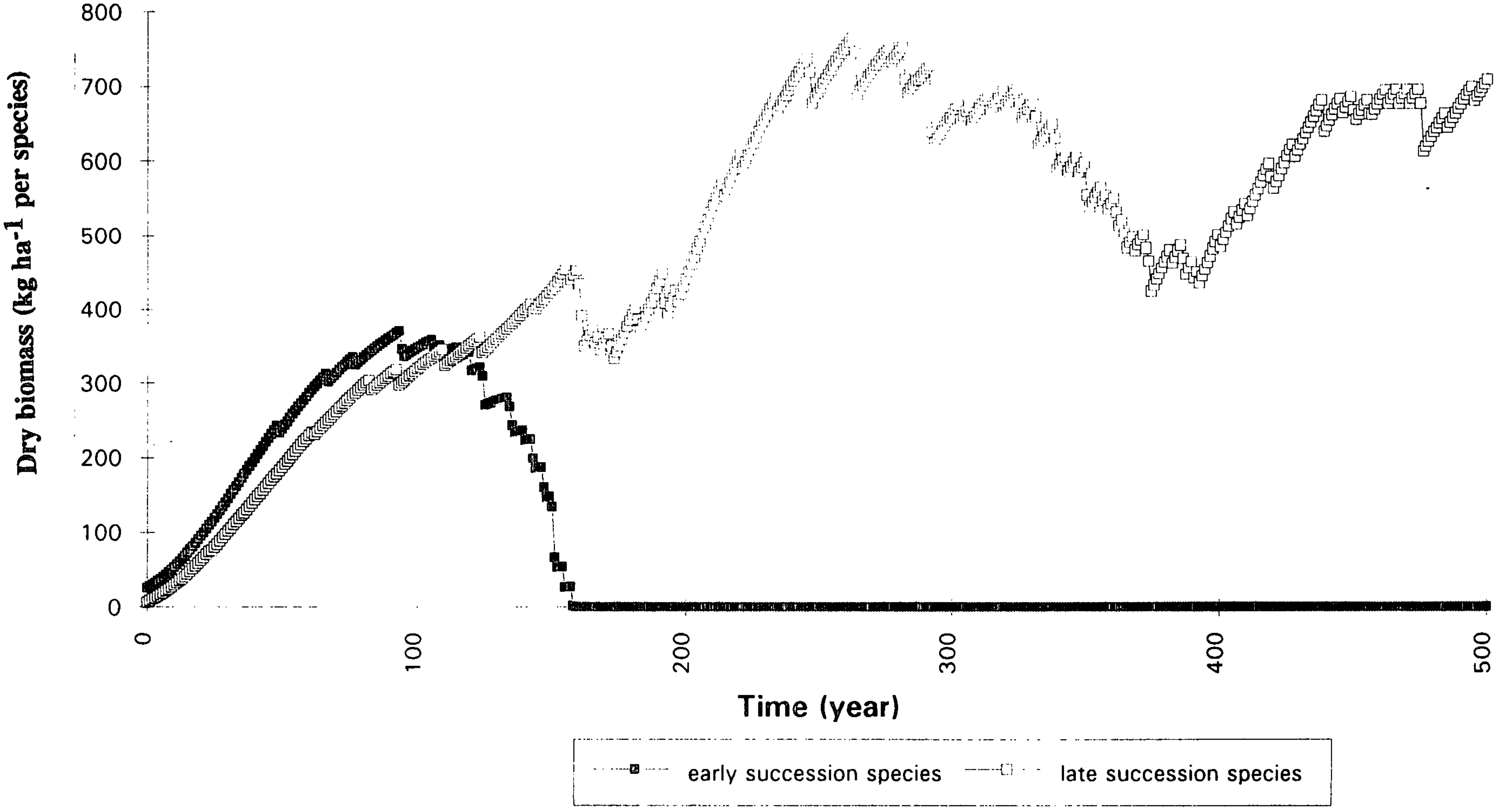
Mode	Symbol	Description	Range of value & unit	Reference
1	D,	diameter at breast height of tree,	0.02 — 10 (m)	0.15 (♠)
	H,	tree height,	1.3 — 100 (m)	15 (♠)
	N_t,	total tree number in the stand,	1 — 10000 (stem ha^{-1})	1625 (♠)
	...	...	...	...
2	M_l,	leaf biomass,	0.001 — 100 (kg DM stem^{-1})	6 (♠)
	M_s,	stem biomass,	0.001 — 100 (kg DM stem^{-1})	47 (♠)
	m_r,	meristem size of root,	0.0001— 0.1 (kg DM stem^{-1})	0.05 (♥)
	...	...	...	...
3	g_{smax},	maximum leaf stomatal conductance,	9 — 340 (mmol m^{-2} s^{-1})	50 (♣)
	P_m,	leaf maximum photosynthetic rate,	0.6 — 1.7 (mg CO_2 m^{-2} s^{-1})	0.7 (◆)
	...	...	...	...
4	V_{cmax},	maximum carboxylation rate,	0 — 200 (μmol CO_2 m^{-2} s^{-1})	98 (◆)
	V_{jmax},	maximum electron transport rate,	0 — 1000 (μmol m^{-2} s^{-1})	467 (◆)
	C_i,	intercellular CO_2 partial pressure,	0 — 70 (Pa)	32.5 (◆)
	...	...	...	

♠ European Pine Model Workshop data set, edited by Mohren & Bartelink (1992) (unpublished),
♥ Thornley (1991),
♣ Jones (1986),
◆ Farquhar *et al* (1980).

An example of a simulation output for a mixed-age and mixed-species forest in a succession time scale is shown in Fig. 3.8, with input data from Table 3.3. In this example, two hypothetical species with contrasting characteristics were allowed to grow together in a stand, whilst the environment was held constant. The saw-tooth shape of the biomass increment by species curve is caused by biomass loss from individual trees on death. The early succession species are replaced by late succession species during forest development when all trees of early species are dead. This is

Fig. 3.8 Forest succession

The succession process in an assumed two-species forest, whereby early species is replaced by late species resulting from different physiological and ecological characters (Table 3.3).



because the early species may have a better dispersal ability (more seed production, longer dispersal distance, etc.), and therefore a better chance to establish first in the new site. As long as the stand is closed, the late species will have a stronger regeneration ability in the understory. Light is recognised as a major factor in species replacement, especially in forest succession (Bazzaz, 1979), and late species have a higher photosynthetic rate at a low light, larger mature size (Table 3.3), and lower light compensation point (Bazzaz, 1979), which place them in a stronger position during inter-species competition.

TABLE 3.3

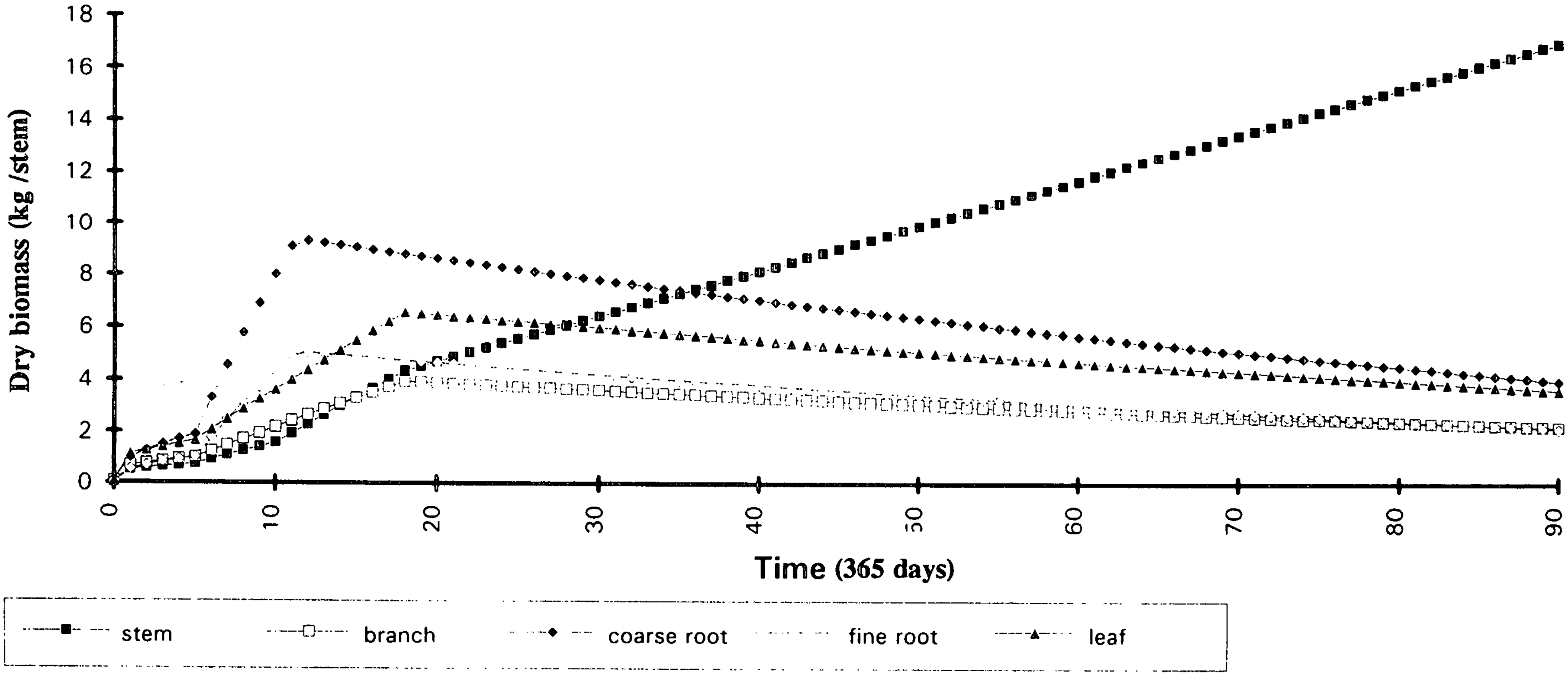
Physiological and ecological characteristics of an early- and a late- succession species (Based on Bazzaz (1979)).

Characteristics	Early succession species	Late succession species	Unit
Maximum photosynthetic rate	20	4	μmol CO_2 m^{-2} s^{-1}
Apparent quantum efficiency	0.02	0.04	μmol CO_2 μmol $photon^{-1}$
Dark respiration rate	1.3	0.2	μmol CO_2 m^{-2} s^{-1}
Seed number	3000	1000	seed $stem^{-1}$
Maximum *DBH* of a tree	0.40	0.60	m
Maximum tree height	30	40	m

An example of the simulation output of FORDYN for tree growth is shown in Fig. 3.9. All the growth curves are initially sigmoidal, with the stem component having a positive growth rate all the time, whereas others reach a maximum and then decline. This decline is caused by litter production. Root growth attains its maximum structure earliest, followed by branch, leaf and stem. This is because carbon and nitrogen concentration decline after an early increase, and also possibly because of a decreased leaf area which can support the meristem (Thornley, 1991). When forest growth reaches a certain stage, nitrogen content of the soil becomes limiting for photosynthetic rate. In addition, after the potential size of meristem is reached, the meristem activity of the tree also begins to decline. Therefore, when photosynthetic assimilation cannot meet the demand of litter loss and maintenance, the biomass will decline as shown in root and leaf parts. The woody component can maintain a longer positive growth period because it has a very small litter loss, but a smaller

Fig. 3.9 Tree growth

Tree growth processes are described following the transport-resistance approach as shown in Fig. 3.4 (Thornley, 1991). Each tree part has a different development speed and reaches its maximum value in different stage of the tree's life.



maintenance demand compared to leaf and root. When the total maintenance demand exceeds that which can be supplied by photosynthetic assimilation, the tree dies.

A simulation example used mode 3 of FORDYN to show leaf photosynthetic rate over a day and is shown in Fig. 3.10: daily total photosynthetic production of leaves in the crown throughout a day is accumulated by a 3-point Gaussian scheme based on the hourly light distribution curve during one day and the length of the day.

The responses of CO_2 photosynthetic assimilation to environmental changes based on cell biochemical processes are shown in Fig. 3.11. The parameters are taken from Farquhar *et al.* (1980), Friend (1991), and Gross *et al.* (1991):

The list of parameters used for biochemical submodel of photosynthesis (subroutine *PHO4*)

Symbols	Definition (Units)	Values
Environmental parameters:		
FLUX	irradiance (μmol $m^{-1}s^{-1}$)	1000
Pa	atmospheric CO_2 pressure (Pa)	35
Patm	atmospheric pressure (Pa)	1000000
Pi	dummy intercellular CO_2 partial pressure (Pa)	30
Po2	atmospheric O_2 pressure (Pa)	21000
Physiological and biochemical parameters:		
av	initial slope of extended Michaelis-Menten form for activation of Rubisco by light (dimensionless)	0.04
Gamma	CO_2 compensation point (Pa)	4
Glc	leaf conductances to water vapour (mol m^{-2} s-1)	0.1
Kc	Rubisco turnover number (s^{-1})	1.1
Kcc	Michaelis-Menten constants for CO_2 (Pa)	31
Ko	Michaelis-Menten constants for O_2 (Pa)	15500
Ln	leaf nitrogen content (mmol m^{-2})	95
Rmax	maximum pool size of RuBP concentration (μmol m^{-2})	10

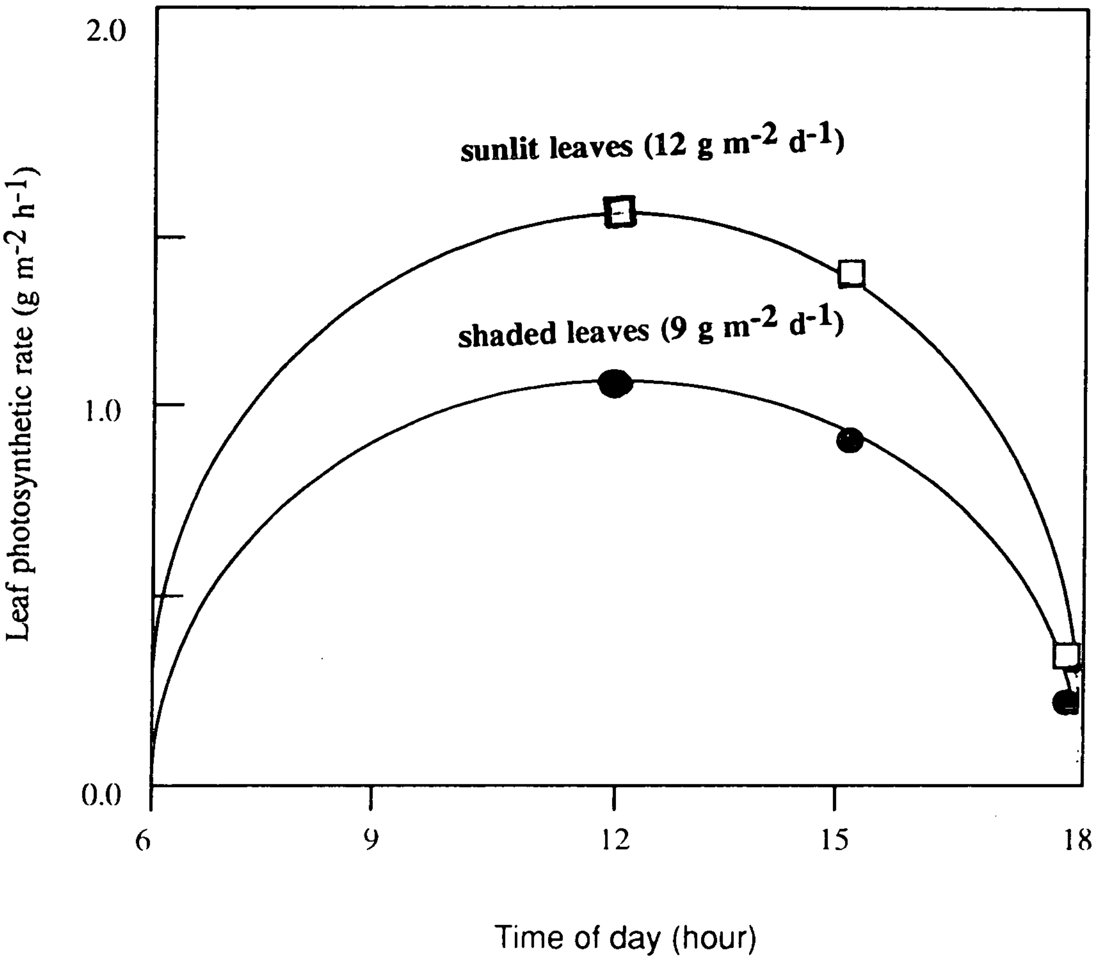


Fig. 3.10 Daily photoproduction by leaves

Daily total day-time photoproduction is calculated from hourly values by a Gaussian 3-point integration scheme, the figure shows example of sunlit leaves that with daily total photoproduction as 12 g m^{-2} d^{-1}, and shaded leaves that with daily total photoproduction as 9 g m^{-2} d^{-1}.

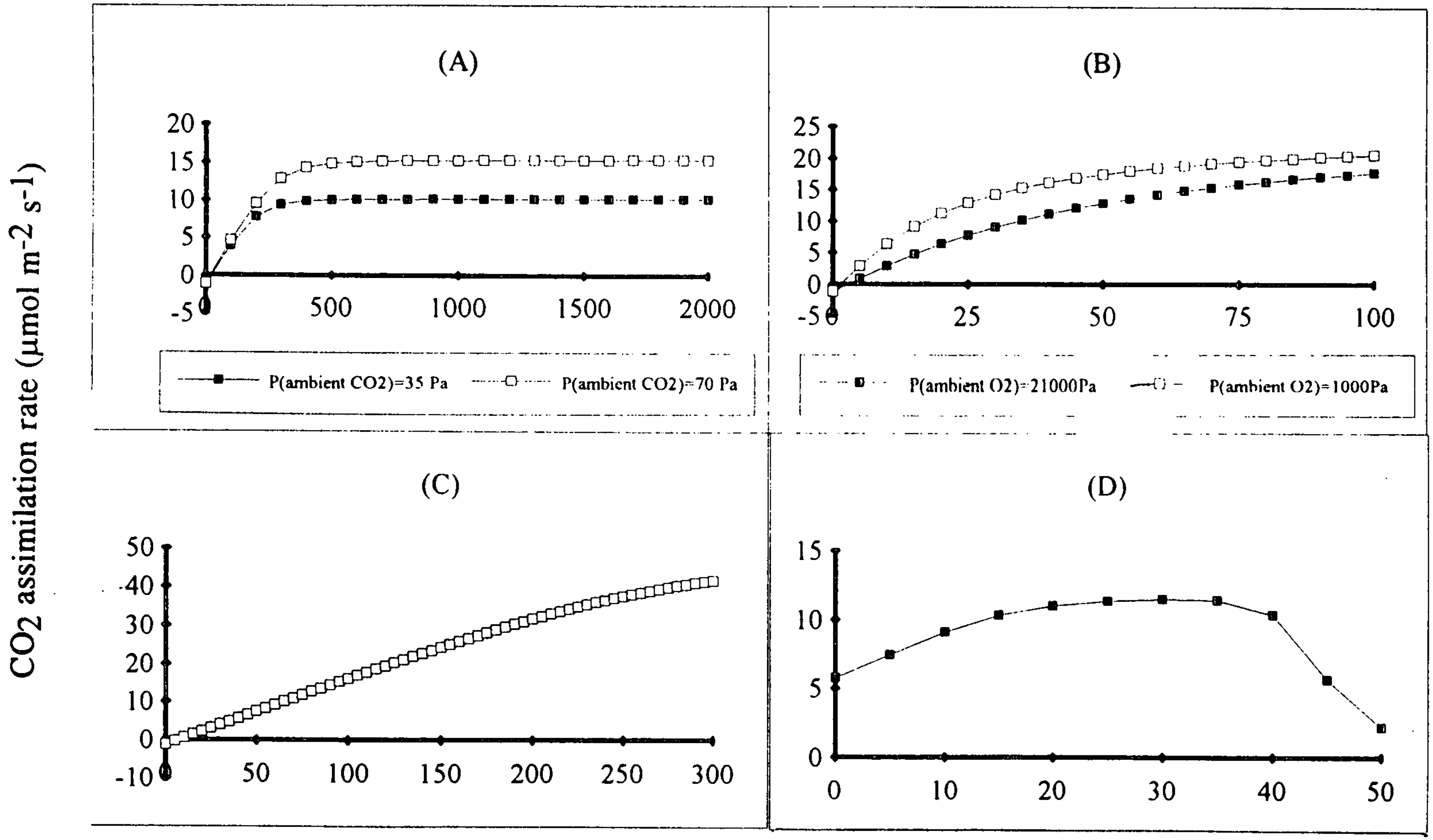


Fig. 3.11 Leaf CO_2 assimilation rate response to environmental factors

(A) response to PPFD (µmol m^{-2} s^{-1}); (B) response to ambient CO_2 partial pressure (Pa), response to leaf nitrogen content (mmol m^{-2}); and response to leaf temperature (°C).

TLEAF	leaf temperature (K)	298.16

Constants:

E	activation energy, and used in equation 3.31 (J mol^{-1})	37000
H4	parameter used in equation 3.31 (J mol^{-1})	220000
Rgc	gas constant (J K^{-1} mol^{-1})	8.314
S	parameter used in equation 3.31 (J K^{-1} mol^{-1})	710
Vck	constant to convert from moles of nitrogen in Rubisco to moles of reaction sites on Rubisco molecules (mol mol^{-1})	7/5500
Vjk	constant that converts moles of nitrogen to moles of chlorophyll (mol mol^{-1})	0.25

Chapter 4 Validation and Sensitivity Analysis of the Model FORDYN

4.1 Introduction

Before applying the model FORDYN to investigate ecological problems (Chapter 5) we need to test and validate the model as far as possible, so we can have more confidence in it. There are various ways in which this may be done. An essential and efficient way to analyse model properties or behaviour is sensitivity analysis. With such experience, one may clarify the crucial aspects of the model and quantify its reliability, robustness and applicability. Furthermore, the results of sensitivity analysis also allow comparison of different models, pointing to strong and weak aspects of the model.

Another way to analyse model properties or behaviour is uncertainty analysis: by contrast, it refers to changes in an input parameter which is not arbitrarily chosen, but based on actual uncertainty of the parameter. This can be caused by the lack of knowledge or natural variation. e.g. the input parameter may vary in a range in a probability density distribution (such as multivariate normal distribution). Thus a probability distribution of outputs can then be related to the specified distribution for the input parameters. For example, Dale *et al.* (1988) used uncertainty analysis to examine assumptions of spatial heterogeneity in the model FORET. However, in this study, I will mainly use sensitivity analysis to analyse the behaviour of FORDYN so as to compare FORDYN with results from other European pine models based on the European Pine Modelling Workshop (EPMW).

In this chapter, I will first test the model FORDYN against measured tree growth in a temperate European mixed-forest in Glentress, Edinburgh, Scotland. I will then further verify the behaviour of the model by simulating a Scots pine (*Pinus sylvestris*) ecosystem with data provided by the EPMW. Sensitivity analysis was carried out and the simulation results are compared with results from other European pine models based on common criteria and data input. Finally, I will discuss some other features of model behaviours and structure, which may shed further light on the overall validity of the model.

4.2 Simulation of a Temperate European Mixed Forest

4.2.1 Background to the Site

Glentress forest, near Edinburgh, was established in 1952 by a gentlemen's agreement between Professor M. L. Anderson and Sir H. Beresford Peirse. The aim was to create a mixed forest of irregular structure similar to the beech-spruce-fir protection forests of the Swiss Jura, transforming the existing even-aged stand over a period of 60 years.

Glentress forest is located on steep rounded hills which are typical of the Tweed valley, with total area of 117 hectares. The underlying Ordovivian sediments give rise to generally well-drained soils, grading from colluvial acid brown earths on the lower slopes to podzolised peaty iron-pan soils at the top of the hills, with an altitudinal range from 240-560 m. The general aspect of the local ridge-valley system is south west, giving site aspects ranging from 100 to 300 degrees, and the area is moderately exposed (Windthrow Hazard Class II-IV) with exposure being accentuated by wind funnelling up the valleys. Annual precipitation varies between 12000 and 1500 mm, with snow falling on about 60 days and lying for about 20 days a year. The mean annual temperature is 7.2 °C, and ground frosts occur, on average, on 100 nights a year. The ground vegetation on the lower colluvial slopes is of a grass-herb type with ferns (*Holcus/Dryopteris*) and *Deschampsia caespitosa* in small mid-slope flush areas. On the higher slopes grass-heath conditions (*D. flexuosa/Vaccinium myrtillus*) previal with *Calluna* increasingly important towards the top and in openings. Early plantings included European larch (*Larix decidua*) on the Caresman Hill (1878), a shelterbelt of Scots pine and European larch on the exposed Smithfield radge and patches of Douglas fir (*Pseudotsuga menziesii)* and Sitka spruce (*Picea sitcheasis*) in the valley of Glentress burn (1903). After acquisition by the Forestry Commission in 1920's the main species planted were Douglas-Fir on the lowest ground with Japanese larch (*Larix kaempferi*) and European larch on the middle slopes. Scots and Corsican pines (*Pinus laricio*) were planted on the upper slopes, but were extensively beaten-up or replaced with Norway spruce (*Picea abies*) and Sitka spruce in the 1940's.

4.2.2 Data Collection and Analysis

To simulate forest growth in Glentress forest, and to test the model FORDYN, a sample plot was established in block A in Glentress forest (Fig. 4.1). Species distribution in this plot is dominated by Douglas-fir, Norway spruce, Japaness larch, and a rather small broadleaf component, e.g. sycamore (*Acer pseudoplatanus*). Douglas fir and larch were planted in 1926, and Norway spruce in 1945 and thereafter.

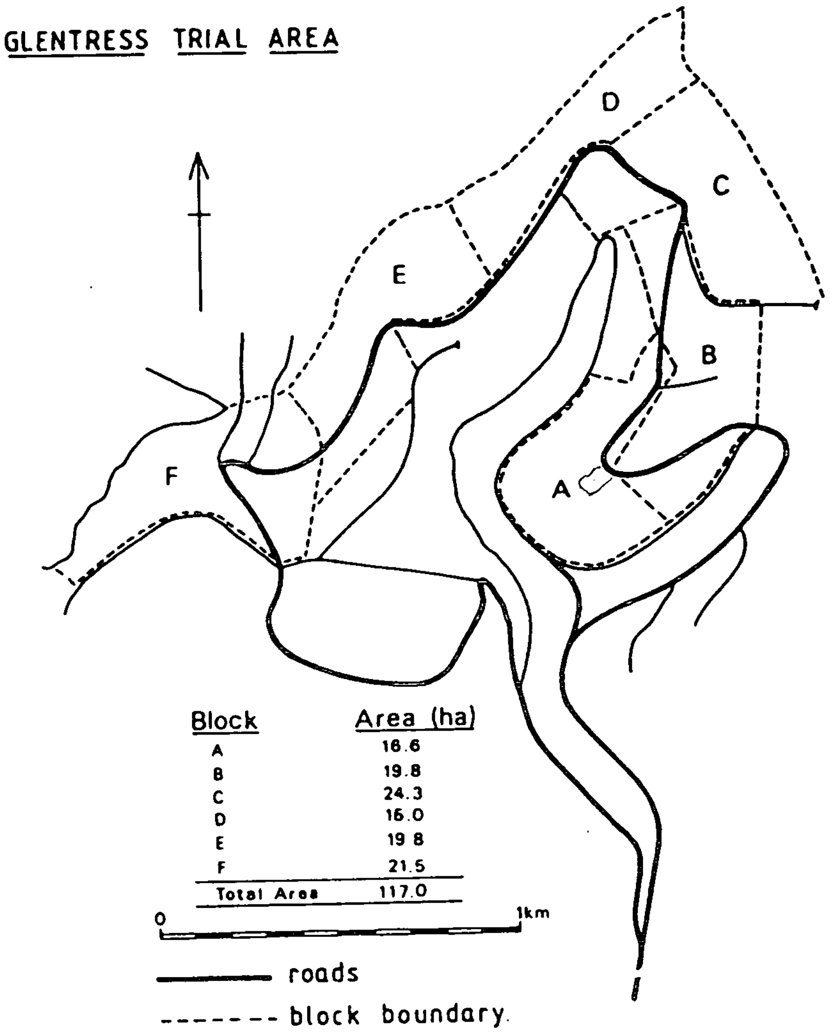
A rectangular sampling plot was set along the slope in Block A. The plot size was 60×20 m^2, with the longer boundary along the slope, starting from the bottom of the slope. The slope is 21^0, and the bearing of the slope from the north is 41^0. There are five species in the plot, they are Douglas-fir, Japanese larch, Norway spruce, sycamore, and Western hemlock (*Tsuga heterophylla*), Douglas fir mostly on the lower part of slope, Norway spruce on the upper slope, and Japanese larch in the middle; sycamore and Western hemlock have a scattered distribution.

For stand structure measurement, each individual tree in the stand was located by (x, y) co-ordinates in the plot. For tree growth measurement, dendrometer girth bands were used for measuring DBH increment. Tree height was measured by a clinometer, and the radius of crown profile of each individual trees in the plot was measured by an anascope. The measurements of tree growth were carried on 31 July 1991, 27 July 1992, 28 May 1993, and 13 August 1993.

Some examples of the data files used for this simulation are to be found in Appendix VII.

The simulation was mainly concerned with tree growth of Norway spruce, as most physiological parameters needed for this species are available from published data (Bossel & Schäfer, 1989) (Table 4.1), and this species occurs in a nearly pure stand on the upper slope of the plot. Values of parameters for other species were guessed.

The climate data used for this simulation are based on UK weather data provided by the European Pine Modelling Workshop.



Block	Area (ha)
A	16.6
B	19.8
C	24.3
D	16.0
E	19 8
F	21.5
Total Area	117.0

Fig. 4.1 Map of Glentress plot (coloured part in block A)

TABLE 4.1

Parameters used to derive the input for simulation of Norway spruce (based on Bossel & Schäfer, 1989)

name	description	unit	value
Tree geometry			
*HD	height-DBH ratio	dimensionless	80
ILFRTF	initial leaf-root ratio	dimensionless	2
FLFRTF	final leaf-root ratio	dimensionless	6
YLFSTR	maximum leaf-stemwood ratio	dimensionless	0.5
Photosynthesis			
PMAX	maximum photosynthetic rate	μmol m^{-2} s^{-1}	3.16
BL	light extinction coefficient	dimensionless	0.4
Specific respiration rate			
SPRELF	specific respiration rate of leaf	y^{-1}	2.2
SPRERT	specific respiration rate of fine root	y^{-1}	2.2
SPREWD	specific respiration rate of wood	y^{-1}	0.25
TNORM	reference temperature for temperature effect	^{0}C	20
TO	temperature for zero activity	^{0}C	-5

* the same as the measured result.

4.2.3 Simulation Results and Discussion

The model FORDYN was used to simulate tree growth by using simulation mode 2 (Fig. 2.4 in Chapter 2), because mode 1 cannot simulate forest dynamics in a time step of less than one year, and modes 3 and 4 involve too many low level parameters (like cell biochemical parameters) that are difficult to obtain. The run started on 31th July 1991, and continued for two years with a time step of 30 days. Simulated DBH of Norway spruce was compared with measured results for 27 July 1992, 28 May 1993, and 13 August 1993. The measured DBH of each tree in the Glentress stand can be found in Appendix VIII.

Fig. 4.2 shows the comparison between measured and simulated DBH increment of each tree of Norway spruce from 31/7/91 to 27/7/92. For the simulation of DBH increment, some physiological parameters are still difficult to get even by simulation mode 2, such as initial meristem size and meristem activity parameters. In these cases, we have to guess the values in the normal range of these parameters.

The data are considerably scattered, because of error in the measurement system (Fig. 4.2). The slope of the relationship is 0.85±0.28, and is not significantly different from unity.

In conclusion, it has been difficult to design a rigorous test of this model. However, as far as can be assessed from measurements of girth over only one year, the model prediction of DBH increment is not demonstrably different from the actual growth.

Nevertheless, to validate the overall behaviour of the model, we still need to investigate different aspects of the model. Thus, sensitivity analysis is to be done in the following discussion, and various aspects of validity will be discussed in the final section of this chapter.

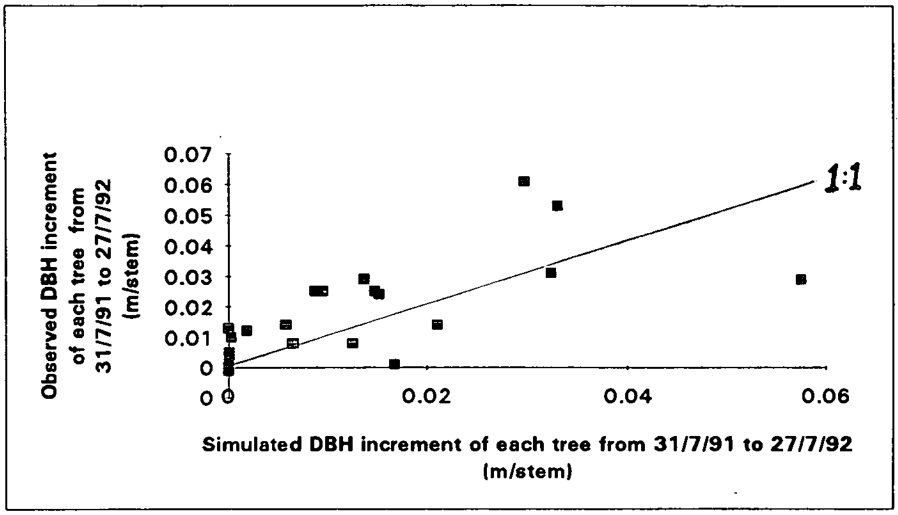


Fig. 4.2 Observed-simulated DBH increment of Norway spruce

The relationship between observed and simulated results of DBH increment of Norway spruce in Glentress plot from 31/7/91 to 27/7/92, with the R^2 is about 0.6, and the slope of the relationship is 0.85±0.28.

4.3 Simulation of Scots Pine Stand Dynamics

4.3.1 Introduction

To make predictions of the development of European forests requires a causal analysis of the effects of changing environment on the functioning of trees. Both theoretical and empirical results can be combined together with stand models which include the trees and soil. As a part of the recent FERN project (Forest Ecosystem Research Network, 1986-1991), a European Pine Modelling Workshop (EPMW) was organised to undertake a comparative evaluation of forest models around Europe for an analysis of an important European ecosystem — forest dominated by Scots pine (Table 4.2). The common data set provided by the workshop for this exercise is suitable for evaluating the validity of FORDYN, and for comparing its behaviour with that of the other models.

4.3.2 Data

The common data set is based on stand and climate data from Finland (Jyväskylä) (Ludlow *et al.*, 1995), with a corresponding yield table by Koivisto (1959). The physiological data supplied in Table 4.3 were taken from the literature, and are not specific to Finland (Ludlow *et al.*, 1995).

TABLE 4.2

European pine models that used in EPMW for simulation of European pines.

Model	Author	Reference
Forestry Commission Growth Model	Ludlow *et al.*	Forestry Commission, UK.
FORGROW	Mohren *et al.*	Instituut voor Bosbouw en Groenbeheer "De Dorschkamp", Wageningen, Rapport nr. 524, 1990.
MAESTRO	Wang & Jarvis	*Agricultural and Forest Meteorology*, 51: 257-280, 1990.
SIMFOR	Nikinmaa	Acta Forestalia Fennica 235.
TREEDYN	Bossel & Schäfer	*Ecological Modelling*, 48: 221-265, 1989.

TABLE 4.3

List of parameters used for simulation of Scots pine by European pine models, which are provided by EPMW. Units are 'as given'.

Photosynthesis

Name	Description	unit	value
*PMAX	maximum photosynthetic rate	mg CO_2 dm^{-2} h^{-1}	6
	PPFD when photosynthetic rate reaches 50% of the maximum value	μmol m^{-2} s^{-1}	360
	PPFD when photosynthetic rate reaches 90% of the maximum value	μmol m^{-2} s^{-1}	1000
	temperature for optimal photosynthesis	^0C	12
	minimum temperature for photosynthesis	^0C	-5

Phenology

Name	Description	unit	value
	average length of growing season	days	150

Respiration

Name	Description	unit	value
	specific respiration rate of foliage at 15 ^{0}C	h^{-1}	0.5
	specific respiration rate of fine root at 20 ^{0}C	h^{-1}	0.45
	specific respiration rate of sapwood at 15 ^{0}C	h^{-1}	0.45
TO	temperature for zero respiration	^{0}C	-5
	dry matter conversion efficiency, accounting for growth respiration	g DM g^{-1}	0.8

Light attenuation

Name	Description	unit	value
ELL	light extinction coefficient for use with projected leaf area	-	0.4
LEAFWA	specific leaf area	m^2 kg^{-1}	
	by projected leaf area		4
	by total leaf area		10

Tree structure

Name	Description	unit	value
BW	wood density	kg DM m^{-3}	400
	foliage dry mass to stem sapwood area ratio	kg m^{-2}	516.7
	foliage dry mass to branch sapwood area ratio	kg m^{-2}	450
	foliage dry mass to transport root sapwood area ratio	kg m^{-2}	200
	no. of tree rings within the living sapwood	-	20
	carbon content of dry matter	%	50

Allocation data

Name	Description	unit	value
	below ground fraction of the annual biomass increment	-	0.2
	initial leaf to root ratio	-	1
	final leaf to root ratio	-	2
	maximum leaf to stem-wood ratio	-	1.46

Tree dimension

Name value	Description	unit	
HD	height to base-stem diameter ratio for forest grown trees	m m^{-1}	90
	height to base-stem diameter ratio for open grown trees	m m^{-1}	45
HMAX	maximum stand height	m	26
	maximum crown projection area	m^{-2}	35

Root system

Name	Description	unit	value
RTFSR	fine root specific turnover rate	y^{-1}	1.0
RTCSR	coarse root specific turnover rate	y^{-1}	0.1
	average specific root length	m g^{-1}	0.35
	fine root radius	cm	0.05
	rooting depth	m	1
	rooting density	kg m^{-2}	0.2

Nutrient uptake and relocation

Name	Description	unit	value
UN	root specific nitrogen uptake rate	kg N kg^{-1}	0.01
	assimilate relocation (should be omitted)	-	-
	nitrogen relocation of needle	%	60
	nitrogen relocation of branch	%	40
	nitrogen relocation of fine root	%	0
	nitrogen relocation of sapwood	%	0

Scenario parameters

Name	Description	unit	value
DECR	litter deposition rate	y-1	0.3
NPREC	external nitrogen input	kg N ha^{-1}	10

Nutrient

nutrient content in % of dry mass						
	N	P	K	Mg	Ca	S
foliage	1.1	0.1	0.35	0.08	0.3	0.1
branches	0.4	0.05	0.2	0.036	0.3	0.05
sap/heart wood	0.065	0.05	0.35	0.01	0.0 55	0.01
coarse root	0.13	0.017	0.075	0.069	0.078	0.01
fine root	0.38	0.075	0.2	0.88	0.2	0.14

Initial stand data

Name	Description	unit	value
IYEAR	stand age	year	40
SNTREE*10	stand density	trees ha^{-1}	1625
DBH	average DBH	m	0.15
H	average height	m	14.0
	dominant height	m	14.9
	canopy closure	%	100
CR	av. crown radius	m	1.4
CP	av. crown profile	m^{-2}	0.15
CL	crown length	m	10
LEAF	total needle dry mass	kg ha^{-1}	5300
STEM	total stem dry mass	kg ha^{-1}	66780
BRANCH	total branch dry mass	kg ha^{-1}	8800
ROOT	total root dry mass	kg ha^{-1}	23000
ROOTF	fine root	kg ha^{-1}	3000
ROOTC	coarse root	kg ha^{-1}	20000

Thinning scheme

thinning age	50	60	70	80	90
remaining tree no. (/ha)	1235	915	675	540	470

---

* parameters that are used directly, while others are used indirectly to derive parameters needed for simulation by the model FORDYN.

4.3.3 Simulation of Tree Growth by Different Simulation Modes

4.3.3.1 Model Structure by Modes

As shown before, different simulation modes of FORDYN differ in the level of processes involved (by time-step), and thus different submodels or model structures are represented (see Appendix IV & V). In this sensitivity analysis study, simulation mode 2 is used so as to be compared with other European pines models in equivalent conditions.

4.3.3.2 Data by Modes

As the model FORDYN is an 'individual tree-based' forest model, individual trees are specified. Here, we set all trees to be in the same size and evenly distributed in space so that the structure is equivalent to a yield table (Shugart & West, 1980) because most other European pine models are 'stand models' (Table 4.1). The plot size was 100×10 m^2, with an initial total of 163 trees in the stand (equivalent to 1625 trees per hectare) on a 2.5 m by 2.5 m grid. Five subsequent thinning every 10 years reduced this density to 47 trees in the plot (470 trees per hectare) (see Table 4.3).

When the simulation mode is changed, as mentioned above, the model structure will be changed correspondingly, as well as the data input (Appendix IV & V).

For simulation mode 2, forest development processes were described with time steps of days. Therefore environmental variation within a year is represented, such as monthly average photon flux density, and air temperature.

For simulation mode 3, leaf physiological properties are needed for calculating hourly photosynthesis within a day, e.g. maximum, minimum and optimal leaf temperature for stomatal and mesophyll conductance.

The data needed for calculation of leaf CO_2 assimilation rate based on a biochemical model are provided in the input file TREE4INT, e.g. atmospheric pressure, O_2 pressure, ambient CO_2 concentration, and dummy intercellular CO_2 partial pressure.

4.3.3.3 Results and Discussion

The model FORDYN has been used to simulate tree growth for 90 years by different simulation modes with the same data set. The simulation results are compared to the yield table given by Koivisto (1959) as shown in Fig. 4.3.

From Fig. 4.3 one can see that diameter increment of Scots pine simulated by FORDYN in different simulation modes can be made to give good agreement with the result of the yield table. Apart from simulation mode 1, parameterisation has been made to initial meristem size, and activity constant of meristem for simulation modes 2, 3, and 4, so as to verify the DBH growth for further sensitivity analysis as follows.

4.4 Sensitivity Analysis of FORDYN

4.4.1 Introduction

Sensitivity analysis normally refers to analysis of the relation between the change in input and output of a model, e.g. what will be the result in dry matter increment if there is a 20% increase in CO_2 concentration in atmosphere. Input parameters are usually arbitrarily chosen. Input parameters or variables are changed by applying the approach suggested by Ludlow *et al.* (1995).

In this study, sensitivity analysis of FORDYN was applied to a standard Scots pine ecosystem based on the method suggested by EPMW (Ludlow *et al.*, 1995) (see the following section), and simulation results are compared with these European pine models (Table 4.2).

As most European pine models are some sort of carbon balance model, some measures of tree growth are used to evaluate model sensitivity (Ludlow *et al*, 1995).

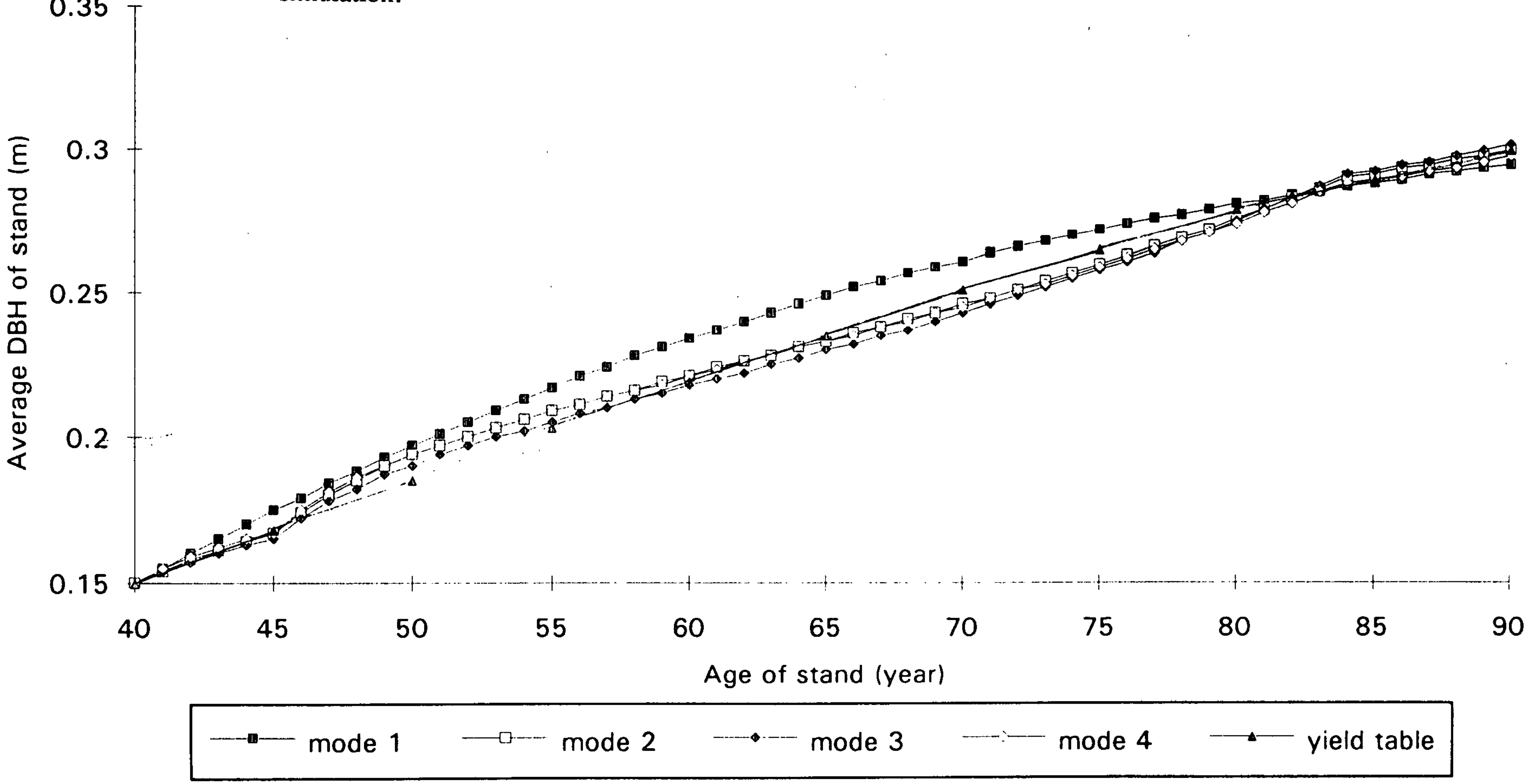
All simulation results are based on simulation mode 2.

There are several steps for sensitivity analysis in this study:

i) Specification of evaluation criteria that represent model behaviour;
ii) Specification of the input parameters or variables that have to be analysed;
iii) Specification of the input variation that will be used (e.g. 20%);

Fig. 4.3 Tree growth by different simulation modes of FORDYN

Simulated results and yield table for the average DBH growth of Scots pine stand that used in EPMW, whereby four simulation modes (modes 1, 2, 3, and 4) of FORDYN are used for the simulation.



iv) Run of the simulation model, using single parameter variation, or using various combinations of input parameters;

v) Comparison of changes in model outcome with respect to changes in model input specifications.

4.4.2 Criteria of Sensitivity Analysis

The criteria used for sensitivity vary with the objective of the analysis: when the total model outcome is to be evaluated, then criteria referring to the entire model should be chosen. Submodels are evaluated, and output variables closely related to each submodel behaviour should be used. For a certain process being studied, both rate and state variables are relevant.

For the European pine models, three periods are used for the analysis (1-year, 10-year and 50-year) so as to achieve appropriate emphasis on tree physiological processes or stand dynamic processes. The main processes included in the carbon balance models of stand growth normally consist of: canopy assimilation, maintenance and growth respiration, assimilate allocation, dry matter accumulation and leaf-area development. The main climate variables included in the models are radiation and temperature.

Table 4.4 contains a list of criteria that have been recommended for using in sensitivity analysis of European pine models (Ludlow *et al.*, 1995), and used for this simulation as well.

TABLE 4.4

Criteria for sensitivity analysis of European pine models, which is recommended by EPMW for simulation of Scots pine. Each parameter is used as simulation input by changing ±20%, and each criterion (rate and state) is used as output for assessing the model behaviour.

Canopy assimilation	
parameters:	gross photosynthesis (net photosynthesis + dark respiration of the foliage) at light saturation; leaf area index.
rate criteria:	average daily gross canopy assimilation of CO_2 (kg ha^{-1} d^{-1})

(1-year-simulation);
average annual total gross canopy assimilation of CO_2 (Mg ha^{-1} y^{-1}) (10- and 50-year-simulations).
state criteria: average annual total gross canopy assimilation of CO_2 (Mg ha^{-1}) (1-year-simulation).

Maintenance respiration

parameters: maintenance respiration coefficients (kg CH_2O kg DM^{-1})
rate criteria: average annual total maintenance respiration (Mg CH_2O ha^{-1} y^{-1}) (10- and 50-year-simulations);
average dry matter growth rate (kg ha^{-1} d^{-1}) (1-year-simulation);
average dry matter grow rate (Mg ha^{-1} d^{-1}) (10- and 50-year-simulations).
state criteria: annual maintenance respiration (Mg CH_2O ha^{-1}) (1-year-simulation);
annual total dry matter increment (Mg ha^{-1}) (1-year-simulation);
total foliage biomass (Mg ha^{-1}) (10-year-simulation);
total foliage biomass (Mg ha^{-1}) (50-year-simulation).

Stand dynamics

parameters: assimilate allocation (shoot/root, and foliage/wood).
state criteria: leaf area index (10- and 50-year simulations);

average ratio of annual dry matter increment (Mg ha^{-1} y^{-1}) and annual total intercepted photosynthetically active radiation (MJ ha^{-1}) (1-, 10- and 50-year simulations).

Soil organic matter dynamics (including nitrogen content)

parameters: decomposition contents (total soil organic matter), atmospheric deposition rate of nitrogen.

rate criteria: total amount of CO$_2$ produced in decomposition of soil organic matter (Mg ha^{-1} y^{-1});
rate of nitrogen immobilisation in soil organic matter
(1-, 10- and 50-year simulations).

state criteria: total amount of carbon in the organic layer (litter, fermented material and humus) and in mineral soil (dead roots and stable humus) (Mg C ha^{-1});
(10- and 50-year simulations).

Radiation and temperature

parameters: average total incoming radiation during the year

rate criteria: average annual total of gross canopy assimilation of CO$_2$ (Mg ha^{-1} y^{-1}) (10- and 50-year simulations);
average annual total maintenance respiration (Mg ha^{-1} y^{-1}) (10- and 50-year simulations);
average dry matter growth rate (Mg ha^{-1} y^{-1}) (10- and 50-year simulations);

state criteria: annual total of gross canopy assimilation of CO$_2$ (Mg ha^{-1}) (1-year simulation);
annual total maintenance requirements (Mg CH$_2$O ha^{-1}) (1-year simulation);
annual total dry matter increment (Mg ha^{-1})

(1-year simulation).

For this sensitivity analysis, we increased and decreased by 20% the original input parameters as listed above, to get a corresponding absolute value and relative value of output. The simulation results and discussion are in the following section.

4.4.3 Results and Discussion

4.4.3.1 Canopy Assimilation

The two parameters: gross photosynthesis at light saturation (or maximum photosynthetic rate) and leaf area index are chosen as subjects for use in sensitivity analysis. Average daily canopy assimilation of CO_2 was used as the output criterion for evaluating carbon uptake.

Simulation results are listed in Table 4.5, together with the corresponding results by models FORGROW and MAESTRO (Ludlow *et al.*, 1995). Units for each parameter are found in Appendix IV.

TABLE 4.5

Sensitivity analysis of canopy assimilation, based on Table 4.3.

Models	Input	Output/running time			
		1-year	1-year	10-year	50-year
FORDYN	*PMAX	PHOPD	PHOPY	PHOPY	PHOPY
	100%	166	23.3	22.8	22.7
	-20%	133 (80%)	18.6 (80%)	18.2 (80%)	18.1 (80%)
	+20%	200 (120%)	27.9 (120%)	27.3 (120%)	27.2 (120%)
FORGROW	100%	127	20.5	21.8	#-
	-20%	107 (84%)	17.2 (84%)	10.0 (46%)	-
	+20%	145 (114%)	23.4 (114%)	30.5 (140%)	-

MAESTRO	100%	177	29.9	-	-
	-20%	140 (79%)	19.7 (66%)	-	-
	+20%	219 (124%)	42.5 (142%)	-	-
	*PMAX	PHOPD	PHOPY	PHOPY	PHOPY
	LAI				
FORDYN	100%	166	23.3	22.8	22.7
	-20%	133 (80%)	18.6 (80%)	18.7 (82%)	18.2 (80%)
	+20%	200 (120%)	27.8 (120%)	26.8 (118%)	27.1 (119%)
FORGROW	100%	127	20.5	21.8	-
	-20%	100 (79%)	16.2 (79%)	8.1 (37%)	-
	+20%	151.1 (119%)	24.4 (119%)	32.0 (147%)	-
MAESTRO	100%	177	29.9	-	-
	-20%	158 (89%)	23.6 (79%)	-	-
	+20%	191 (108%)	34.7 (116%)	-	-

*PMAX=maximum leaf photosynthesis rate (μmol m^{-2} s^{-1}), PHOPD=daily total photoproduction (kg CH_2O ha^{-1} d^{-1}), PHOPY=annual total photoproduction (Mg CH_2O ha^{-1} y^{-1}).
no simulation applied.

From Table 4.5 one can see that, in all three models, canopy assimilation (either daily or annual total photoproduction) is quite sensitive to PMAX and LAI. However, both FORGROW and MAESTRO have a changed sensitivity to PMAX, whereas FORDYN has a nearly unchanged sensitivity to PMAX in its different simulation periods. This is because FORDYN has a relatively constant leaf biomass in the late stage of stand growth (as in this simulation, see Table 4.6 in the following section) based on a transport-resistance approach (Thornley, 1991), while FORGROW has an increased leaf biomass as long as PMAX is increased (Table 4.5). This positive feedback leads to a more sensitive leaf photosynthetic production response to PMAX in the longer time interval as shown in the above result.

4.4.3.2 Maintenance Respiration

In order to calculate net dry mass increment from gross photosynthesis, respiration has to be taken into account. It is such an important part in gas exchange of plant that some plants are known to lose by respiration about half of carbon they fix by photosynthesis (Farrar, 1985; Lambers, 1985; Givnish, 1988; Lehto & Grace, 1994).

As shown in Chapter 3, respiration can be treated as growth and maintenance respiration parts (McCree, 1970), where maintenance respiration is the respiration required even when the plant is not growing, for example to maintain concentration differences across membranes, for re-synthesis of degraded proteins, and to fuel base metabolic activity (Penning de Vries, 1975; de Wit *et al.*, 1978).

For sensitivity analysis of maintenance respiration in this study, respiration rates of tree parts were selected as the change in input, while average annual total maintenance respiration, average dry mass growth rate, total foliage biomass growth, and total stand biomass growth were used as output criteria (Table 4.6).

TABLE 4.6

Sensitivity analysis of maintenance respiration, based on Table 4.3.

Models	Input	Output/running time			
		1-year	1-year	10-year	50-year
FORDYN	*#r*	BIOMI/d	Σ(MRESP)/y	Σ(MRESP)/y	Σ(MRESP)/y
	100%	92	3.7	4.8	7.5
	-20%	94 (103%)	2.9 (79%)	3.8 (80%)	6.2 (82%)
	+20%	89 (97%)	4.4 (119%)	5.7 (118%)	8.8 (118%)
			Σ(BIOMI)/y	Σ(BIOMI)/y	Σ(BIOMI)/y
			11.6	12.2	10.1
	r	BIOMI/d	Σ(MRESP)/y	Σ(MRESP)/y	Σ(MRESP)/y
			11.9 (103%)	12.5 (103%)	10.9 (108%)
			11.2 (97%)	11.9 (97%)	9.2 (92%)

				LEAF	SBIOM
				3.26	175.4
				3.26 (0%)	187.6 (107%)
				3.26 (0%)	164.3 (93%)

	#r	BIOMI/d	Σ(MRESP)/y	Σ(MRESP)/y	Σ(MRESP)/y
FORGROW	100%	71	8.0	8.1	-
	-20%	77 (108%)	6.9 (86%)	7.9 (97%)	-
	+20%	65 (91%)	9.0 (113%)	7.3 (90%)	-
			Σ(BIOMI)/y	Σ(BIOMI)/y	Σ(BIOMI)/y
			10.8	11.1	-
			11.8 (109%)	13.8 (124%)	-
			9.8 (91%)	8.2 (74%)	-
				LEAF	SBIOM
				6.11	-
				8.1 (132%)	-
				3.79 (62%)	-

MAESTRO	*r*	BIOMI/d	Σ(MRESP)/y	Σ(MRESP)/y	Σ(MRESP)/y
	100%	56	4.9	5.2	4.3
	-20%	60 (107%)	4.1 (83%)	4.5 (87%)	4.0 (92%)
	+20%	52 (92%)	5.7 (117%)	5.8 (112%)	4.5 (105%)
			Σ(BIOMI)/y	Σ(BIOMI)/y	Σ(BIOMI)/y
			8.5	9.7	8.3
			9.1 (107%)	10.7 (110%)	9.0 (108%)
			7.8 (92%)	8.7 (90%)	7.2 (87%)
				LEAF	SBIOM
				5.29	-

LEAF	SBIOM
5.82 (110%)	-
4.76 (90%)	-

#*r*=specific leaf respiration rate (d^{-1}), specific root respiration rate (d^{-1}), and specific wood respiration rate (d^{-1}); Σ(BIOMI)/d=daily average biomass increment (Mg CH_2O ha^{-1} d^{-1}); Σ(BIOMI)/y=annual average biomass increment (Mg CH_2O ha^{-1} y^{-1}); Σ(MRESP)/y=annual average maintenance respiration (Mg CH_2O ha^{-1} y^{-1}); LEAF=leaf biomass (Mg CH_2O ha^{-1}); SBIOM=total stand biomass (Mg CH_2O).

From the above results, one can see that increased maintenance respiration rate normally will decrease growth rate or biomass increment. These three models have different sensitivities to the maintenance respiration resulting from different tree growth processes described in each model.

It needs to be noted that, both FORGROW and MAESTRO show an increasing trend of leaf biomass during stand growth, whilst FORDYN seems less sensitive at this stage of stand (simulation time starts from stand age 40 years old). This is because in FORDYN, tree growth rate largely depends on meristem activity, and reaches its maximum meristem size or activity at an early stage of tree growth, then there is generally a slightly decline of meristem activity, thus limiting foliage biomass growth (Thornley, 1991).

4.4.3.3 Stand Dynamics

For the sensitivity analysis of stand dynamics, assimilate allocation (shoot-root and foliage-wood ratios) is used as the input change, and leaf area index, and dry matter increment per unit of intercepted PAR (photosynthetic active radiation) were chosen as output criteria.

Simulation results of FORDYN are compared with results from the European pine models of FORGROW and SIMFOR as that shown in Table 4.7.

TABLE 4.7

Sensitivity analysis of stand dynamics, based on Table 4.3.

Models	Input	Output/running time		
		1-year	10-year	50-year
FORDYN	#SHOOT/ROOT	Σ(BIOMI/PAR)/y	Σ(BIOMI/PAR)/y	Σ(BIOMI/PAR)/y
	100%	1.37	1.51	1.30
	-20%	1.37 (100%)	1.56 (103%)	1.27 (98%)
	+20%	1.36 (99%)	1.47 (97%)	1.33 (102%)
			LAI	LAI
			1.61	0.60
			1.34 (83%)	0.50 (83%)
			1.87 (116%)	0.70 (117%)
FORDYN	#FOLIAGE/WOOD			
	100%	1.37	1.51	1.30
	-20%	1.35 (99%)	1.58 (105%)	1.27 (98%)
	+20%	1.38 (101%)	1.45 (102%)	1.32 (102%)
			LAI	LAI
			1.60	0.60
			1.30 (81%)	0.49 (82%)
			1.90 (119%)	0.71 (118%)
FORGROW	SHOOT/ROOT	*Σ(BIOMI/PAR)/y	Σ(BIOMI/PAR)/y	Σ(BIOMI/PAR)/y
	100%	1.25	1.21	-
	-20%	1.28 (102%)	1.22 (101%)	-
	+20%	1.23 (98%)	1.61 (133%)	-
			LAI	LAI
			2.1	-
			2.2 (103%)	-
			2.0 (97%)	-
	FOLIAGE/WOOD	Σ(BIOMI/PAR)/y	Σ(BIOMI/PAR)/y	Σ(BIOMI/PAR)/y
	100%	1.25	1.21	-
	-20%	1.23 (98%)	1.04 (86%)	-
	+20%	1.28 (102%)	1.39 (115%)	-
			LAI	LAI
			2.5	-
			0.25 (10%)	-
			5.0 (200%)	-

SIMFOR	SHOOT/ROOT	Σ(BIOMI/PAR)/y	Σ(BIOMI/PAR)/y	Σ(BIOMI/PAR)/y
	100%	-	-	-
	-20%	-	-	-
	+20%	-	-	-
			LAI	LAI
			2.4	1.6
			2.38 (99%)	1.54 (96%)
			LAI	LAI
			2.42 (101%)	1.63 (102%)
	FOLIAGE/WOOD			
	100%	-	-	-
	-20%	-	-	-
	+20%	-	-	-
			LAI	LAI
			2.4	1.6
			2.6 (109%)	1.9 (120%)
			LAI	LAI
			2.3 (94%)	1.3 (80%)

SHOOT/ROOT=shoot-root ratio of assimilate allocation (dimensionless), FOLIAGE/WOOD=foliage-wood ratio of assimilate allocation (dimensionless), Σ(BIOMI/PAR)=biomass increment per unit of radiation received, or energy conversion efficiency (dimensionless) (with that, 1Mg=20000MJ), LAI=leaf area index (dimensionless).

* the unit used here is by Mg/MJ.

From the above simulation results one can see that by increasing shoot-root allocation ratio, all three models have an increase of leaf area index (LAI), while, for light use efficiency, or energy conversion efficiency, there is a slight decline for both FORGROW and FORDYN in the longer time simulations. This may be the result of the decline of meristem activity in FORDYN.

When foliage-wood ratio is increased, both FORDYN and FORGROW show an increased response of leaf area index.

These results of stand dynamics largely depend on model structure, especially the way that assimilate allocation is treated. FORDYN represents this process as a transport-resistance approach, and is different from the other European pine models, which use a goal-seeking strategy to maintain fixed ratios of such things as leaf area per sapwood area, and carbon to nitrogen. The transport-resistance approach is considered to be superior, as it allows the allocation pattern to change dynamically in response to resource availability.

4.4.3.4 Soil Organic Matter Dynamics

The dynamics of soil organic matter, including nitrogen content, in the plant-soil system, is an important process in forest ecosystems. Nitrogen dynamics and other soil organic matter dynamic processes are represented in the subroutines *NSYSL1* and *NCYCL2* in the FORDYN program (see also Fig 3.3).

Here, we have used as the input changes in the decomposition rate of soil organic matter and the atmospheric deposition rate of nitrogen. For assessment of change in the output, we report the total amount of CO_2 produced in decomposition of soil organic matter, the rate of nitrogen immobilisation in soil organic matter, and the total amount of carbon in the organic matter layer and in the mineral soil.

Unfortunately, no other European pine model was applied to simulate soil organic matter dynamics. Thus, we report only the simulation result from FORDYN (Table 4.8).

TABLE 4.8

Sensitivity analysis of soil organic matter dynamics, based on Table 4.3.

Models	Input	Output/running time			
FORDYN	*DECR	1-year	COMAT+CLIAT	NSOM+NLITR	
	100%		2.27	6.82	
	-20%		1.81 (80%)	6.83 (100.1%)	
	+20%		2.72 (120%)	6.81 (99.9%)	
		10-year	COMAT+CLIAT	NSOM+NLITR	CSOM+CLITR
			1.03	6.48	94.68
			0.96 (93%)	6.54 (101%)	96.88 (102%)
			1.06 (103%)	6.41 (98%)	92.78 (98%)
		50-year	COMAT+CLIAT	NSOM+NLITR	CSOM+CLITR
			0.29	5.52	77.07
			0.26 (90%)	5.72 (104%)	80.06 (104%)
			0.33 (114%)	5.33 (97%)	74.28 (96%)

NPREC	#Σ(BIOMI)/years				
	10-year (age=50yr)	20-year	30-year	40-year	50-year
100%	9.8	7.9	7.6	7.6	7.0
-20%	8.9 (91%)	6.6 (84%)	6.4 (84%)	7.1 (93%)	6.8 (97%)
+20%	10.6 (108%)	8.8 (111%)	8.1 (106%)	7.8 (103%)	7.1 (102%)

---

* DECR=decomposition rate of soil organic matter (y^{-1}), COMAT=humus decomposition rate (Mg N ha^{-1} y^{-1}), CLIAT=litter decomposition rate (Mg N ha^{-1} y^{-1}), CSOM=carbon in soil organic matter (Mg C), CLITR=carbon in forest litter (Mg C ha^{-1}), NPREC= nitrogen input by deposition (Mg N), NSOM=nitrogen in humus (Mg N ha^{-1}), NLITR=nitrogen in litter (Mg N ha^{-1}), Σ(BIOMI)/years=annual average biomass increment (Mg ha^{-1} y^{-1}).

criteria designed for this study rather than that used in European Pine Models.

From the above simulation results one can see that increase in the decomposition rate of soil organic matter can lead to an increase of CO_2 production from soil by decomposition (COMAT+CLIAT), and to a reduction of the amount of carbon stored in soil organic matter and in mineral soil (CSOM+CLITR).

More nitrogen input to the soil (NPREC) generally will increase forest growth rate. This is because the enhanced nitrogen supply increases uptake by fine roots of trees, therefore more nitrogen can be transported to tree parts, and thus leading to enhanced meristem activity and tree growth (see more in section 3.2.2 in Chapter 3).

In addition, forest growth or biomass increment rate is more sensitive to nitrogen inputs in the earlier stages (e.g. within 10 to 20 years). This is because meristem activity is more active in the earlier stages, and thus more sensitive to nitrogen, which normally contributes to meristem activity.

These results show that FORDYN has a good response to soil nitrogen dynamics.

4.4.3.5 Radiation and Temperature

Sensitivity analysis of radiation and temperature in this study use total average incoming radiation during the year and daily average temperature as inputs and, annual total gross photosynthesis, maintenance respiration, and dry matter increment as output criteria.

Simulation results are shown in Table 4.9, but no other simulation results by European pine models are available for comparison.

TABLE 4.9

Sensitivity analysis of radiation and temperature, based on Table 4.3.

Models	Input	*Output/running time		
		#PHOPY	Σ(MRESP)/y	Σ(BIOMI)/y
FORDYN	PARV	1-year		
	100%	23.5	3.7	11.7
	-20%	20.5 (87%)	3.7 (99%)	10.1 (86%)
	+20%	26.1 (111%)	3.7 (101%)	13.0 (111%)
		10-year		
		22.6	4.7	12.1
		19.7 (87%)	4.6 (98%)	11.0 (91%)
		13.0 (111%)	4.8 (102%)	13.0 (107%)
		50-year		
		22.4	8.2	9.9
		19.5 (87%)	7.7 (94%)	8.3 (84%)
		24.9 (111%)	8.6 (105%)	11.4 (102%)
		1-year		
	9.0 (100%)	23.5	3.2	11.7
	7.2 (-20%)	21.9 (94%)	2.8 (88%)	11.0 (96%)
	10.8 (+20%)	24.2 (105%)	3.7 (116%)	11.8 (104%)
		10-year		
	9.0 (100%)	22.3	4.2	11.9
	7.2 (-20%)	21.1 (95%)	3.7 (88%)	11.7 (98%)
	10.8 (+20%)	23.4 (105%)	4.7 (112%)	12.1 (102%)
		50-year		
		22.1	7.2	9.5

ATEMP	#PHOPY	Σ(MRESP)/y	Σ(BIOMI)/y
	20.9 (95%)	6.3 (88%)	9.2 (97%)
	23.2 (105%)	8.2 (114%)	9.6 (101%)

PHOPY=annual average gross photoproduction (Mg CH_2O ha^{-1} y^{-1}),
Σ(MRESP)/y=annual average maintenance respiration (Mg CH_2O ha^{-1} y^{-1}),
Σ(BIOMI)/y=annual average biomass increment (Mg CH_2O ha^{-1} y^{-1}),
PARV=average incoming radiation (J m^{-2}),
ATEMP=daily average temperature (^0C).

From the above simulation results, it appears that increases in both radiation and temperature can lead to an increase in gross photosynthesis, maintenance respiration, and biomass increment. As shown in Fig. 4.4 (output from a 10-year simulation as in Table 4.8), one can see that, photosynthesis is more sensitive to radiation with a steeper slope (Fig. 4.4(A)), and maintenance respiration is more sensitive to temperature with a steeper slope (Fig. 4.4(B)). These are in accord with our knowledge and experience.

4.5 General assessment of the model FORDYN

In order to assess the general validity of FORDYN, I will discuss its structural, behavioural, empirical, and application validities (as suggested by Bossel *et al.* (1989)) in the following:

Structural validity.

'Structural validity' refers to the representation of the essential processes of the real system, their interconnections and feedback. It is the intent to integrate the essential structure of interactions within the forest ecosystem in a hierarchical context. Great concern is taken in the model to link the levels of processes such as forest succession, physiological tree growth processes, physiological functioning, and cell biochemical processes (Fig. 2.3 in Chapter 2). In fact, these four levels of processes have been studied separately before. e.g. in level 1, dispersal process refers to Levin *et al.*, (1984), mortality to Shugart *et al.* (1977); in level 2, assimilate allocation refers to Thornley (1991), nitrogen dynamics in plant-soil system to Bossel & Schäfer (1989), water balance in term of stomatal conductance-soil water relation (Khalil & Grace, 1993); in level 3, daily total photoproduction refers to Goudriaan (1977) and

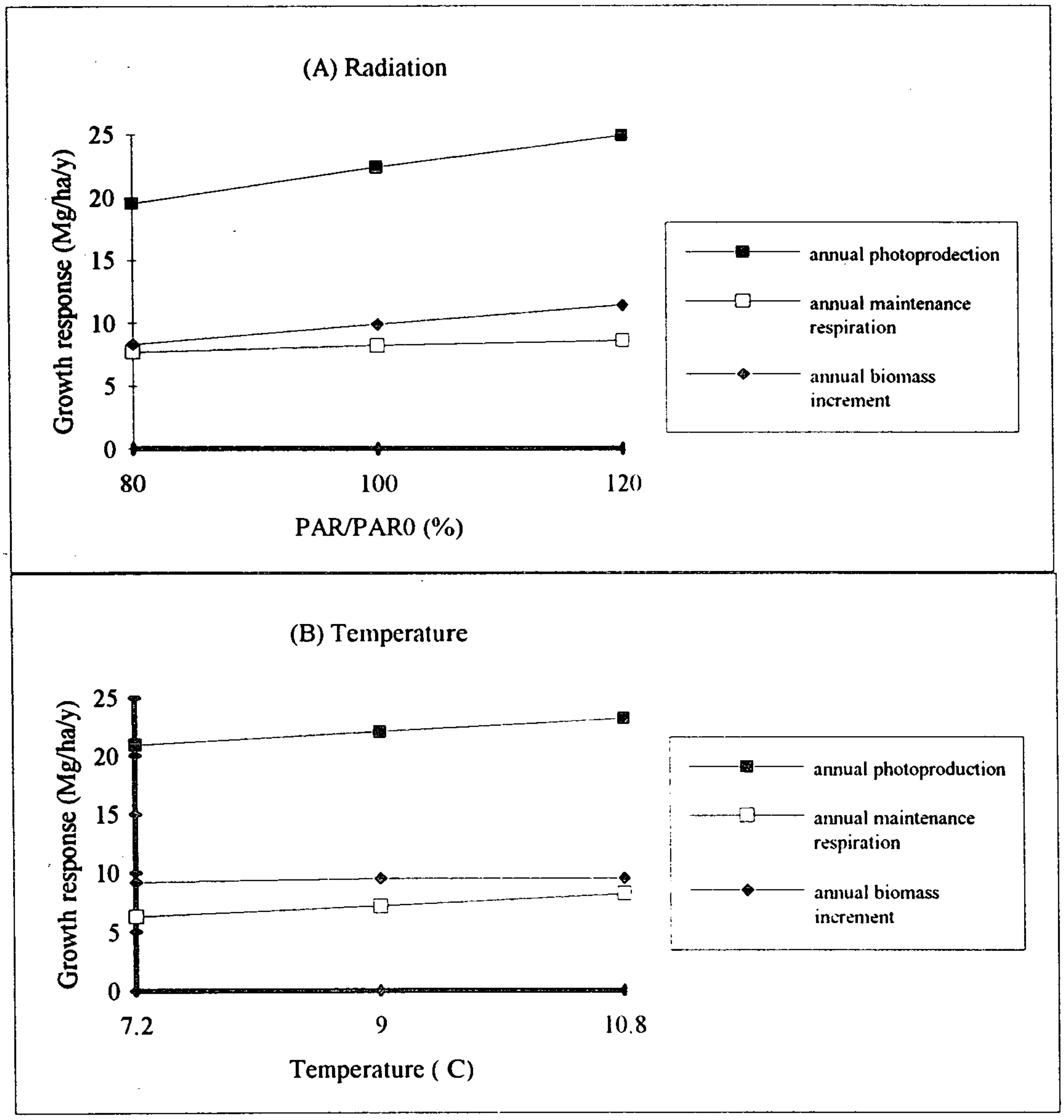


Fig. 4.4 Tree growth response to radiation and temperature

tree growth processes such as annual photoproduction, annual maintenance respiration and annua biomass increment response to: (A) radiation change (noted as PAR/PARO (%), with PARO=50 J m^{-2}); (B) temperature (°C).

Miranda (1981); and in level 4, cell biochemical CO_2 assimilation processes refers to Farquhar *et al.* (1980, 1982). In addition, realism of the biological processes is the sole context in linking these levels. e.g. to scale up from level 3 to level 2, daily photosynthetic production drives the daily assimilation of each tree; and from level 4 to level 3, daily photoproduction is driven by instantaneously CO_2 assimilation rate in a time during a day. All these links between levels as described in Chapter 3 are created on the basis of our current understanding and knowledge (revision of model structure and parameter values may be desirable over the years, as knowledge grows).

Behavioural validity.

'Behavioural validity' refers to the representation of the behavioural spectrum of the real system. FORYDN can produce a reasonable simulation result on the four levels of processes (forest succession, process-based tree growth, leaf physiological functioning, and cell biochemical processes) as discussed in Chapter 3 (Fig. 3.6, 3.8, 3.9, and Fig. 3.10). Also, it is capable of simulating behaviour of both a pure stand like Scots pine (as used in EPMW) and European mixed-forest. Sensitivity analysis shows the model has a acceptable response to canopy assimilation, maintenance respiration, stand dynamics, soil organic matter dynamics, radiation and temperature, and does not substaintially disagree with other published and validated models like FORGROW and MAESTRO (although that in itself should not be regarded as a test of the model). FORDYN is also responsive to thinning effects as sensitivity analysis simulations (section 4.4 in this chapter) are under the same thinning scheme. Therefore, the model can produce correct behaviour for both man-made and natural (mixed) forest, with regard to both stand and soil dynamics, ecological and physiological processes, and it can simulate these processes under management (e.g. thinning) and environmental change (e.g. CO_2 increase) (see next chapter). We may conclude that the model is behaviourally valid.

Empirical validity.

'Empirical validity' refers to the correct representation of empirically determined time-series. In many cases, a full one-to-one comparison between simulation and observation is hardly possible. The empirical validity must be judged by assessing the overall reliability of the numerical results; they are within the expected range, and in agreement with empirical observation and general knowledge.

It has been shown in both this chapter and Chapter 3 (section 3.6), that FORDYN can produce acceptable responses and behaviour on different levels of forest ecosystem processes.

Application validity.

'Application validity' refers to the good agreement of simulation result and the purpose of the model. FORDYN was designed to integrate different levels of forest dynamics processes, so that it is capable of simulating the wide range of behaviour of the forest ecosystem, e.g. scaling up physiological processes to ecosystem level. It has been shown FORDYN then can produce similar results in different simulation modes (section 4.3.3 in this chapter), where different level of processes or resolution are represented. This is also true in simulating management effects (thinning effect in this chapter) and environmental change (effect of CO_2 increase in next chapter). We can say FORDYN can do what it is supposed to — to simulate forest dynamics on the basis of different level of processes and their response to management effect and environmental change.

Sensitivity analysis has been made on aspects of canopy assimilation, maintenance respiration, stand dynamics, soil organic matter dynamics, radiation and temperature. Simulation results of FORDYN have been compared with other European pine models (especially to those validated and mature models, e.g. FORGROW and MAESTRO) that use the same data set, and similar results are found. Simulation results may vary from model to model and from criteria to criteria, resulting from difference between model structure and assumption. This is not to say that all possibilities for sensitivity analysis have been exhausted, for example, new research findings from the field of denchronology can sometimes pinpoint the sensitivity of the system to climatological variables such as temperatures or rainfall, and hence expose weaknesses in any model of tree growth. Overall, it is generally acknowledge that models of trees and ecosystems are hard to evaluate, because of the scale involved.

As it has been shown above, FORDYN is robust, and responsive. Thus it provides a framework for further development and application to many ecological and environmental scenarios, as well as some forest management problems. e.g. the potential to predict spatial distribution of forest under changing climate by considering effects of temperature and other factors on forest growth, and forest response to elevated atmospheric CO_2 by scales (as it will be shown in following chapter).

Chapter 5 Simulating Responses of a Forest Ecosystem to Atmospheric CO_2 increase: application of the model FORDYN

5.1 Introduction

The scientific goal of understanding forest dynamics, and the management goal of being able to forecast stand dynamics and timber output, both require a model of stand structure and development in which individual trees are permitted to influence the local environment. To approach both goals, we need a new simulation approach that can help us to understand how species composition and growth rates vary over time, to predict the timber output, and the scheme for a sustained management under a changing climate (Grace, 1991). The model FORDYN developed in this study provides a simulation approach that can meet this demand.

In this chapter, FORDYN is used to assess the effects of elevated atmospheric CO_2 on forest stand. The objectives are:

- to examine and predict the likely effects of the projected increase in global atmospheric CO_2 concentration on a forest ecosystem over different spatial and temporal scales (scaling up from short term physiological processes to long term ecological processes); and
- to compare these effects on the basis of the same stand condition and environment variables as used in EPMW (see Chapter 4).

5.2 The Problem

There is a growing interest in studying the effects of increasing global CO_2 concentration on forest development. Data obtained from bubbles in ice cores provide evidence of long-term changes in CO_2 concentration (Neftel *et al.*, 1985; Figield, 1988). Global atmospheric CO_2 concentration was about 270 to 280 μmol mol^{-1} in the mid 18th century, and now exceeds 355 μmol mol^{-1}, increasing at *ca* 1.2 μmol mol^{-1} per year (Conway *et al.*, 1988). It expected to increase to approximately 700 μmol mol^{-1} by the middle of the 21st century (Eamus & Jarvis, 1989).

The effects of this increase in atmospheric CO_2 concentration on trees and forests may be very important, because forests cover about one-third of the land area of the world and carry out a substantial part of the global photosynthesis (Kramer, 1981). Eamus and Jarvis (1989) indicated that there are four reasons for being concerned about the rise in CO_2 and its effects on trees and forests:

i) enhancement of biological knowledge about the functioning of tree species of major ecological and economical importance;
ii) impact on the productivity and value of the economic product;
iii) impact on the ecology and environment of woods and forests; and
iv) downstream, socio-economic consequences.

Reviews of previous experimental studies on the effects of elevated CO_2 on tree and forest processes are found in Eamus and Jarvis (1989), Mussekman and Fox (1992), Mousseau and Saugier (1992), and Ceulemans and Mousseau (1994). It has been shown that most of our knowledge about the effects of CO_2 on plants is at the short term physiological and biochemical scales, while it is at long term stand scale that we want to know the effects of any CO_2 increase. Long term processes are normally impossible to measure. Therefore, a modelling approach has been strongly recommended to encompass a wide range of knowledge on ecosystem processes and to assess the consequences of the increase in CO_2 at the forest stand level.

5.3 Modes of Reaction of Plants to CO_2

The main physiological function of CO_2 is as the substrate and activator for photosynthetic carbon assimilation, and so an increase in concentration of CO_2 in the external air may be expected to increase the supply of substrate by diffusion into the leaf. Quite a lot is known about the biochemistry and biophysics of these processes (e.g. Farquhar *et al.*, 1980), and we would like to utilise this information.

The consequences of elevated global atmospheric CO_2 concentration can be viewed over a range of spatial and temporal scales as shown in Table 5.1. For example, an increase in CO_2 may affect the primary photosynthetic carboxylation through changing ribulose bisphosphate carboxylase-oxygense (Rubisco) activity at the cell scale over seconds or minutes; assimilation of CO_2 and transpiration of water are influenced by CO_2 at a time scale of hours; whereas, assimilate (carbon) allocation and nitrogen uptake are affected at the tree scale over weeks and months.

In the following, I will investigate the effects of changing ambient CO_2 at these scales. All simulations are based on simulation mode 4 (see Chapter 3). The

Table 5.1
The range of temporal and spatial scales suggested in the study of the effects of elevated CO_2 upon trees, WUE=water use effciency, following Eamus & Jarvis (1989).

	Temporal scale				
Spatial scale	Seconds/Minutes	Hours/Days	Weeks/Months	Years/Decades	Centuries
Cell	enzyme activation; fluorescence; carboxylation; transport/partitioning	enzyme kinetics; organelle structure	acclimation of cellular processes		
Leaf/Shoot		assimilation; transpiration; stomatal action	acclimation of assimilation; senescence		
Seedling/Tree			growth and carbon allocation; nutrient uptake; root/shoot dynamics	crown properties; branching	
Plantation/ Woodland		canopy properties of photosynthesis, transpiration, light interception	nutrient uptake; WUE; productivity	canopy structure; competition; harvest index	
Forest/ Ecosystem				yield; rotation length; WUE	natural and artificial selection; land use; species composition

physiological parameters and stand data used are based on Scots pine as in Chapter 4 from the European Pine Modelling Workshop. The climate data were set as follows: PPFD as 1000 µmol m^{-2} s^{-1}, ambient partial pressure of O_2 as 21 000 Pa, atmospheric pressure as 1 000 000 Pa, and temperature as 25 °C. Nitrogen and water contents in the soil were assumed to be non-limiting. In each of the following simulations, these conditions were held constant unless indicated. Each simulation was carried out to predict the response of forest (at different levels) to ambient CO_2 concentrations varying from 100 to 800 µmol mol^{-1}.

5.4 Cell Level

5.4.1 C_3 Photosynthesis

Emphasis in many experiments at the cellular scale has been on the influence of CO_2 concentration on fluorescence induction phenomena, enzyme activity of Rubisco, carbon partitioning within celluar pools and cellular transport properties (Eamus & Jarvis, 1989). The enzyme Rubisco has been better studied: it has both oxygenase and carboxylase activities, and the balance between these two activities depends on the supply of CO_2 and O_2 to the carboxylation sites inside the leaves. The CO_2 concentration influences Rubisco activity *via* its role as a substrate as well as through its influence upon the enzyme activation state (Eamus & Jarvis, 1989).

For short-term studies in which the plant does not have sufficient time to acclimate to the elevated CO_2, experiments have shown that a doubling of the ambient CO_2 concentrationan leads to an increase of carbon assimilation rate from 20 to 300% (Eamus & Jarvis, 1989).

In the model FORDYN, effects of CO_2 on assimilation processes at the cell biochemical level are represented as simplified Rubisco-limited carboxylation and oxidation processes based on the C_3 pathway, with the scheme described in section 3.2.4 in Chapter 3. In the following simulation study, I investigate how photosynthesis responds to changing ambient CO_2 concentration, and what are the effects of temperature and nitrogen.

In the following simulation, photosynthetic rate is simulated when ambient CO_2 concentration changes from 100 to 800 µmol mol^{-1}. Simulation results are shown in Fig. 5.1. In Fig. 5.1(A), temperature is set as 10 and 35 °C for assessing the effect of temperature on photosynthetic rate. In Fig. 5.1(B), leaf nitrogen is set

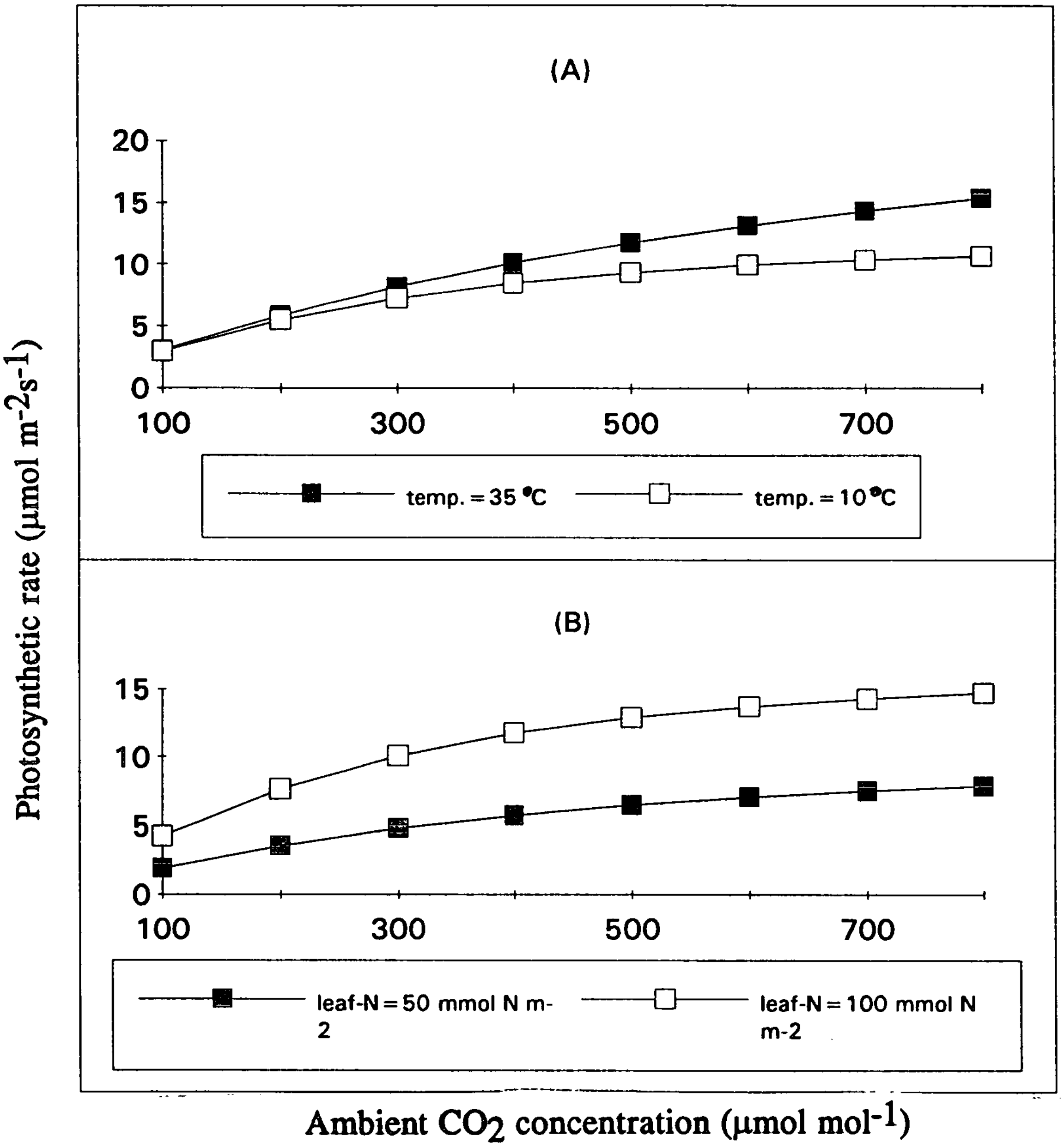


Fig. 5.1 Photosynthesis response to ambient CO_2 concentration
(A) temperature effect on photosynthetic rate, with leaf nitrogen set to 100 mmol N m^{-2};
(B) leaf nitrogen effect on photosynthetic rate, with temperature set to 25 °C.

as 100 and 50 mmol N m^{-2} for assessing the effect of nitrogen stress on photosynthetic rate and temperature as 25 ^0C. Leaf conductance is set as 0.1 mol m^{-2} s-1,

5.4.2 Simulation Results and Discussion

5.4.2.1 Temperature Effect

Fig. 5.1(A) shows that CO_2 assimilation rate is less sensitive to elevated CO_2 at low temperature (10 °C) than at high temperature (35 °C), which is similiar to the conclusion by Long (1991). This is because higher leaf temperature can enhance maximum electron transport rate, and thus maximum carboxylation rate (see also section 3.2.4.2 and Fig. 3.10(D) in Chapter 3).

5.4.2.2 Nitrogen Stress

From Fig. 5.1(B) one can see that photosynthetic rate increases substantially when CO_2 concentration is increased. The simulated photosynthetic rate increases about 45% when ambient CO_2 concentration is doubled from 350 to 700 μmol mol^{-1} with leaf nitrogen as 100 mmol N m^{-2}. However, the higher leaf nitrogen concentration of 100 mmol N m^{-2}, leads to a higher CO_2 assimilation rate (than that of 50 mmol N m^{-2}) because of increased nitrogen allocation to Rubisco.

5.5 Leaf Level

5.5.1 Acclimation of Photosynthesis

When plants are grown for a period of time, say weeks or months, in elevated CO_2, they normally become 'acclimated'. Then the 'sensitivity' of photosynthesis to CO_2 concentration of many plants may be changed by comparson with plants grown in ambient CO_2 (Ceulemans & Mousseau, 1994).

The physiological explanation of this photosynthetic acclimation process may be: i) reduction in the amount or activity of Rubisco; ii) inhibition of the production and/or the consumption of NADPH and ATP, as a result of chloroplast disruption by starch accumulation (Wulff & Strain, 1982); and iii) fewer stomata (Eamus & Jarvis, 1989). On a whole plant level, it was proposed that this acclimation process may be attributed to source-sink phenomena (Ceulemans & Mousseau, 1994; Mousseau & Enoch, 1989; El Kohen *et al.*, 1993; Körner & Arnone, 1992). In some other examples, downregulation phenomena are frequently found to be related either to poor nutritional conditions or limiting pot size, resulting in restriction by nutritional conditions and less physical space available for root growth. (Ceulemans & Mousseau, 1994).

However, in this study, the acclimation of photosynthesis is focused on the leaf physiological level of processes, and stomatal conductance is kept constant. This is because the effect of CO_2 concentration on stomatal conductance is still uncertain, conflicting data having been obtained (Eamus & Jarvis, 1989). Other processes such as soil nutritional condition, and root development are assumed not to be limiting.

The A-C_a response curve can provide convincing evidence for acclimation of photosynthesis under long term exposure to elevated CO_2 (Long, 1991). Based on Farquhar *et al.* (1980), the shape of A-C_a curve at low CO_2 relates to Rubisco activity, and the upper range of A-C_a curve (photosynthesis response to high CO_2) is limited by RuBP or orthphosphate (P_i) regeneration. Thus, acclimation may involve changes in shape of the A-C_a curve: i) change in the amount or activity of Rubisco; ii) change in RuBP or P_i regeneration capacity.

As for i), a decrease of activity and amount of Rubisco has been reported (Sage *et al.*, 1989; El Kohen, 1993). Nitrogen allocation to Rubisco is relevant to Rubisco activity (Sage *et al.*, 1989). Leaf nitrogen content is another factor that may affect photosynthetic capacity, but is now generally accepted that the nitrogen concentration in leaves and other organs of plants grown under elevated CO_2 is lower than that in plants cultivated at ambient CO_2 — the so called 'dilution effect' (Overdieck, 1990). Therefore, in this simulation, I use the Rubisco activity state, which is represented as the Michaelis-Menten coefficient for CO_2 ($K_{m,co2}$), as an effective indicator of the acclimation to elevated CO_2 (See also Sage *et al.*, 1989).

As for ii), the acclimation of photosynthesis is also found to be related to inhibition of Pi regeneration (Sage *et al.*, 1989). The changes in RuBP or P_i regeneration are limited by the electron transport capacity (although our understanding of the relation between P_i regeneration and electron transport is still not complete (Ceulemans & Mousseau, 1994)), and the electron transport capacity (depending on production and consumption of NADPH and ATP) is affected by starch accumulation in the leaves (Wulff & Strain, 1982). So, in this simulation, the change of RuBP regeneration or electron transport limited processes is described by changing a parameter θ, the curvature of light dependence of regeneration of the RuBP pool (see Gross *et al.*, 1991).

Therefore, as shown in Fig. 5.2(A)-(E), there are different possible acclimation patterns depending on different changes (or recovery ability) in Rubisco activity and RuBP regeneration after long term exposure to elevated CO_2. The possible acclimation patterns caused by increased or upregulated Rubisco activity are not shown here, as there is no experimental evidence for such change.

In the simulations in Fig. 5.2, acclimation of photosynthetic rate comes into effect when ambient CO_2 concentration changes from 100 to 800 μmol mol^{-1}. According to a 'look up table' which contains the 'assumed acclimation effect', it is assumed that both the Michaelis-Menten coefficient for CO_2 and the curvature of light dependence of RuBP pool regeneration can be changed to describe acclimation to CO_2. In (A), it is assumed that Rubisco is downregulated ($K_{m,co2}$ is adjusted from 31 to 40 Pa) and RuBP regeneration capacity is unchanged (θ is kept as 0.8). In (B), it is assumed that Rubisco is downregulated ($K_{m,co2}$ is adjusted from 31 to 40 Pa) and RuBP regeneration capacity is upregulated (θ is adjusted from 0.8 to 0.96). In (C), it is assumed that Rubisco is downregulated ($K_{m,co2}$ is adjusted from 31 to 40 Pa) and RuBP regeneration capacity is also downregulated (θ is adjusted from 0.8 to 0.7). In (D), it is assumed that Rubisco activity remains unchanged or be able to completely reactivated ($K_{m,co2}$ is kept as 31 Pa), and RuBP regeneration capacity is upregulated (θ is adjusted from 0.8 to 0.9). In (E), $K_{m,co2}$ is kept as 31 Pa, and θ is adjusted from 0.8 to 0.7.

This acclimation effect is only brought into play when the tree is exposed to a changed CO_2 concentration over a period of more than one year.

5.5.2 Simulation Results and Discussion

Fig. 5.2(A)-(E) show the simulation results of the possible acclimation of leaf photosynthesis to changing ambient CO_2. Photosynthesis is acclimated during long-term exposure to increased ambient CO_2, with either a regulated Rubisco activity or RuBP regeneration capacity, and therefore a changed photosynthetic rate occurs at any given CO_2 concentration. There will be either a changed initial slope of the A-C_a curve, a changed maximum carboxylation rate, or a changed sensitivity to high CO_2. The overall sensitivity of photosynthesis to high CO_2 may be expressed as a biotic growth factor β (defined as the proportional change in photosynthetic rate when CO_2 is doubled from 350 to 700 μmol mol^{-1} (Bacastow and Keeling, 1973).

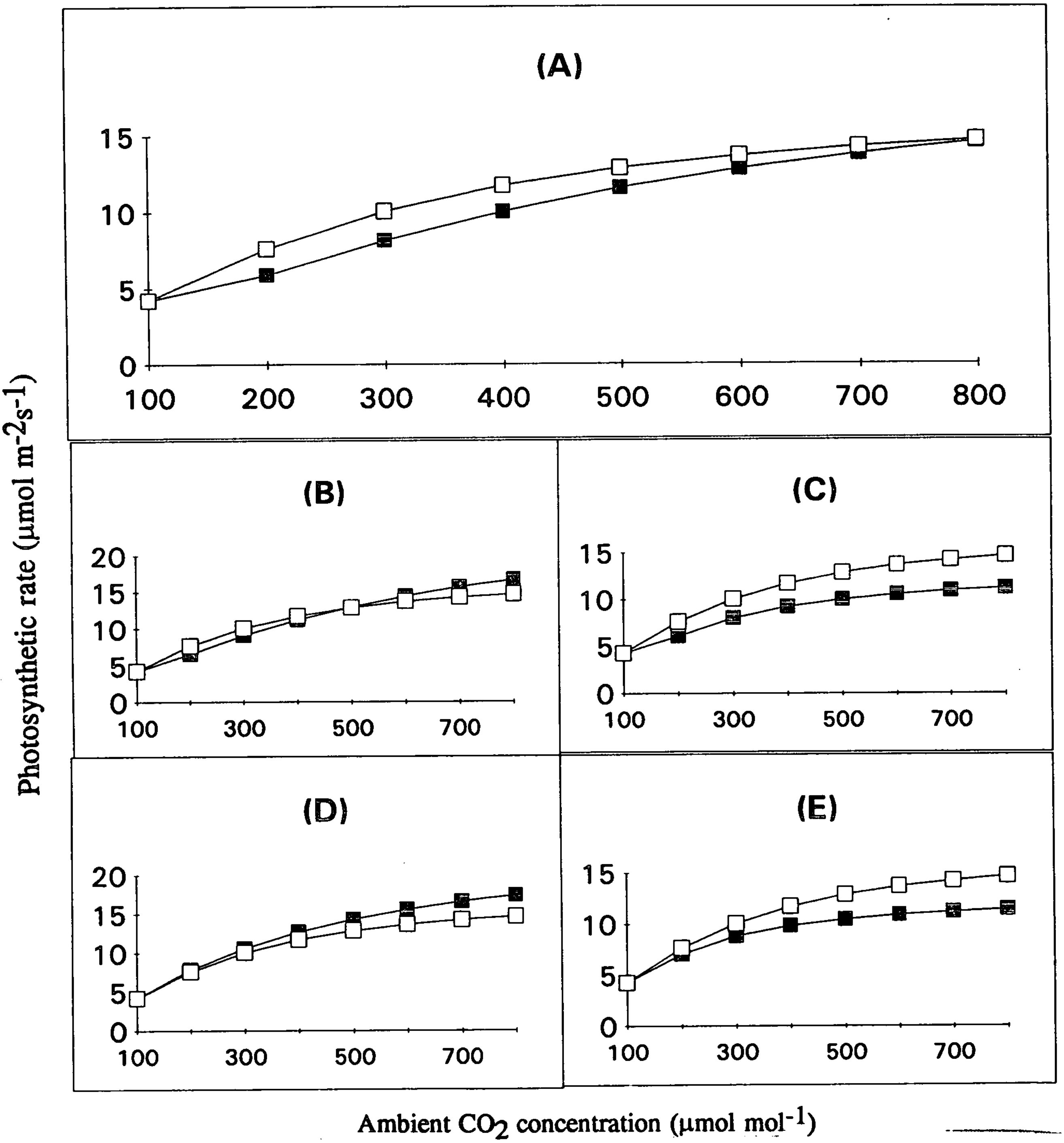


Fig. 5.2 The acclimation effect of photosynthesis to ambient CO_2 concentration

(A) Rubisco activity downregulated, RuBP regeneration capacity unchanged; (B) Rubisco downregulated, RuBP regeneration upregulated; (C) Rubisco downregulated, RuBP regeneration downregulated; (D) Rubisco unchanged, RuBP regeneration unchanged; and (E) Rubisco unchanged, RuBP regeneration downregulated. Open symbols are for photosynthesis under ambient CO_2 concentration, filled symbols are for acclimated photosynthesis.

In Fig. 5.2(A), the 'initial slope' of A-C_a curve (which is calculated as the slope of A-C_a curve at the point when C_a equals to 100 μmol mol^{-1} in this simulation) declines from 0.81 to 0.51, the maximum carboxylation rate is not changed, and β increases from 0.45 to 0.50. This acclimation pattern was observed in *Phaseolus vulgaris* by both Sage *et al.* (1989) and von Caemmerer and Farquhar (1984). In Fig. 5.2(B), slope of the A-C_a curve declines from 0.81 to 0.55, the maximum carboxylation rate increases, and β increases from 0.45 to 0.64. This acclimation pattern was observed in *Chenopodium album* (Sage *et al.*, 1989). In Fig. 5.2(C), the initial slope of the A-C_a curve declines from 0.81 to 0.44, the maximum carboxylation rate declines, and β decreases from 0.45 to 0.39. This acclimation pattern was observed in *Brassica oleracea* (Sage *et al.*, 1989). In Fig. 5.2(D), the initial slope of the A-C_a curve increases from 0.81 to 0.86, the maximum carboxylation rate increases, and β increases from 0.45 to 0.51. This acclimation pattern was observed in *Solanum tuberosum* (Sage *et al.*, 1989). The acclimation pattern in Fig. 5.2(E) is similar to Fig. 5.2(C) but with a smaller decline in initial slope (from 0.86 to 0.67 compared to 0.81 to 0.44 in Fig. 5.2C).

It has been proposed that a plant can regulate Rubisco activity, electron transport, and P_i regeneration to balance the non-limiting processes with limiting processes (Sage, 1990). Nevertheless, it seems that different species show quite different mechanisms in regulating these non-limiting and limiting processes, and thus show different acclimation patterns as above. Our knowledge of the impact of elevated CO_2 on photosynthetic processes, e.g., on the primary sugar loading from starch accumulation in tree leaves, is still incomplete (Ceulemans & Mousseau, 1994).

Nevertheless, in the following simulation, it is assumed that, when trees are grown under elevated CO_2 over a period of more than one year, both Rubisco activity and the capacity to regenerate RuBP will decline, and thus photosynthesis takes the acclimation pattern of Fig. 5.2(C). This acclimation pattern will be further used in the following simulations at tree and stand levels.

5.6 Tree Level

5.6.1 Tree Growth Processes

The effects of CO_2 increase on tree growth processes include tree growth rate, assimilate allocation, shoot-root ratio, and nitrogen uptake, with time scales ranging from weeks to months. The observed response of tree growth rate to doubling CO_2 ranges from 20 to 120% with a median of *ca* 40% (Eamus & Jarvis, 1989). Both leaf and root growth are increased.

Unfortunately, nearly all experiments on this subject are rather short-term ranging from a few months to a year (Eamus & Jarvis, 1989). It is still uncertain how much growth rate, assimilate allocation, and nitrogen uptake will change over a time scale of years.

In this simulation I examine the response of tree growth processes, such as relative tree growth rate, assimilate allocation and assimilate allocation under nitrogen stress, to changing the ambient CO_2 concentration.

The following simulation is based on the physiological and stand data that were used for the Scots pine stand from EPMW as in Chapter 4. Soil nitrogen is assumed saturating in assessing the effects of changing ambient CO_2 on tree growth rate and assimilate allocation, and has been set at saturating and half-saturating levels in assessing the effect of changing CO_2 on assimilate allocation under nitrogen stress. Each of these tree growth processes is simulated with ambient CO_2 concentration changing from 100 to 800 $\mu mol\ mol^{-1}$. Run durations are all 10 years, and the results are shown in Fig. 5.3.

5.6.2 Simulation Results and Discussion

5.6.2.1 Growth Rate

Fig. 5.3(A) shows tree growth in response to ambient CO_2 concentration after 10 years. Tree biomass growth rate (annual biomass increment/total tree biomass) is accounted on a yearly basis. There is a 33 % increase of tree growth rate when ambient CO_2 concentration is doubled from 350 to 700 $\mu mol\ mol^{-1}$.

The increase of tree growth rate occurs because increased photosynthesis at the leaf scale produces more carbon assimilate (Fig. 5.3), and higher meristem activity (section 3.2 in Chapter 3), and, therefore, a higher biomass increment rate.

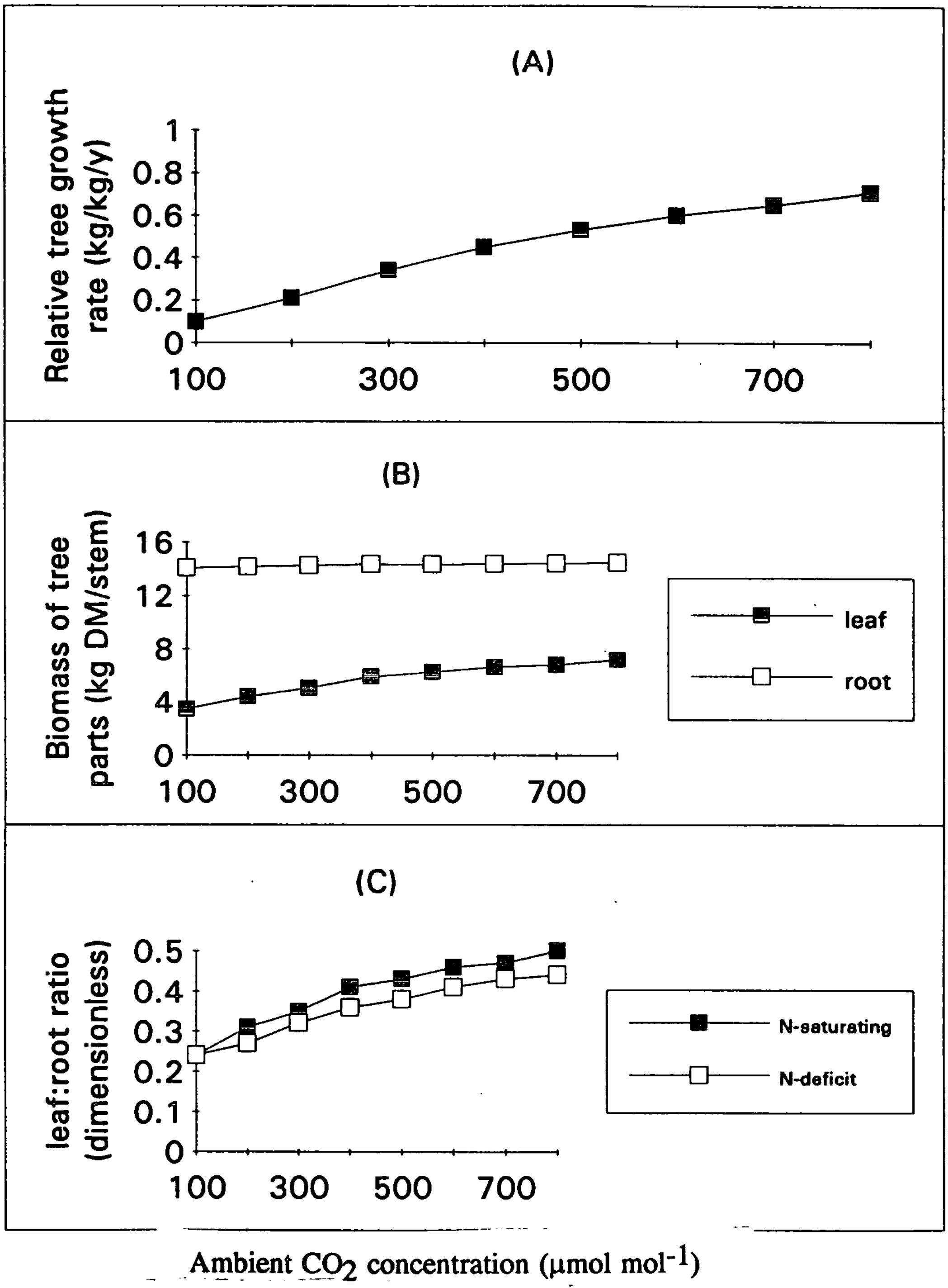


Fig. 5.3 The response of tree growth processes to ambient CO_2 concentration
(A) response of tree growth rate; (B) response of leaf and root biomass growth; and
(C) response of leaf:root ratio.

5.6.2.2 Assimilate Allocation

Fig. 5.3(B) shows assimilate allocation (leaf and root) in response to ambient CO_2 concentration. From the figure, one can see that an increase in ambient CO_2 concentration leads to more total leaf biomass increment per tree, as well as to a larger increment of root biomass. At the same time the leaf biomass increases faster than root biomass.

This result is supported by other experiments. For examples, an increase in CO_2 concentration resulted in an increase in leaf number, leaf area and leaf mass per plant (Tolley & Strain, 1984; Sionit *et al.*, 1985); as well as an increase in the dry mass of coarse and fine roots (Higginbotham *et al.*, 1985). It has been observed that increased CO_2 has a direct effect on root initiation and growth (J. F. Farrar, unpublished). However, further experimental work on whether the effects on leaf growth result from direct action of CO_2 on leaf initiation, or from an enhanced supply of substrate is needed (Tolley & Strain, 1984).

In the model FORDYN, it was assumed that the intrinsic tree growth rate of leaf and root are proportional to the carbon concentration. Therefore, enhanced CO_2 assimilation rate as in Fig. 5.1 and Fig. 5.2 can 'stimulate' the growth of meristems in the leaf and root (as well as other tree parts) and therefore enhance the growth rate of leaves and roots (Thornley, 1991).

5.6.2.3 Assimilate Allocation Under Nitrogen Stress

The allocation of carbon is usually expressed as the leaf:root ratio. Nitrogen is an important factor in assimilate allocation during tree growth. In previous simulations, nitrogen has been assumed to be non-limiting in elevated ambient CO_2. In this simulation, I examine the effect of nitrogen stress on assimilate allocation in response to a change in ambient CO_2 concentration.

Fig. 5.3(C) shows the leaf:root ratio in response to changing ambient CO_2 concentration in different nitrogen supply conditions (saturating and half-saturating) in the soil. From the figure one can see that saturating nitrogen gives a higher leaf:root ratio, and half-saturating nitrogen (deficit) gives a lower leaf:root ratio during growth. This occurs in the model because of the transport-resistance subroutine (Thornley, 1991), and because the increased nitrogen supply is insufficient (in the nitrogen deficit condition) in relation to the supply of carbon (i.e. the increased ambient CO_2 concentration).

This result is supported by some experimental work that shows that when nutrients are supplied in adequate amounts, increase in CO_2 concentration leads to an increase in the shoot:root ratio (Tolley & Strain, 1984; Sionit *et al.*, 1985; Brown & Higginbotham, 1986).

5.7 Stand and Ecosystem Level

5.7.1 Stand Development

An experimental approach to assess the effects of increased CO_2 concentration on processes at the scale of a forest stand (with time scales ranging from years to decades) is not practical, and thus the modelling approach is the only option. However, the models that are currently available can either describe long-term forest development (but with insufficient information about internal feedback), or can represent short-term internal feedbacks (e.g. process-based tree growth models) but are limited in their ability to predict long-term forest dynamics. Therefore, there is a need to scale up. We need a more compact, scale-based, or hierarchical forest modelling approach to assess the consequences of the increase in CO_2 at the forest stand level. FORDYN is a model that is designed for this purpose.

In this simulation, I examine the changes of forest stand response to increase in atmospheric CO_2 concentration, including stand productivity, total nitrogen uptake by all trees in the stand, N:C in the plant, nitrogen pool in the plant, and nitrogen pool in the litter and soil.

In each of the following simulations, all physiological, biochemical, stand, soil and climate parameters are held the same as were used for Scots pine in Chapter 4, and the ambient CO_2 concentration is changed from 100 to 800 μmol mol^{-1}. Run durations are all 20 years. The results are shown in Fig. 5.4.

5.7.2 Simulation Results and Discussion

5.7.2.1 Stand Productivity

Fig. 5.4(A) shows the result of simulating stand biomass growth in response to changing ambient CO_2 concentration. Stand growth increases with ambient CO_2

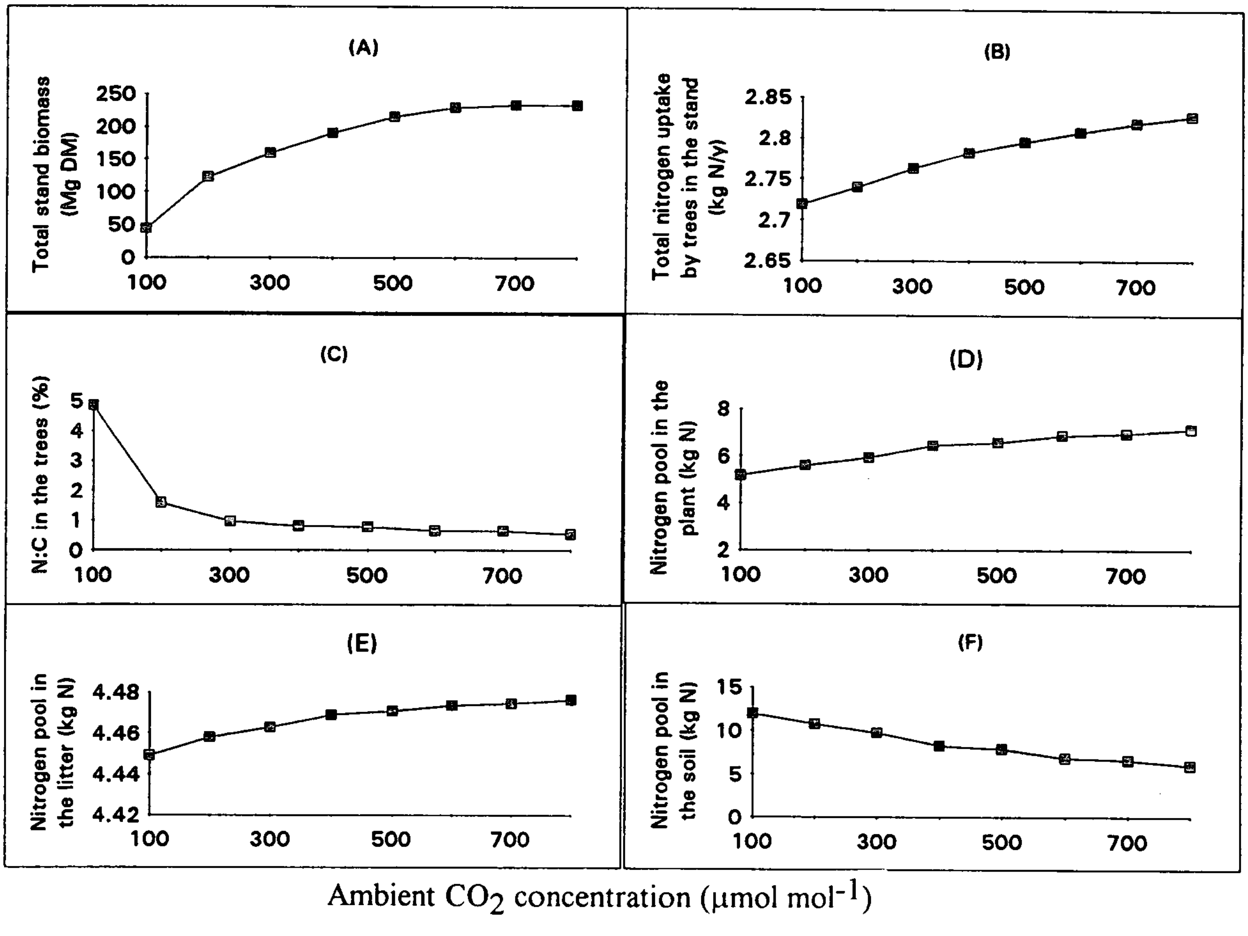


Fig. 5.4 Stand and ecosystem dynamics response to ambient CO_2 concentration (A) response of stand biomass; (B) response of total nitrogen uptake by trees; (C) response of N:C in the trees; (D) response of nitrogen pool in the trees; (E) response of nitrogen pool in the litter; and (F) response of nitrogen in the soil. The stand area is 0.1 ha.

concentration. There is a 29% increase in stand biomass when ambient CO_2 concentration is doubed from 350 to 700 μmol mol^{-1}.

This result comes about because elevated CO_2 leads to a higher rate of photosynthesis (Fig. 5.1, 5.2) and a corresponding higher stand growth rate (Fig. 5.3(A)). However, the stand biomass increase is less than that at previous lower levels of processes as in Fig. 5.1 to 5.3, as there is enhanced competition for limited resources such as nitrogen in the soil and light inside the stand. As a feedback there will be a resource limit to the growth of trees, and thus to stand growth. This is an example of how feedback from a higher level can constrain processes at a lower level.

5.7.2.2 Nitrogen Uptake

Fig. 5.4(B) shows nitrogen uptake by trees in response to ambient CO_2 concentration. There is a simulated increase of nitrogen uptake of 24% when ambient CO_2 concentration is doubled from 350 to 700 μmol mol^{-1}.

As shown in Fig. 5.3(B), increased root biomass in response to increasing ambient CO_2 concentration will increase the area of fine root that is used to take up nitrogen from soil, and therefore more nitrogen will be absorbed by the trees.

However, this response may be weakened (see the following) because reduced leaf nitrogen concentration (Fig. 5.4(C)) and thus nitrogen concentration in the litter may ultimately lead to a lower rate of mineralization in the soil (Fig. 5.4(E)), which will impose greater nutrient limitations to the nitrogen uptake rate.

5.7.2.3 N:C in the Plant

Fig. 5.4(C) shows the N:C ratio in the trees in the stand in response to ambient CO_2 concentration. There is a 30 % decrease of N:C ratio in the plant when ambient CO_2 concentration is doubled from 350 to 700 μmol mol^{-1}.

It is commonly observed in experiments that the nitrogen concentration in leaves decreases under elevated ambient CO_2 concentration (Curtis *et al.*, 1989, 1990), even though total nitrogen uptake by the plant (Fig. 5.4(B)) and the nitrogen pool in the plant (see below) may increase.

5.7.2.4 Nitrogen Pool in the Plant

Fig. 5.4(D) shows the nitrogen pool in the plant in response to ambient CO_2 concentration. There is a 13% increase of nitrogen pool size in the plant when ambient CO_2 concentration is doubled from 350 to 700 μmol mol^{-1}.

This is because increased ambient CO_2 concentration leads to increased nitrogen uptake by the plant as in Fig. 5.4(C), while the nitrogen loss normally from leaf turnover is much less than the nitrogen uptake by the roots, and therefore the total nitrogen amount or nitrogen pool increases.

5.7.2.5 Nitrogen Pool in the Litter

Fig. 5.4(E) shows the nitrogen in the litter in response to changing ambient CO_2. There is a 0.3 % increase of nitrogen in the litter when ambient CO_2 is doubled from 350 to 700 μmol mol^{-1}.

This response is not as evident as in the previous simulation. It seems that the enhanced nitrogen content of the plant can increase the amount of nitrogen returning from plant to soil, but this is evidently still not big enough to change the total nitrogen pool size in the litter. However, this may further affect nitrogen re-utilisation through humification and mineralization in the soil. Therefore, as a feedback, it may influence nitrogen uptake by the roots, causing a reduction in tree growth.

5.7.2.6 Nitrogen Pool in the Soil

Fig. 5.4(F) shows the nitrogen pool in the soil in response to ambient CO_2 concentration. There is a 37 % decrease when ambient CO_2 concentration is doubled from 350 to 700 μmol mol^{-1}.

This is because increased ambient CO_2 concentration enhances the growth of tree roots in the stand (Fig. 5.3(B)), and therefore total nitrogen uptake by all trees will be increased (Fig. 5.4(B)). While nitrogen return from the plant to the soil may increase a little (Fig.5.4(E)), it is not enough to maintain the size of the soil nitrogen pool. The decreased nitrogen pool in the soil will normally produce a nitrogen stress, and have effects on tree growth processes such as are shown in Fig. 5.3(C).

5.8 Synthetic Assessment of CO_2 Effects on Forest Ecosystem

To synthesise the effects of elevated CO_2 on forest, it is necessary to compare these effects at different scales. Fig. 5.5 shows the predicted response of forest to elevated atmospheric CO_2 by scale. All simulation results in Fig. 5.5 are based on previous simulation results from Fig. 5.2(C), Fig. 5.3(A), and Fig. 5.4(A) under the same stand and environmental conditions.

A biotic factor β, as defined in section 5.5.2, is used for assessing the effects of CO_2 increase on different levels of forest dynamics.

In Fig. 5.4, the percentage change of each variable, measured as β, of leaf photosynthesis (short-term and long-term), tree growth rate, and stand biomass production are compared in response to a changing of CO_2 concentration from 350 to 700 μmol mol^{-1}. The value of β for these four simulations of response are 0.45, 0.39, 0.33, and 0.29, respectively. This simulation study has provided a clear picture of the difference in magnitude of the responses of forest dynamic processes to atmospheric CO_2 increase at different scales, under the same stand and environmental conditions.

From Fig. 5.5 one can see that the sensitivity of forest to elevated CO_2 declines with increasing level. This is because of interacting processes and feedbacks between levels. The responses of processes at low hierahchical levels are always limited or constrained by the processes at higher levels, e.g. increased ambient CO_2 concentration can increase tree growth rate (Fig. 5.3(A)) and leaf biomass (Fig. 5.3(B)), this in-turn leads to a reduced soil nitrogen pool size (Fig. 5.4(F)), and a declined nitrogen concentration in the trees (Fig. 5.4(C)). As a feedback, the declined nitrogen concentration in the trees will produce nitrogen stress on both leaf photosynthesis (Fig. 5.1(B)) and tree growth process (Fig. 5.3(C)).

5.8 Discussion

The complexity of global environmental changes, such as elevated atmospheric CO_2, are especially difficult to address, since they involve translating information across a variety of spatial and temporal scales. To avoid 'transposition of scale' (O'Neil, 1988), and to understand these interactions and make predictions at larger scales requires modelling, especially hierarchical modelling.

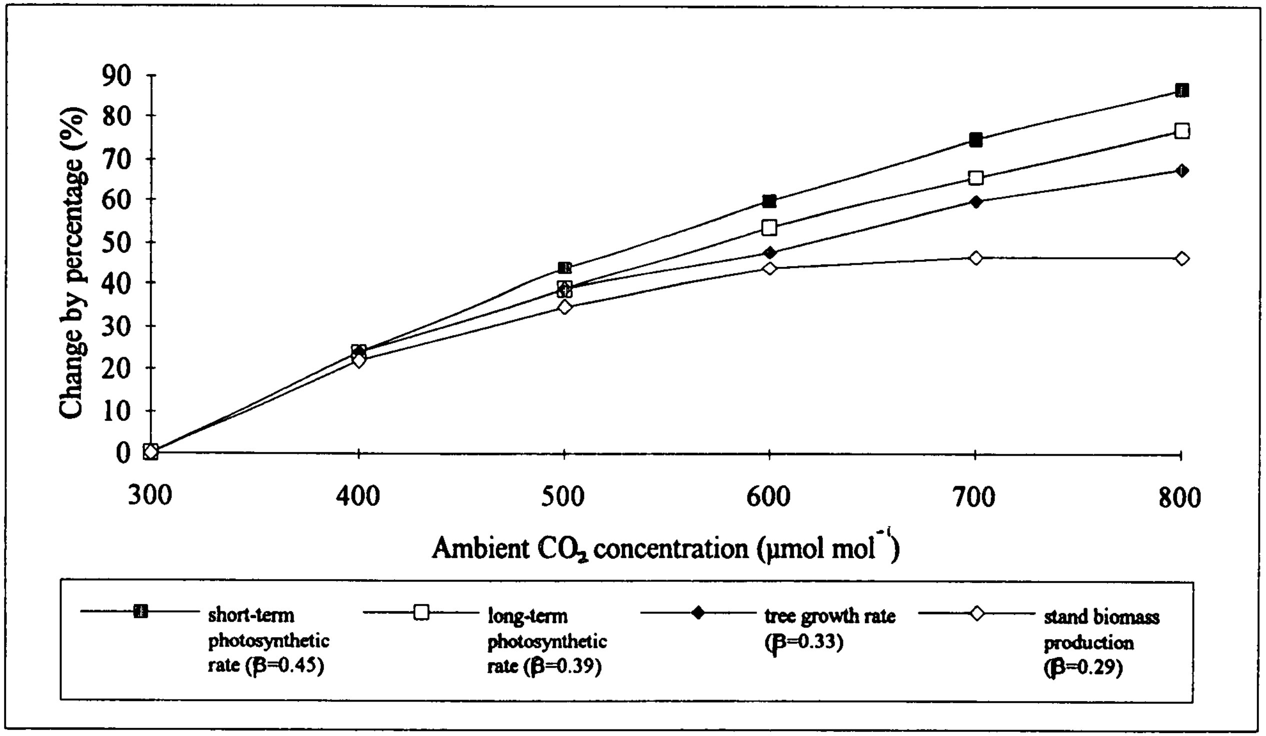


Fig. 5.5 Simulated forest processes at different scales in response to changing ambient CO_2 concentration

Short-term and long-term photosynthesis, tree growth rate, and stand biomass, based on the Scots pine stand used in EPMW, have been calculated in response to ambient CO_2 concentration change. A biotic factor β is used for assessing the effect of the CO_2 increase (Bacastow & Keeling, 1973). β is defined as the proportional change in each variable brought about by doubling CO_2 from 350 to 700 μmol mol^{-1}

As shown in this study, a hierarchical approach to forest ecological modelling can help to identify the mechanistic interactions of system components at lower levels, and address their effects at higher levels. It, therefore, provides a most effective way of translating effects from the physiological level of organisation to the ecosystem level and of accounting for the relations between these effects.

It is evident that models that address high level phenomena can rarely be tested. In the case of forest models in the boreal zone, there is some prospect of using historical, palynological data for such testing, at least over the last 10 000 years or so, when temperature has probably been the main influence, not CO_2. Unfortunately, phenomena at even larger scales (or higher levels) come into play. In this case, soil formation would have to be modelled because the soil resources have developed over this time scale.

Chapter 6 Discussion and Conclusions

6.1 Perspective of Scaling Issue

Questions of spatial and temporal scale are unavoidable in biological systems, particularly when one is interested in understanding processes and the implications among processes. It has been argued that the problem of scales is a central problem in ecology (Levin, 1992). Scaling up from leaf to ecosystem and beyond is recognised as one of most fundamental challenges in predicting effects of global change (Norman, 1980).

Scaling refers to the use of information at one spatial and temporal scale to infer behaviour or properties at another scale. Scaling is not simply integration or aggregation of values at one level to achieve estimates at a more encompassing level of consideration. Rather, scaling represents the transcending concepts that link processes at different levels of space and time. Scaling aims to identify and express changes of a process across scales, by defining mechanistic processes at a smaller scale, and finding its effects or phenomena at the higher scale. This way of combining mechanisms that are understood precisely at small scales into synthetic assessments over larger scales of space and time can be a grand expression of scientific confidence (Field & Ehleringer, 1993). However, the process of scaling exposes where adequate information is still lacking. Actually, scaling is an art form of science, involving identification of those factors that are less important, what constitutes noise in the transition aross scales, and what is, therefore, best excluded. Scaling identifies what processes are important in understanding the whole system, and should therefore be retained.

A recent book, *Scaling Physiological Processes, Leaf to Globe*, edited by Ehleringer and Field (1993), represents an important contribution towards understanding the potential impacts of global changes. In this book, the state of knowledge concerning strategies and techniques available for scaling are summarised; e.g. in the second major section, some techniques and approaches for scaling processes described at the leaf scale to infer characteristics at the canopy scale are discussed. Norman (1993) outlines a strategy for dealing directly with the complexity and provides an example of a hierarchical approach for scaling leaf photosynthesis to canopy photosynthesis; the 'bottom-up' and 'top-down' models are discussed in detail (Jarvis, 1993); Running and Hunt (1993) explain the scaling lessons learned in the development of their forest-ecosystem model over the past several years. However, most authors demonstrated that ecophysiology can make major contributions to analysis of ecosystems on large spatial and long temporal scales, rather than presenting a definitive answer to the general problem of scaling in terms of a modelling context, e.g. how to organise those concurrent phenomena at multiple scales into an ecosystem model.

In this study, efforts have been made to apply hierarchical approaches to organise scales in forest ecosystem simulation. It has been my aim to demonstrate that a hierarchical approach can help to integrate scales of ecosystem processes in a modelling context, to explore the scaling methodology or rules, to indicate the errors to avoid in scaling, and to show the potential of this approach to current environmental studies.

6.2 How to Link Levels

In an effort to build models that can simulate multi-level (or multi-scale) systems like ecosystems (Allen & Starr, 1982; O'Neil *et al.*, 1986), and to meet the current demand for scaling up (Ehleringer & Field, 1993), a hierarchical approach is recognised as an effective tool to explore the ways in which processes and system properties are aggregated, and translated among and within subsystems.

Differences in organisation and dynamic behaviour between levels make scaling or linking levels very challenging. There is a need to find a more efficient way of integrating levels, e.g. to link levels through phenomena, to set some scaling rules that allow ecologists or modellers to keep track of terms and data between levels, and give due warning to the possible errors that could arise.

6.2.1 Linking Levels Through Phenomena

A scientific investigation about the system structure depends on our own observation. Normally, we choose the processes and levels of interest or importance, and they may be observed in different ways or they may differ in behaviour. To link these levels in a realistic way is challenging. There are different tools available for this linking or scaling, which include correlation, extrapolation and modelling (Levin, 1992). No matter which tool is used, the criteria of observed processes or phenomena should be kept consistent between levels. Thus it is crucial to search for common phenomena that link levels.

As shown in Chapter 2, stem growth is a link between level 1 and level 2 in the model FORDYN (Fig. 2.3). It is a phenomenon that is treated consistently at both levels (or in other words, tree growth can be represented by either size increment, or net assimilate production). In level 1, it corresponds to the DBH increment of tree size. In level 2, it is an accumulation of assimilate allocated to the stem in the same time step.

6.2.2 Scaling Rules

Through this scaling study, two aspects have been found to be important in applying hierarchy theory. We need not only an integration of lower level processes to represent a higher level of processes through linking phenomenon, but also to find feedback from higher to lower levels. Thus two scaling rules are suggested:

i) processes with different temporal scales should be represented as *nested time loops*, so that one can find the cause of a process at the next lower level, and consequence at the next higher level;
ii) setting *constraints from the higher level* of activity to determine the limits of activity at the lower level, either explicitly or implicitly, will define the boundaries of the process at the lower level.

To address a problem at a certain level or scale, we need to explore the mechanism or underlying processes at its lower level. The descriptions of the phenomena from both levels should be consistent. As lower levels of underlying processes of the phenomena have smaller time steps or bigger behaviour frequencies (see Chapter 2), they need to be integrated through time steps to get the equivalent representation of the phenomena at the higher level. This normally can be described in a nested time loop, e.g. yearly assimilate production on level 1 is an integration of daily assimilate production on level 2 (Chapter 3).

However, in a real modelling context, scaling up from one level to the next may be represented by different forms of integration. For example, in FORDYN, the following methods have been used:

- Integration over time by summing.

Annual biomass increment is calculated by summing daily change.

- Integration over time by multiplication.

  In Level 2, the amount of photosynthesis during one fraction-of-a-year time period is obtained by multiplying a daily rate by the number of days in that period.

  In Level 4, hourly photosynthesis is obtained by multiplying the rate per second by the number of seconds in an hour.
- Integration over time by Gaussian integration.

  In Level 3 and 4, the daily total photosynthesis is obtained by a 3-point Gaussian integration approach from hourly photosynthesis.

Apart from integration from lower levels to higher levels as in i), there is also a need to find feedback from higher levels to lower levels, or set constraints from higher levels to lower levels. The point of this consideration is that scaling-up represents a process of transcending concepts between levels, rather than just a simple aggregation of lower levels. This implies consideration of levels of processes as a whole, so that the feedback and interactions between different levels of phenomenon are taken into account. See examples in section 3.4 of Chapter 3.

6.2.3 Errors to Avoid

There are several pitfalls in the scaling study:

First, it is important to avoid 'transposition of scale' (O'Neil, 1988). Sometimes, there is a danger in direct scaling, of making predictions at a higher level simply from the results obtained at lower level, e.g., to predict the response of stand growth to elevated CO_2 as equivalent to that achieved at leaf or cell biochemical level (Chapter 3.3).

Second, it is important to avoid inconsistency in the definition of phenomena between levels. For example, the annual stem biomass increment per tree implies a link between level 1 and level 2 in FORDYN as shown in Fig. 2.3 in Chapter 2. When scaling from level 2 to level 1, one should realise that it is biomass increment of the *stem* that changes tree size of DBH and H in level 2, rather than the *whole tree* biomass increment, because the latter also includes leaf biomass increment that is equivalent to increase in leaf area index in level 1.

Third, one should realise the weaknesses of the top-down and bottom-up modelling approaches. In top-down models, the output is constrained totally though an experimentally determined relationship with a crucial driving variable. This kind of modelling approach tends to be more empirical (Jarvis, 1993). The limitation of this approach is that predictions cannot be made safely outside the range of the variables encountered, and moreover there is only limited mechanistic insight. So, one should explore the lower level by modelling mechanistic processes in a well organised hierarchical model.

The bottom-up modelling approach has disadvantages too. Bottom-up models begin with a smaller spatial or temporal scale than the output. They are open-ended in their model output. A limitation of this modelling approach in that the model can be very sensitive to error in certain inputs (Jarvis, 1993), and too complicated to be of general use in scaling to higher levels. An improved approach is to set an upper limit or constraint to the process concerned in a hierarchical context.

6.3 Future Challenges and Applications

Global change and forest decline have provided an impetus for forest modelling. The limitations of the traditional ways of forecasting forest yield are becoming evident (Bossel, 1991). What is needed is a modelling system that simulates the forest response to a changing environment, and can scale up from physiological processes to higher levels, ultimately to the globe. As a result, there are new challenges and applications in front of us.

6.3.1 Modelling Methodology: a hierarchical approach

A hierarchical approach can help to clarify and simplify complex ecosystem processes as shown in Chapter 2.

Forest modelling aims to simulate forest pattern and processes, whereby each of those dynamic processes is characterised by the time-scale of its components, e.g. forest succession is in decades to centuries, tree growth is in seasons to decades, phenology is in days to months, and stomatal processes is in minutes to hours, etc. Different modelling objective determines which of those processes are emphasised. To obtain a realistic mechanistic and valid behavioural description of forest dynamics, scales of processes must be identified. Understanding, representing, and organising scales of biological processes in forest ecosystem is an essential problem in forest science and forest modelling. A valid model structure based on natural biological processes is the precondition to study many ecological problems.

6.3.2 Research Prospects: scaling-up physiological processes

As noted above, to assess the potential effects of environmental change (global CO_2 increase, global warming, and air pollution etc.), there is a need to understand the problem of scale in ecological processes (Levin, 1992). The effects of climate change operate at the molecular level of the living organism, yet it is at the ecosystem or population level that we want to know the consequence of climate change (Ågren *et al.,* 1991). It is argued that through scaling ecophysiology can make major contributions to analysis of ecosystems on larger spatial and temporal scales (Ehleringer & Field, 1993).

For management of this kind of large-scale modelling, a well organised modelling team is necessary. As suggested by Kiester (1991), in addition to one or more modellers, an experimental physiologist with a short-term physiological view, a field ecologist with a long-term view, and a computer scientist (not just a programmer) to deal with issues of language, expressiveness, and communication, are all required.

6.3.3 Application Prospects: software development

New developments in computer software and hardware, artificial intelligence (AI), and programming methodology can be expected to help not only the modeller to deal the increasing complexity of ecological problem, but users to acquire a more friendly simulation tool.

Modelling, in its computerised form, increasingly will become a key knowledge component in all forms of decision making in modern life (Zeigler, 1984). The historical development of forest models has been greatly catalysed by increased availability of computers. Large quantitative mathematical models based on physical and physiological principles and ecological theory are impossible without the high speed computer.

An increasing usage of the declarative program represents a significant technological advance. In knowledge processing, qualitative and quantitative knowledge about system components and their relationships are entered into a knowledge base, whereby the highly modularised design of the program allows the model to be modified without changing the whole program, therefore saving time.

On the user side, logic-based approaches and other AI techniques can help to make modelling accessible to the ecologist and forest manager with no modelling experience (Muetzelfeldt *et al.*, 1987; Robertson *et al.*, 1991)

In addition, animated three-dimensional colour graphics of forest dynamics also provide a vivid interface for assessing forest development and provides users with assistance in formulating sustainable management policies.

The software that bears the features outlined above will greatly enhance applications of forest modelling. The trend is reflected in the founding of the journal *AI Applications in Natural and Resource Management*, and in various essays by Muetzelfeldt *et al.* (1987), and Robertson *et al.* (1991).

6.3.4 Problems Facing Us in the Scaling Study

In this scaling study, through development of the hierarchical model FORDYN, some new problems have been exposed to our ecological modelling community:

- knowledge gaps that limit scaling studies: e.g.
  - C, N, and water coupling relations and their functional effects on tree growth; the ideas and assumptions of Thornley (1991) and Dewar (1993) need experimental support; and
  - phenological aspects of tree physiological processes such as photosynthesis (e.g. photoinhibition) and assimilate allocation, and especially the difficulty of identifying and understanding developmental rhythms such as those involved in budbreak, flowering, and senescence of leaves.

- limits to computational time:

  In the 1960's and 70's, the development of the forest model was catalysed by the introduction of high speed computers. Today, even more computing power is needed for scaling up.

  It is often suggested that it is unrealistic to simulate more than two levels of processes because of the computation time needed; e.g. as shown in Table 6.1, the scaling ratio of time (the ratio of time scales changed) is enormous:

TABLE 6.1

Scaling ratio of time scales in the model FORDYN:

level	1	2	3	4	Scaling ratio (dimensionless)
time scale (second)	10^{0-2}	10^{3-5}	10^{6-9}	10^{9-11}	10^{9-11}
or	seconds	hours	years	centuries	

- difficulties in collecting the enormous amount of data needed for validation and application resulting from the complexity of the model; and

- the 'art' of scaling-up needs to be better understood:
  it is crucial to know what fine detail is relevant to the higher levels, and what is noise.

6.4 Conclusions

By addressing the problem of hierarchy or scale in simulation of forest ecosystem dynamics, some experience and insights have been obtained:

- A practical model named FORDYN, involving four levels, cell biochemical processes of photosynthesis, leaf physiological processes, tree growth processes, and forest succession processes, has been proposed. It appears to be the first forest model to straddle all these four levels.

- For many purposes, not all the levels are needed. The user may select one of four modes to utilise whatever information he/she may have. The model structure is flexible and permits less elaborate simulation schemes.

- The FORDYN has provided a test-bed to explore current ideas about scaling, which are considered to be important in ecological research.

- An attempt has been made to validate the model in its fully developed form, using stand data on *Pinus sylvestris* from the European Pine Modelling Workshop, and some data on stand growth collected locally.

- The model has also been applied to make predictions about the response of forest to elevated CO_2 and it indicates a reduction in response sensitivity to CO_2 as one proceeds from leaf level to stand or ecosystem level; the reduction is attributable to an increase in feedback between levels.

- Last, but not the least, an example of unification of population biology and ecosystem science has been provided (For a long time previously, these two subdisciplines have been separately studied). The model FORDYN can represent both structure and dynamics of the populations of each tree species in a forest, and ecosystem functions, such as nitrogen, carbon, and water exchanges between forest and environment, on the common basis of biological processes.

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Appendices

I. List of Tables

II. List of Figures

III. List of Parameters and Variables Used in the Program of FORDYN

Name	Description	Unit
A1	CO_2 assimilation rate	μmol CO^2 m^{-2} s^{-1}
A2	CO_2 assimilation rate	μmol CO^2 m^{-2} s^{-1}
aa	intermediate variable	radians
AA1	intermediate variable	m
AC	intermediate variable	m^2
aj	quantum yield	*-
ALFA	intermediate variable in wind calculation	-
AMPLTD	average atmospheric CO_2 concentration	ppm
ANGOT	daily extraterrestrial radiation	J m^{-2}d^{-1}
AOB	intermediate variable	-
AR	ratio of respiring wood to non-respiring wood	-
ASSIP	assimilate gain of each tree per year	kg CH_2O stem^{-1} y^{-1}
ASSIPR	potential assimilate supply rate per tree	kg CH_2O stem^{-1} y^{-1}
ASSUR	specific assimilate use rate per tree	y^{-1}
ATEMP	monthly average air temperature	^{0}C
ATEMP1	annual average air temperature	^{0}C
av	Rubisco activation as a function of R	-
AVRAD	total daily radiation	J m^{-2} d^{-1}
b1	species-based coefficient for H-DBH relation	m
b2	species-based coefficient for H-DBH relation	dimensionless
b3	species-based coefficient for H-DBH relation	m^{-1}
BANK	seed production in a gap	-
BATMP	base temperature for phenological development	^{0}C
bb	intermediate variable	radians
BB1	intermediate variable	m
BIOM	biomass of a tree	kg CH_2O stem^{-1}
BIOM0	=BIOM	kg CH_2O stem^{-1}
BIOMG	gross biomass increment of each tree	kg CH_2O stem-1 y-1

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BIOM0	=BIOM	kg CH_2O $stem^{-1}$
BIOMG	gross biomass increment of each tree	kg CH_2O stem-1 y-1

BIOML	loss of biomass of a tree	kg CH_2O stem-1 y-1
BIOMS	average biomass per tree by species	kg CH_2O stem^{-1}
BIOMT	total biomass of a species	kg CH_2O
BIOMX	maximum single tree biomass of a species	kg CH_2O stem^{-1}
BK	light extinction parameter	-
BNLOC	specific nitrogen relocation of branch	-
BRANCH	biomass of branch	kg CH_2O stem^{-1}
BRANCHS	average branch biomass per tree by species	kg CH_2O stem^{-1}
BRK	average maintenance respiration rate of biomass	y^{-1}
BW	wood weight per volume of tree by species	Mg CH_2O m^{-3}
C	specific parameter for DBH-LAI relation	m^{-2}
Calw	carbon transport conductance between shoot and wood	-
CASS	assimilate availability factor per tree	-
Cawr	carbon transport conductance between wood and root	-
CD	crown radius-DBH ratio of each tree by species	-
Cdd	parameter used in wind speed calculation	-
CDmax	maximum crown radius-DBH ratio by species	-
Ci	intercellular CO2 concentration	μmol mol^{-1}
CL	crown length	m
CLEAF	carbon mass per leaf area	kg C m^{-2}
CLEAF0	carbon substrate in shoot	kg C stem^{-1}
CLIAT	litter decomposition rate	y^{-1}
CLIOM	carbon transfer rate in humification	kg C y^{-1}
CLITR	carbon in litter	kg C
CLL	=CL	m
CLR	crown length-radius ratio	-
CLUSTF	clustering variable in radiation calculation	-
CNI	nitrogen availability factor of each tree	-
CNLIT	carbon/nitrogen ratio in litter	-
CNSOM	C/N ratio in soil organic matter	-
CO2AIR	ambient CO2 concentration	μmol mol^{-1}
CO2CP	CO2 compensation point	ppm
CO2FN	intermediate variable of CO2 concentration calculation	ppm
CO2MAX	maximum atmospheric CO2 concentration	ppm
CO2MID	intermediate variable of CO2 concentration calculation	ppm

CO2MIN	minimum atmospheric CO2 concentration	ppm
COMAT	humus decomposition rate	y^{-1}
COSLD	intermediate variable	-
COUP	coupling factor in caculation of transpiration	-
CP	crown profile of a tree	m^2
CP1	a function for calculation of CO2 compensation point	ppm
CPAIR	molar heat capacity at dry air at sea level	J mol^{-1} kPa^{-1}
CPP	crown profile of subject tree	m^2
CR	crown radius of a tree	m
CRNLOC	specific nitrogen relocation of coarse root	-
CROOT	carbon substrate in root	kg C stem^{-1}
CRR	crown radius of subject tree	m
CSOM	carbon in soil organic matter	kg N y^{-1}
CSP	density of wood in carbon by species	kg CH_2O m^3
CWOOD	carbon substrate in wood	kg C stem^{-1}
D1	density-dependent dispersal parameter of a species	-
D2	distance-dependent dispersal parameter of a species	-
DARE	dark respiration of leaf of a species	mol m^{-2} s^{-1}
DARK	dark respiration rate of a tree	g C stem^{-1}d^{-1}
DATMP	mean daily temperature	^{0}C
DAY	the day of a year	-
DAYL	day length	h
DBH	diameter in breast height of a tree	m
DBHG	DBH increment	m
DBHS	average DBH of a species	m
DEC	declination of the sun	degree
DECR	decomposition rate	y^{-1}
DELM	the total silhouette area of crowns in the stand	m^{-2}
DELTA	intermediate variable in calculation of transpiration	-
DEN	density of the stand	stem ha^{-1}
DK	rate of dark respiration at zero ^{0}C	mol m^{-2} s^{-1}
DML	=sqrt(DMLF)	m^2
DMLF	single side leaf area	m^{-2}
DOM2	intermediate variable	-
DSINB	integral of SINB over a day	-

DSINBE	intermediate variable	-
DSTEP	simulation time step by days within a year	d
DT	=DSTEP	d
DTCR	crown radius of the dead tree whereby gap produced	m
DTCR	radius of crown profile of dead a tree in the gap	m
DTT	dispersal distance	m
DTX	X coordinate of dead tree in the gap	m
DTY	Y coordinate of dead tree in the gap	m
DVS	phenological stage	-
DVSTB	phenological development based on temperature sum	-

E	activation energy	J mol^{-1}
ELL	low light use efficiency	-
EPSLON	intermediate variable in calculation of transpiration	-
EST	intermediate variable in calculation of transpiration	-
ET1	equilibrium transpiration rate	mol m^{-2} s^{-1}
ET2	imposed transpiration rate	mol m^{-2} s^{-1}

FBRAF	fraction of branch of each tree	-
fc	carbon content of meristem and structure	kg C $stem^{-1}$
FFRESP	updated specific respiration rate of leaf by tree	d^{-1}
Fg	intrinsic growth rate of leaf meristem	d^{-1}
FK0	constant determining meristem size of leaf	kg CH_2O m^{-2} C^{-1} N^{-1}
fl	shoot fraction of a tree	-
FLFRTF	specific final leaf-root ration of of a tree	-
FLSHA	fraction of shaded leaves area of subject tree	-
FLSUN	fraction of sunlit leaves area of subject tree	-
FLUX	intermediate variable	w m^{-2}
FLUXSHA	radiation absorbed by shaded leaves	w m^{-2}
FLUXSUN	radiation absorbed by sunlit leaves	w m^{-2}
FLUXSUN1	intermediate variable	w m^{-2}
fn	nitrogen content of meristem and structure	kg N $stem^{-1}$
FNLOC	nitrogen relocation of leaf	-
FNUM2	intermediate variable	-
FOL	fraction of each leaf age class	-
fr	root fraction of a tree	-

FRDIF	fraction of diffuse light from transmission	-
FRRESP	updated specific respiration rate of wood of tree	d^{-1}
fw	wood fraction of a tree	-
FWRESP	updated specific respiration rate of root by tree	d^{-1}
FZ	accumulated leaf area above subject tree in calculation of light competition between trees	m^{-2}

G	germination factor of a species	-
G1	pool of components of the glycolate pathway	$\mu mol\ m^{-2}\ s^{-1}$
GA	boundary layer conductance	$m\ s^{-1}$
GAM	intermediate variable in calculation of transpiration	-
Gamma	compensation point when no non-photorespiration	Pa
GAP	number of seedling in a gap	-
GB	growth respiration factor per tree by species	-
Gcl	utilization of carbon for shoot growth	kg C $stem^{-1}$
Gcr	utilization of carbon for root growth	kg C $stem^{-1}$
Gcw	utilization of carbon for wood growth	kg C $stem^{-1}$
GGAA	=GA1	$\mu mol\ m^{-2}\ s^{-1}$
GGAS	leaf conductance	$\mu mol\ m^{-2}\ s^{-1}$
GGMM	=GA1	$\mu mol\ m^{-2}\ s^{-1}$
GGSS	=GS1	$\mu mol\ m^{-2}\ s^{-1}$
Glc	leaf conductance	$\mu mol\ m^{-2}\ s^{-1}$
Glc0	=Glc	$\mu mol\ m^{-2}\ s^{-1}$
GM	mesophyll conductance	$m\ s^{-1}$
GMMX	maximum leaf temperature for mesophyll conductance	^0C
GMT	temperture limit of leaf mesophyll conductance	-
Gnl	utilization of nitrogen for growth of shoot	kg N $stem^{-1}$
Gnr	utilization of nitrogen for growth of root	kg N $stem^{-1}$
Gnw	utilization of nitrogen for growth of wood	kg N $stem^{-1}$
GS	stomatal conductance	$m\ s^{-1}$
GS1	stomatal conductance	$\mu mol\ m^{-2}\ s^{-1}$
GSL	light limit of leaf stomatal conductance	-
GSLPV	slope of the curve of stomatal response to VPD	$mol^{-1}\ m^{-1}\ s^{-1}\ kPa^{-1}$
GSPXP	stomatal conductance response to predown xylem potential	-
GST	temperture limit to leaf stomatal conductance	-
GSVP	VPD limit to leaf stomatal conductance	-

H	height of a tree	m
H4	parameter used in Jmax-temperature ralation	-
HARD	height and base diameter ratio of a tree	-
HARDM	maximum height and base diameter ratio of a tree	-
HCANPY	average tree height of the stand	m
HD	tree height-DBH ratio of a species	-
HH	=H	m
HMAX	maximum tree height of a species	m
HMH	mature tree height of a species	m
HOUR	time by hour within a day	-
HR	humification ratio	-
HS	average tree height of a species	m
HUMC	organic content in soil	kg C y^{-1}
HUMINR	humus mineralization rate	y^{-1}
ICRLIM	increment limit of assimilate supply	y^{-1}
IGAUS3	3 point Gauss scheme	-
IGAUS5	5 point Gauss scheme	-
IHI	intermediate variable	-
ILO	intermediate variable	-
IM	intermediate variable	-
INGRP	specific wood increment rate	y^{-1}
INI	=NITC	y
INSW	a switch function	-
INTGRL	a integral function	-
IYEAR	initial year of simulation	-
IZ	radiation onto the crown of subject tree	w m^{-2}
J	species no.	-
JJ	=J	-
Jmax	light saturated potential rate of electron transport	$EqChl^{-1}s^{-1}$
Jr	coefficient used in Jmax-temperature relation	J mol^{-1}
K	tree number	-
K0	Michaelis-Menten constant for O2	Pa

LFGRP	leaf growth rate factor	-
LFRTD	total leaf and fine root demand per tree	kg CH_2O stem^{-1} y^{-1}
LFTUR	leaf turnover rate per tree by species	y-1
Lgd	daily leaf growth rate	d^{-1}
Lgy	leaf growth rate	y^{-1}
LINT	a linear interpolation function	-
LITAV	total amount of litter in the stand	kg
LITLF	total leaf litter	kg
LITRT	total root litter	kg
LITWD	total wood litter	kg
LL	intermediate variable	-
Lms	loss in meristem to intrinsic differentiation by leaf	kg stem^{-1}
LN	=K	-
Ln	leaf nitrogen content	kg N stem^{-1}
Lns	nitrogen concentration rate of leaf	kg N stem^{-1}
LWP	leaf water potential	mPa
LWPmin	minimum leaf water potential	mPa
LYEAR	final year of simulation	-

M	intermediate variable	-
MAXGS	maximum stomatal conductance of a species	mol m^{-1} s^{-1}
ML	seedling no. in gap	-
MP	intermediate function for calculating species no. of new seedling	-
MRLEAF	daily leaf maintanence respiration of each tree	g CH_2O stem^{-1} d^{-1}
MRROOT	daily root maintanence respiration of each treeg	g CH_2O stem^{-1} d^{-1}
MRWOOD	daily wood maintanence respiration of each tree	g CH_2O stem^{-1} d^{-1}
MS	species no. of the seedling in the gap	-

N	intermediate variable	-
NAGE	leaf age class	-
Narw	nitrogen transport conductance between wood and root	-
NAV	plant available nitrogen in soil	kg N
NAVR	nitrogen availability rate from soil	kg N y^{-1}
NAVSR	nitrogen uptake rate from soil	kg N y^{-1}
Nawl	nitrogen transport conductance between wood and shoot	-
NBRANCH	nitrogen in branch of a tree	kg N stem^{-1}

Nchl	proportion of leaf nitrogen in chlorophyll	-
NCPLANT	N:C in the plant	-
ND	intermediate variable	-
NDD	=DSTEP	d
NDLEAD	nitrogen demand for leaf growth	kg N stem^{-1}
NDROOT	nitrogen demand for fine root growth	kg N stem^{-1}
NDROOTT	total nitrogen demand for fine root	kg N y^{-1}
NDTNO	no. of dead tree in ther gap	-
NDTOT	total nitrogen content in dead tree	kg N
NDWD	nitrogen content in dead wood by species	kg N stem^{-1}
NDWOOD	nitrogen demand for wood increment	kg N stem^{-1}
Neff	nitrogen efficiency factor of tree growth	-
NEW	intermediate function for calculating species no. of new seedling	-
NEWS	intermediate function for calculating species no. of new seedling	-
NFIX	total nitrogen fixation rate by trees	kg N stem^{-1} y^{-1}
NFIXM	maximum nitrogen fixation rate per tree by species	kg N stem^{-1} y^{-1}
NG	gap no. in the stand	-
NIGHT	night length	h
NIRLOC	relocation of nitrogen for litter by species	-
NISR	potential nitrogen supply rate	kg N y^{-1}
NITAV	total amount of avilable nitrogen in litter for decomposition	-
NITC	nitrogen deficiency time constant	y
NLEACH	nitrogen leaching rate	kg N y^{-1}
NLEAF	nitrogen content in leaves of each tree	kg N stem^{-1}
NLEAFT	total nitrogen content in dead leaf	kg N
NLF	nitrogen content in green leaf	kg N kg CH_2O^{-1}
NLINP	nitrogen mineralization in litter	kg N y^{-1}
NLIOM	nitrogen transfer rate in humification	kg N y^{-1}
NLITR	nitrogen in forest litter	kg N
NLLEAF	nitrogen loss rate in leaf litter	kg N stem^{-1}
NLROOT	nitrogen loss rate in root litter	kg N stem^{-1}
NLTOT	total nitrogen loss rate	kg N y^{-1}
NLWOOD	nitrogen loss rate in wood litter	kg N stem^{-1}
NOLF	nitrogen content in yellow leaf	kg N kg CH_2O^{-1}
NOMNP	nitrogen mineralization from humus	kg N y^{-1}
Nother	proportion of leaf nitrogen other than Nrub and Nchl	-

NPP	net photoproduction per tree	g CH$_2$O stem^{-1}d^{-1}
NPPD	net daily photoproduction	g CH$_2$O stem^{-1}d^{-1}
NPPD1	intermediate variable	g CO2 stem^{-1} d^{-1}
NPPY	net annual photoproduction	kg CH$_2$O stem^{-1}y^{-1}
NPREC	nitrogen input by deposition	kg N y^{-1}
NRDWOOD	nitrogen in non-respiring wood of a tree	kg N stem^{-1}
NRLEAF	nitrogen relocation rate from leaf	kg N stem^{-1}
NROOT	nitrogen in fine root of each tree	kg N stem^{-1}
NROOTT	total nitrogen content in dead root	kg N
NRROOT	nitrogen relocation rate from fine root by tree	kg N stem^{-1}
NRRWOOD	nitrogen in respiring wood of a tree	kg N stem^{-1}
NRT	nitrogen content of fine root of each tree	kg N stem^{-1}
NRTOT	total nitrogen relocation	kg N y-1
NRWD	nitrogen content in dead wood	kg N
NRWD	nitrogen content in respiring wood by species	kg N stem^{-1}
NRWOOD	nitrogen relocation rate from dead wood by tree	kg N stem^{-1}
NSEEDL	seed number in the stand	-
NSOM	nitrogen in soil organic matter	kg N
NT	number of competitor for light competition	stem
NTMAX	potential new born seedling no. allowed in the stand	-
NTOT	total nitrogen in tree biomass	kg N y^{-1}
NTREE	total tree number of a species	stem
NTREEDN	total amount of nitrogen in dead trees in the stand	-
Nu	nitrogen uptake rate from soil by the fine root	kg N d^{-1}
NUP	actual nitrogen uptake rate	kg N y^{-1}
NUPD	total nitrogen uptake demand from soil in the stand	kg N y^{-1}
NUPDT	total nitrogen uptake demand for tree growth in the stand	kg N y^{-1}
NUR	specific nitrogn uptake rate	-
NWOODT	total nitrogen content in dead wood	kg N
NYEAR	time by year during simulation	-

Paccl	acclimated photosynthesis rate	-
PAI	pi=3.141516	-
PAR	photosynthetic active radiation	w m^{-2}
PARDIF	flux density of diffuse component of PAR	w m^{-2}
PARDIR	flux density of direct component of PAR	w m^{-2}

PARSUM	daily sum of radiation received by tree	J stem $^{-1}$ d^{-1}
Patm	atmospheric pressure	Pa
PAWER2	intermediate variable	-
PHOP	photosyntheic rate of a tree	µmol CO_2 stem^{-1} s^{-1}
PHOPD	daily photoproduction of each tree	g CH_2O stem^{-1} d^{-1}
PHOPH	hourly photoproduction of each tree	g CO2 stem-1 h-1
PHOPH1	=PHOPH	g h^{-1} stem^{-1}
PHOPL	instantaneous leaf photosynthetic production	µmol m^{-2} s^{-1}
PHOPY	annual photoproduction of each tree	kg CH_2O stem^{-1} y^{-1}
Pi	intercellular CO_2 partial pressure	Pa
Pi0	=Pi	Pa
PMAG	updated maximum photosynthetic rate with leaf age effect	-
PMAGTB	photosynthesis-leaf age relation table	-
PMAX	updated maximum photosynthetic rate	µmol CO_2 m^{-2} s^{-1}
PMAXO	maximum PMAX in ideal condition	µmol CO_2 m^{-2} s^{-1}
PMDVST	photosynthesis-phenology relation table	-
PMTMPT	photosynthesis-temperature relation table	-
PMXAGE	leaf age effect on photosynthesis	-
PMXDVS	leaf-age correction factor of photosynthesis	-
PMXTMP	temperature effect on photosynthesis	-
Po2	partial pressure of O_2	Pa
PSHA	photoproduction by shaded leaves	µmol CO_2 m^{-2} s^{-1}
Psi	curvature of extended Michaelis-Menten form for activation of Rubisco by light	-
PSUN	photoproduction of sunlit leaves	µmol CO_2 m^{-2} s^{-1}
PSUN1	intermediate variable	µmol CO_2 m^{-2} s^{-1}
PXP	intermediate variable	-

q	=VEX	-
Q10	coefficient on respiration-temperature relation	-
QFE	apperent quantum flux density	mol m^{-2} s^{-1}

R	pool of reduced intermediates including RuBP	mol m^{-2} s^{-1}
RA	conversion factor from degree to radians	-
RAD	base radius of each tree	m
RATE	intermediate variable	-

RCOEQ	quantum flux density coefficiency for dark respiration	$m^2\ s^{-1}\ mol^{-1}$
RCOET	temperature coefficient for dark respiration	-
Rcs	carbon concentration rate of root	kg C $stem^{-1}$
RDDIR	absorbed direct component of direct radiation	w m^{-2}
RDIF	absorbed diffuse radiation	w m^{-2}
REFH	reflecton coefficient for horizontal leaves	-
REFS	reflection coefficient for spherical leaves/includes angle distribution	-
RELOC	assimilate relocation rate	d^{-1}
RELOG	assimilate relocation by day of each tree	g CH_2O $stem^{-1}$ d^{-1}
RESP	daily respiration rate of each tree	g CH_2O $stem^{-1}$ d^{-1}
RESPG	daily growth respiration of each tree	g CH_2O $stem^{-1}$ d^{-1}
RESPM	maintenance respiration	g CH_2O $stem^{-1}$ d^{-1}
Rg	intrinsic growth rate of root meristem	d^{-1}
Rgc	parameter used in Jmax-temperature ralation	-
Rgd	dialy root growth rate	d^{-1}
RGR1	tree growth rate for mode 1	$stem^{-1}$ y^{-1}
RGR2	tree growth rate for modes 2, 3, & 4	$stem^{-1}$ y^{-1}
Rgs1	coefficient for stomatal conductance-soil water content relation	$m^3\ m^{-3}$
Rgs2	coefficient for stomatal conductance-soil water content relation	$m^3\ m^{-3}$
Rgy	root growth rate	y^{-1}
rh1	phloem resistance coefficient between shoot and wood	-
Rh1	phloem resistance to sap flow between shoot and wood	-
rh2	phloem resistance coefficient between wood and root	-
Rh2	phloem resistance to sap flow between wood and root	-
RK0	constant determining meristem size of root	kg DM m^{-2} $[C]^{-1}$ $[N]^{-1}$
RLEACH	plant-available nitrogen leaching rate of soil	y^{-1}
Rmax	maximum size of RuBP-pool	$\mu mol\ m^{-2}\ s^{-1}$
Rms	loss in meristem to intrinsic differentiation by root	kg CH_2O $stem^{-1}$
Rns	nitrogen concentration rate of root	kg N $stem^{-1}$
ROOT	fine root mass of each tree	kg CH_2O stem-1
ROOTF	root fraction of a tree	-
ROOTG	fine root renewal and growth of each tree by day	kg CH_2O $stem^{-1}$ d^{-1}
ROOTI	fine root growth of each tree by day	kg CH_2O $stem^{-1}$ d^{-1}
ROOTL	fine root loss rate of each tree by day	kg CH_2O $stem^{-1}$ d^{-1}
ROOTLIM	maximum root biomass per tree by species	kg CH_2O $stem^{-1}$
ROOTm	root meristem size	kg CH_2O $stem^{-1}$

ROOTMpot	potential root meristem size	kg CH_2O $stem^{-1}$
ROOTS	average root biomass by species	kg CH_2O $stem^{-1}$
RTDIR	absorbed total direct radiation	w m^{-2}
RTTUR	fine root turnover rate per tree by species	y^{-1}
RWOOD	respiring wood mass of each tree	kg CH_2O $stem^{-1}$
RZ	crown length	m
S	parameter used in Jmax-temperature ralation	-
SBIOM	total tree biomass of stand	kg CH_2O
SBIOM1	=SBIOM	kg CH_2O
SBIOMX	maximum biomass of stand	kg CH_2O
SC	solar constant	w m^{-2}
SCV	scattering coefficient	-
SDDF	density dependent seed production of a source tree	-
SEED	an initial value for random integer generator	-
SHADEC	shading area of competitor in calculation of competition	m^2
SHADES	shaded area of subject tree in calculation of competition	m^2
SHOOTm	shoot meristem size	kg CH_2O $stem^{-1}$
SINB	sine of the solar elevation	-
SINLD	intermediate variable	-
SL	scaling factor	-
SNTREE	total tree number in the stand	stem
SNTREE01	=SNTREE	stem
SNTREE1	intermediate variable	stem
SOILc	soil water capacity	m^3
SOILh	soil water potential	m^3 m^{-3}
SOILw	soil water volume	m^3
SPECNO	species number in the stand	-
SPRELF	specific leaf respiratory rate	d^{-1}
SPRESRT	specific fine root respiratory rate	d^{-1}
SPREWD	specific wood respiratory rate	d^{-1}
SPWSL	soil weight	kg m^{-3}
SST	intermediate variable for initialisation new born seedling in the stand	-
SSY	potential seed production per tree of a species	seed
STATE	intermediate variable	-
STBR	birth rate of stand	-

STBT	total seedlings established in the stand	stem
STDR	death rate of stand	-
STDT	total dead trees of stand	stem
STEM	stem biomass by tree	kg CH_2O stem^{-1}
STEM0	=STEM	kg CH_2O stem^{-1}
STEMI	stem biomass increment of each tree per year	kg CH_2O stem^{-1}y^{-1}
STEMS	biomass of stem of each tree	kg CH_2O stem^{-1}
SVP	saturated vapour pressure	mbar
SWP	soil water potential	kg kg^{-1}

TA	intermediate variable	^{0}C
TAIR	air temperature	^{0}C
TBT	total seedlings established in the plot of a species	stem
TC	total amount of carbon in soil organic matter	kg C
Tclw	carbon transfer from shoot to wood	kg N stem d^{-1}
TCO2	total amount of CO_2 produced in decomposition of soil organic	kg CO_2
Tcwr	carbon transfer from wood to root	kg C stem^{-1} d^{-1}
TDF	effect of tree size on seed production	-
TDT	total dead trees of a species	stem
TEMP	=ATEMP, or ATEMP1	^{0}C
THGM	maximum leaf temperature for mesophyll conductance	^{0}C
THGS	maximum leaf temperature for stomatal conductance	^{0}C
TLEAF	leaf temperature	^{0}C
TLGM	lowest leaf temperature for stomatal conductance	^{0}C
TLGS	lowest leaf temperature for mesophyll conductance	^{0}C
TMAX	maximum daily temperature	^{0}C
TMIN	minimum daily temperature	^{0}C
TMPACC	effective daily increment of temperature sum	^{0}C
TMPACC	effective daily increment of TMPSUM	^{0}C
TMPSUM	sum of daily temperature	^{0}C
TMPSUM	temperature sum	^{0}C
TN	nitrogen immorbilization in soil organic matter	kg N
TNDLW	total leaf biomass of all age classes of a tree	kg CH_2O
TNORM	reference temperature for temperature effect on	^{0}C
TNORS	reference temperature for soil process	^{0}C
Tnrw	nitrogen transfer from root to wood	kg N stem^{-1} d^{-1}

Tnwl	nitrogen transfer from wood to shoot	kg N $stem^{-1}$ d^{-1}
TO	temperature for zero activity of respiration	^0C
TOGM	optimal leaf temperature for mesophyll conductance	^0C
TOGS	optimal leaf temperature for stomatal conductance	^0C
TOPSL	topsoil depth	m
TRANSPA1	intermediate variable	J H_2O m^{-2} s^{-1}
TRANSPD	trspiration rate of each crown by day	g H_2O $stem^{-2}d^{-1}$
TRANSPF	transpiration rate by tree	mol H_2O $stem^{-1}$ s^{-1}
TRANSPH	trspiration rate of each crown by hour	g H_2O $stem^{-2}$ h^{-1}
TRANSPL	leaf transpiration rate	mol H_2O m^{-2} s^{-1}
TRANSPL	transpiration rate	g H_2O m^{-2} h^{-1}
TRANSPL1	transpiration rate	mol H_2O m^{-2} s^{-1}
TREEDC	total amount of carbon in dead trees in the stand	kg C
TREEDN	total nitrogen content in dead trees	kg N
TREENO	tree number in the stand	-
TRES	specific temperature effect on respiration	-
TRSS	temperature effect on soil processes	-
TSO	temperature for zero soil activity	^0C
TTD	distance between subject tree and competitor	m
TX	co-ordinates of each tree in X axis	m
TY	co-ordinates of each tree in Y axis	m
UGWDF	underground wood biomass fraction per year by species	-
Un	nitrogen uptake rate	kg N kg DM^{-1}
V0	Rubisco activation at zero light is a function of R	-
VAP	actual capor pressure	mbar
Vcar	rate of carboxylation	μmol m^{-2} s^{-1}
Vck	constant that converts moles of nitrogen in Rubisco to moles of reaction sites on Rubisco molecules	mol mol^{-1}
Vcmax	maximum rate carboxylation at full activation of Rubisco	m^{-2} s^{-1}
Veq_cmax	equilibrum carboxylation	μmol m^{-2} s^{-1}
VEX	convexity of photosynthetic light response curve	-
Vj	electron transport-limited rate of carboxylation	μmol m^{-2} s^{-1}
Vjk	constant that converts moles of nitrogen to moles of chlorophyll	mol mol^{-1}

Vjmax	maximum rate of regeneration of RuBP-pool	$m^{-2} s^{-1}$
VLAMTA	latent heat of vaporization of water	$J mol^{-1}$
VPD	vapor pressure deficit	mbar
Wc	RuBP-saturated rate of carboxylation	$\mu mol m^{-2} s^{-1}$
Wcs	carbon concentration rate of wood	$kg C stem^{-1}$
WDLSR	dead wood loss rate per tree by species	y^{-1}
Wg	intrinsic growth rate of wood meristem	d^{-1}
WGAUS3	weight of each point in 3 point Gauss scheme	-
WGAUS5	weight of each point in 5 point Gauss scheme	-
Wgd	daily wood growth rate	d^{-1}
Wgy	wood growth rate	y^{-1}
WINDAH	hourly wind speed	$m s^{-1}$
WINDZ	hourly wind speed at a tree height in the stand	$m s^{-1}$
WK0	constant determining meristem size of wood	$kg CH_2O m^{-2} [C]^{-1} [N]^{-1}$
Wms	loss in meristem to intrinsic differentiation by wood	$kg DM stem^{-1}$
WNDL1	leaf weight of the first leaf age class	$kg CH_2O m^{-2}$
WNDL2	leaf weight of the second leaf age class	$kg CH_2O m^{-2}$
WNDL3	leaf weight of the third leaf age class	$kg CH_2O m^{-2}$
Wns	nitrogen concentration rate of wood	$kg N stem^{-1}$
WOOD	wood mass of each tree	$kg CH_2O stem^{-2}$
WOOD1m	wood meristem size	$kg CH_2O stem^{-1}$
WOODF	wood fraction of a tree	-
WOODG	wood renewal and growth of each tree per year	$kg CH_2O stem^{-1} d^{-1}$
WOODI	wood increment of each tree by day	$kg CH_2O stem^{-1} d^{-1}$
WOODL	wood dead loss of each tree by day	$kg CH_2O stem^{-1} d^{-1}$
WOODMpot	potential wood meristen size	$kg CH_2O stem^{-1}$
WPREC	average precipitation per month	$mm H_2O month^{-1}$
WPREC1	water input into soil by rainfall	$m^3 H_2O d^{-1}$
WTRAN	soil water loss from transpiration of trees	$m^3 H_2O stem^{-1} d^{-1}$
WUE	water use efficiency	$\mu mol CO_2 \mu mol H_2O^{-1}$
XA	intermediate variable for calculating location of new seedling	m
XB	intermediate variable for calculating location of new seedling	m
XML	maximum length in X axis of sample plot	m
XX	=TX	m

YA	intermediate variable for calculating location of new seedling	m
YB	intermediate variable for calculating location of new seedling	m
YLFRTF	specific maximum leaf-stem ratio of a tree	-
YML	length in Y axis of sample plot	m
YSTEP	time step by years	y
YY	=TY	m
Z1	intermediate variable	µmol m^{-2} s^{-1}
Z2	intermediate variable	µmol m^{-2} s^{-1}
ZBC	length of clear bole	m
Zl	proportion of growth rate to meristem in leaf	-
Zr	proportion of growth rate to meristem in root	-
Zw	proportion of growth rate to meristem in wood	-
ZZ	=H	m

IV. Program Structure by FORTRAN of FORDYN

```
***************************************************************************
      PROGRAM FORDYN
***************************************************************************
      CALL CONTRO
      CALL OPEN

      IF (SCALE.EQ.1) THEN
            CALL INPUT1
            CALL READAT1
      ENDIF

      IF (SCALE.EQ.2) THEN
            CALL INPUT2
            CALL READAT2
      ENDIF

      IF (SCALE.EQ.3) THEN
            CALL INPUT3
            CALL READAT3
      ENDIF

      IF (SCALE.EQ.4) THEN
            CALL INPUT4
            CALL READAT4
      ENDIF

*11111111111111111111111111111111111111111111111== forest succession:
      DO 1000 NYEAR=IYEAR,LYEAR,YSTEP
            CALL THINNING
            CALL GAUSS

      IF (SCALE.NE.1) THEN
*22222222222222222222222222222222222222222222222222==tree growth:
```

```
      WTRAN=0
          DO 366 ND=0,365,DSTEP
             DAY=DAY+DSTEP
             CALL ASTROL
             CALL METEO

             DO 750 J=1,NSPEC
               CALL PHENO(J)
               CALL FOLIAGE(J)
 750  CONTINUE

             DO 800 K=1,SNTREE01
                 IF (SCALE.EQ.2) THEN
                    CALL RADIAT
                    CALL PHOSYN2(K,J,PHOPD,TRANSPD)
                 ELSE

*3333333333333333333333333333333333333333333333333== leaf physiology:
               DO 20 IN=1,IGAUS3
                 HOUR=12+INT(DAYL*0.5*XGAUS3(IN))
                 CALL RADIAT

                 IF (SCALE.EQ.3) THEN
                   CALL PHOSYN3(K,J,PHOPH,TRANSPH)
                 ENDIF

*4444444444444444444444444444444444444444444444444== cell biochemistry:
                 IF (SCALE.EQ.4) THEN
                   CALL PHOSYN4(K,J,PHOPF1,TRANSPF1)
                 ENDIF

*     1 µmol CO2 s-1 m-2 = 0.1584 g CO2 h-1 m-2 ;
*     1 mol H2O s-1 m-2 = 6.48*(1E+4) g H2O h-1 m-2
             PHOPH(K)=PHOPF1*0.1584
             TRANSPH(K)=TRANSPF1*6.48*(1E+4)
*444444444444444444444444444444444444444444444444444444444444444
```

```
*    daily photoproduction of each tree,  unit: g CO2 stem-1 d-1
         PHOPD(K)=PHOPD(K)+PHOPH(K)*DAYL*WGAUS3(IN)

*    daily transpiration of each tree, unit: g H2O stem-1 d-1
         TRANSPD(K)=TRANSPD(K)+TRANSPH(K)*DAYL*WGAUS3(IN)
 20    CONTINUE
*33333333333333333333333333333333333333333333333333333333333333333333333
              ENDIF

*    unit: g CO2 d-1 stem-1 ---> g CH2O d-1 stem-1
              PHOPD(K)=PHOPD(K)*(30./44.)

               CALL RESPN(K,J)
               NPPD=PHOPD(K)-RESP(K)
*    water uptake through transpiration of trees:
              WTRAN=WTRAN+TRANSP(K)*18/(1+E6)

               CALL ALLOC(K,J,NPPD,TRANSPD1,SWP,DT)
               CALL NCYCL1(K,J)

*    annual net assimilation of each tree,  unit: kg CH2O stem-1 y-1
              PHOPY(K)=INTGRL(PHOPY(K),NPPD/1000.,DSTEP)
         PHOPD(K)=0
 800    CONTINUE
*    water balance:
        SOILw = SOILw-WTRAN+WPREC1
366    CONTINUE
*2222222222222222222222222222222222222222222222222222222222222222222222222
        ENDIF

          DO 880 K=1, SNTREE01
              IF (SCALE.EQ.1) THEN
              CALL RADIAT(K,J)
              CALL PHOSYN1(K,J)
              ENDIF
 880  CONTINUE
```

```
      DO 900 K=1,SNTREE01
          IF (SCALE.EQ.1) THEN
            CALL GROWTH1(K,J)
            CALL MORTAY1(K,J)
            IF (RGR1(K).LE.0.0) THEN
              CALL RECRUT1
           ENDIF
        ELSE
          CALL GROWTH2(K,J)
          CALL MORTAY2(K,J)
            IF (RGR2(K).GT.0) THEN
              CALL RECRUT1
            ENDIF
        ENDIF
900 CONTINUE

     IF (NSEEDL.EQ.0.OR.NG.EQ.0) THEN
          SNTREE1=SNTREE01-NG+LL
     ELSE
          CALL RESRUT2
     ENDIF

     IF (SCALE.NE.1) THEN
          CALL NCYCL2
     ENDIF

     CALL OUTPUT01
1000 CONTINUE
*111111111111111111111111111111111111111111111111111111111111111111111111111111
   CALL CLOSE

   STOP
   END
```

V. Computer Program of FORDYN

See attached disc.

VI. Examples of the input files used for Glentress forest simulation

```
              ***  GEOGRINT  ***
------  input file for geographical data
 spec: 1=D. fir; 2=J. larch; 3=N. spruce;  4=W. hemlock; 5=sycamore.
*******************************************************************
------------------------------------------------------------------------------
XML      YML
60       20
```

```
               ***  STANDINT  ***
------  stand input file of Glentress stand
 spec: 1=D. fir; 2=J. larch; 3=N. spruce;  4=W. hemlock; 5=sycamore.
**********************************************************************
----------------------------------------------------------------------------------
TREENO      SPECNO       TX     TY      CR
1           1            6.5    5        2.6
2           1            8.8     1.2     3.7
3           1            3.7     11      3
4           1            8.3     10.2    4.2
5           1            17.2   8        3.8
6           1            20.9   2.1      3.8
7           2            31.7   3.8      3.7
8           2            17.5   1        4.6
9           2            33.9   8.1      4.6
10          2            34.4   19.1    3.6
11          2            34.2   11.4    3.5
12          2            34.3   12.4    1.3
13          2            33.3   13.5    2.7
14          2            34.9   13.2    1.7
15          2            33.2   14.5    2.8
16          2            34.4   15.1    1.7
17          2            36.6   14.7    2.6
18          2            35.8   13.2    1.7
19          6            38.6   13.2    2.7
20          3            41.8   16.5    3.1
```

21	3	41.8	10.1	3.7
22	6	42.0	12.5	2.9
23	6	41.1	12.6	2.6
24	3	46.0	3.3	2.9
25	3	48.2	4.5	2.6
26	3	50.3	4.2	2.6
27	3	54.4	4.6	2.8
28	3	55.5	6.1	2.1
29	3	56.1	9.7	2.7
30	3	57.3	10.8	2.5
31	3	58.4	7.3	2.9
32	3	59.4	1.7	2.6
33	4	1.3	6.8	0.5
34	4	4.2	5.3	0.3
35	3	6.0	4.6	1.3
36	3	2.5	9.9	1.1
37	3	2.1	12.3	0.7
38	3	3.3	12.1	0.4
39	3	3.7	12.2	0.5
40	3	5.3	10.6	0.8
41	5	4.2	1.8	0.3
42	5	6.4	17.3	0.9
43	5	7.7	16.7	0.8
44	3	8.1	3.0	0.4
45	3	8.8	0.2	0.7
46	3	6.4	8.1	0.4
47	3	13.1	12.0	1.5
48	5	13.1	7.0	1.4
49	3	16.0	7.0	0.5
50	3	15.9	7.2	0.5
51	3	18.3	8.3	0.5
52	3	18.7	8.6	0.6
53	3	20.5	10.2	0.7
54	5	3.0	6.6	0.3
55	3	7.0	11.2	1.2
56	3	27.7	18.4	1.6
57	3	30.0	17.3	2
58	1	32.0	17.7	2
59	1	33.5	19.6	0.9
60	1	32.7	19.7	0.8
61	1	32.0	19.2	0.6
62	1	31.8	19.3	0.8
63	3	59.9	17.4	3.8

```
            ***  TREE0INT  ***
------ input file for tree morphology
 spec: 1=D. fir; 2=J. larch; 3=N. spruce;  4=W. hemlock; 5=sycamore.
******************************************************

------------------------------------------------------------------------------
TREENO  SPECNO      DBH (cm)    H (m)
1           1         44           30.8
2           1         57.7         30
3           1         50.4         32.6
4           1         48.2         29.2
5           1         52.4         32.2
6           1         59.9         30
7           2         36.7         25
8           2         37.5         25
9           2         27           24
10          2         13.2         24
11          2         19.4         20.2
12          2         13.1         13.6
13          2         16.8         24.2
14          2         13.8         14.4
15          2         28.2         24.2
16          2         9.6          10
17          2         27.2         24.2
18          2         20.4         21
19          3         16.2         13
20          3         28.8         23
21          3         53.4         43
22          3         19.5         15.6
23          3         30           24
24          3         14.5         11.6
25          3         19.5         15.6
26          3         16.8         13
27          3         10.6         8.5
28          3         19.5         15.6
29          3         26.4         21
30          3         19.9         16
31          3         22.2         17.6
32          3         19.9         16
33          4         0.2          2.8
34          4         0.6          1.2
35          3         3            3
```

36	3	2.5	2.3
37	3	2.1	1.7
38	3	0.9	0.7
39	3	1.4	1.1
40	3	2.8	2.2
41	5	1.2	1.2
42	5	3	3.2
43	5	3	3.2
44	3	1.4	1.1
45	3	3	2.4
46	3	1.6	1.3
47	3	5.1	4.1
48	5	4.8	3.8
49	3	3.7	1.8
50	3	2.3	1.8
51	3	1.6	1.3
52	3	2.5	2
53	3	3.1	2.5
54	5	1.8	1.8
55	3	3.4	3.4
56	3	5.6	4.3
57	3	8.2	4.5
58	1	5.8	3.7
59	1	3	3
60	1	2	2.5
61	1	1.3	1.5
62	1	2	2.7
63	3	16.5	13.2

VII. DBH measurement in Glentress plot

TREE NO.	days after first measurement in 31/7/91 /date of measurements			
	0	361	666	744
	31/07/91	27/07/92	28/05/93	13/08/93
1	44	44.4	45	45.5
2	57.7	59.6	60.8	62.3
3	50.4	51.4	52.8	53.5
4	48.2	49.3	50.3	52.8
5	52.4	54.9	56.8	58.3
6	59.9	51.8	63.4	64.2
7	36.7	36.8	37.1	37.9
8	37.5	37.6	37.8	38.5
9	27	28.5	29.9	30.9
10	13.2	13.6	13.4	13.7
11	19.4	20.7	21.5	22.6
12	13.1	13.1	13.1	13.1
13	16.8	17.4	18.1	19.1
14	13.8	13.6	13.6	13.6
15	28.2	31.8	33.7	36
16	9.6	9.8	10.1	10.6
17	27.2	29.2	30.4	32
18	20.4	21.5	22.8	24.3
19	16.2	17	17.7	18.6
20	28.8	34.9	38.1	40.1
21	53.4	56.3	58.2	60.5
22	19.5	20.3	20.4	20.5
23	30	33.1	35.1	37.5
24	14.5	15.9	17.5	20
25	19.5	22	23.5	25.8
26	16.8	19.3	21.3	22.8
27	10.6	11.8	13	14.1
28	19.5	22.4	24.3	26.5
29	26.4	31.7	34.5	36
30	19.9	22.3	24.4	26.1
31	22.2	23.6	26.7	28.1
32	19.9	20	25.3	25.4
33	0.2	0.3	0.4	0.4
34	0.6	0.8	1	1.1
35	3	4.3	5.1	5.5
36	2.5	2.8	3.2	3.4
37	2.1	2.4	2.8	3

38	0.9	1.2	1.4	1.5
39	1.4	1.6	1.8	1.9
40	2.8	3.1	3.5	3.7
41	1.2	1.6	2	2.2
42	3	3.6	4	4.2
43	3	3.6	4.1	4.3
44	1.4	1.6	1.8	1.9
45	3	3.2	3.4	3.5
46	1.6	1.8	2	2.1
47	5.1	5.6	6.3	6.5
48	4.8	5.4	5.8	6
49	3.7	4	4.3	4.4
50	2.3	2.4	2.5	2.5
51	1.6	1.7	1.9	2
52	2.3	2.2	2.1	2.2
53	3.1	3.3	3.7	3.8
54	1.8	2.2	2.6	2.8
55	3.4	3.6	2.9	4.2
56	5.6	6	6.4	6.6
57	8.2	9.2	10.2	11
58	5.8	7.3	10.1	11.3
59	3	4.3	7.3	8.5
60	2	3.5	6.5	7.5
61	1.3	2.8	5.6	6.8
62	2	3.5	6.3	7.5
63	16.5	19	21	22.5

Publications

Luan, J., Grace, J., and Muetzelfeldt, R., 1992. Scales of organisation in forest ecosystem modelling, presented at the 6th European Ecological Congress, *Mésogée,* Vol. 52, pp 88, Museum d'Histoire Naturelle, Palais Longchamp, 13004 Marseille, France.

Abstract

There is an increasing interest in studying ecological systems over a wide range of spatial and temporal scales. Advances in ecophysiology need to be incorporated into ecosystem level studies in order to contribute ideas about the impact of global change. An integration between models which run at physiological and ecological scales seems highly desirable and long overdue. This contribution describes a plant ecophysiological simulator that scales up from the physiological-functioning scales (with some limited attention to biochemistry) to the scale of community succession.

The model discussed here is a physiologically-based three dimensional 'gap model' FORDYN. This is probably the first model that can simulate long term ecosystem (forest) dynamic changes on the basis of calculations made by 'scaling up' from the physiological level. It is designed to predict forest ecosystem succession, with individual and species attributes, with a resolution that enables modelling of hourly environmental responses to critical variables like radiation, temperature, and CO_2. The model is used to examine some specific forest ecosystems. The ecological implication of the simulation results are also discussed.