Ecophysiological studies on four species of tropical trees

BY

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Abstract

This study deals with the regeneration processes and the management of tropical moist forests. It is focused on the response to environmental variables of four tree species grown under different light regimes. Growth, photosynthesis and transpiration were analysed. Models of stomatal conductance and photosynthesis were fitted to obtain physiological parameters. These parameters together with environmental data were used as inputs for the simulation model, which predicted the growth of two species under field conditions. Ecophysiological studies and simulation models are discussed in terms of the mechanisms of forest regeneration and management practises.

The aims were to present a selected set of data obtained under natural and controlled environment conditions and to integrate such information into a theoretical framework, with which to obtain research priorities and to assess feasibility of management practices, e.g. enrichment planting.

The field work is an enrichment planting experiment where, at different thinning regimes, growth, mortality and environmental conditions were monitored. The controlled environment experiment consisted of growing tree seedlings at different light regimes and subsequently assessing their growth and gas exchange responses to light, humidity and temperature. Also, biomass allocation and leaf nitrogen content were assessed in both experiments. Finally, the growth of two species under field conditions was simulated.

The field experiment was particularly helpful in assessing the possibility of manipulating secondary forests canopies to optimize growth and mortality in enrichment planting schemes. The parameters obtained in the controlled environment experiment were very useful in the comparision of the species when grown at different light conditions. They were also important constituents of the simulation model. Although the performance of the species in the field was inadequately predicted, the simulation model was an invaluable tool for synthetizing the information collected, and it was also helpful in defining areas for further research.

the response of the species was, in general, as expected for secondary-forest and primary-forest species: primary-forest and late-secondary forest species, *B.alicastrum* and *S.macrophylla* respectively, displayed lower growth rates, and lower photosynthetic and transpiration rates than the secondary-forest species, (*C.alliodora* and *C.odorata*). Secondary-forest species were more plastic in their responses i.e. they displayed larger changes when shaded. Dry matter allocation patterns were complex and generalizations were difficult to draw. Nevertheless, all species tended to allocate more dry matter to stem and leaves when shaded. Secondary-forest species tended to favour leaf area and stem height while primary-forest species increased stem density.

Declaration

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

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CHAPTER 1

GENERAL INTRODUCTION.

1.1. Problem definition.

Tropical moist forests (TMF) are the most complex and diverse terrestrial ecosystems. Although they represent only 6% of the earth surface, they amount about 40-50% of the planetary stock of species (Myers 1980). Clearly, this biome is of outmost importance to mankind and at the present rates of conversion TMF may disappear by the end of the century (Gomez-Pompa et.al. 1972). This will mean a great reduction of life's diversity and lead to a permanent shift in the course of evolution (Myers 1980). This conversion is widely believed to be having direct and immediate effect on the environment, increasing soil erosion, flooding and droughts; and may have unforseen long-term consequences, like changes in the weather and loss of productivity, that may hinder Man's ability to sustain life in tropical regions (Farnworth & Golley 1974). Spontaneous settlers, shifting-cultivators and fuel-wood harvesters are blamed as the major contributors to the destruction of TMF. However, international enterprises e.g. cattle ranching, logging and local governmental development schemes are far more damaging due to their larger scale and the use of heavy machinery.

In Mexico TMF were estimated, at the beginning of this century, to cover about 110 000 km^2, approximately 5% of the country (Rzedowski 1978). Nowadays, the only substantial areas of TMF are the Lacandon forest, covering some 13 000 km^2, two areas at the Isthmus of Tehuantepec, about 2 500 km^2 each, and Los Tuxtlas with a few thousand hectare. These remnants are undergoing rapid conversion to farm and pastureland, mainly because of government-sponsored colonization programmes and cattle ranching (Ewell & Poleman 1980).

Shifting-cultivation has been practised for millennia and has not generally resulted in long-term elimination of TMF (Nations & Nigh 1978). However, in some areas the number of shifting cultivators has increased to a point where the forest is not allowed sufficient time for regrowth and soils become exhausted. Hence, farmers are obliged to move to primary forests or to the cities. Firewood cutting does not appear to rank as an important factor in

conversion of TMF. Only a small percentage of fire-wood is taken from TMF areas, and a still smaller percentage from primary forests. In most cases it is obtained from savanna woodlands, scrub and brush patches, and local woodlots (Myers 1980).

There has been a growing demand from developed nations for tropical timber, from 4 million m^3 in 1950 to a predicted 95 million m^3 by the year 2000. Although the commercial loggers tend to harvest selectively, only removing a small proportion of wood types available, they damage and impoverish large areas in their operations. These operations can destroy up to 2/3 of the remaining trees and roads, haulage tracks and dumping zones can account for 10-30% of the forest area (Burgess 1973). TMF contain few species conventionaly used for pulping, however, new technology now allows wood chips from many other species to be converted into pulp. As a result an increased pressure is expected on these forests in future years (Myers 1980). Cattle ranching plays a substantial role, the dominant role in Latin America, in conversion of TMF. This factor is becoming more important, mainly due to the demands of the international beef trade. Many ranches become unprofitable within less than 10 years, because the productivity of the sown grassland declines, which encourages ranchers to clear further patches of forest. This represents a new broad-scale variation of shifting agriculture (loc.cit.).

Improving farming methods and hence productivity of croplands might aleviate the pressure upon primary forests. For example, the change from non-sustainable use of forest environments to intensive and established forms of agriculture in the form of multiple sustained yield systems. These systems, in which a broad range of crops including trees are grown, have been used by ancient civilizations and are now suggested as means to increase productivity (Nations & Nigh 1978). The selective and integrated use of the forest includes other activities such as grazing, wildlife management and fishing. Plantations may also reduce the pressure on primary forests; however, at present only 5000 km^2 are established each year, which would supply only one third of the forest production required to relieve extreme exploitation of TMF during the next two decades (Myers 1980). Furthermore, plantations are costly to establish, attract diseases and pests, and require fertilizer to maintain productivity (Evans 1982). The most appropriate strategy is to establish plantations in the forests that have been already exploited and are now poor-quality secondary forests, degraded grasslands, or areas overburdened by forest farmers. Two factors

make this difficult to achieve; firstly plantation investors seek to locate their concessions within an extensive tract of primary forest, so that they can exploit the timber to capitalize their plantation; secondly, previously cleared forest areas are generally occupied by settlements of one sort or another, and it is politically difficult to uproot people in order to plant trees (Myers 1980). In these degraded areas, enrichment planting and agroforestry systems e.g. Taungya, are possible alternatives (Evans 1982). These options may reduce establishment costs and provide short-term benefits. These systems also utilize the local labour force and can complement multiple sustained yield systems.

Management involves disturbing or altering a system with the intention of achieving a specified result. It is particularly important to assess the potential success of a species in the field. That is, their tolerance ranges and their response to a variety of environmental factors. Studies in natural and controlled environments, using ecophysiological and modelling techniques, enable us to predict species potential success in the field by understanding their response to the environment (Landsberg 1986). Research on growth requirements of tree seedlings and saplings will improve our knowledge regarding the response of a particular species to the environment and help to select species that are appropriate for the management system chosen.

1.2. The tropical moist forest.

In geographical terms, these forests are approximately located between 23° latitude on either side of the equator. They may be defined as follows (Walter 1979): 'evergreen forests' grow in areas receiving not less than 100 mm of precipitation in any month for two out of three years, with mean annual temperature about 24 °C and essentially frost-free; in these forests some trees may be deciduous; the forests usually occur at altitudes below 1300 m; and in mature areas of these forests, there are several more or less distinctive strata. Forest ecosystems appear to be hypersensitive to availability of moisture, especially to the annual distribution. Thus, when a short dry period occurs, the endogeneous rhythm of tree species adapts to the climatic rhythm. As a result the vegetation exhibits definite seasonal changes in appearance, i.e. many trees loose their leaves, or sprout or flower at the same time. This variation has been called 'seasonal rain forest'. If the dry season becomes even longer, the type of forest changes. The upper tree storey is made up of deciduous

species, whereas the lower stories are still evergreen, so that it can be termed 'tropical semi-evergreen forest'. These definitions can also take account of a number of further variations, such as ecological factors (edaphic formations and swamp forests), divergences of structure and physiognomy (dense and open forest), and evolutionary aspects (primary and secondary forests).

1.2.1. Forest growth cycle.

In a closed forest, when a tree dies or falls, a gap forms. The canopy of a forest is continually changing as the trees grow and die. As a result, TMF may be described as a heterogeneous mosaic of regeneration areas of different ages (Oldeman 1983). They are characterized by having multi-layered and closed canopies, where gaps in the canopy trigger the regeneration processes (Whitmore 1982). When a gap is formed, the environmental conditions underneath change drastically. These changes enhance establishment, growth and reproduction of the trees below (Hartshorn 1980). Three phases can be distinguished in the forest growth cycle: gap, building and mature (Oldeman 1983). There are different ecological groups of tree species adapted to regenerate in gaps of different size (Denslow 1980). The principal characteristic of each group is the amount of light required by seedlings (Whitmore 1982). Seed biology, tree architecture and aspects of ecophysiology are also important. The filling process of a gap is called secondary succession, during which dominance is characterized by progressively more shade tolerant species (Bazzaz & Pickett 1980). The environment above and below ground differs between big and small gaps and two groups can be defined among tree species: those which regenerate in the open and big gaps and those which regenerate in small gaps and closed forest (Whitmore 1982). Response to light is one of the most important attributes of these species groups which are often called shade-intolerant and shade-tolerant species (Bazzaz & Pickett 1980).

1.3. Physiological ecology and modelling.

Management of TMF and degraded TMF requires a knowledge of the forest growth cycle, regeneration processes and the life history of the species. The study of these factors may range from individual physiological responses to

population dynamics and the matter and energy fluxes of the ecosystem. These responses, dynamics and fluxes are difficult to determine due to the multiplicity of factors affecting them and the long periods of time involved (Longman & Jenik 1974). For these reasons, both ecophysiological studies and simulation models are essential to understand the mechanisms underlying the species adaptation to the environment. Ecophysiological studies can contribute greater certainty about the consequences of disturbing forests, and mechanistic models, after adequate testing, may be used to extrapolate the consequences of conditions outside the range under which the original experimental work was carried out (Landsberg 1986). Even if it is not possible to develop accurate, reliable models, the attempt to formulate them leads to valuable insights into the functioning of the system being modelled, it is also a useful guide to the design of experiments.

1.4. Aims and scope.

The aims of this work are: to obtain, analyse and synthesize information from both natural and controlled environment experiments; to incorporate this information into a common framework, a model; and simulate the performance of the species studied under field conditions. This may contribute to the knowledge and understanding of tropical forest ecosystems, and help define areas for further research.

The study is concerned with the light response of four tropical tree species. Environmental factors other than light were assumed 'optimum' although they may reduce the plant's ability to utilize light.

To achieve these aims the work was divided in three sections:

a) Natural Environment (chapter 2). The field work, on enrichment planting was carried out in a ten-year secondary forest derived from a TMF in the south-east of Mexico. Three thinning treatments in different canopy layers were made, and the four species were planted within these treatments. Growth rates, mortality and dry matter allocation were evaluated during a period of three years. In addition, light and temperature were monitored during one year.

b) Controlled Environment (chapter 3). The responses to shade of tropical

tree saplings (the same species as in the previous experiment) were studied using a controlled environment cabinet. Two treatments were established: high and low light levels, which simulate two of the field conditions. The photosynthetic and stomatal responses to environmental variables were assessed. Growth analysis and dry matter allocation studies were also carried out.

c) Simulation Model (chapter 4). The results from the previous experiments were integrated in a common framework, a model, and used in a simulation exercise. Models of climate, radiation interception, photosynthesis and dry matter allocation were used to simulate the performance of the species studied under field conditions.

CHAPTER 2

ENRICHMENT PLANTING IN A SECONDARY FOREST.

2.1. Introduction.

Undisturbed areas of Tropical Moist Forest (TMF) are nowadays small and inaccessible. Previous TMF areas in Mexico are now used for human settlements, raising crops and cattle-ranching. Degraded TMF and secondary forests are common and natural regeneration of desired species has proved difficult to achieve in these forests (Fox 1976). Taungya and enrichment planting have been proposed as alternatives to plantations, saving the costs of complete land clearance and establishment (Evans 1982). Enrichment planting overcomes inadequate natural regeneration while largely retaining the forest structure and cover. This is achieved by supplementing the forest with lines or groups of desired species. Full overhead light, adequate lateral space and control of weeds is essential. Nevertheless no absolutely successful method has been devised (Evans 1982).

Research on growth requirements of tree seedlings and saplings will undoubtedly improve our knowledge of tropical tree regeneration patterns and enrichment planting methods. Different tree species vary in their requirements, particularly for light and nutrients, and sites vary in their environmental characteristics for example their canopy and soil structure. Therefore, species must be selected that are appropriate, and ecophysiological studies may help to avoid costly mistakes. Species can be varied at will but site characteristics are more difficult to manipulate. While canopy structure is modified and controlled before planting, soil conditions can hardly be changed. As a result, soil may be seen as a constraint while light can be modified, at least crudely, through the canopy structure.

The aims of this work are not directly focused on enrichment planting methods, where financial and economic variables are very important, but are aimed at obtaining knowledge on the response of saplings to the environment. We have the possibility of manipulating canopy layers to improve the establishment and growth of the desired species.

A 10-year-old secondary forest derived from TMF was planted with four

TMF tree species. The effect of removing some canopy layers on the growth and mortality of saplings is analysed. There were three treatments -open, shade and deep shade- and the response of the introduced saplings was assessed and related to the canopy structure.

Within each treatment the following environmental variables were monitored:

1.- Light: daily integral of photosynthetically active radiation (Q) above the canopy (measured for one year).

2.- Temperature: Maximum and minimum temperatures in all treatments (measured weekly for one year).

3.- Canopy transmissivity: hemispherical photographs (done once for all treatments).

Growth analysis, dry matter allocation and nitrogen content of the introduced saplings were assessed and the following characteristics analysed:

Growth:

a) Height and mortality (measured yearly over three years by destructive sampling).

b) Fresh-dry weight of leaves,stem and roots; leaf area, stem length and crown dimensions (measured yearly using stratified destructive sampling over two years).

Nitrogen content of leaves:

once after the second harvest.

2.2. Materials and methods.

2.2.1. Site description.

The Uxpanapa region was, before 1974, one of the last and most important areas of TMF in Mexico (Fig. 2.1). It lies between the meridians 94° 05′ and 94° 95′ west longitude, and the parallels 17° 10′ and 17° 25′ north latitude. Its

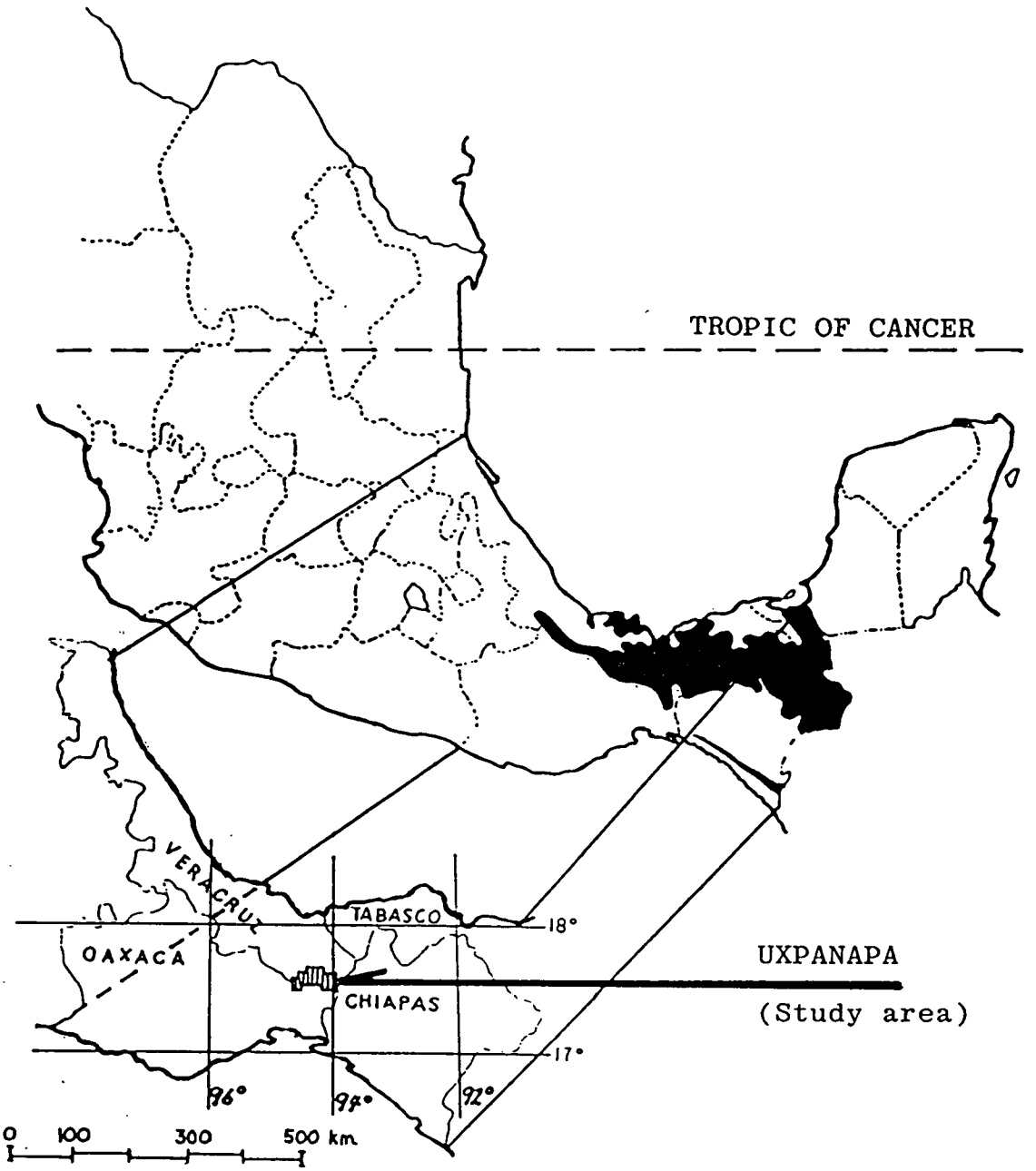


Fig. 2.1 Distribution of Moist Tropical Forest areas in Mexico (shaded area) and location of the study area within this region.

height above sea level varies between 100-200 m with an average value of 130 m (Marquez et. al. 1981). In general, the underlying geology consists of sedimentary rocks: limestone and sandstone. There are three soil types -alluvial, lateritic and carstic- the lateritic being the most frequent. The climate is hot and moist with summer rains and a dry spring season. The annual precipitation mean is 3640 mm and the mean annual temperature is 24.2 °C with monthly oscillations of 5-7 °C (Fig. 2.2).

The TMF of this region is variable, with evergreen, semi-evergreen, riparian and bamboo communities. The dominant species are: *Ceiba pentandra, Terminalia amazonia, Pouteria zapota, Manilkara zapota, Sterculia mexicana and Dialium guianense*. Between 1974 and 1976 a government resettlement scheme changed the face of this area. Using heavy machinery, 100 000 ha of the forest was clearcut, the objectives being firstly to relocate 50 000 peasants (who were moved from their original home because of a dam construction project) and secondly to develop a large intensive cereal-cropping project (Ewell & Poleman 1980). It had already been suggested that the project was dangerous and unrealistic (Gomez-Pompa 1979), because TMF are fragile in their energy and matter turnover, soils are shallow and unsuitable for mechanized agriculture and improved cereal seeds do not cope well with the humid tropical conditions. In addition, the peasants were forced to move and were not used to the new conditions of climate, machinery and social organization.

This area is now important for the study of regeneration patterns and proposed management schemes (Amo-del 1984). Some agriculture ministry sectors are shifting from cropping to cattle-ranching and others are experimenting with rubber plantations while the peasants have mainly returned to their traditional 'slash & burn' cropping systems. The result is that most of the area is now used as pastureland, for shifting cultivation, or is covered by several stages of secondary succession with relics of TMF. As a result the area is an interesting place to study the dynamics of secondary succession and the possibility of encouraging regeneration to a more productive stage. Enrichment planting is thought to be one possibility, although ecophysiological studies are necessary to find the limitations and requirements of desirable species for improved growth and survival.

This enrichment planting experiment was carried out in a 10-year-old

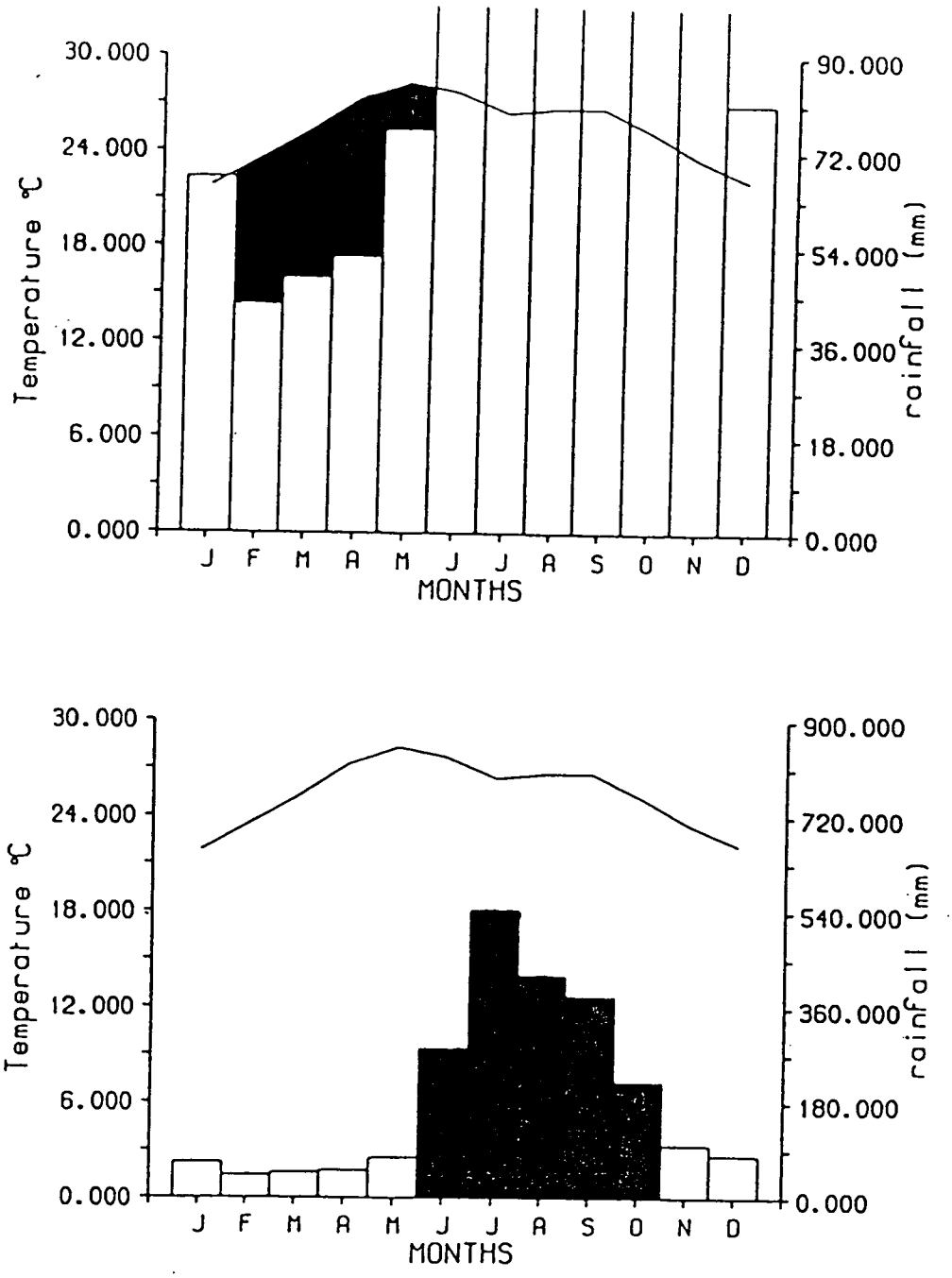


Fig. 2.2 Mean monthly temperature (continuous line) and monthly rainfall (bars) in the study area (Uxpanapa). The shaded areas indicate: the dry season (above) and the wet season (below), see text for explanation.

secondary forest. The area (20 ha) was fallowed in 1973, after which minor fellings were carried out. The area has a moderate slope of 4–15°; the soils are lateritic, clayed, very acid and with a high cation exchange capacity. Nutrient content of the vegetation and soils are negatively correlated: nutrient levels in the soil rise sharply after tree cutting and burning, falling back to normal levels once the vegetative cover establishes over a period of time (Williams 1982). The total biomass (at 8 years old) was 5268 g m^{-2}, 315 in the understorey (big herbs and shrubs) and 4953 in the overstorey (trees). 40% of the overstorey biomass was *Heliocarpus appendiculatus*, with 17% of *Cecropia obtusifolia* (loc.cit.).

A structural analysis of this forest (Ramos et.al. 1982) showed that the tree canopy can be subdivided into three height classes: *Cecropia obtusifolia* and *Heliocarpus appendiculatus* dominate the uppermost canopy, two melastomataceae species, *Bellucia spp.* and *Miconia hyperprasina* dominate the middle canopy, and many species share the lowest canopy with no clear dominance. The shrub layer is mainly represented by several species of *Piper*, along with other genera. The upper and, to a lesser extent, the middle canopies give the principal structural characteristics of this forest. Dominance index (Muller–Dombois & Ellenberg 1974) is 10–20 times higher in the top canopy than the medium, which is about 10 times higher than the lowest canopy (Ramos et.al. 1982). The tallest trees are composed of typical pioneer species (shade–intolerant) which form a continuous and more or less homogeneous layer. The middle canopy is dominated by secondary forest species (shade–tolerant) and the lowest is composed of late–secondary and primary forest species (shade–tolerant). These two are rather discontinuous and present a high variability in crown dimension and position, with small gaps and patches of dense vegetation being common. Although the lowest canopy is not important in determining the overall structure of the forest at this stage it is extremely important to the dynamics of the forest as it contains juvenile stages of potential dominants in a future mature forest. From an ecological point of view the forest has a good potential for regeneration, since after 10 years there are plenty of juvenile trees arising from its previous mature phase. Silviculturally, however, these may not be the most productive species suitable for use in a regeneration project.

2.2.2. Species description.

The species used for enrichment planting were chosen to represent a wide range of ecological groups, from early secondary to late secondary forest trees. The nomenclature used is related to the vegetation they belong to and their position within the canopy i.e. primary or secondary forests and shade tolerant or intolerant species. All the chosen species are common and abundant in Mexico's TMF and are present in the study area. They have economic value and a future productive potential. The following descriptions and figures (2.3–2.6) were taken from Pennington & Sarukhan (1968).

– *Cordia alliodora* (Ruiz & Pav.) Cham. Boraginaceae.

Form: This tree reaches 25 m in height and 90 cm in diameter at breast height (dbh); it has a straight trunk, round crown and ascendant branches (vertical in the upper crown).

Ecology: It is present in secondary vegetation derived from evergreen and semi-evergreen TMF. It has a very fast growth rate and grows up to an altitude of about 500 m.

Phenology: Flowering is between August and April, fruiting between September and April, and its leaves are shed between April and May.

Strategy: Early secondary forest species, shade-intolerant.

– *Cedrella odorata* L. Meliaceae.

Form: Up to 35 m in height and 1.7 m in dbh. This tree has a straight trunk with small buttresses, ascendant thick branches and a round, dense crown.

Ecology: It is very abundant in secondary vegetation derived from evergreen and semi-evergreen TMF.

Phenology: The flowering season is between May and August; leaves are shed after the maturation of the fruits, just before flowering.

Strategy: Secondary forest species, shade-intolerant.

- *Swietenia macrophylla* King. Meliaceae.

Form: Up to 70 m in height and 3.5 m in dbh, the trunk is straight but slightly fluted, with well developed buttresses up to 2–3 m height. It has thick ascendant and winding branches, with an open, round crown.

Ecology: It forms part of the evergreen and semi-evergreen TMF and is sometimes one of the emergent trees. It grows from sea level up to 750 m.

Phenology: It flowers from April to June, the fruits ripening from November to January, and in semi-evergreen TMF it sheds its leaves in the dry season.

Strategy: Late secondary, primary-forest species, shade-intolerant.

- *Brosimum alicastrum* Sw. Moraceae.

Form: Up to 40 m in height and 1.4 m in dbh. This tree has a straight trunk with well developed butresses, ascendant branches hanging at the end, and a pyramidal, dense crown.

Ecology: This is one of the dominant species of evergreen and semi-evergreen TMF in Mexico. It grows from the sea level up to 800 m.

Phenology: Flowering normally take place from November to February but sometimes occurs outside this period. Fruits ripen from March to May. Generally evergreen. They can shed their leaves in the dryest areas of their distribution.

Strategy: Primary forest species, shade-tolerant.

Ecological descriptions allow us to arrange the species within a successional gradient from pioneer to primary forest species. However, confusion arises when location of the species in an ecological gradient is confused with growing or physiological characteristics i.e. fast-growing or shade-tolerance. Although these characteristics are related it is important to describe and understand them separately.

Fig. 2.3 Cordia alliodora; leaves and floral characteristics. It also shows the species distribution in Mexico.

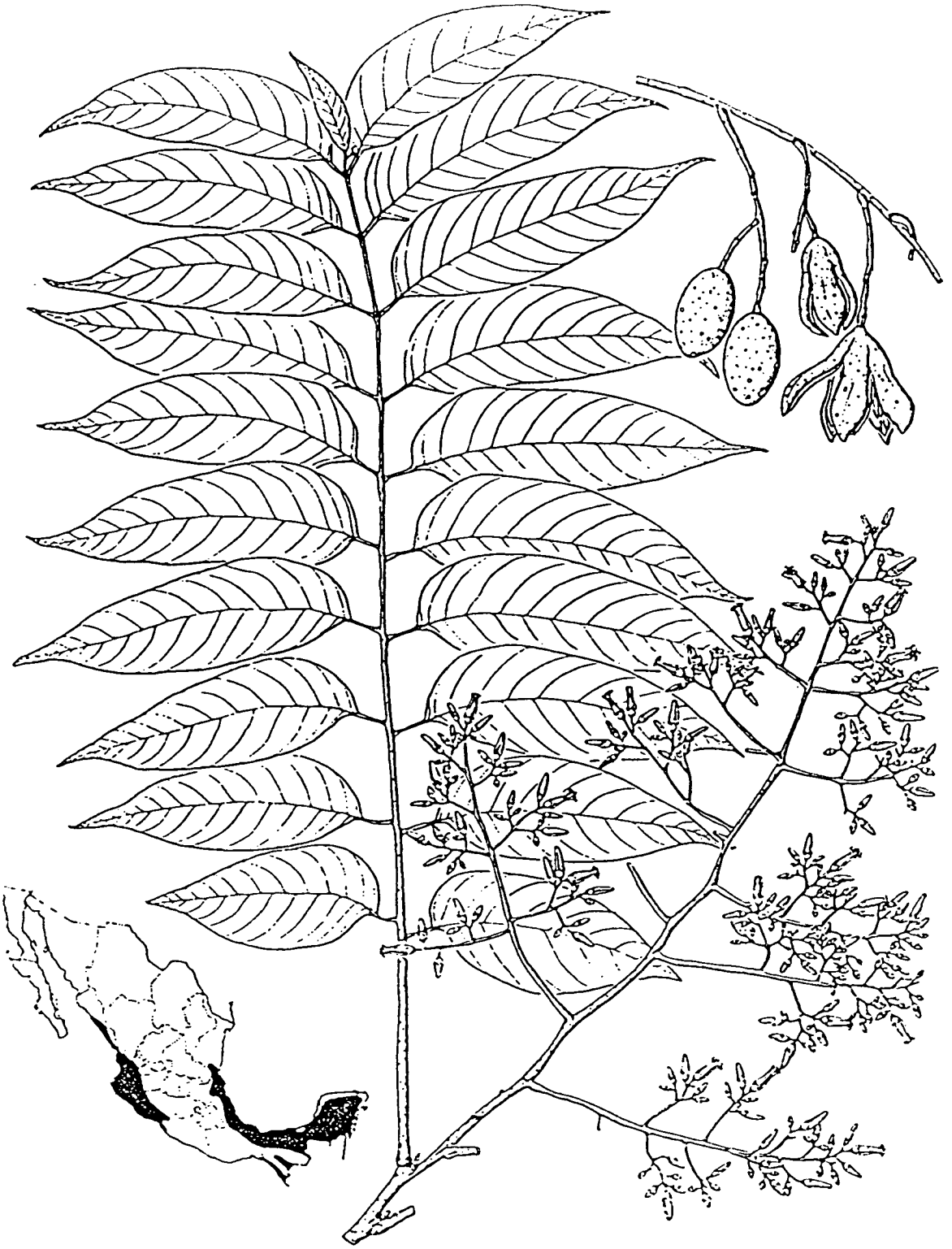


Fig. 2.4 Cedrela odorata; leaves, floral and fruits characteristics. Also the species distribution is shown.

Fig 2.5 Swietenia macrophylla; leaves, floral and fruit characteristics. The species distribution in Mexico is also shown.

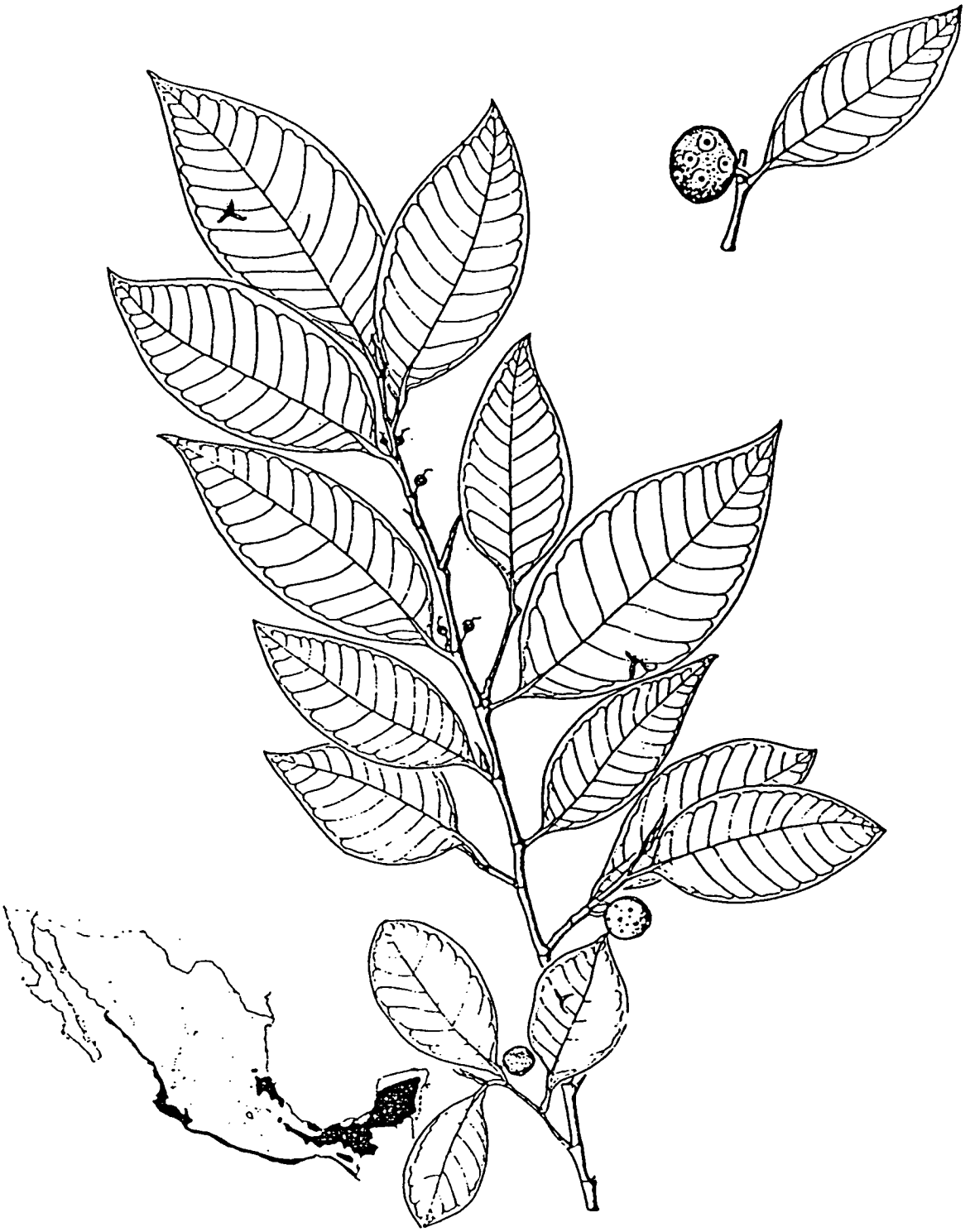


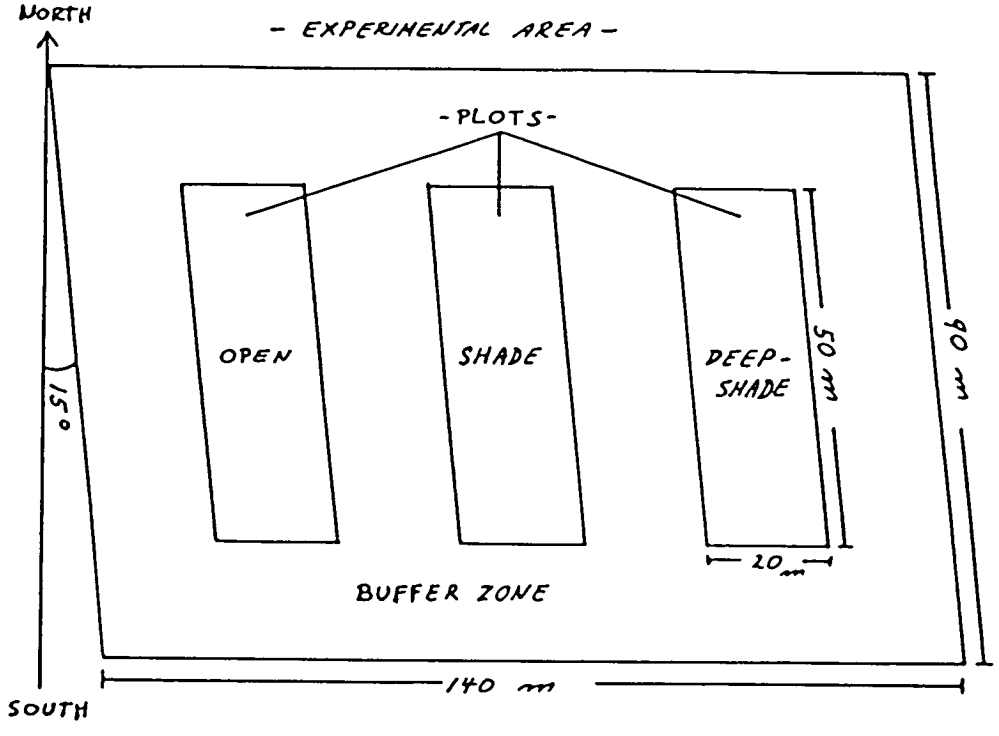
Fig 2.6 Brosimum alicastrum; leaves, floral and fruit characteristics. The species distribution within Mexico is also shown.

2.2.3. Experimental details.

2.2.3.1. Secondary forest.

The experimental area (140 x 90 m) was located on a 15° slope facing north. Within this area, three plots were prepared with different canopy structures, each measuring 50 x 20 m and surrounded by a 'complete' canopy buffer zone (Fig. 2.7). The entire area was fenced with barbed wired to avoid undesirable visits (cattle).

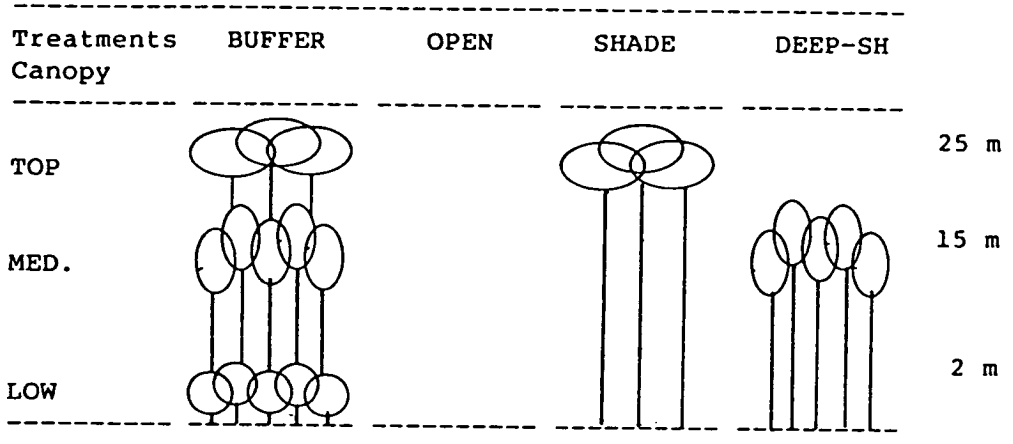
Figure 2.7 Treatment plots (gaps) within the undisturbed 'buffer' zones.



Although the structural analysis of this forest revealed four canopy layers these were redefined as top, medium and low. The 'top' canopy layer was composed of the dominant pioneer trees, whose height and dbh values were 10–24 m and 12–27 cm respectively. The 'medium' canopy layer was composed of all the trees below the 'top' layer, that is, both the middle and lower

canopies. Finally, the 'low' canopy layer was composed of shrubs and herbs. Three treatments a) open, b) shade and c) deep-shade were applied as follows: for the 'open' treatment all canopy layers were clear-cut and removed; in the 'shade' treatment, trees below 12 cm dbh were removed; in the 'deep-shade' treatment trees above 12 cm dbh and all shrubs and herbs were cut down and removed (Fig. 2.8).

Figure 2.8 Diagram showing the forest canopy layers and the layout of the treatments.



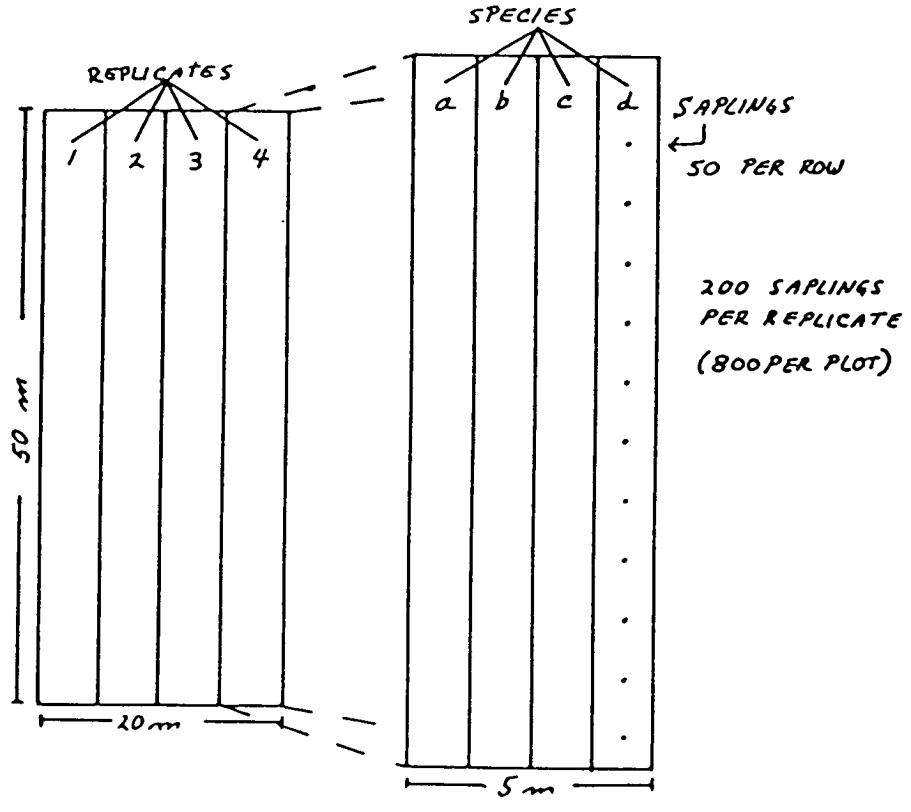
2.2.3.2. Plant material.

Germination.- Seeds of Mexican provenance were used to germinate three species: *C.alliodora, C.odorata* and *S.macrophylla*. *C.alliodora* was collected near the site, the rest was supplied by the National Institute of Forestry Research, Mexico (INIF). Seeds of *B.alicastrum* were difficult to collect or find in sufficient amount, so that, saplings were used instead. They were provided by the National Institute of Biotic Resources Researches (INIREB).

A small nursery was built near the enrichment planting site, seeds were germinated there and saplings kept till the weather conditions were optimum. Once the rainy season was well advanced the seedlings and saplings were transferred to the experimental plots.

Enrichment planting.- Saplings and seedlings were planted with a ball of soil between the 13th and 18th of November 1982, each species being planted at 1 m spacing in lines 50 m long and 1 m apart. Four replicates were established in every plot, making a total of 800 individuals per treatment (200 of each species) as shown in Fig. 2.9. A subsequent replanting was carried out after three months.

Figure 2.9 Planting layout within each treatment plot.



Weeding.- After planting several weedings were necessary. These were done by hand, uprooting and removing the plants from the site. During the first year weeding was carried out every two months in the open treatment. During subsequent years, and in the other treatments, weeding was carried out when necessary.

2.2.3.3. Data collection.

Environment.- Daily integrals of Q were obtained using a Δ-T quantum sensor and a millivolt integrator (§ 2) which were read during one year (1984-1985) the sensor being located on the roof of an adjacent building to simulate 'above canopy' conditions. Three hemispherical photographs were taken within each treatment at 1 m height (regularly spaced along the center of the plots) in order to describe the light environment within the treatments.

Maximum and minimum temperatures were recorded every week during one year (1984-1985) for 'open' conditions. Attempts to measure RH% were discontinued because of damage to the instruments from animals and condensation.

Plant material.- Growth measurements were taken three months after replanting (six months after planting) once the saplings were well established. At this stage the first non-destructive measurements were done: mortality and height. Then every year the same plants were measured, counted and a stratified destructive sample (harvest) was carried out on five plants (of each species for each treatment). Due to the small sample, 'average' or 'modal' plants (by eye) were chosen. Height and crown dimensions were measured, plants were divided into roots, stem and leaves and fresh-dry weights obtained. A sample of leaves was used to determine specific leaf areas and nitrogen content by acid digestion (Crooke & Simpson 1971). Leaves were oven-dried at 80 °C for two days and then weighted, roots and stems were dried at the same temperature until no further weight reduction was noticed (about 2-3 weeks). Up to 30% of the roots may have been left during excavation.

2.2.4. Data analysis.

2.2.4.1. Environmental factors.

Photosynthetic photon flux density.- Daily integrals were displayed as a frequency distribution for each season (dry and wet), and from these, average values for three 'average' days (clear, cloudy and overcast) were obtained. Hemispherical photographs were used to estimate the transmissivity (%transmittance) of the canopy layers for diffuse and direct beam radiation,

which were calculated for three angular elevations (15°, 45° and 75°). The method used was a modification of the standard grid method (Sestak et.al. 1971, Ross J. 1981). This consists of measuring the vegetation cover in different regions of the hemispherical photograph, using masks and a Δ-T area meter (§ 2).

Temperature.- frequency distribution of maximum and minimum temperatures for each season were obtained. From them, average values for clear, cloudy and overcast days were calculated.

Seasons.- The length in months of the dry and wet seasons were determined from climate diagrams (Fig. 2.2) relating average monthly temperature and rainfall (Walter 1979).

2.2.4.2. Growth.

Height and mortality.- Growth and mortality within a population are not equally distributed among the individuals. As a result, size frequency distributions change with time, becoming skewed or bimodal (Harper 1977); mean values obscure plant to plant variation which is observed in frequency distributions (loc.cit.). Estimates of height relative growth rates **(HRGR)** and frequency distributions of height (loge) were obtained (Ford 1975). Additionally, the change of frequency distribution with time was estimated.

Because of initial skewed distributions (when the first height data were taken) data were transformed to natural logarithms (loge). The aim of this procedure was to obtain a nearly-normal (Gaussian) distribution, enabling means to be easily compared. This transformation was not good enough to normalize the initial distributions, hence comparisions between treatments and species were inaccurate. To overcome this problem, the change of frequency distribution with time was obtained. This frequency distribution is obtained by estimating the area of the distribution in t_2 not overlapped with t_1. This technique allows us to compare changes in distributions when the initial distributions are not the same. Mortality is expressed as a proportion of the total population for each species and treatment. Mortality rates are the change of this proportion with time, in this case expressed in a year basis.

Weight.- The assimilated CO_2 which is not lost by respiration nor by

translocation represents an increase in total leaf dry matter, this accumulation process being the basis of plant production. Growth of plants is usually determined from dry weight change by destructive sampling. This technique is adequate for assesing long-term net photosynthetic production and is also useful for analysing carbon allocation patterns and height-surface-weight relationships, all very important for determining plant performance (Jones 1983). The mechanisms controlling the partitioning of assimilates among the different plant parts are very important in determining plant performance in a given environment. The physiological mechanisms which control partitioning are hardly known and we therefore lack a satisfactory basis for model building. Nevertheless, descriptive data on dry matter allocation (LWR, SWR, RWR, etc.)* are available and provide us with a basis for discussion. Growth analysis is useful for analysing physiological adaptations of different species in terms of their partitioning of carbohydrate into leaves, stem and roots.

In order to analyse the efficiency of plants to produce new material, the mean relative growth rate **(RGR)** was obtained. The RGR expresses the increase in plant weight per unit of plant weight per unit of time. The following expression was used (Hunt 1978).

$$RGR = (\text{Loge } W_2 - \text{Loge } W_1) / (t_2 - t_1)$$

where;

Loge W_2 = Natural logarithm of dry weight (g) at time t_2.
Loge W_1 = Natural logarithm of dry weight (g) at time t_1

Experimental values were substituted into this expression. Standard errors (s.e.) were calculated using Hunt's (1978) technique of pairing. Although this technique might underestimate the variance, it is often used (Causton & Venus 1981).

* These abbreviations defined on p. 26.

Another useful index of the productive efficiency of the plants is the mean net assimilation rate **(NAR)** which relates the biomass production to the leaf area, i.e. the net gain in weight per unit leaf area (Hunt 1978). The expression for the mean NAR is as follow:

$$NAR = [(W_2 - W_1) / (t_2 - t_1)] * [(\log_e LA_2 - \log_e LA_1) / (LA_2 - LA_1)]$$

where;

LA.- Leaf area (cm^2).

This expression estimates the carbon assimilation capacity of the leaves, which is also called the unit leaf rate. It allows for respiratory losses at night and from non-photosynthetic tissues and is thus not equivalent to net assimilation (An) measured in single leaves (Jones 1983).

The leaf area ratio **(LAR)** is an estimate of the leafiness of the plant. It is defined as the ratio of total leaf area to whole plant dry weight. RGR, NAR and LAR together summarize the plant performance. LAR can be expressed as follows:

$$LAR = [(LA_2 / W_2) + (LA_1 / W_1)] / 2$$

LAR represents the ratio of photosynthesizing area to respiring material within the plant. All of the above ratios show a dependence upon environmental factors, the level of illumination being very important. NAR and LAR have been found to be linearly related to the logarithm of percentage light intensity; where the slopes determine the trend obtained for RGR (Hunt 1978). Woody plants exhibit inherently lower ratios than the majority of herbaceous species and the same is expected for late compared with early successional species.

Specific leaf area **(SLA)** is the mean area of leaf per unit of leaf weight; it is a measure of the leaf density or relative thickness. Leaf weight ratio **(LWR)** is an index of the leafiness of the plant on a weight basis. SLA is generally more sensitive than LWR to environmental variables. Variation in light intensity is the foremost factor affecting SLA: shade causes an increase in SLA which may offset decreases in NAR. Differences in LAR between species show the 'productive investment' of the plant (loc.cit.). The expressions for SLA and LWR are:

$$SLA = LA / LW$$

$$LWR = LW / W$$

where;

LA.- leaf area.
LW.- Leaf dry weight.
W.- Total dry weight.

Stem weight ratio **(SWR)** and root weight ratio **(RWR)** represent the proportion of dry weight allocated to each part and are also very helpful for assesing the effects of environmental parameters. The expressions to calculate these ratios are similar than for LWR.

2.3. Results.

2.3.1. Environment.

2.3.1.1. Photosynthetic photon flux density (Q).

Higher and less variable daily Q values were observed from May to July, with values after this month dropping and variability increasing. The lowest values and highest varibility was found between November and April (Fig. 2.10). The 'dry' season presents a negatively skewed bimodal distribution with modal values around 8-12 and 28-32 mol m^{-2} day^{-1}; the wet season displayed a bell-shaped curve with modal value around 15-20 mol m^{-2} s^{-1} (Table 2.1). The frequency of cloudy days is high in both seasons but clear and overcast days

are more frequent for the dry and wet season respectively.

Table 2.1 frequency distribution of Q daily values (mol m^{-2} day^{-1}) for the dry and wet season .

Dry season (February-May).-

Q classes	frequency (days)	
2 - 4	3	***
4 - 8	8	********
8 - 12	8	********
12 - 16	12	************
16 - 20	3	***
20 - 24	18	******************
24 - 28	13	*************
28 - 32	17	*****************
32 - 36	29	*****************************
36 - 38	10	**********

For three 'average' days.

	Q classes	frequency (days).
overcast	2 - 15	26
cloudy	15 - 30	50
clear	30 - 38	45

Wet season (June-January).-

Q classes	frequency (days).	
2 - 5	18	******************
5 - 10	27	***************************
10 - 15	30	******************************
15 - 20	47	**
20 - 25	30	******************************
25 - 30	23	**********************
30 - 35	19	*******************
35 - 40	13	*************
40 - 45	1	*
45 -	0	

for three 'average' days.

	Q classes	frequency (days).
overcast	2 - 15	75
cloudy	15 - 30	100
clear	30 - 42	33

Transmissivity of the canopy increases from the ground (complete canopy) through the medium and top canopy layers to the open (above canopy) (Fig. 2.11). It also increases from low elevation angles to the zenith (Table 2.2). Values for the complete canopy are as low as 2-4% and around 60-70% for the open canopy. Values for direct and diffuse radiation are very similar except for the penetration of direct radiation at low elevations (15°) with extremely low values.

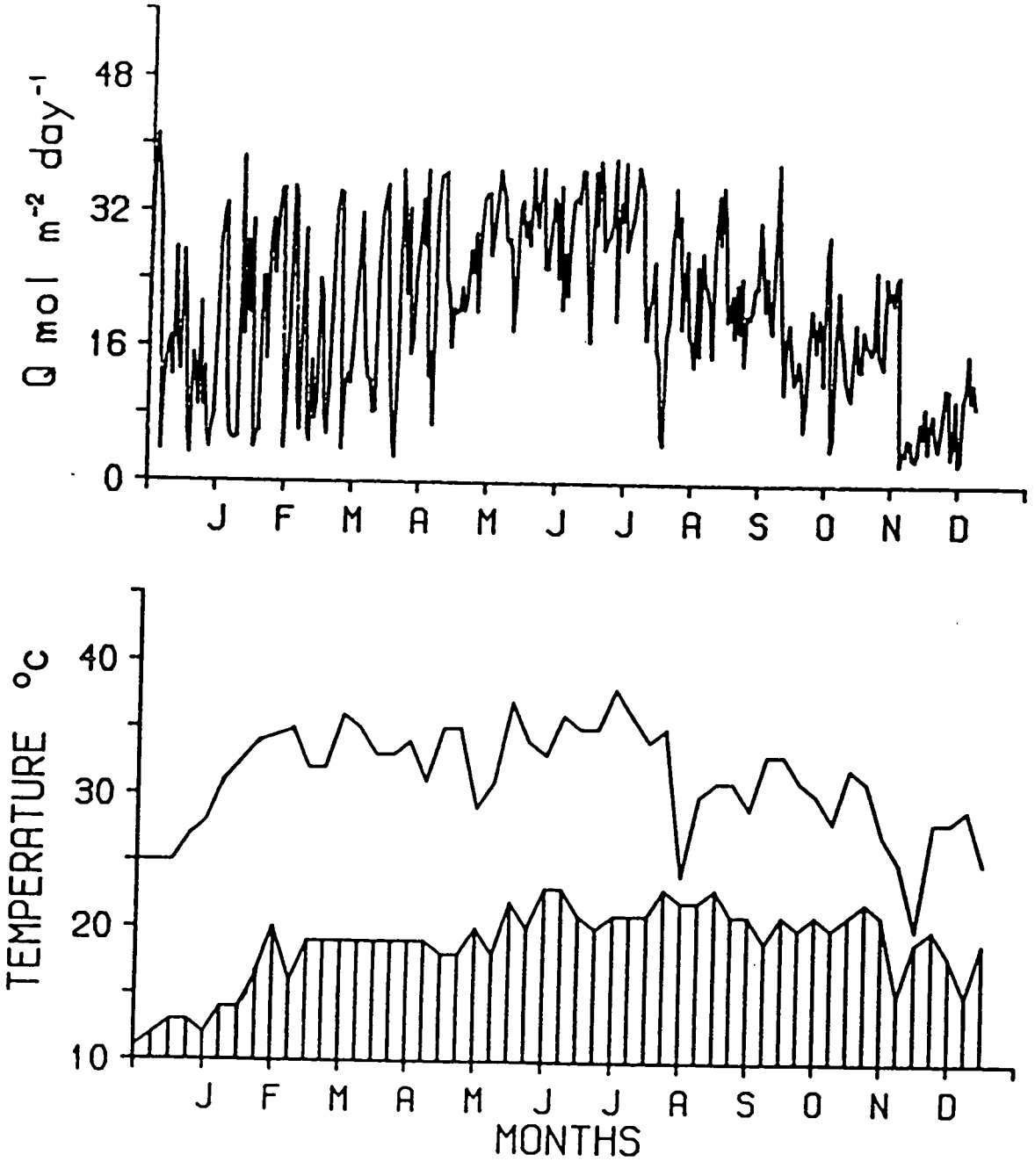


Fig. 2.10 Daily integrals of photosynthetic photon flux density (above) and weekly maximum-minimum temperature levels (below) in the study area. These are above canopy conditions.

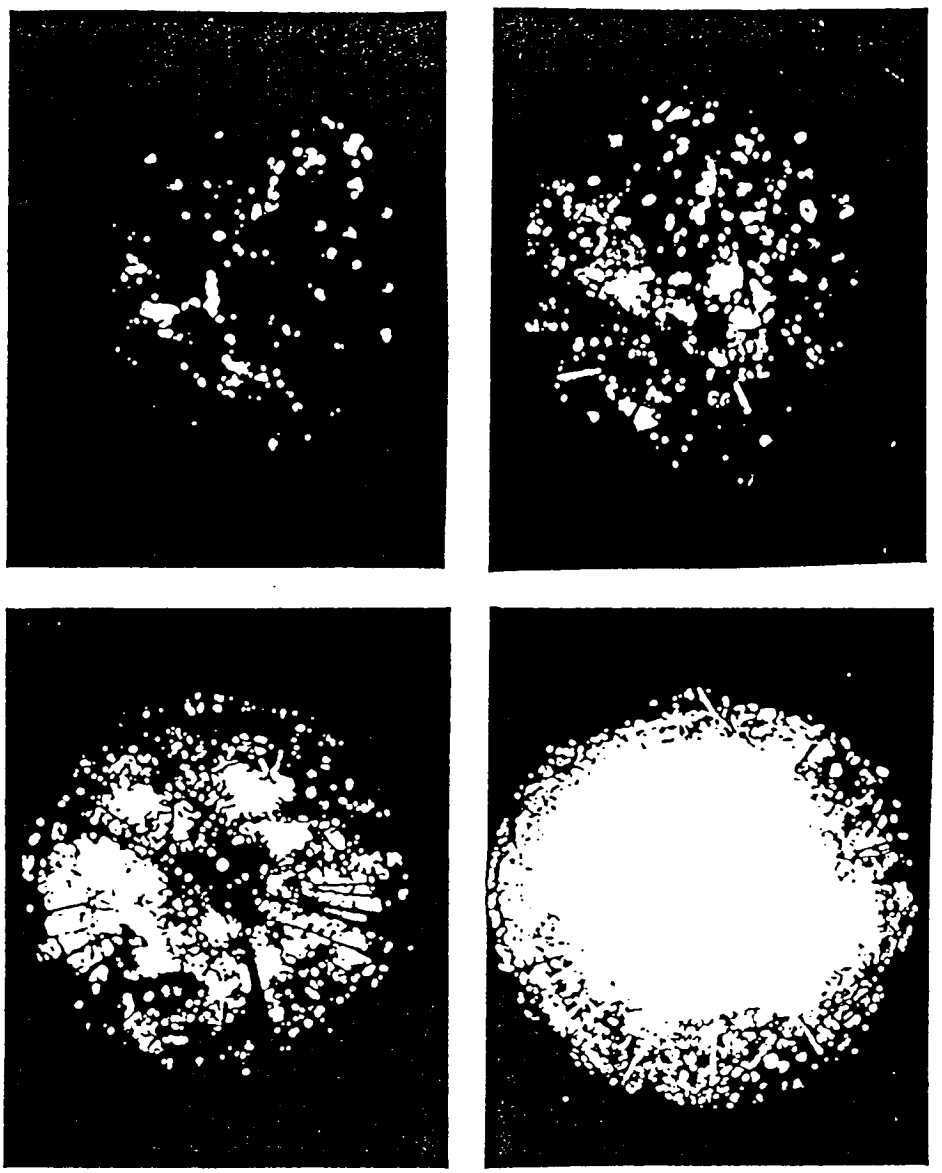


Fig. 2.11 Hemispherical photographs showing canopy light transmitance inside the experimental plots. Complete canopy (above left), medium canopy (above right), top canopy (below left) and open canopy (below right).

Table 2.2 Transmissivity of different layers of canopy to radiation at different elevation angles.

Canopy	Elevation (degrees) 15	45	75	0-90
		Diffuse radiation		
Open	38.0 (07.5)	80.3 (07.7)	96.7 (02.3)	72
Shade	11.0 (01.0)	45.7 (06.7)	64.3 (22.9)	40
Deep-sh	02.8 (01.3)	18.7 (01.8)	32.7 (03.9)	18
Complete	00.7 (00.1)	05.3 (01.4)	05.3 (01.3)	04
Mean	13	37	50	
		Direct beam		
Open	24.1 (07.4)	76.4 (13.4)	89.7 (10.3)	63
Shade	06.7 (02.6)	36.2 (06.4)	60.0 (28.0)	34
Deep-sh	02.3 (01.2)	10.2 (03.7)	35.9 (03.9)	16
Complete	00.9 (00.6)	03.1 (01.2)	03.3 (01.6)	02
Mean	08	31	47	

Mean values and (s.e.), n=3.

2.3.1.2. Temperature.

The highest maximum temperature levels were found between February and August, with minimum temperatures peaking between June and November (Fig. 2.10). This fact leads to larger temperature differences between January and May and smaller differences between July and December.

The distribution of maximum temperatures during the dry season is bimodal with modal values around 27-28 °C and 34-35 °C; for the wet season the distribution is fairly normal with a mean value around 30 °C (Tables 2.3-2.4). Minimum temperature distribution in both seasons is negatively skewed with modes around 19-20 °C.

Table 2.3 Frequency distribution of weekly maximum and minimum temperatures, dry season (February-May).

Maximum temperature.-

Classes	frequency (weeks).
27 - 28	3 ***
28 - 29	1 *
29 - 30	0
30 - 31	2 **
31 - 32	2 **
32 - 33	2 **
33 - 34	2 **
34 - 35	4 ****
35 - 36	1 *
36 - 37	0

frequency distribution for three 'average' days.

	Classes	frequency (weeks).
overcast	27 - 30	4 ****
cloudy	30 - 33	6 ******
clear	33 - 36	7 *******

Minimum temperatures.-

Classes	frequency (weeks).
12.0 - 12.8	1 *
12.8 - 13.6	0
13.6 - 14.4	2 **
14.4 - 15.2	0
15.2 - 16.0	0
16.0 - 16.8	2 **
16.8 - 17.6	0
17.6 - 18.4	2 **
18.4 - 19.2	8 ********
19.2 - 20.0	2 **

frequency distribution for three 'average' days.

	Classes	frequency (weeks).
overcast	12 - 15	3 ***
cloudy	15 - 18	4 ****
clear	18 - 20	10 **********

Table 2.4 frequency distribution of maximum and minimum temperatures for the wet season (June-January).

Maximum temperatures.-

Classes	frequency (weeks).
20 - 22	1 *
22 - 24	1 *
24 - 26	5 *****
26 - 28	5 *****
28 - 30	4 ****
30 - 32	6 ******
32 - 34	5 *****
34 - 36	5 *****
36 - 38	2 **

frequency distribution for three 'average' days.

	Classes	frequency (weeks).
overcast	20 - 24	2 **
cloudy	24 - 32	20 **********
clear	32 - 38	12 **********

Minimum temperatures.-

Classes	frequency (weeks).
11.0 - 12.0	2 **
12.0 - 13.5	2 **
13.5 - 15.0	2 **
15.0 - 16.5	0
16.5 - 18.0	2 **
18.0 - 19.5	3 ***
19.5 - 21.0	15 ***************
21.0 - 22.5	4 ****
22.5 - 24.0	4 ****

frequency distribution for three 'average' days.

	Classes	frequency (weeks).
overcast	11 - 15	6 ******
cloudy	15 - 20	10 **********
clear	20 - 24	18 **********

'Average days'.- Assuming that clear days have higher Q and temperatures than cloudy and overcast days (Fetcher et.al. 1985) the following table was build. Values were obtained from the frequency distribution tables.

Table 2.5 A summary of Q, maximum and minimum temperature values for three average days during the dry and wet seasons.

Season	Dry				Wet			
	Q	Tmax	Tmin	f	Q	Tmax	Tmin	f
clear	34	34	19	45	36	35	22	40
cloudy	22	31	16	50	22	28	17	117
overcast	6	28	13	25	6	22	13	88

Q.- mol m^{-2} day^{-1}.
Temperature.- °C.
f.- frequency (days).

2.3.2. Species performance.

2.3.2.1. Non-destructive sampling.

The frequency distribution of the natural logarithms of heights clearly displays the differences in initial sizes (Figs. 2.12-2.14). With the exception of *B.alicastrum* the species had skewed and bimodal distributions. The subsequent changes in height (same figs.) also show different distributions: *B.alicastrum* keeps its normal distribution over time and between treatments but its positive kurtosis (low spread) is lost in the open canopy after the third year; *S.macrophylla* displays positive skewness (to the left) and bimodal distributions which become rather flat after the second year; *C.odorata* changes from bimodal and negative skewness to bimodal with negative kurtosis (flattened); *C.alliodora* starts and ends with negatively skewed distributions but with some bimodality.

The change of height frequency distribution with time (Fig. 2.15), also displays positively skewed and fairly normal distribution patterns in the cases of *B.alicastrum* and *S.macrophylla* . *C.odorata* has a slightly positively skewed bimodal distribution in the shade and open treatments and a flat normal in the

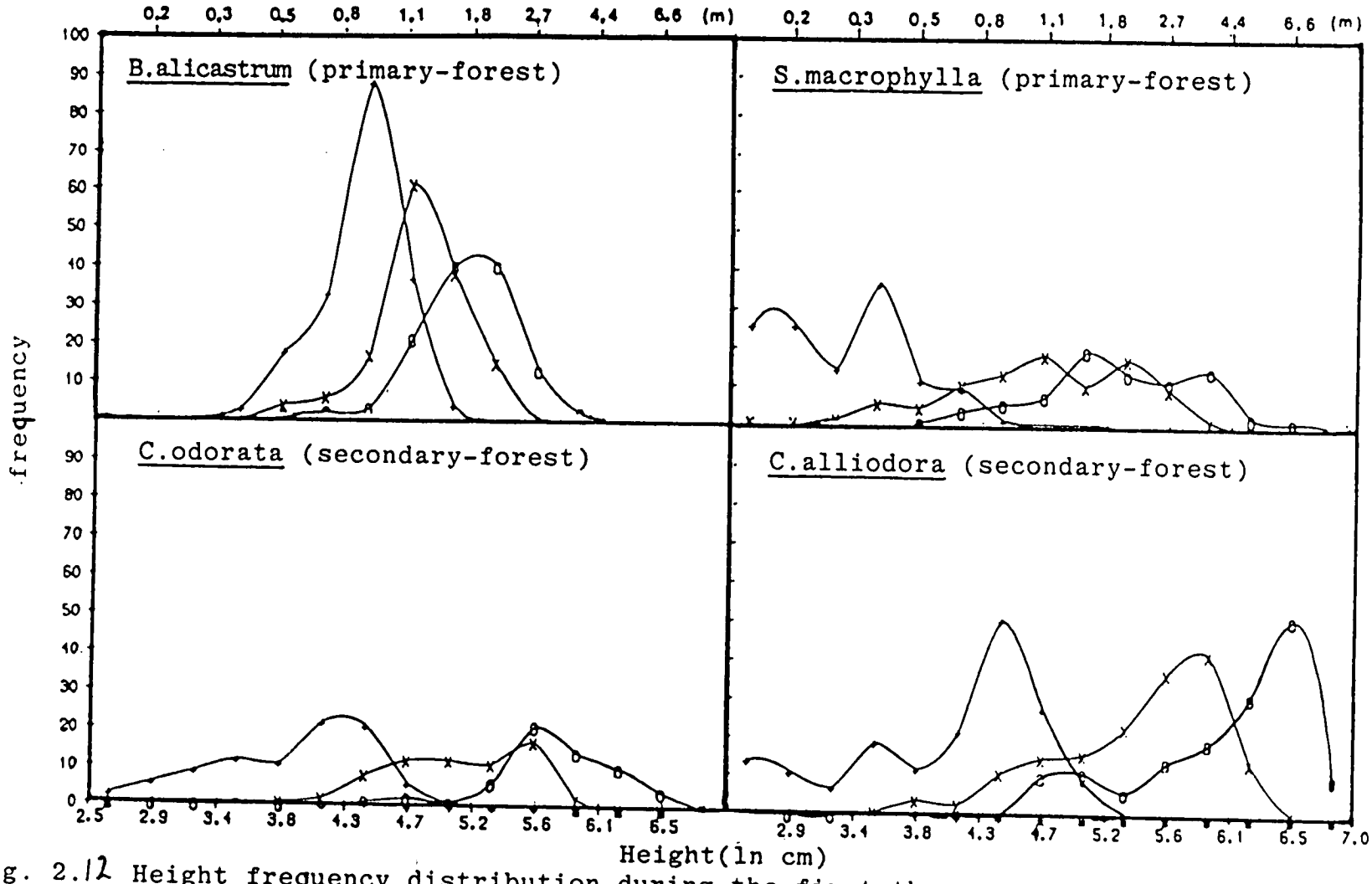


Fig. 2.12 Height frequency distribution during the first three years of growth for the open canopy. Distribution for the starting point (+), first (x) and second (o) years are shown.

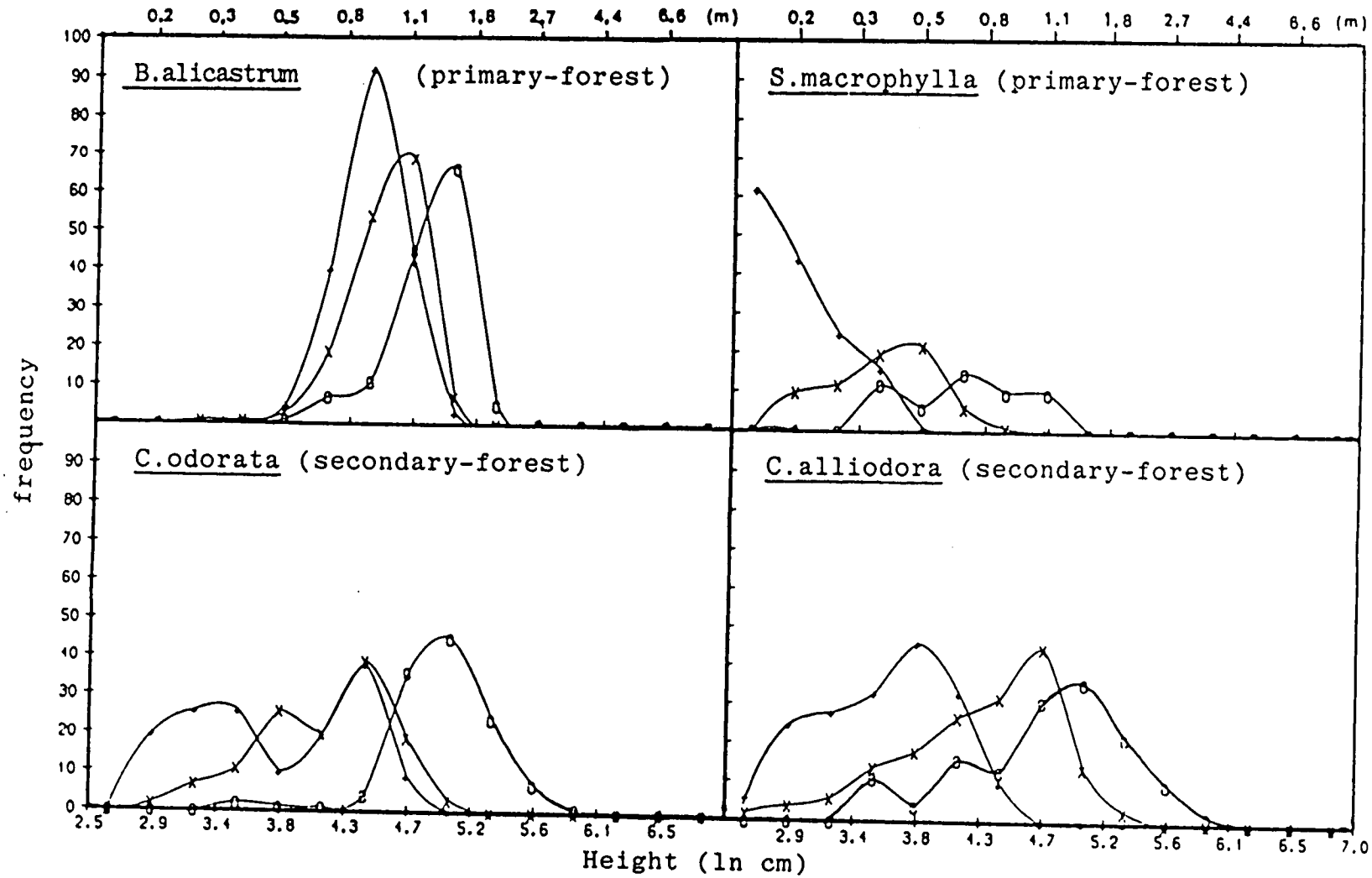


Fig. 2.13 Height frequency distribution during the first three years of growth under 'shade.' Distributions for the starting point(+), first(x) and second(o) years are shown.

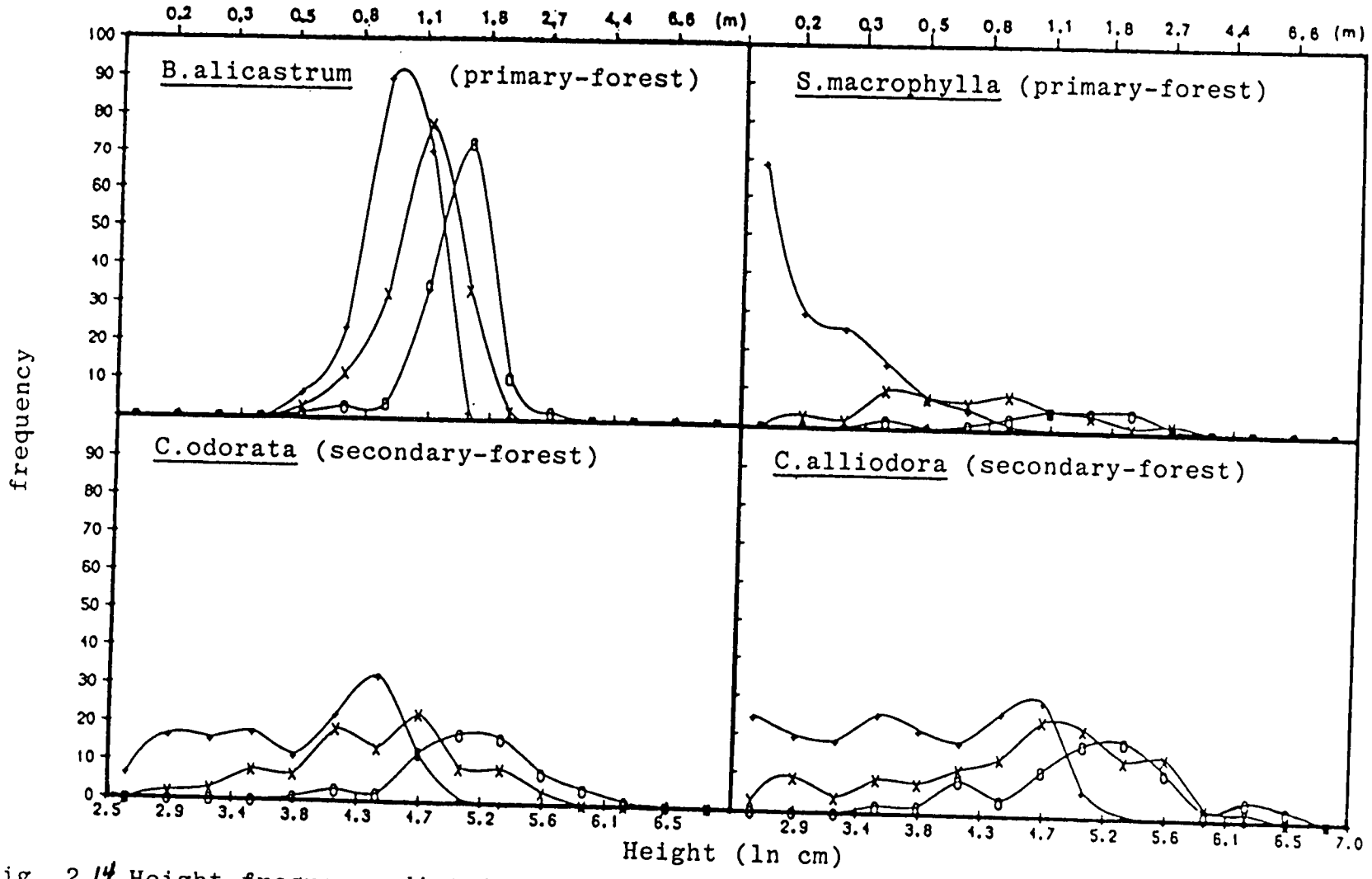


Fig. 2.14 Height frequency distribution during the first three years of growth under 'deep-shade'. Distributions for the starting point(+), first(x) and second(o) years are shown.

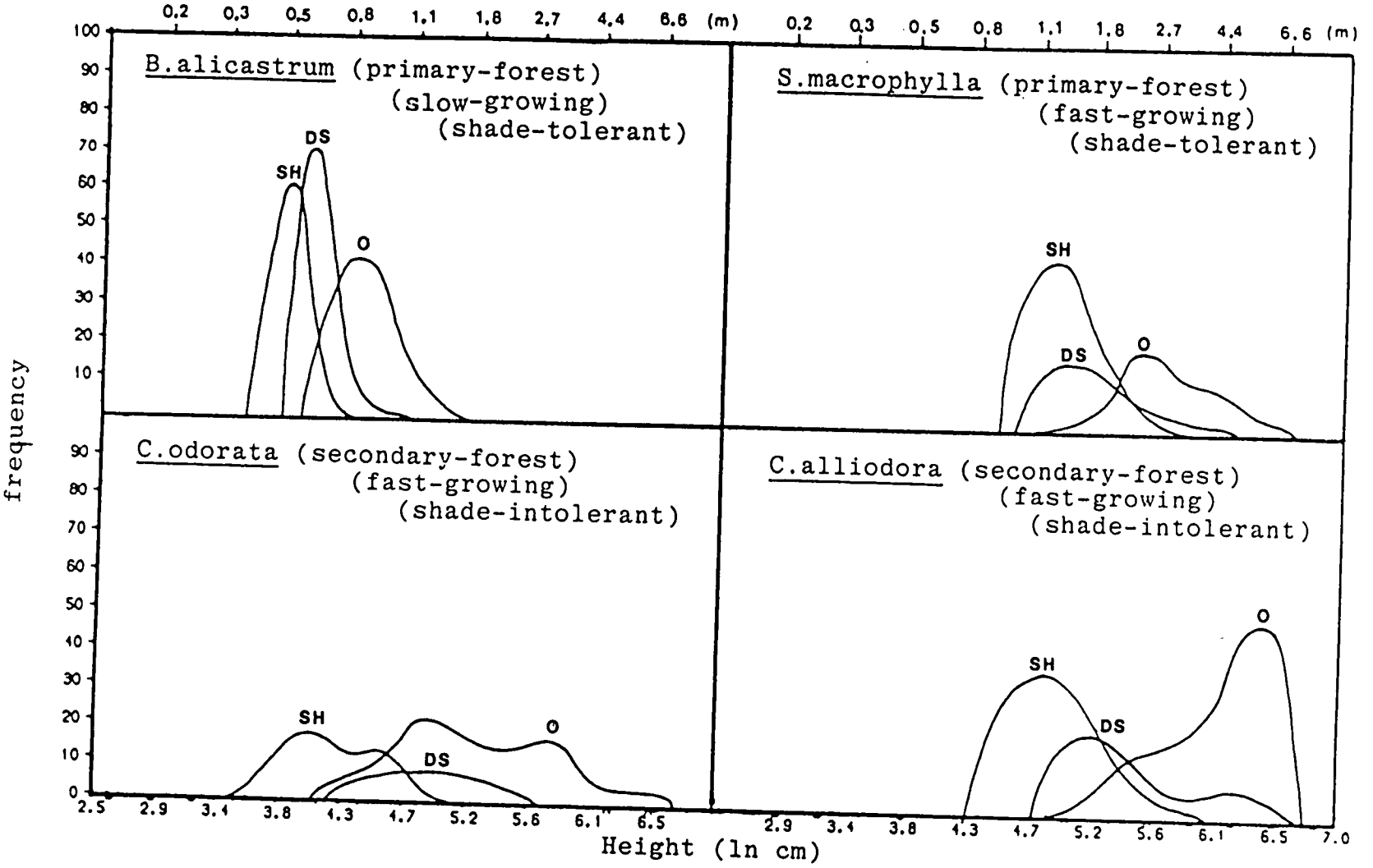


Fig..2.15 Frequency distribution of height change after two years of growth. Three treatments: open (o), shade (sh) and deep-shade (ds) are shown.

deep-shade. *C.alliodora* shows a strongly negatively skewed bimodal distribution in the open, while positive skewness and bimodal in the shade and deep-shade. In general, highest modal values are displayed in the open treatment, followed by the deep-shade and with the lowest the shade treatment. When comparing areas under the distribution, some of the above differences disappear due to high overlapping e.g. *S.macrophylla* and *C.alliodora* for deep-shade and shade treatments and *C.odorata* for deep-shade and open treatments.

Mean height relative growth rates (HRGR) follow the same trend as the modes of the frequency distribution change i.e. highest values for the open, followed by the deep-shade treatment (Fig. 2.16). Higher HRGR are found in the first year compared with the second year, differences between species and treatments are also smaller in the second year. The low growth rate of *B.alicastrum* (primary-forest species) in relation to the others is clearly seen. Mean values of height (loge) and HRGR are given in Table 2.6 (§ 1).

Mortality rates are higher for the first year and the secondary-forest species (Fig. 2.16). *C.alliodora* and *C.odorata* (secondary-forest) display their highest mortality in the deep-shade treatment while the lowest in the open, *S.macrophylla* and *B.alicastrum* (primary-forest) showed highest mortality under deep-shade and open conditions while their lowest values are under the shade treatment. Mortality rates for *B.alicastrum* are very low and do not differ between treatments, very high values are displayed by *C.odorata* followed by *C.alliodora*. Table 2.7 contains mortality and mortality rates for all species and canopy treatments (§ 1).

2.3.2.2. Destructive sampling.

Several problems were faced during harvesting: First, leaf fall was observed in the open treatment, in particular *C.odorata* and to a lesser extent *C.alliodora* and *S.macrophylla* while *B.alicastrum* showed signs of chlorosis but no leaf fall; Second, heavy insect attacks were observed in *C.odorata* and to a lesser extent in *S.macrophylla*, especially in the open treatment, it was mainly in the leaves and buds; Third, lichen and moss growth was observed on the leaves of *B.alicastrum* in the shade treatment and to a lesser extent in the deep-shade. Leaf fall and insect attack certainly affect the growth analysis but the

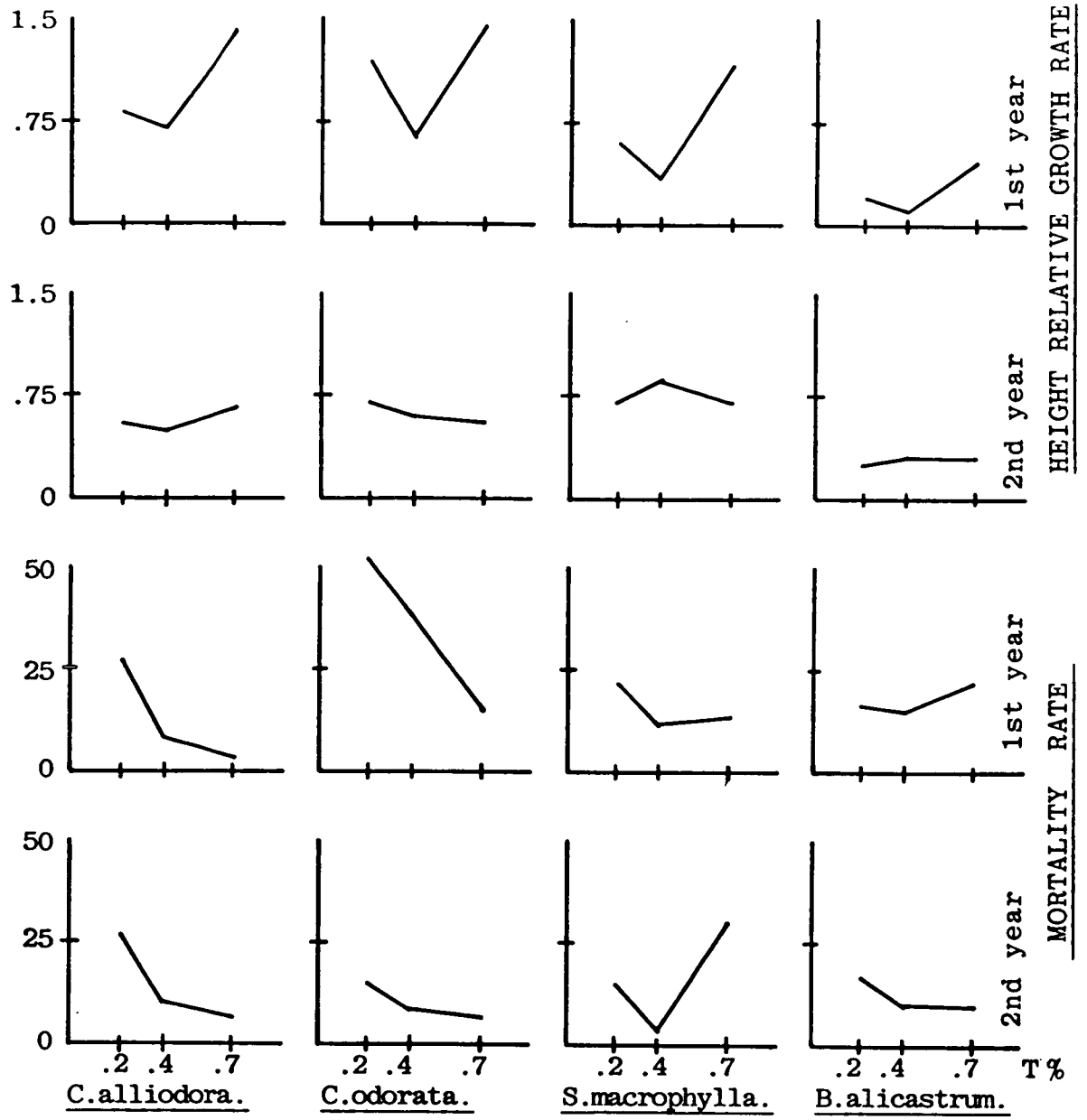


Fig. 2.16 Mean height relative growth rates (above) and mortality rates (below), during the first three years of growth are displayed for different species and treatments: open (70% transmittance), shade (40%) and deep-shade (20%).

effect is dificult to assess. Growth of moss and lichens may affect nitrogen content determination and thus make interpretation difficult. Figure 2.17 shows a summary of plant performances obtained by growth analysis, Means and s.e. of raw data and the derived ratios are given in tables 2.8 and 2.9 (§ 1).

RGR.- In general, secondary-forest species tend to have higher values than primary-forest species. *C.odorata* and *C.alliodora* show their highest RGR in the deep-shade and lowest RGRs in the open. *S.macrophylla* displays its highest RGR in the open while *B.alicastrum* in the shade. The two most secondary-forest species show their minimum RGR in the open! (contrary to expectations and to observations of the height data). It is important to note that the initial weight from which RGR are calculated was different between species and treatments, especially for the open canopy, and to remember that leaf fall ocurred before harvest.

NAR.- As with RGR, higher values are associated with secondary-forest species, the same trend as in RGRs is observed between treatments.

LAR.- The area of leaves tends to increase greatly with shading, from the open to the deep-shade, and from secondary to primary-forest species. However *C.odorata* had its highest value in the shade treatment. *B.alicastrum* appears to be rather insensitive to shade (with smaller changes than the other species).

SLA.- Similarly to LAR, this ratio increases consistently with shading and from primary to secondary-forest species. Again *B.alicastrum* is the least plastic while *C.odorata* the most responsive.

LWR.- *B.alicastrum* shows opposite behaviour to the other species with highest LWR values in the shade and lowest in the open. Here again the secondary-forest species show the most plastic response to the different treatments.

SWR.- Values are very similar between species and treatments with slightly higher values for *C.odorata* and in the open and deep-shade. Lowest values are displayed in the shade but in most cases differences are very small (Fig. 2.18).

RWR.- Similarly to SWR differences between species and treatments are

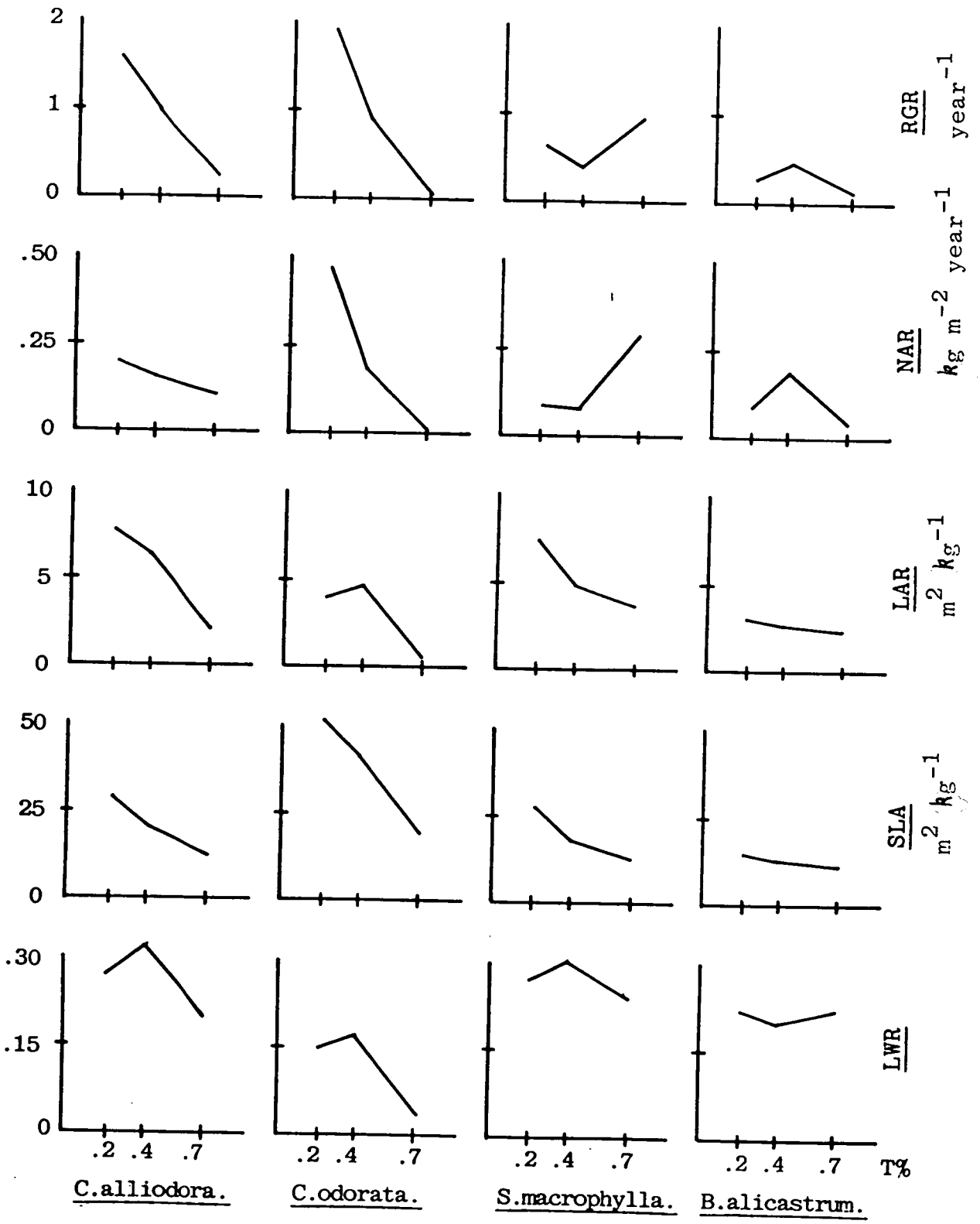


Fig. 2.17 Relative growth rate (RGR), net assimilation rate (NAR), leaf area ratio (LAR), specific leaf area (SLA) and leaf weight ratio (LWR), during the first year of growth are displayed for different species and treatments: open (70% transmittance), shade (40%) and deep-shade (20%).

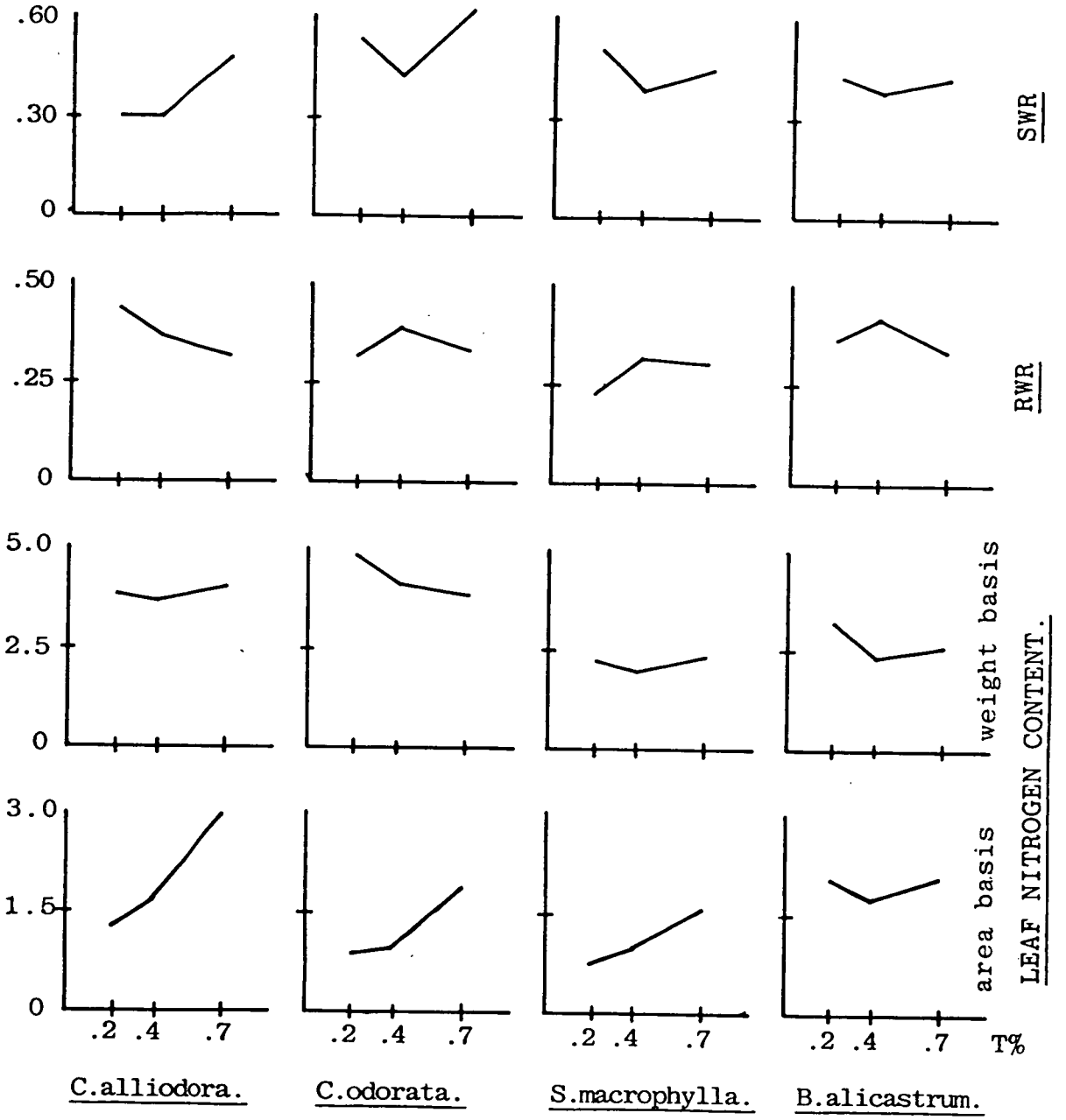


Fig. 2.18 Stem weight ratio (SWR), root weight ratio (RWR) and leaf nitrogen content: in % of dry matter (above) and in g per 100 cm^2 (below), during the first year of growth for different species and treatments: open (70% transmittance), shade (40%) and deep-shade (20%).

small, but an opposite response is shown with higher values associated to the shade treatment (Fig. 2.18).

2.3.2.3. Nitrogen content.

Higher nitrogen contents (N/dry matter, %) were displayed by secondary-forest than primary-forest species, with mean values around 4 and 2.5 respectively (Fig. 2.18). Differences between treatments are small and most of them are not statistically significant ($p = 0.05$) but there is a tendency for the shade treatment to be lower. When expressed in a leaf area basis (N/LA, g m^{-2}) the pattern is reversed with the highest values displayed by the primary-forest species and for the open treatment.

2.4. Discussion.

2.4.1. Environmental factors.

Daily integral values of radiation (Q) ranged from 3 to 41 mol m^{-2} during a one year period; in a 5000 m^2 clearing in Costa Rica values ranged from 14 to 34 mol m^{-2} during a 13-day period study (Chazdon & Fetcher 1984). Mean daily totals of 35.4 were found in open conditions during one month (Pearcy 1983). The short periods of time used in the above studies is probably overestimating mean values. Mean values for the dry and wet season were 24 and 19 mol m^{-2} respectively; Chazdon & Fetcher (1984) found mean values of 28 and 23 mol m^{-2} respectively. In both cases the dry season shows about 25% higher values. The dry season is characterized by high and very variable values, in addition its frequency distribution is not normal. Thus, mean values are not adequate to describe the radiation regime, yearly courses and/or frequency distribution give a better picture.

Transmissivity has been studied mainly for understorey conditions and some gaps of different size (Pearcy 1983, Chazdon & Fetcher 1984), whose values for understorey conditions range from 1 to 3.8%, in this work values ranged from 2 to 4% (complete canopy). These values are relatively high and could be the result of the method used in this work to estimate canopy transmittance (hemispherical photographs), nevertheless they are within the

range obtained in other tropical forests. Transmissivity of different canopy layers is not documented for tropical forest and although values obtained (40 and 20% for the top and medium canopy respectively) resemble values obtained in gaps, light conditions (quality, quantity and variability) are substantially different.

Mean values for minimum and maximum temperatures (°C), 18-32 and 19-30 for dry and wet seasons respectively, are similar to the mean values obtained in Costa Rica (Fetcher et.al. 1985), 19-27 and 22-31 for dry-wet seasons respectively. Nevertheless values are not directly comparable due to the character of the temperature frequency distributions (skewed and bimodal) and that Fetcher et.al. (1985) used mean values without considering maximum and minimum values.

The dry season is characterized by high and variable Q values, low precipitation (below 100 mm per month) and large temperature differences. These conditions may increase transpiration and eventually lead to low leaf water potentials (LWP) with consequent stomatal closure (if soil water content is not replenished). Although radiation is high and less variable in the wet season temperature differences are small and precipitation is high. Under these conditions transpiration is lowered and LWP rises, maintaining stomatal opening. Nevertheless floods may occur impairing root functioning and increasing the risk of fungal attacks. Within the canopy some of these effects are ameliorated but others are exacerbated. Light transmission decreases from the top to the bottom where temperatures are lower and humidity higher; while low light levels are disadvantageous for photosynthesis lower temperatures and the related high humidity may provide optimum conditions for gas exchange.

2.4.2. Species performance.

2.4.2.1. Non-destructive sampling.

Different initial heights and distributions of heights make the analysis complex and the estimated parameters imprecise. Although the loge transformation normalized and diminished the spread of data it was far from being ideal, partly due to the change in distribution when the plants are

growing and competing which leads to skewed and bimodal distributions (Ford 1975, Cannell et.al. 1984); competition is expressed as density dependant mortality associated with low RGR of supressed individuals.

The change of height frequency distribution allow us to analyse these changes regardless of the initial state. Larger changes are displayed by the secondary-forest species (Fig. 2.15), particularly in the open treatment. Distributions are, in general, positively skewed which suggest species sensitive to density dependent competition. Similar behaviour has been observed for *Picea sitchensis* and *Pinus contorta* at high densities (Ford 1975). When planted at wider space, distributions may become negatively skewed (loc.cit.), as *C.alliodora* in the open, or bimodal as *S.macrophylla* and *C.odorata* in the open. It is clear that under shade and deep-shade the species are under 'density-stress' and in the open, some individuals 'escape' competition, forming a dominant group (*C.alliodora*, open), while the rest become 'supressed' individuals. *B.alicastrum* which maintains a normal distribution over time and treatments, suggest low levels of density dependant competition ('stress' tolerant), slightly positively skewed distribution in the open though. It is interesting to note that there is a small group of very large plants in the deep-shade (*C.alliodora*) reflecting the mini-gaps mentioned in this treatment.

Lowest mortality values were displayed by *B.alicastrum*, with the treatments having no effect, highest values were for *C.odorata* especially in deep-shade. Two groups develop from analysing mortality; a) *B.alicastrum* and *S.macrophylla* with highest and lowest mortalities in the open and shade respectively and b) *C.odorata* and *C.alliodora* with their highest and lowest mortality in the deep-shade and open respectively. Th results are very interesting since too much radiation is apparently killing some plants; Augspurger (1983) concludes that " seedlings of 15 species survive better in sun than shade; none survive better in shade than sun". The 'sun' and 'shade' treatments in this work are about 20 and 1% transmittance! respectively. Hence, it is important to define and refer if possible to more quantitative terms i.e. transmissivity. Although photoinhibition has been observed at high Q levels (Langenheim et.al. 1984), the high mortality in the open treatment could be caused by drought conditions brought about by high radiation and temperature. The observed leaf fall in this treatment documents this statment.

It is important to mention here some other plant characteristics which

could help to assess their performance in the field. Vigour is difficult to define but easy to see and in this case *C.odorata* and to some extent *S.macrophylla* were characterized by lack of vigour in most of the treatments. This could be caused by insect attack which lowered the performance of these species.

2.4.2.2. Destructive sampling.

Patterns of dry matter allocation are important in analysing the response of a species introduced to a particular environment. Growth analysis describes the performance of a plant from a different point of view and is very suitable for comparing species and treatments. Also slow-fast growth and low-high plasticity descriptions are possible when analysing RGR. Growth analysis on trees growing in field conditions is not common, as a result, methodology is just developing and there are no data with which to compare.

Due to the sampling problems, comparisons are unprecise. Several factors can be mentioned which made the sampling inaccurate: stratified destructive sampling procedures where biased when assesing the 'average' plant, since they did not represent 'dominant' and 'supressed' plants; another factor is the decidous nature of these species in drought conditions; although sampling was planned to avoid this danger, leaf fall was obvious during the second harvest of *C.odorata* and the effect on the other species *S.macrophylla* was unclear and difficult to assess.

In spite of the problems already mentioned, differences in shade tolerance and plasticity are clearly displayed from *C.odorata* (shade-intolerant) to *B.alicastrum* (shade-tolerant) where, there is a trend in lower rates and growth parameters (RGR, NAR, LAR and SLA) and smaller changes (less plasticity, fig. 2.17). Response to the different light levels is more difficult to assess, nevertheless SLA can be analysed without including the effect of leaf fall.

The effect of shade and differences between species is clearly displayed through the analysis of SLA; values increase with shade and the more shade-intolerant the species is. For secondary-forest species SLA ranges from 51 to 20 $m^2\ kg^{-1}$ for deep-shade (20% transmittance) to open (70%) conditions, for a primary-forest species SLA ranges from 15 to 12 respectively. Fetcher et.al. (1985) found that the range for a pioneer species (*H.appendiculatus*) was from 41 to 19 for 'partial shade' (20% transmittance) to 'full sun' and from 30 to

21 for a 'small-gap' species (*D.panamensis*), which resemble very close the values obtained with *S.macrophylla*. Values for three Amazonian emergent trees (Langenheim et.al. 1984) had smaller differences between 'shade' (6%) and 'sun' (100%) conditions (around 17 to 11 respectively), adittionally in one case the 'sun' treatment displayed higher values than in 'shade'. Kwesiga & Grace (1986) demonstrate that SLA is very sensitive to the red/far-red ratio particularly in shade-intolerant species. The 'shade' treatments in this work are under a natural canopy, thus the R/FR is low, in Fetcher's and Langenheim's works, shade treatments were done with neutral density shade cloth and presumably at high R/FR but in the former the plants were placed under a cocoa grove for one month before they were 'shade' treated (2 months). It is clear that we need more controlled conditions and precise descriptions of the light regime under which experimental plant are grown. However, SLA is a very sensitive and simple index of shade tolerance and plasticity, which could be very useful in assessing those characteristics in the field since it is cheap and easy to obtain.

SWR and RWR show opposite responses and all the species responded similarly: the lowest values for SWR are seen in the shade while the highest are in the open and deep-shade treatments. Whether dry matter is put into height, diameter or density is an interesting question. The responses observed suggest that shoot-root ratio decreases from open conditions to moderate shade but it will increase under deep-shade conditions. A 'trade-off' between leaf,stem and roots develops and the balance depends on many factors; the use of dry matter for expansion in size increase in length area or density are other balances to be solved.

2.4.2.3. Nitrogen content.

Values obtained in this experiment are within the average values obtained for phytomass in general (around 2-4% of the dry matter, Larcher 1980). With the exception of *C.odorata* deep-shade which had rather high values. Values of primary-forest species are within the range displayed by some temperate and sub-tropical trees e.g. 1.0-1.2% (Pine), 1.7-2.1% (Apple) and 2.2-2.8% (Orange) (Kramer & Kozlowski 1979). For secondary-forest species values are similar to other secondary-forest species e.g. 3.2-4.2% for *Trema micrantha, Cecropia obtusifolia, Heliocarpus appendiculatus & Cassia doylei* (Williams 1982). All

species' leaves in the sun contained more nitrogen per unit leaf area than leaves of shade plants (Fig. 2.18). The same response and similar values were obtained by Langenheim et.al. (1984) for seedlings of three Amazonian emergent species. When expressed on a leaf area basis the response of the species is larger and opposite than on a dry weight basis, suggesting important structural changes which enable leaves to harvest light more efficiently.

Differences between species are large and consistent enough to suggest that adaptations in nitrogen content in leaves are present. Such adaptations may help some species to tolerate poor growing conditions e.g. low nitrogen contents in soil or shading. Less N means less structural proteins and enzymes which will result in lower growth rates but more efficiency in energy expenditure. High N contents may help plants to be competitive and achieve high growth rates but only in good growing conditions. The differences between treatments are small and not consistent, confounded with other variables e.g. litter fall from the neighbouring trees, own phenology and the growth of lichens and moss. Nevertheless, the deep-shade treatment tends to show higher values. Evidence of specific differences is clear and the range of variation, due to environmental effects, is also shown.

2.5. Conclusions

1.- Differences between the dry and wet seasons are well described by yearly courses and/or frequency distributions of: a) radiation, b) rainfall and c) temperature. Environmental factors differ for similar days (clear, cloudy and overcast) for each season.

2.- Canopy layers differ markedly in their transmissivity and their homogeneity, due to crown structure and distribution. The top layer displays the highest transmittance and is more homogeneous than the rest hence, easier to manipulate in order to change light conditions in the understorey.

3.- Frequency distributions of height and mortality rates are useful in assessing the competitive status of individuals in a population and their response to environmental variables, in particular the change of distribution with time. They also provide information for its management, i.e. thinning certain size classes to relax competition on others.

4.- Growth analysis can be used to assess the partitioning of assimilates in the field in relation to various environmental factors, however sampling techniques are a major problem. Specific leaf area (SLA) is a good indicator of shade tolerance and plasticity of response to changes in light quality and quantity.

5.- Nitrogen content, in general, reflects the energy investment of a species to harvest light in a given environment. Lower values and smaller changes were displayed by primary-forest species. These values are consistent with the results from growth analysis where primary-forest species display the lowest values and they change little under shade.

6.- From height frequency distributions and mortality three shade tolerance categories can be defined: a) tolerant, b) slightly tolerant and c) intolerant. It is also possible to describe growth as fast or slow. In addition the relative changes of these characteristics in relation to changes in the environment (plasticity) is of great value in assessing the adaptability of a species to a particular environment.

Summary of the response to shade for the different species.

Species	Habitat (forest type)	Growth rate	Shade sensitivity	Shade tolerance
C.odorata	secondary	fast	very high	very low
C.alliodora	secondary, late-secondary	fast	high	very low
S.macrophylla	late-secondary, primary	fast	high	low
B.alicastrum	primary	slow	low	high

7.- Best and worst conditions can be obtained from the interaction of species and canopies, enabling management schemes to be derived e.g. enrichment planting.

For this particular experiment the following guidelines are suggested:

a) only two species are worth continuing with (*B.alicastrum & C.alliodora*).

b) the introduction of saplings under a thin 'nurse' canopy e.g. shade treatment (40% transmittance) will minimize mortality and help establishment.

c) it is important to plant when environmental conditions are optimal e.g. July–August.

d) after establishment (6–12 months) the 'nurse' canopy needs to be removed e.g. by girdling to avoid sapling damage.

e) enrichment with two species, one shade–tolerant and the other intolerant is suggested.

CHAPTER 3

RESPONSE TO SHADE IN TROPICAL TREE SAPLINGS.

3.1. Introduction.

The sequence of species that establishes and grows after the disturbance of a tropical moist forest canopy is called secondary succession. The different establishment periods and growth rates reflect the species physiology and their response to the environment. Hence, understanding of secondary succession requires physiological information on the response of different species to environmental variables. Information regarding the ecophysiology of seedlings and saplings is sparse for tropical trees (Mooney et.al. 1984). Light quality and quantity is a major factor driving secondary succession (Whitmore 1983). Although the light response is the most documented physiological response in tropical trees (Bazzaz & Pickett 1980), physiological parameters have seldom been obtained through fitting available models on photosynthesis (Kwesiga et.al. 1986).

Probably the most adequate way of characterizing the light requirements of tropical moist forest tree species is with a gradient from shade-tolerance to shade-intolerance. Because plant light requirements change as individuals grow and it might be cumbersome to use such classification, the simpler dichotomy of primary or secondary-forest species will be used for the saplings studied in this work.

Physiological information can be obtained in the field or using controlled environment chambers. Although such chambers 'reproduce' the environment, they may differ in some respects from the natural environment. Nonetheless, the environmental conditions of interest can be varied at will, singly or in groups, being of great value when the aim is to obtain response curves or to fit models. Because portable gas analyser systems were not available in Mexico and some physiological parameters were needed for the modelling exercise, the controlled environmental approach was chosen. This experiment is concerned with the ecophysiology of four tropical tree species: *Brosimum alicastrum*, *Swietenia macrophylla*, *Cedrela odorata*, and *Cordia alliodora*, which were described in Ch. 2. These species are found in different environments

from 'primary' to 'secondary' forest, and represent a range of physiological traits, i.e. maximum stomatal conductance, light saturation point, etc. As light quality and quantity is a most important factor in these environments, physiological adaptations to light are expected.

The effect of two different light regimes on the growth, development and gas exchange characteristics of these species is evaluated, characterizing a) photosynthesis, b) stomatal conductance, c) growth and dry matter partitioning, and d) nitrogen content of leaves under both, high/low photosynthetic photon flux density (Q) and high/low red to far-red ratio (R:FR). These light regimes simulate conditions above the canopy or in the open, 'sun', and conditions below the canopy or in the understorey, 'shade', respectively (Ch. 2).

For each species at both light regimes the following responses were assessed:

a) Photosynthetic response to Q.

b) Stomatal responses to : Q, temperature, and saturated vapour pressure deficit (SVPD).

c) Growth : Height, number of leaves, leaf area and fresh-dry weight of roots, stems and leaves.

d) Nitrogen content of leaves.

3.2. Materials and methods.

3.2.1. Plant material.

Seeds of Mexican provenance were used, those of *C.alliodora* were collected near the field site (Ch. 2), and the rest were supplied by the National Institute of Forestry research, INIF, Mexico, from a nearby forest field station.

Approximately one hundred seeds of each species were sown in 50/50 peat-sand mixture under the mist bench conditions of a glass-house at the Department of Forestry and Natural Resources on 11/9/85. Temperature in the glass-house was maintained at 20-25 °C and the mean value of Q was 68 ±8 $\mu mol\ m^{-2}\ s^{-1}$ at bench height (18 h /day). Germination took place in pulses:

C.odorata start germination after two weeks, *B.alicastrum* after three weeks and *S.macrophylla* took six weeks. After eight weeks *C.alliodora* did not show any sign of emergence so another batch of seeds was heat-treated to promote germination, by boiling in water for one minute (Vazquez-Yanes 1976) before they were sown. The results were the same after another period of eight weeks.

After emergence, 20-30 seedlings of each species (except *C.alliodora*) were potted on fertilized compost, 75% peat - 25% sand (UC mix IID; Baker 1957). By December the seedlings were repotted into bigger containers (10 x 12 cm plastic pots) and by January 20th twelve saplings of each species were brought into the growth chamber. Six saplings per species were used for each of the light treatments. A *C.alliodora* clone from the Institute of Terrestrial Ecology (ITE, Bush Estate, Penicuik, Scotland) was used to obtain cuttings to root. After one year, cuttings were pruned and later repotted (16 x 18 cm plastic pots) and established before they were brought to the growth cabinet.

3.2.2. Controlled environment chamber.

The experiment was carried out in a growth cabinet (Fisons, §2; Fig. 3.1), important features of this cabinet are:

a) Light.

It has 21 high intensity metal halide lamps (Wotan, type HQ 1-2, 250 W-NDL) and 12 pearl bayonet tungsten 100 W lamps. They produce a photosynthetic photon flux density (Q) of about 1000 µmol m^{-2} s^{-1} (973 ± 96) at 20 cm from the cabinet double glazed ceiling, and around 600 µmol m^{-2} s^{-1} (630 ± 15) at 110 cm from the ceiling, see table 3.1. Macam quantum sensors (§ 2) were used for the Q measurements. The combination of lamps gave a R:FR (655-665 / 725-735 nm) of ≃ 1.95 irrespective of the distance from the ceiling. The spectral composition of this light can be seen in Fig. 3.2. Spectral measurements were carried out with a Techtum quantum spectroradiometer (§ 2).

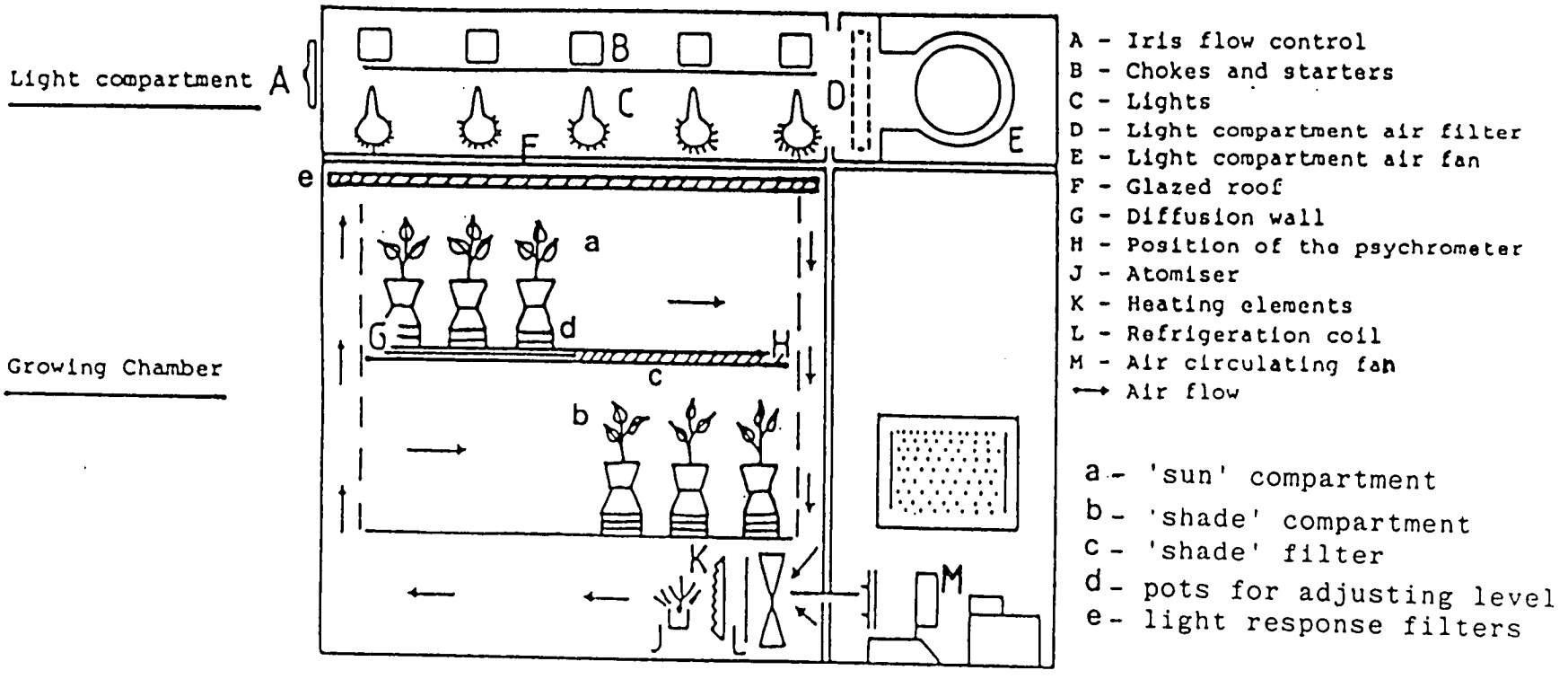


Fig. 3.1 Diagram showing some important features of the Fisons cabinet and the disposition of the compartments for both, 'sun' and 'shade' treatments with the potted seedlings inside.

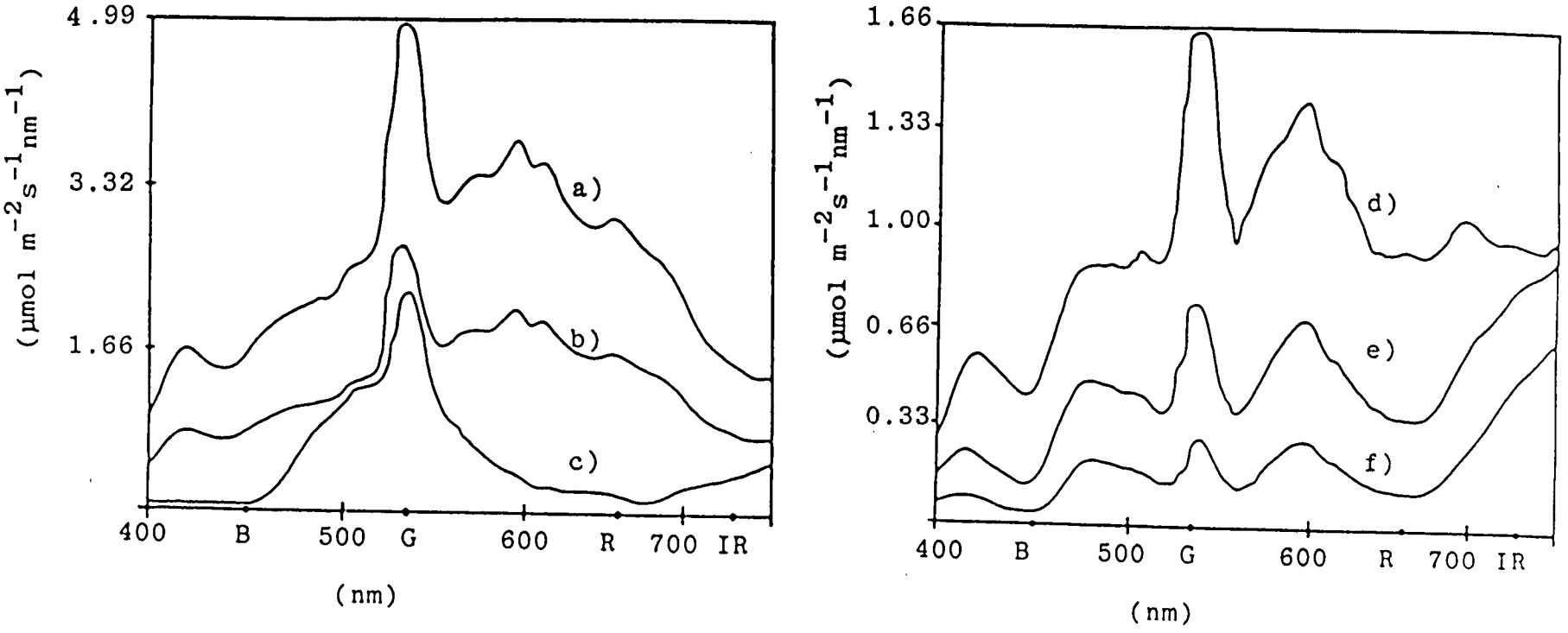


Fig. 3.2 Spectral composition of Fison's cabinets lights with and without filters.

a) Fison's cabinet lights without filters.
b) with two layer of muslin.
c) with one layer of green 'cinemoid' filter.
d) with 50% transmittance 'Rosco' filter.
e) with 25% transmittance 'Rosco' filter.
f) with 12.5% transmittance 'Rosco' filter.
For details of filters and measurements see text.

Table 3.1. Means and (s.d.) of Q values from the top of the Fison's cabinet. Units are µmol m^{-2} s^{-1}.

Distance from ceiling	Q	n=9	
0 cm	520 to 3700		
10	1100	(290)	
20	973	(96)	
30	900	(37)	
50	763	(29)	
110	630	(15)	
120 *	549	(31)	* 60 cm from the bottom of the cabinet.

b) Temperature.

Theoretically, air temperature can be controlled to an accuracy of 0.5 °C in the range of 0-50 °C . The band-width over which the control is effective is adjustable from 1% to 10% of the full scale of the controller (50 °C for the dry bulb and -25 °C for the wet bulb depression). In spite of all these controls, the heat load from the lamps, and the horizontal and laminar air flow (approx. 1 m s^{-1}) creates a gradient, with the temperature higher at the right end of the cabinet. Furthermore, differences in the radiation load and ventilation between the treatment compartments, due to different heights , filters and frames, creates differences in temperatures. In spite of all these differences, air temperature between the treatments during the experiment never exceeded 1-2 °C.

c) Humidity.

Air flows over wet and dry resistance thermometers, located within a movable psychrometer. These thermometers are connected to an electronic controller, which compares the differential temperature with the desired set point. This control adjust the humidity by spraying water onto the heating elements causing the water to vaporize (increasing humidity), or condensating water on surfaces at or below dew point temperature (decreasing humidity). Differences in relative humidity between treatments were mainly caused by the difference in temperature and were always smaller than 5%.

d) Carbon Dioxide.

Two air vents are provided at the rear of the cabinet. By opening them the air in the cabinet can be changed up to several times per hour. As a result, the amount of carbon dioxide, CO_2, is essentially the same as the ambient room concentration and very similar to the outside concentration.

3.2.3. Gas exchange analyser.

A portable system for the measurement of CO_2 assimilation and transpiration of single leaves was used (ADC, § 2). This open gas exchange system consist of four units: an Infrared Gas Analyser, IRGA, a leaf chamber, an air supply (pump), and a data-processor with logger. It is a commercially available unit and was used unmodified as recommended by the manufacturers.

3.2.4. Experimental details.

First, the environmental conditions of the cabinet during the 'growth' period and the subsequent change of those conditions during the 'treatment' sessions are described. Then, details of the gas exchange system during the measurements is mentioned. Leaf ontogenetic stage and insertion levels are analysed and finally, growth analysis and nitrogen content measurements are described.

3.2.4.1. Environmental conditions.

To simulate light under field conditions, particularly values of Q, R:FR, and spectral composition, it was necessary to manipulate several factors: a) distance of saplings to the ceiling of the cabinet, b) neutral screens, c) selective filters, and d) daylength. The distance of the plants to the ceiling was controlled by the use of shelves and plastic pots (Fig. 3.1). Layers of muslin and nylon fabric were used as neutral screens; green 'cinemoid' filter and a set of gray 'Rosco' filters (§ 2) were used to obtain different spectral compositions. A summary of values obtained with the interplay of the above factors is shown in Tables 3.1 – 3.3. Spectral characteristics of neutral screens and filters are shown in Fig. 3.2. Once the best combination of factors was found a series of

wooden frames was built to accommodate them into the cabinet (Fig. 3.1.).

Table 3.2. Values of Q (µmol m^{-2} s^{-1}) and R:FR (655-665 / 725-735 nm) at 30 and 120 cm from the ceiling for different combinations of shade screens and filters.

Q	R:FR	Muslin	Nylon	'Rosco' Filt. 50%	25%	12%	'Cinm' Green	Peg-board	Light Treats.	Shade Screens
				(30 cm from top)						
852	1.96	---	---	---	---	---	---	---	'sun'	---
542	1.96	1	---	---	---	---	---	---	---	---
405	1.96	2	---	---	---	---	---	---	---	5
339	1.96	3	---	---	---	---	---	---	---	---
705	1.96	---	2	---	---	---	---	---	---	6
303	0.97	---	2	1	---	---	---	---	---	---
169	0.97	2	---	1	---	---	---	---	---	---
209	0.97	1	2	1	---	---	---	---	---	4
91	0.97	2	1	1	---	---	---	---	---	3
61	0.97	3	1	1	---	---	---	---	---	2
77	0.45	2	---	---	1	---	---	---	---	---
46	0.25	2	---	---	---	1	---	---	---	---
22	1.96	---	1	---	---	---	---	1	---	1
				(120 cm from top)						
550	1.96	---	---	---	---	---	---	---	---	---
152	0.39	---	---	---	---	---	1	---	---	---
99	0.45	---	---	---	1	---	---	---	'shade'	---
45	0.28	---	---	---	---	1	---	---	---	---

For details of filters and measurements see text.

Table 3.3 Transmittance of the different filter materials at several wavelengths measured at 30 cm from the top in the Fison's cabinet. (Transmittances are calculated from 10 nm wavelength band-width, i.e. 450 for 445-455 nm.) Units are µmol m^{-2} s^{-1} nm^{-1} for each of the wavelengths and µmol m^{-2} s^{-1} for Q (400-750 nm).

	Filter wavelenghth (nm)				
	450	530	660	730	400-750
without filter	1.57	4.95	2.99	1.52	852
muslin (2 layer)	0.72	2.67	1.61	0.82	405
'Rosco' (50%)	0.47	1.70	0.97	0.99	303
(25%)	0.14	0.75	0.37	0.83	153
percentages	Blue	Green	Red	Fred	PAR
Muslin	46	54	54	54	47
'R' 50%	30	34	32	65	36
'R' 25%	9	15	12	55	18

1.- Growth period.

Open (sun) and understorey (shade) conditions were simulated as follows:

Photosynthetic photon flux density.

A range from 3 to 41 mol m^{-2} day^{-1} was found during field measurements with an average value around 20 mol m^{-2} day^{-1}. Maximum values in a clear day may reach up to 2000 µmol m^{-2} s^{-1} and the average daylength is around 12 hours (See chapter 2 for a detailed description of field conditions). Average values were used in the simulation of 'field' conditions inside the growth cabinet: the maximum value of Q ≈ 1000 µmol m^{-2} s^{-1} was less than the maximum found in the field, but is still high (most tropical tree species are light saturated at this value). Furthermore, with a daylength of 12 h an input of about 40 mol m^{-2} day^{-1} was obtained, which is equal to the highest daily integrals on the field. This Q level and daily integral was assumed to be an appropriate representation of a 'clear day'.

As a result of a) uneven distribution of light near the ceiling of the cabinet, b) high radiation loads near the ceiling, with undesirable overheating effects c) expected growth of saplings during the experiment and d) the fact that the target leaf is about the fourth leaf from the top of the plant, the Q level at the 'target' leaf was between 750-850 μmol m^{-2} s^{-1}.

Light conditions below the canopy in the field site are around 4-40% of the values above the canopy, depending on height (Ch.2). 'Shade' conditions in the experiment were about 70-90 μmol m^{-2} s^{-1} representing around 10% of the 'sun' treatment. This value was assumed to represent understorey conditions: although higher than many tropical forest understoreys, it is usually below the published light saturation point of most tropical tree species.

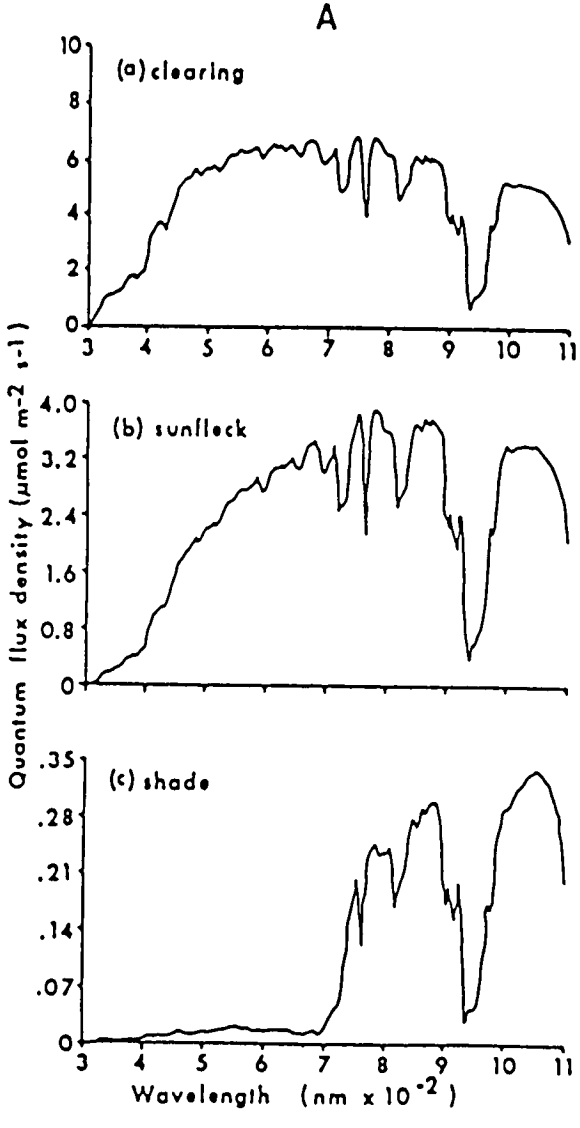
Red to far red ratio.

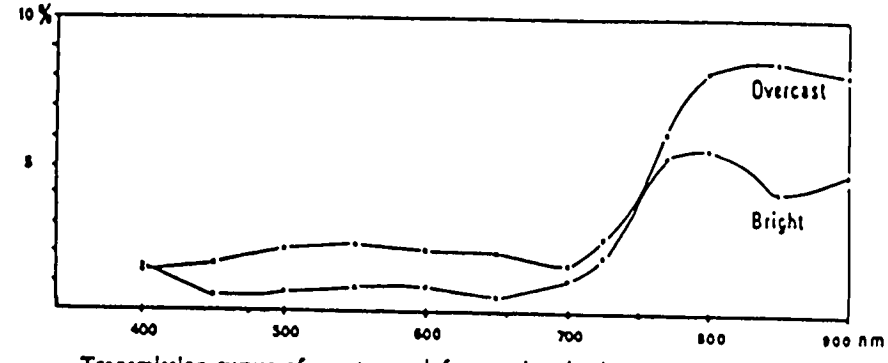
Values of R:FR were not measured in the field. However, values of R:FR for open conditions and below different canopies are fairly constant and well known (Monteith 1976, Morgan & Smith 1981). These authors mention ranges from about 0.1 to 1.2, with average values of about 1.1 above the canopy. Values below the canopy are more variable depending on leaf area index, clumping of leaves, etc. and may range from about 0.08 to 0.9 but average values range from 0.2 to 0.4. Values obtained in tropical rain forests lie within these ranges: 1.23 in a clearing and 0.42 in the shade (Chazdon & Fetcher 1984).

A R:FR of 1.96 (Table 3.4) was used for the 'sun' treatment. Although quite high, it is essentially the same as a R:FR of 1 (for a plant), since the ratio of the two forms of phytochrome does not change above 1.2. For the 'shade' treatment a better approximation was achieved, with a R:FR=0.45 (Table 3.4).

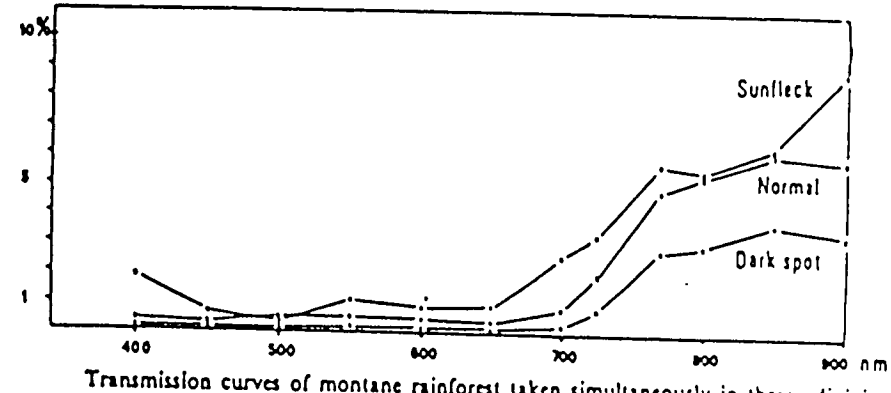
Spectral distribution.

As mentioned before nothing could be done to change the 'sun' light conditions. Although, light in the Fison's cabinet resembles 'natural' light in a clear day, there is a high peak in the green region (Fig. 3.2) which was left unchanged. The 'shade' compartment was well controlled and a spectral composition very close to the ones found in nature was achieved (Figs. 3.3, 3.4).





Transmission curves of montane rainforest taken in the same spot with bright and overcast conditions.



Transmission curves of montane rainforest taken simultaneously in three adjoining spots.

B

Fig. 3.3 Spectral distribution of light in a tropical rain forest in Costa Rica,A, (Chazdon 1984) And in a montane tropical rain forest in Java,B, (Stoutjesdijk 1972).

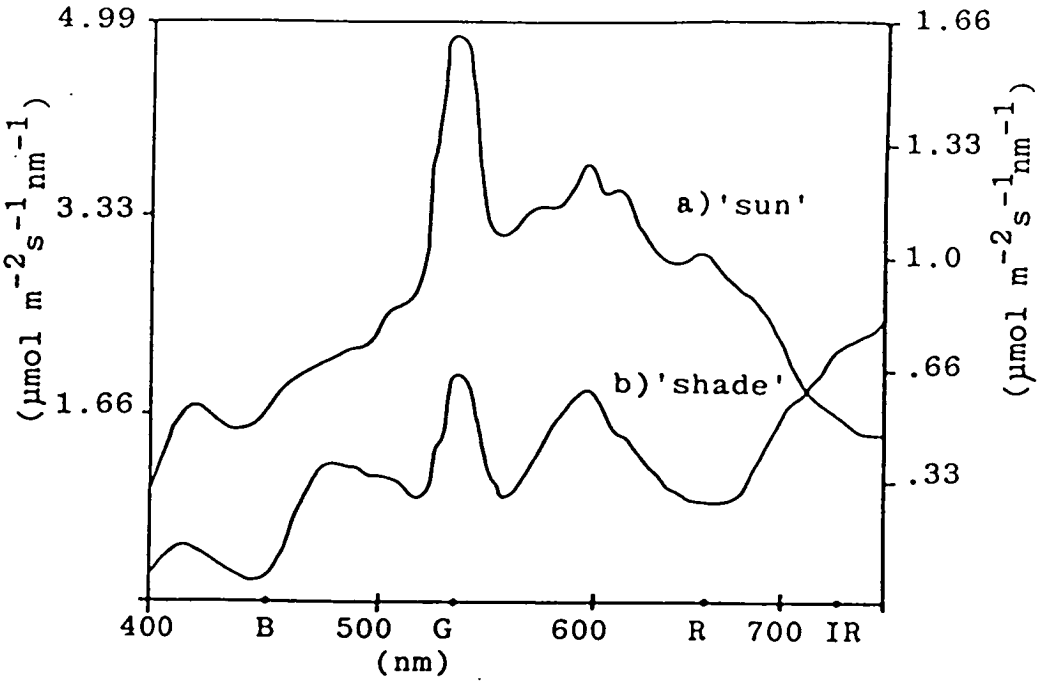


Fig. 3.4 Spectral composition of both 'sun' and 'shade' treatments within the Fison's cabinet.

	'DAY' (12 h)		
	'SUN'	'SHADE'	
PAR	763 (79)	71 (6)	n=9
R/FR	1.96	0.45	
TEMP. °C	27 (0.5)	28 (0.3)	n=6
RH %	71-72	69-70	
PAR (day)	33	3	
	'NIGHT' (12 h)		
TEMP. °C	18		
RH%	90		

Table 3.4 Summary of environmental conditions at plant height inside the growth chamber. PAR is in µmol m^{-2} s^{-1}, PAR(day) in mol m^{-2} day^{-1}(12 h), standard errors in brackets and number of determinations (n).

Temperature and humidity.

Very large variations in temperature and humidity are experienced by leaves at the top of the canopy in relation with leaves present at the bottom of the canopy. No attempt was made to simulate these factors since both affect stomatal conductance and are strongly correlated with light.

It was decided to work with average conditions at the top of the canopy in a clear day. Average conditions of temperature and RH% lie around 28 °C and 75% respectively, representing a VPD of about 1.0 kPa (Fetcher et.al. 1985).

Soil.

Soil properties are very important to the performance of plants in the field. It is impossible to simulate soil field conditions in a growth cabinet, even using the same soil. However, it is possible to assess the performance of plants under 'optimum' soil conditions, where ample supply of nutrients and water is given. Because the latter may not be true when the roots fill the pot and plants may run short of nutrients, foliar nitrogen was measured after the light response. This allows us to compare the nutrient status of glass-house grown plants with the field-grown plants.

The saplings were watered every day to full capacity and additional nutrient supply was applied every week (1-100 ml H_2O solution of 'liquid feed', § 2).

Pests.

Signs of red spider and white fly were found three weeks after the plants were placed inside the cabinet and subsequently plant were sprayed with a water miscible, 'Pynosect 30', insecticide, containing 'Resmethrin and Pyrethrins' (§ 2). Readings were taken at least two weeks after the spray sessions in order to avoid interference or undesirable effects of the insecticide.

2.- Treatment conditions.

Photosynthetic photon flux density.

Light levels were modified by putting different filters on the ceiling of the cabinet (Fig. 3.1.). The combination of filters for each of the seven Q levels can be seen in Table 3.2, Temperature and air VPD inside the cabinet were

maintained constant and equal to the conditions during the growing period.

Dark respiration was measured one hour before the lights were switched on. Temperature was increased to 28 °C (day temperature) one hour before, hence maintaining the same temperature during the whole light response. Readings for all plants in both treatments were taken at each step of changing light levels.

Q levels were always increased from zero (dark respiration) to the highest light level (730 μmol m^2 s^{-1})). This value was chosen as the highest intensity because there was a risk of damaging the plants grown under 'shade' conditions. Each species reading was done at a time, measuring both treatments in one day.

Light level steps were shorter at lower Q levels, improving the amount of information where the response is steeper thus enhancing the curve fitting procedure. A stabilization period of one hour was allowed between each change of light level and the next reading.

Saturated vapour pressure deficit (SVPD).

Humidity was modified by controlling the differential temperature of the dry and wet bulb thermometers. For the lowest values of SVPD was necessary to use a rotary drier unit (§ 2) attached to the cabinet. This unit was left running overnight to have dry air from the beginning of the day, avoiding time delays.

In spite of the cabinet's sensitivity to room temperature and humidity it was possible to control SVPD levels within reasonable limits (Table 3.5). (Temperature and light conditions were maintained constant and equal to the ones used during the growing periods). The four air SVPD levels used for measuring the responses were always decreased from about 2.1–2.2 kPa. to about 0.4 kPa since, it is easier and faster to increase rather than to decrease humidity. This fact is important since the stabilization period of one hour prior the readings was counted once the cabinet reached the desired SVPD value and it was stable.

The range of values represent the values found normally in the field during the day. Minimum values of SVPD are around 0.2 kPa. and maximum values are between 1.5–3.5 kPa (for wet and dry season respectively) (Whitehead et.al.

1981, Grace et.al. 1982). Again at lower SVPD values the steps were shorter because the faster stomatal response at this values.

Table 3.5. Levels and ranges of SVPD, RH% and dry-wet bulb temperature difference for the SVPD response.

dry-wet bulb Temperature	RH%	SVPD (kPa)	Mean SVPD	step
1.5-2	85-90	0.36-0.55	0.45	
				0.4
3.0-3.5	75-79	0.80-0.94	0.85	
				5.5
5.0-6.0	60-65	1.30-1.50	1.40	
				8.0
8.5-9.0	40-45	2.08-2.27	2.20	

Temperature.

To modify this factor whilst keeping SVPD level constant, it was necessary to adjust both the temperature and the humidity controllers. It was decided to use five temperature levels equally spaced around the growing condition temperature (28 °C). The aim was to maintain SVPD at the growing values (9.4 kPa). Values of RH% and dry-wet bulb difference (maintaining a fixed value of SVPD) at the 5 temperatures are shown in Table 3.6.

Temperatures were always increased from the minimum temperature (15 °C) to the maximum (35 °C) At the lower temperature levels it was necessary to use the drying unit and at higher values it was necessary to dampen the floor of the cabinet, since at these values the controllers were not efficient. In spite of all these efforts, oscillations in the temperature controllers resulted in shifts of humidity and therefore in SVPD. As a result it was impossible to maintain the SVPD near the selected value (9.4 kPa.) and the readings obtained reflect the confounding effect of temperature and SVPD (Table 3.6). The analysis of the data was continued as an exercise but the parameters obtained do not represent a 'typical' temperature response.

Table 3.6. Values of temperature, RH%, dry-wet bulb temperature and actual SVPD values for a required value of SVPD (9.4 kPa).

Temp.	RH%	D-W °C	SVPD(actual)
15	45	6	8.9
20	60	5	9.3
25	70	4	9.5
30	77.5	3.5	10.4
35	83	2.5	11.0

3.2.4.2. Gas exchange system.

To maintain environmental conditions within the cabinet nearly undisturbed, the system was moved to the back of the cabinet. Leaf chamber tubes and leads were passed through a hole at the back of the cabinet (Fig. 3.5).

Air was taken from outside the building, then passed through a column (4-50 cm) of calcium chloride (8-15 mesh), partially drying the air and acting as a CO_2-concentration buffer. Another column (3 x 20 cm) filled with 'Drierite'(8 mesh) (§ 2) was used to dry the air down to (1-2 RH%) before entering the air pump. As a result desiccant columns in the pump were not removed either during or between the measurements. 'Drierite' was used because its low ability to absorb and release CO_2, very high in the case of silica gel.

A breathing mask attached to a vacuum pump was used during the gas exchange readings. Operator breath may raise the CO_2 concentration inside the Fison's cabinet room up to 500 ppm in about two hours. This CO_2 concentration can upset both plant stomata and IRGA readings. The IRGA air flow was 200-500 ml min^{-1}.

Dark respiration and low light level measurements were done at minimum flow rate (210 ml min^{-1} while the rest of the readings were done at a flow which maintained the differential CO_2 concentration below 30 ppm (Values greater than this will cause an under-estimation of the assimilation rate). The relation between assimilation, A, and ambient CO_2 concentration is almost

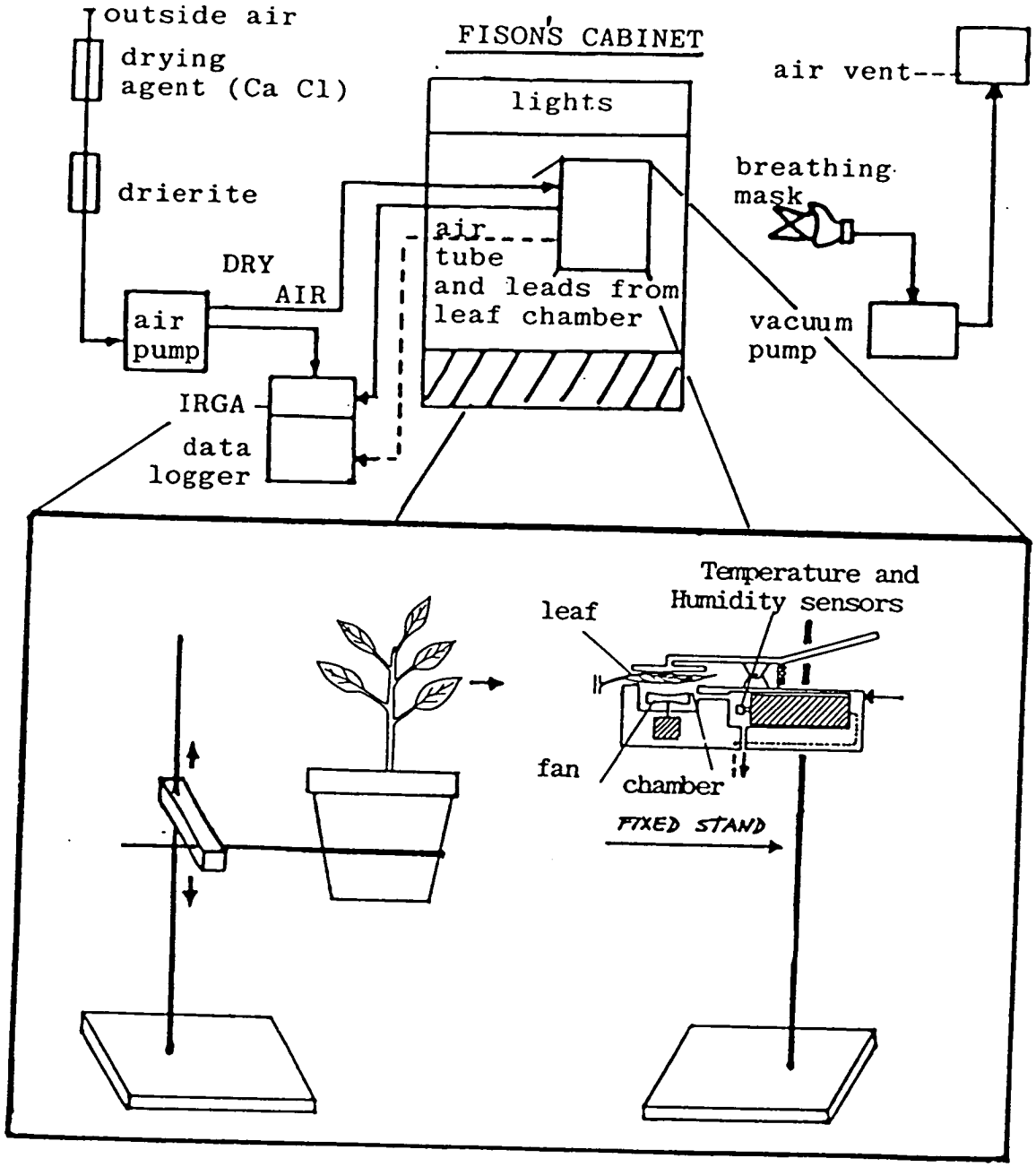


Fig. 3.5 Diagram showing the gas exchange system with the cabinet and also the leaf chamber and one seedling mounted on their stands.

linear up to 1000 ppm, therefore the apparent rate of A is lower than the real rate of A. As the differential CO_2 concentration rises above 30 ppm, the error involved in estimating A become significant. (Sandford, A. pers. comm.)

The leaf chamber was held in a fixed position inside the cabinet. Thus, all readings were done at the same height and therefore the same Q. A stand was used for this purpose, another stand was used to level the plants up and down so that the target leaf fitted into the leaf chamber (Fig. 3.5).

3.2.4.3. Leaf Characteristics.

The second or third 'fully developed' leaf grown under experimental conditions was used (target leaf). Measurements of leaf length were taken weekly and a 'fully developed' leaf was defined as having no significant increase in length during one week. Leaf-insertion number (leaf order from bottom) affects the assimilation capacity of a leaf (Ticha et.al. 1985). Precautions were taken to use the same leaf-insertion number: plants chosen in the glasshouse had the same number of leaves (within not between species), and the second or third fully developed leaf were of the same insertion number (Table 3.6).

The third fully developed leaf (from the top) was used in the case of *C.alliodora*. It was not possible to assess the insertion number since pruned cutting were used instead of saplings.

Table 3.6. Leaf insertion number of target leaves.

Treatment species	'sun'	'shade'
B.alicastrum	6-7	6-7
S.macrophylla	8-9	8-9
C.odorata	11-12	11-12

3.2.4.4. Growth analysis.

A sample of 5 saplings for each species was chosen at the beginning of the experiment (having the same height and number of leaves as the ones for the light response). Height and number of leaves were recorded and the plants were then divided into roots, stem and leaves. Leaf area (Licor 3100, § 2) and fresh/dry weight (ovendried for 48 h at 85 °C) were also determined. *C.alliodora* was not sampled at the beginning of the experiment.

a) Growing period.

At the start and then weekly, height, number of leaves, and length of new leaves were recorded. These measurements were carried out while the second or third leaf was fully developed and the assimilation and stomatal responses were recorded.

b) Harvesting.

Once the gas exchange readings were completed, the particular species was harvested and growth analysis carried out as above. This procedure was repeated for each species except *C.alliodora* which only leaves and stem were harvested.

3.2.4.5. Nitrogen analysis.

Total leaf nitrogen content was determined at the start and then at the end of the experiment, three samples for each species and treatments were analysed. Samples were dried in an oven at 85 °C for 2 days and then finely ground in a ball-mill (Glen-Creston, Scotland) then nitrogen analysis by acid digestion was carried out (Crooke & Simpson 1971).

Results are expressed both in a dry-weight and leaf area basis.

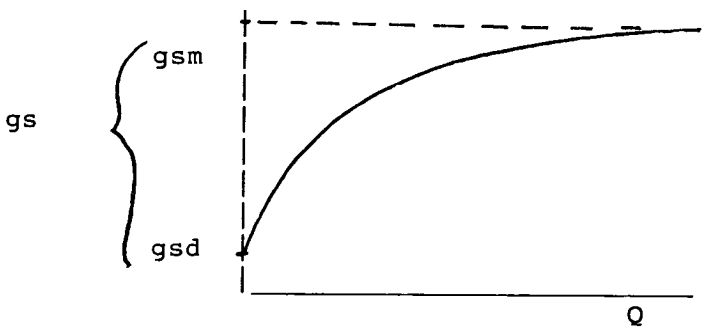
3.3. Data analysis.

3.3.1. Stomatal conductance.

It has become common to fit models of photosynthesis to experimental data of the kind collected with an IRGA, so that physiological parameters may be estimated by optimization procedures. Physiological knowledge of stomatal functioning is not adequate to provide a mechanistic model linking stomatal conductance, g_s, to the main environmental variables, which determine the value of g_s at a particular time (Jarvis 1976). However, several models which describe the idealized responses of g_s to these variables have been published (Jones 1983, Jarvis 1981).

a) Light response curve.

It has been shown that, a rectangular-hyperbola describes fairly well the response of g_s to Q.



The function used in this work is similar to the one used by Landsberg (1986) and has the form:

$$g_s = [g_{sm}\ \alpha\ Q] \ /\ [(\ g_{sm} + \alpha\ Q\ ) + g_{sd}]$$

where;

g_s is the stomatal conductance to water vapour (mol m^{-2} s^{-1}).
g_{sm} is the maximum stomatal conductance (mol m^{-2} s^{-1}).
α is the initial slope of the response (dimensionless).
g_{sd} is stomatal conductance in the dark (mol m^{-2} s^{-1}).
Q is the photon flux density (μmol m^{-2} s^{-1}).

b) VPD response.

A linear reduction in g_s with increasing VPD has been observed in some cases (Jarvis 1976, Miranda 1982). Nevertheless, a negative exponential function fits better to these data. The function used is similar to the one Jones (1983) uses and has the form:

$$g_{sd} = g_{smd} \exp(k_d \, VPD)$$

where;

g_{sd} is the stomatal conductance (mol m^{-2} s^{-1}).
g_{smd} is the maximum stomatal conductance at zero VPD (mol m^{-2} s^{-1}).
k_d is the negative exponential coefficient (dimensionless).
VPD is the leaf-air vapour pressure deficit (kPa).

c) Temperature response curve.

The dependence of g_s on leaf temperature can be represented by a bell shaped curve. There are several models which describe this kind of response (Jarvis 1976, Jones 1983). One of the simplest is described by Landsberg (1977) and has this form:

$$g_{st} = g_{mt} - (k_t (T - T_{opt})^2)$$

where;

g_{st} is the stomatal conductance (mol m^{-2} s^{-1}).
g_{mt} is the maximum stomatal conductance at optimum T (mol m^{-2} s^{-1}).
k_t is the temperature coefficient (dimensionless).
T is the air temperature. (°C).
T_{opt} is the optimum temperature (°C).

3.3.2. Photosynthesis.

The basic physiological parameters that describe photosynthesis by leaves are obtained from the response of net photosynthesis to absorbed quanta of photosynthetic active radiation and to the internal CO_2 concentration, Ci, (Jarvis & Sandford 1986). As this author mentions, the response had hardly been

measured until recently. Instead net assimilation (An) has been expressed in terms of incident quanta, Q, and in terms of air CO_2 concentration, Ca, as in this work.

The rectangular hyperbola function has been used to describe the light response curve of An (Landsberg 1986). Nevertheless, the non-rectangular hyperbola has been used as a better approximation, this function represents better the light response at low levels of Q (Thornley 1976).

$$0 = A^2 \theta - A (\alpha Q + Am) + \alpha Q Am$$

where;

A.- Gross CO_2 exchange rate (µmol m^{-2} s^{-1}).
Q.- Photosynthetic photon flux density (µmol m^{-2} s^{-1}).
Am.- Asymptotic rate of assimilation at saturating Q (µmol m^{-2} s^{-1}).
α.- Quantum efficiency (initial slope, dimensionless).
θ.- convexity parameter (dimensionless).

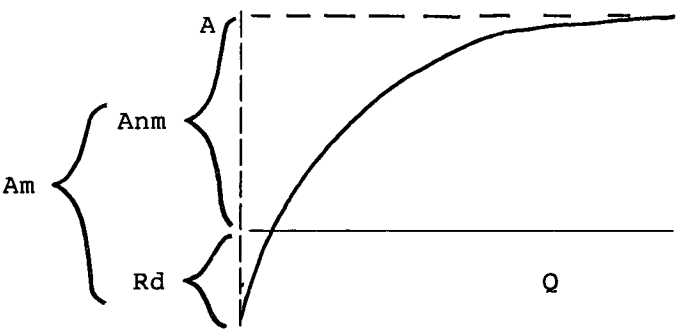
The convexity parameter allows a family of curves to be represented. It can have values from 0 to 1, where 0 results in a rectangular hyperbola and 1 results in the 'Blackman response' function, see Thornley (1976) for details.

In terms of the exchange flux of CO_2 through the stomata:

$$A = An + Rd$$

and

$$Am = Anm + Rd$$



where;

An.- Is the net assimilation rate (µmol m^{-2} s^{-1}).
Anm.- Is the maximum net assimilation rate (µmol m^{-2} s^{-1}).
Rd.- Rate of dark respiration (µmol m^{-2} s^{-1}).

For field data, it is adequate to assume a linear relationship between Anm and the internal CO_2 concentration, Ci, with the mesophyll conductance, g_m, as slope (Griffiths 1983), that is:

$$Anm = g_m (Ci - \Gamma)$$

where;

g_m is in mol m^{-2} s^{-1},
Ci in µmol m^{-2} s^{-1} and
Γ, CO_2 compensation point is in µmol m^{-2} s^{-1}.

Combining equations :

$$0 = \theta (An + Rd)^2 - (An + Rd) (\alpha Q + (g_m (Ci - \Gamma) + Rd)) + \alpha Q (g_m (Ci - \Gamma) + Rd)$$

This equation has a quadratic form when solved for An and has the form:

$$\alpha = \theta$$

$$\beta = Rd (2\Gamma - 1) - \alpha Q - (Ci - \Gamma) g_m$$

$$\gamma = Rd^2 (\theta - 1) + (Ci - \Gamma) g_m (\alpha Q - Rd)$$

Therefore:

$$An = (- \beta - (\beta^2 - 4 \alpha \gamma)^{0.5}) / 2 \alpha$$

Of these variables, Q and Ci can be derived from gas exchange studies, the other variables may be estimated as parameters by solving the equation with observed values of An.

3.3.3. Growth analysis.

The most common rates and ratios which summarize plant performance were used (Causton & Venus 1981). RGR, NAR, LAR, SLA and LWR (among others) were analysed; the functions used were explained in the previous chapter.

3.3.4. Fitting procedures.

Hyperbolic models were fitted to the stomatal and assimilation responses to light. Exponential models were used for the stomatal response to VPD and temperature. All these models are non-linear and were fitted by the 'maximum likelihood program' (MLP, Ross 1981), available within the Genstat package (Alvey et.al. 1983).

Variance analysis was carried out in all the data sets; assimilation, stomatal conductance, growth analysis and, nitrogen content. Treatment effects and differences between species were analysed. In addition, error terms (variance) were used to assess the goodness of fit of the non-linear models. The total variance about the mean ('total') is divided into variance accounted for by the equation ('equation') and variance about the equation ('residual'), the 'residual' is further subdivided into variance due to lack of fit ('lack of fit') and variance due to replicate error ('replicate error'). 'Equation' and 'residual' are compared to see if the equation removes a significant amount of variance, 'replicate error' and 'lack of fit' are compared to see if 'lack of fit' is significant (Ross 1981). The Genstat package was used to carry out the variance analysis.

In the case of data on conductance and photosynthesis which decline at high light levels (see results), such data are deemed to be 'aberrant' because they do not conform to the basic models which present asymptotic levels. Thus in some runs of the anovar and in the model fitting the data at the highest light levels were deleted so as to not jeopardize the overall fit in the rest of the range. This data set are called 'truncated'. It is important to mention that these data were only a few and that they were discussed outside the scope of the models. The results of the anovar and the 'F' test carried out to assess the goodness of fit are presented in appendix 1.

3.4. Results

In the figures that follow the curves drawn through the data points are those calculated from the model after fitting the model to the data as already described. The goodness of fit of the model to the data was adequate except when otherwise noted in the caption. Tables to indicate the level of statistical significance arising from the 'goodness of fit' test are given in appendix 1.

3.4.1. Stomatal conductance.

3.4.1.1. Photon flux density.

Although there was much variation between leaves (Figs. 3.6–3.9), it was evident that all species displayed a stomatal opening in the Q range 0–250 μmol m^{-2} s^{-1}, and that at night the conductance was never as low as zero. The trends can be seen more clearly when mean values and fitted curves are displayed (same figs.). The more 'shade-tolerant' species, *B.alicastrum* and *S.macrophylla*, showed the highest g_s in the 'sun' treatment, while the more 'shade-intolerant', *C.odorata* and *C.alliodora* showed the highest values in the 'shade' treatment. In two species (*B.alicastrum* and *C.odorata*) there was a strong indication of stomatal closure, perhaps reflecting high leaf temperatures and correspondingly high VPD values at the highest irradiation. Maximum values are in the range of 0.12–0.20 mol m^{-2} s^{-1}, although 0.30 was recorded in one determination on *C.odorata* (Fig. 3.8). The fitted parameters and their standard errors are shown in Table 3.10.

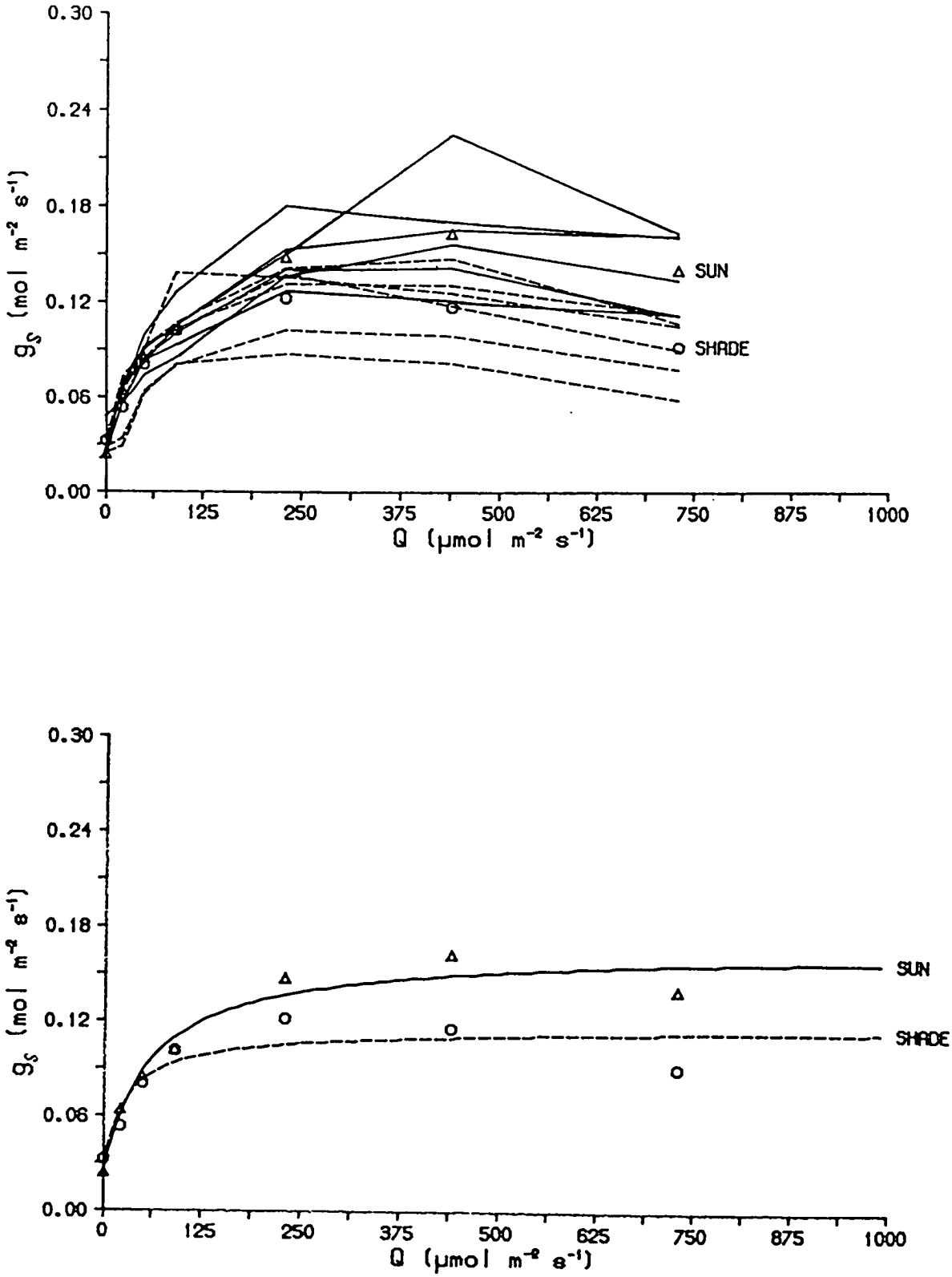


Fig. 3.6 g_s as function of Q. Saplings of B.alicastrum grown at two levels of Q (80 and 800 μmol m^{-2} s^{-1}). Above, each line is an individual leaf response and one single plant. Below, each line represents a rectangular hyperbola model fitted to the data. Means for each light levels are also shown.

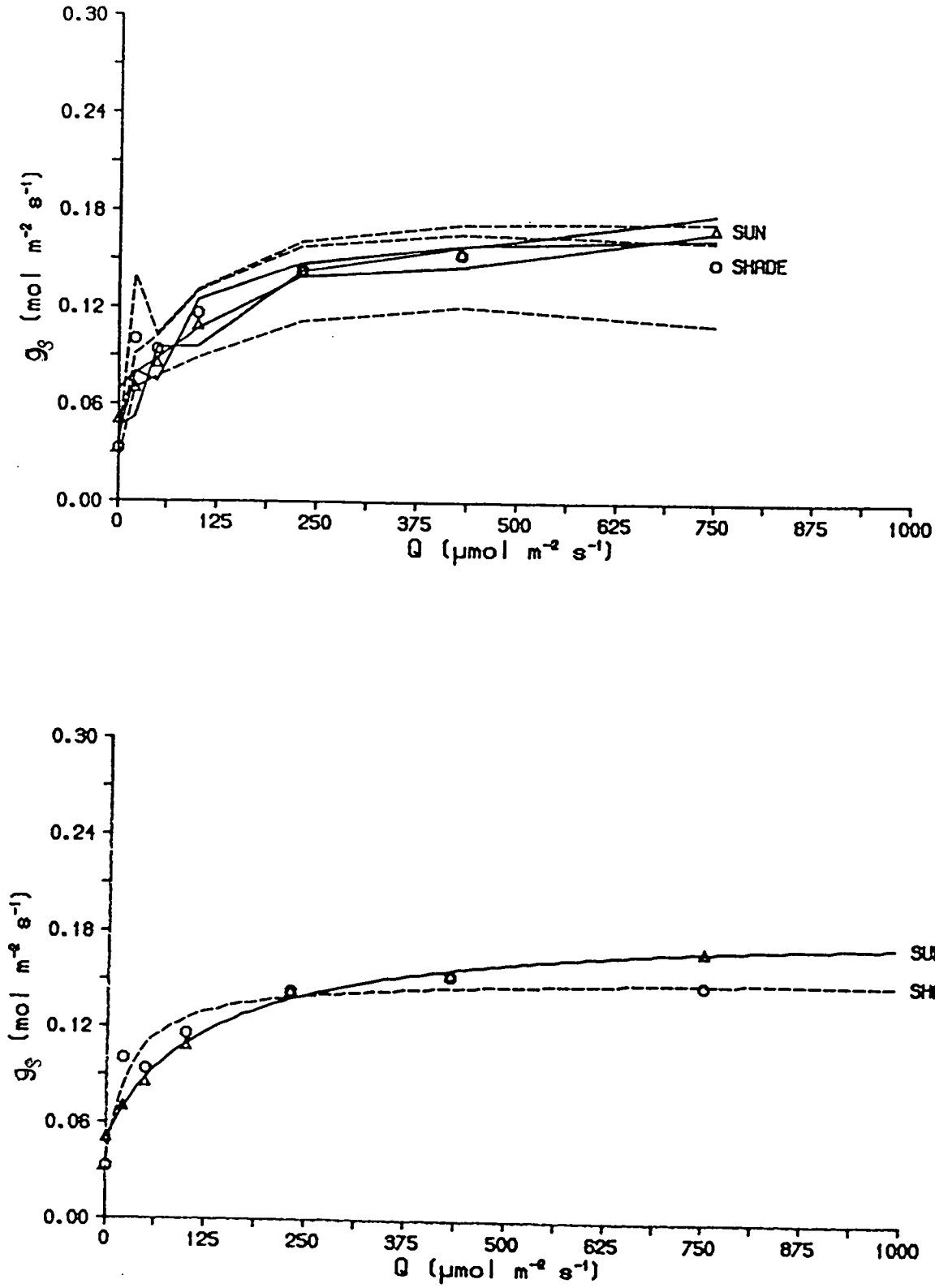


Fig. 3.7 g_s as function of Q. Saplings of S.macrophylla grown at two levels of Q (80 - 800 µmol m^{-2} s^{-1}). Above, each line is an individual leaf response and one single plant. Below, each line represents a rectangular hyperbola model fitted to the data. Means for each light level are also shown.

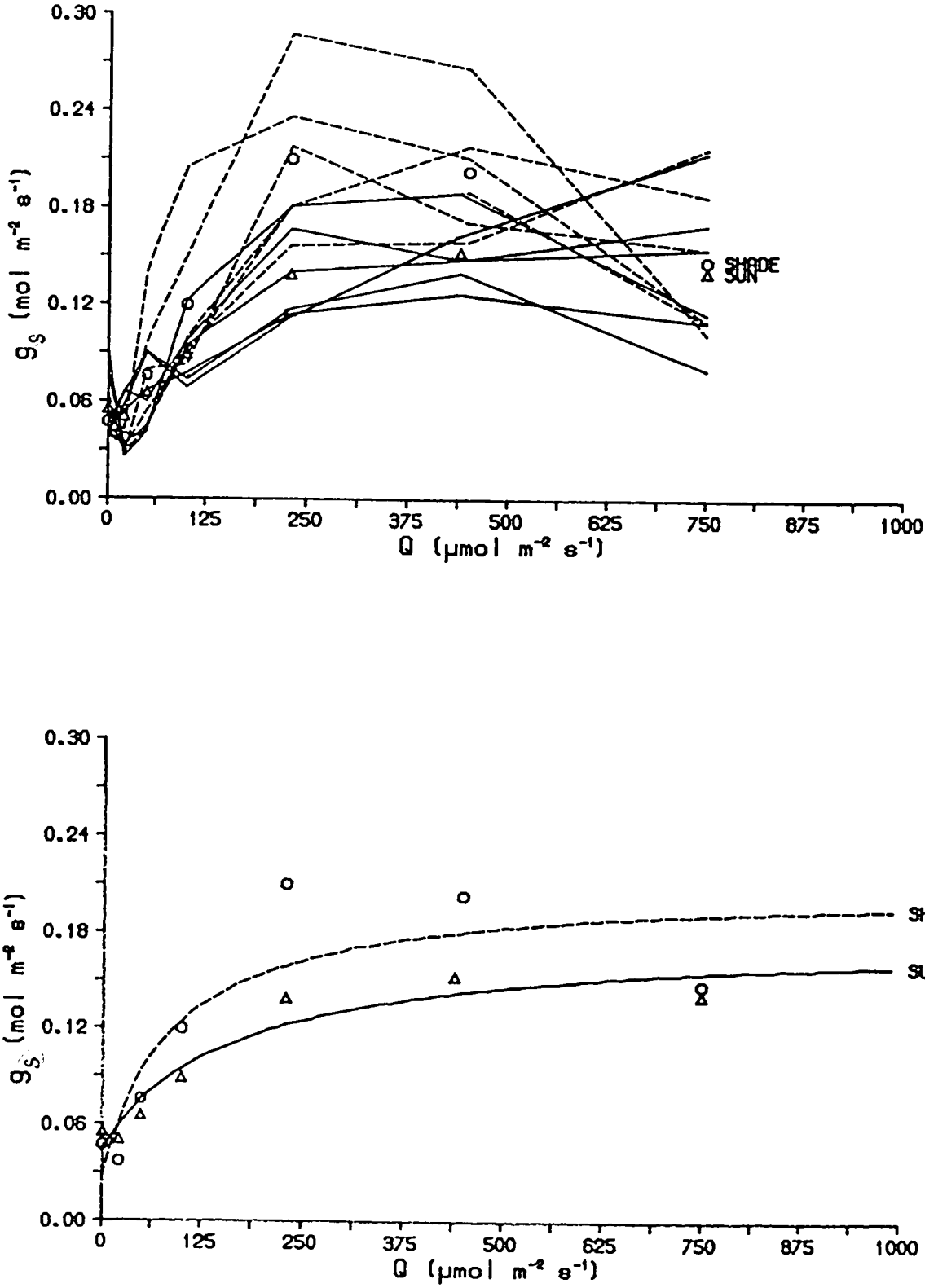


Fig. 3.8 g_s as function of Q. Saplings of C.odorata grown at two levels of Q (80 -800 µmol m^{-2} s^{-1}). Above, each line is an individual leaf response and one single plant. Below, each line is a rectangular hyperbola model fitted to the data. Means for each light level are also shown.

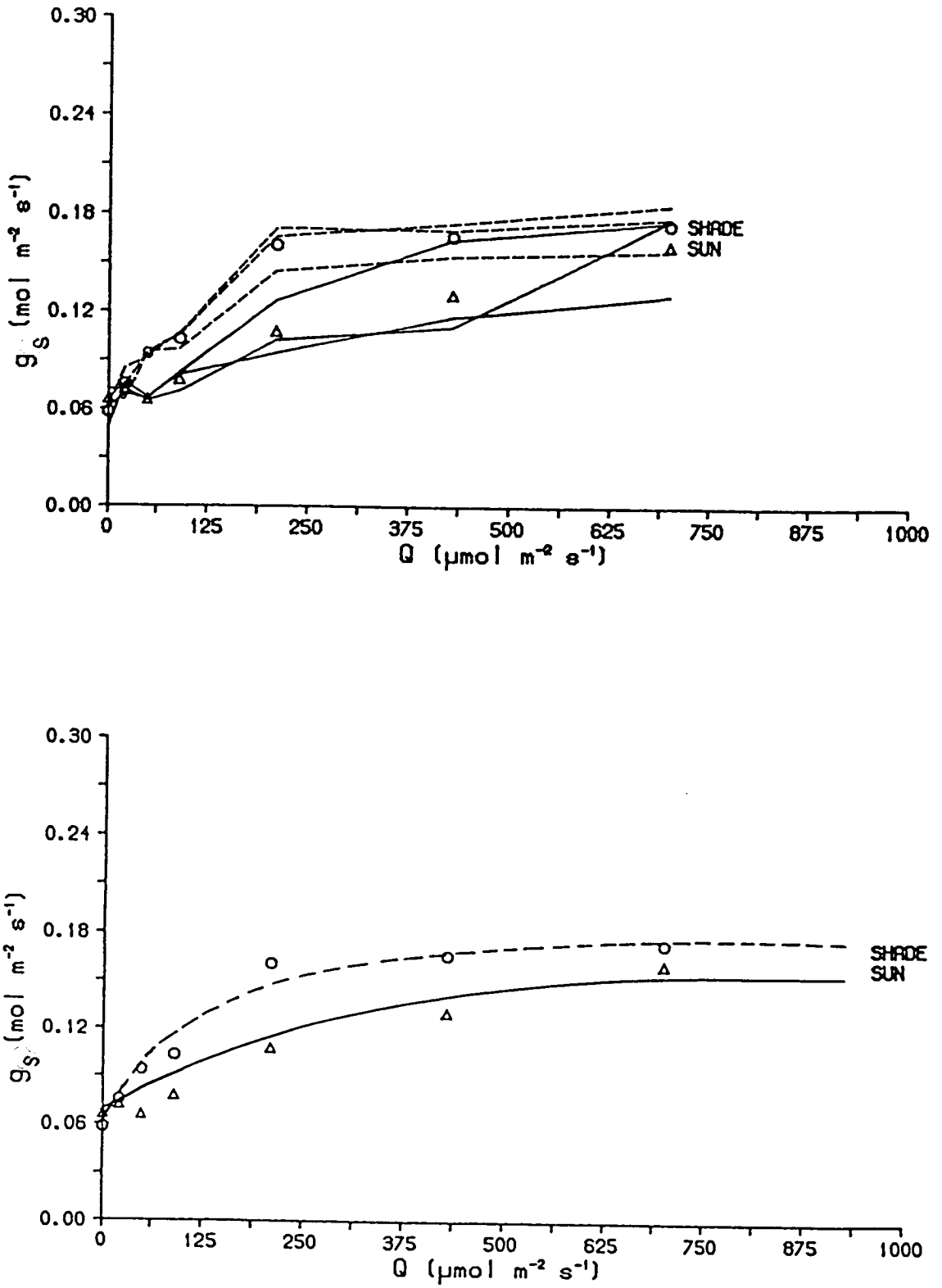


Fig. 3.9 g_s as function of Q. Saplings of C.alliodora grown at two levels of Q (80 -800 μmol m^{-2} s^{-1}). Above, each line is an individual leaf response and one single plant. Below, each line represents a rectangular hyperbola model fitted to the data. Means for each light level are also shown.

Table 3.10 Light response of stomatal conductance. Parameters estimates and (s.e.) of the rectangular hyperbola model.

species	Light	Qs	gsd	a	gsm	RSS.	df.
B.ali.	sun	450	.028 (.007)	.0018 (.0004)	.164 (.012)	.0102	33
------	shade	244	.030 (.007)	.0021 (.0006)	.104 (.010)	.0114	33
S.mac.	sun	612	.051 (.006)	.0010 (.0003)	.139 (.014)	.0019	15
------	shade	281	.037 (.015)	.0036 (.0025)	.118 (.019)	.0094	15
C.odo.	sun	644	.046 (.007)	.0006 (.0002)	.193 (.046)	.0169	33
------	shade	525	.029 (.013)	.0015 (.0004)	.268 (.041)	.0509	33
C.all.	sun	581	.064 (.005)	.0002 (.0001)	.258 (.280)	.0028	15
------	shade	425	.057 (.006)	.0010 (.0002)	.159 (.017)	.0020	15
range		244-644	.028 - .064	.0002 - .0036	.104 - .268		
B.ali.	s & sh	347	.029	.0019	.134		
S.mac.	----	446	.044	.0023	.129		
C.odo.	----	584	.038	.0010	.231		
C.all.	----	503	.060	.0006	.208		
All	sun	572	.047	.0009	.188		
---	shade	369	.038	.0020	.162		

For details about species and light conditions see text.

Qs.- Light saturation point, estimated, (µmol m^{-2} s^{-1}).
gsd.- Mean stomatal conductance at dark (mol m^{-2} s^{-1}).
a.- Mean initial slope (mol H2O / µmol quanta).
gsm.- Mean maximum stomatal conductance (mol m^{-2} s^{-1}).
RSS.- Residual sum of squares.
df.- Degrees of freedom.

3.4.1.2. Vapour pressure deficit.

Primary-forest species displayed higher g_s in the 'sun' treatment irrespective of the VPD level, secondary-forest species showed the same pattern at high VPD but opposite response when VPD is low (Figs. 3.10-3.11). This response reflect higher sensitivity to VPD (k_d) of secondary-forest species, particularly when grown in shade (Table 3.11). It is important to mention that these values represent the mean maximum stomatal conductance when VPD is nil. Thus, this is an optimum condition and may be taken as maximum mean g_{sm} for all other responses, i.e. Q and temperature response (the g_{sm} response for Q and temperature were calculated for VPD values about

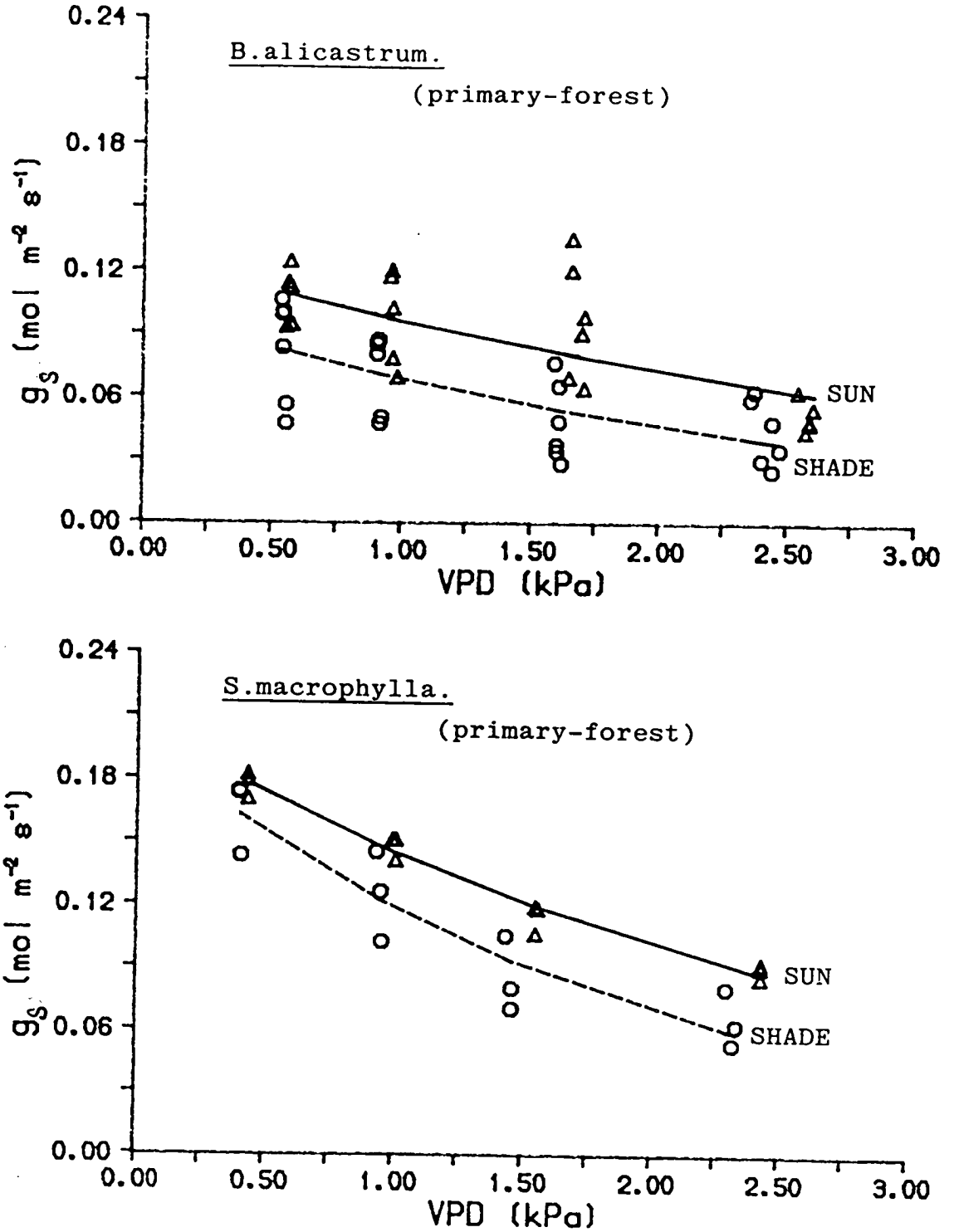


Fig. 3.10 g_s as function of VPD. Saplings grown at two levels of Q: 80 μmol m^{-2} s^{-1} (dashed line) and 800 μmol m^{-2} s^{-1} (continuous line). Lines represent a negative-exponential model fitted to the data (triangles and circles).

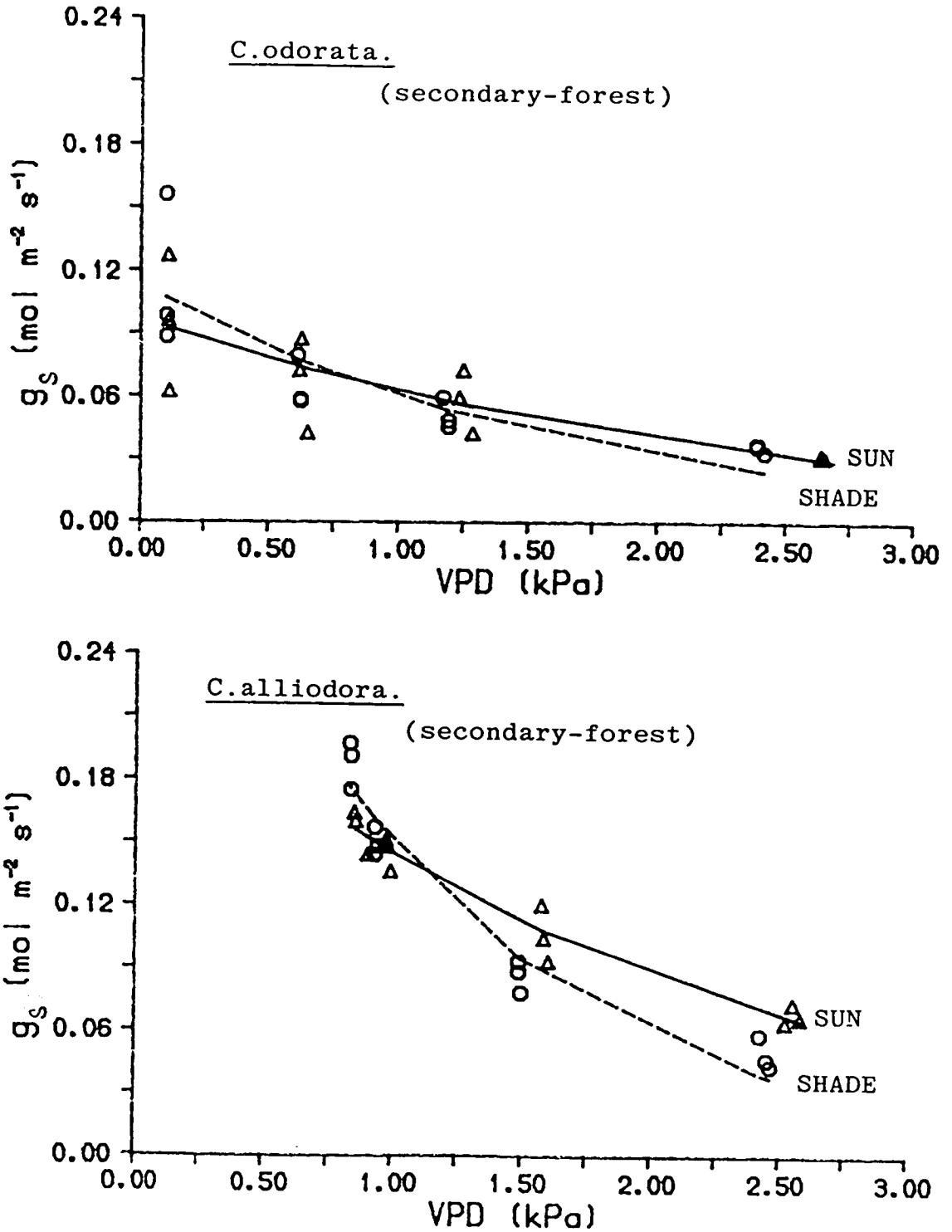


Fig. 3.// g_s as function of VPD. Sapling grown at two levels of Q : 80 µmol m^{-2} s^{-1} (dashed line) and 800 µmol m^{-2} s^{-1} (continuous line). Lines represent a negative-exponential model fitted to the data (triangles and circles).

10 kPa, thus, not in "VPD optimum" conditions).

Values as high as 0.39 mol m^{-2} s^{-1} were estimated for the mean g_{sm} of the shade-intolerant *C.alliodora* (shade) Table 3.11. Lower values were estimated for the shade-tolerants *B.alicastrum* and *S.macrophylla*, 0.1 and 0.2 mol m^{-2} s^{-1} respectively. The shade-intolerant *C.odorata* displayed the lowest values, similarly to the values observed in the light response. Whether this is a property of the species or is due to the insect damage already mentioned is not known.

Table 3.11 . Parameters and (s.e.) of the negative-exponential model for the g_s - VPD relationship.

species	Light	gsm	kd	RSS.	df.
B.ali	sun	.128 (.013)	.278 (.073)	.0104	22
	shade	.102 (.013)	.384 (.109)	.0082	22
S.mac	sun	.208 (.005)	.364 (.022)	.0004	10
	shade	.204 (.015)	.529 (.076)	.0029	10
C.odo	sun	.098 (.011)	.440 (.013)	.0038	10
	shade	.114 (.013)	.648 (.176)	.0045	10
C.all	sun	.240 (.013)	.512 (.041)	.0008	10
	shade	.388 (.037)	.951 (.115)	.0021	10
ranges		.098 - .388	.275 - .951		
B.ali	s & sh	.115	.331		
S.mac	s & sh	.206	.446		
C.odo	s & sh	.106	.544		
C.all	s & sh	.314	.731		
ALL	sun	.168	.398		
	shade	.202	.628		

g_{sm}.- Mean maximum stomatal conductance (mol m^{-2} s^{-1}).
k_d.- negative-exponential coefficient (mol m^{-2} s^{-1} kPa^{-1}).
RSS.- Residual sum of squares.
df.- Degrees of freedom.

3.4.1.3. Temperature.

As a result of the unsuccessful optimization no attempt was made to use the parameters obtained. The model was fitted to all species and both treatments assuming a constant optimum temperature equal to the growing conditions temperature (28 °C). The results are shown in Table 3.12. These are taken just as an approximation of the response and assumed to be equal for all the cases (species and treatments).

Table 3.12. Parameter estimated for the temperature response.

species	Light	To	gsm	kt	RSS.	df.
All	sun & shade	28	.101 (.005)	.001 (.001)	.1675	111

T_o.- Mean optimum temperature (°C).
g_{sm}.- Mean maximum stomatal conductance (mol m^{-2} s^{-1}).
k_t.- Temperature coefficient.
RSS.- residual sum of squares.
df.- degrees of freedom.

3.4.2. Photosynthesis.

3.4.2.1. Photon flux density.

Variation between leaves was smaller for An than for g_s (Figs. 3.12–3.15) thus better fits were obtained i.e. differences between means and fitted curves. All species in 'shade' reached the light saturation level in the range Q= 280–600 µmol m^{-2} s^{-1} and displayed maximum An values, around 4.6–5.3 µmol m^{-2} s^{-1} (Table 3.14). In the 'sun' treatment all the species reached the light saturation level at about 745–780 µmol m^{-2} s^{-1} being its maximum An values around 6.2–8.8 µmol m^{-2} s^{-1} (Table 3.14).

Dark respiration rates were always higher in the 'sun' treatment and for the shade-intolerant species (*C.odorata* and *C.alliodora*) with values around 0.7 µmol m^{-2} s^{-1}. For the 'shade' treatment and the shade-tolerant species values

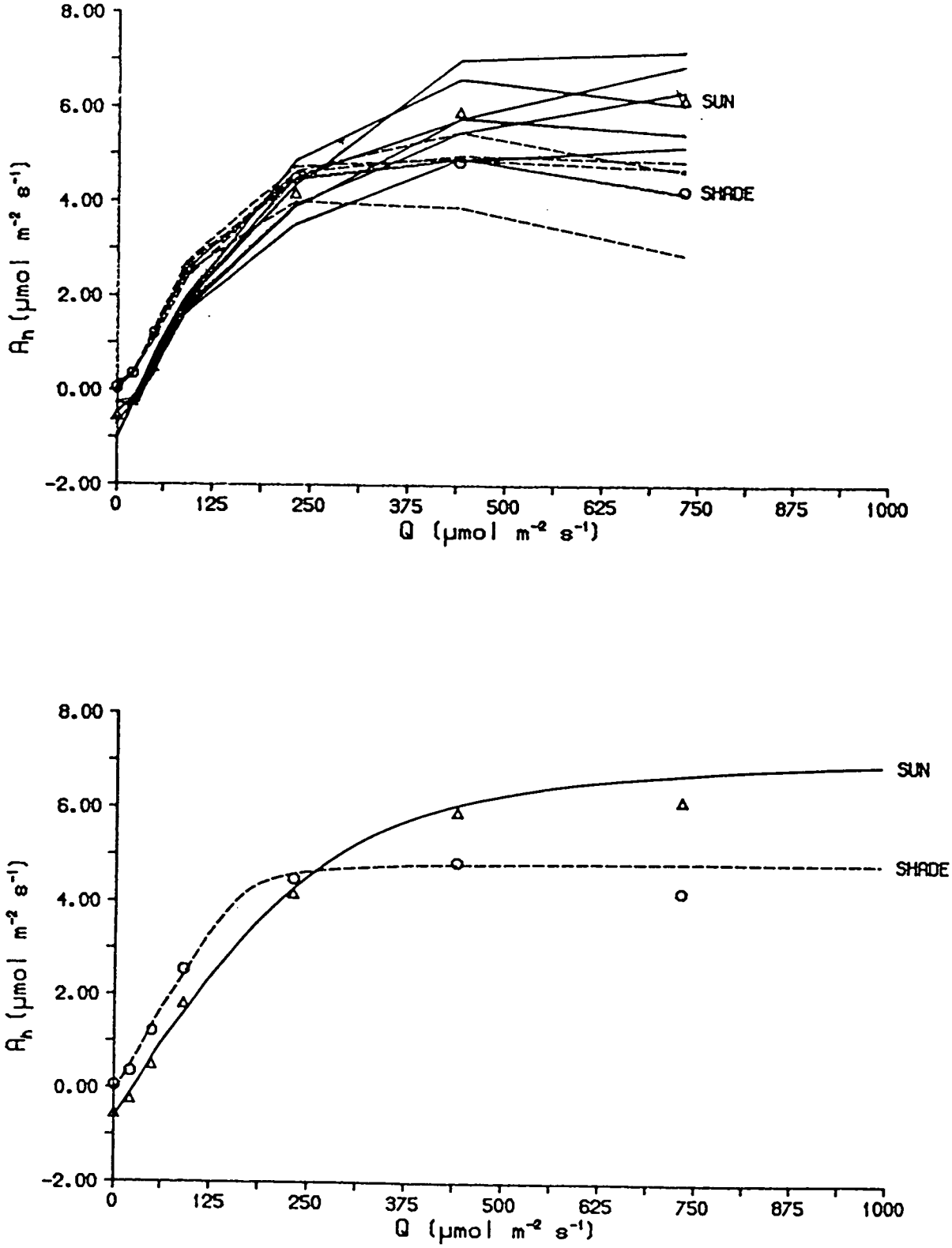


Fig. 3.12 A_n as a function of Q. Saplings of B.alicastrum (shade-tolerant) grown at two levels of Q : 80 µmol m^{-2} s^{-1} (SHADE) and 800 µmol m^{-2} s^{-1} (SUN). Above, each line represents an individual leaf response and one single plant. Below, each line is a non-rectangular hyperbola model fitted to the data. Means for each light level are also shown.

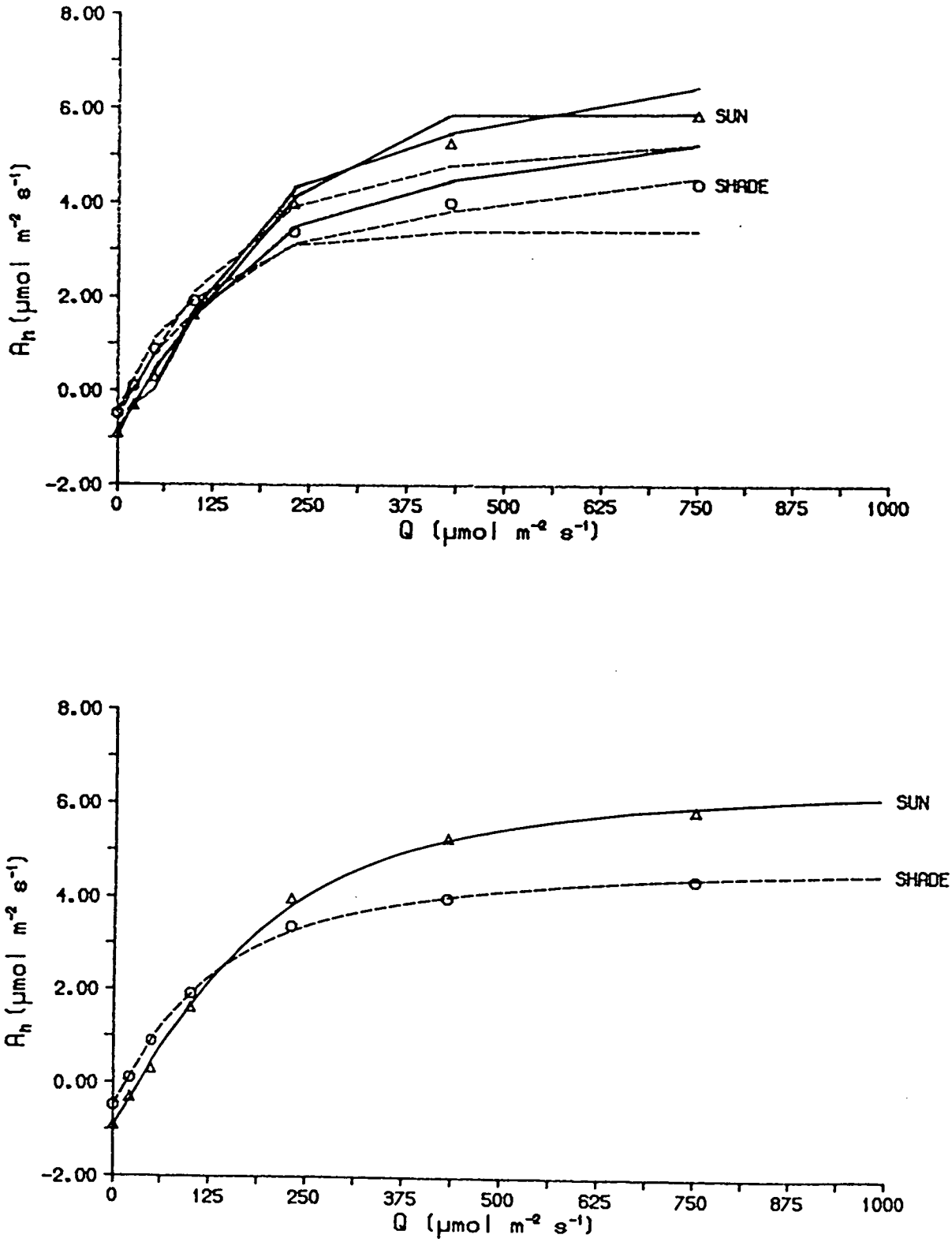


Fig. 3.13 A_n as a function of Q. Saplings of S.macrophylla (shade-tolerant) grown at two levels of Q : 80 µmol m^{-2} s^{-1} (SHADE) and 800 µmol m^{-2} s^{-1} (SUN). Above, each line represents an individual leaf response and one single plant. Below, each line is a non-rectangular hyperbola model fitted to the data. Means for each light level are also shown.

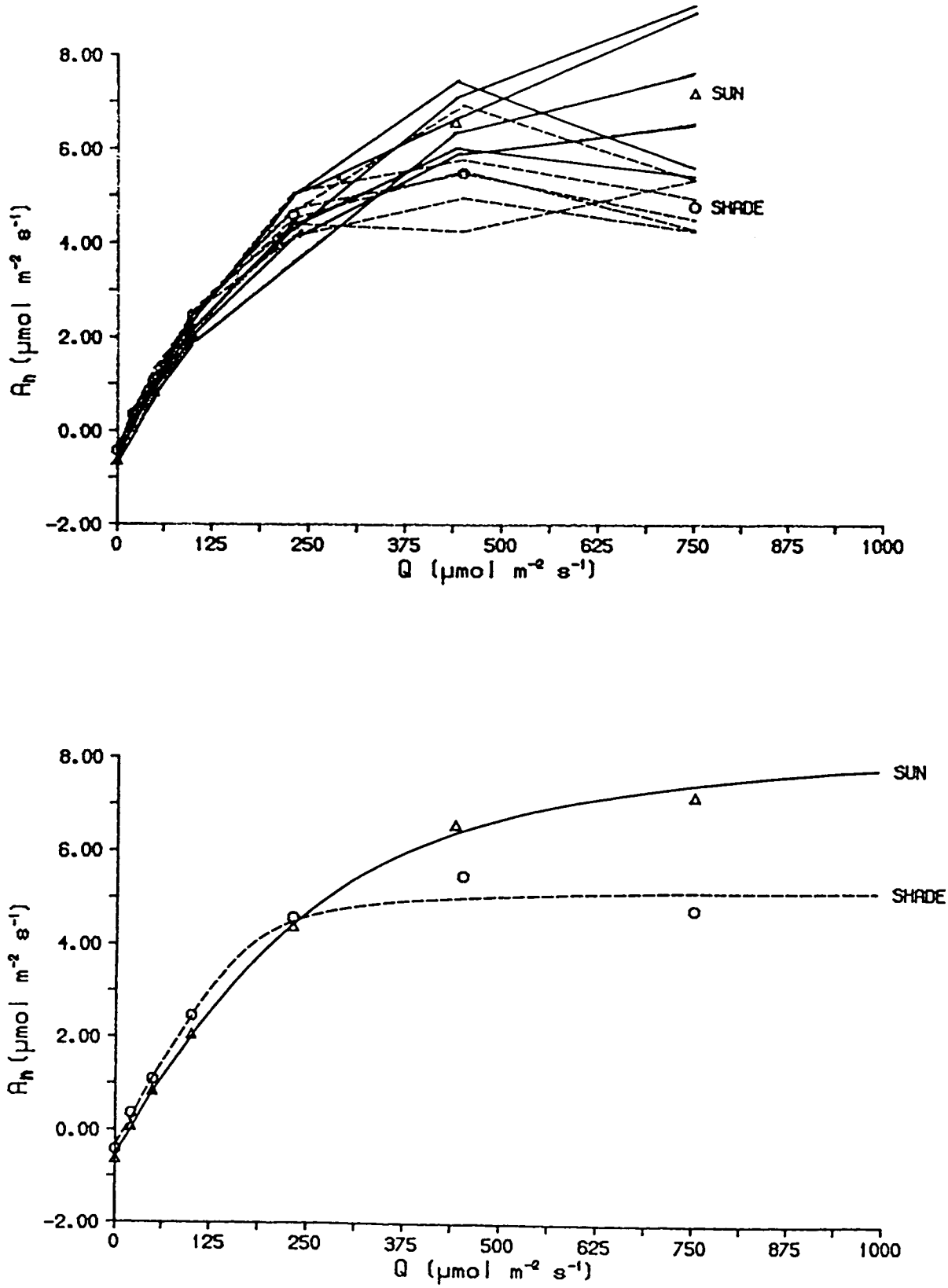


Fig. 3.14 A_n as a function of Q. Saplings of C.odorata (shade-intolerant) grown at two levels of Q : 80 µmol m^{-2} s^{-1} (SHADE) and 800 µmol m^{-2} s^{-1} (SUN). Above, each line represents an individual leaf response and one single plant. Below, each line is a non-rectangular hyperbola model fitted to the data. Means for each light level are also shown.

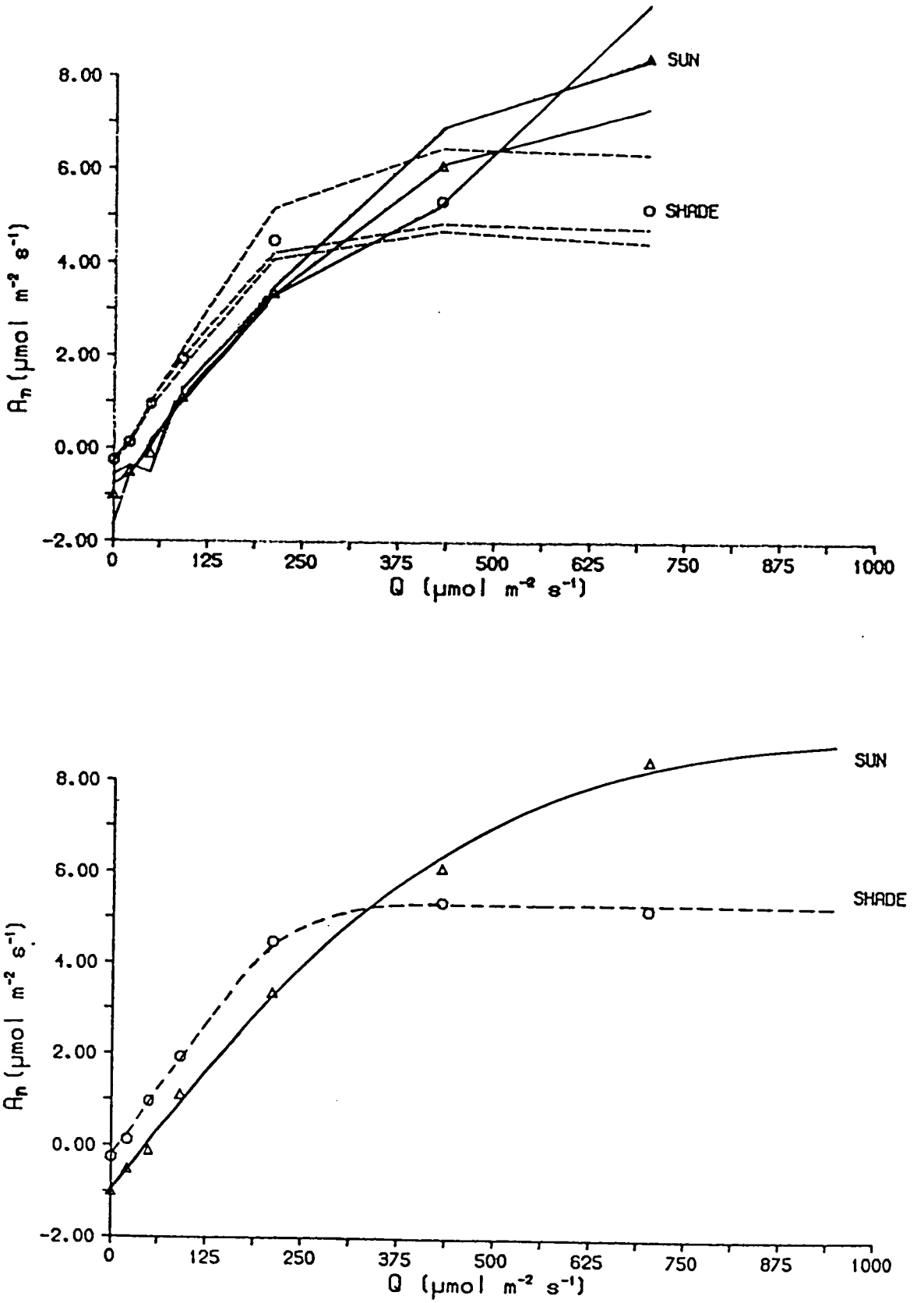


Fig. 3.15 A_n as a function of Q. Saplings of C.alliodora (shade-intolerant) grown at two levels of Q : 80 µmol m^{-2} s^{-1} (SHADE) and 800 µmol m^{-2} s^{-1} (SUN). Above, each line represents an individual leaf response and one single plant. Below, each line is a non-rectangular hyperbola model fitted to the data. Means for each light level are also shown.

were about 0.3 µmol m^{-2} s^{-1}.

At high irradiances both *B.alicastrum* and *C.odorata* display a drop in An (Figs. 3.12 and 3.14) which could be caused by the stomatal closure previously noted. Fitted parameters and their standard errors can be seen in Table 3.13

Table 3.13. Light response curve of photosynthesis. Parameter estimates and (s.e.) for the non-rectangular hyperbola model.

species	Light	Θ	a	gm	Rd	RSS.	D
B.ali.	sun	.693 (.324)	.027 (.004)	.044 (.011)	.655 (.141)	5.724	3
------	shade	.921 (.036)	.029 (.002)	.027 (.001)	.100 (.078)	1.871	3
C.odo.	sun	.022 (.082)	.031 (.001)	.073 (.003)	.575 (.047)	4.127	3
------	shade	.812 (.152)	.032 (.005)	.028 (.003)	.369 (.147)	6.047	3
S.mac.	sun	.917 (.100)	.026 (.004)	.026 (.003)	.879 (.163)	1.778	1
------	shade	.747 (.324)	.029 (.007)	.020 (.004)	.464 (.188)	2.000	1
C.ali.	sun	.807 (.561)	.023 (.004)	.052 (.046)	1.03 (.187)	2.513	1
------	shade	.955 (.105)	.026 (.006)	.026 (.003)	.316 (.245)	4.043	1
Ranges		.022 - .955	.023 - .032	.020 - .073	.100 - 1.03		
B.ali.	s & sh	.807	.028	.036	.378		
C.odo.	----	.417	.031	.050	.472		
S.mac.	----	.832	.027	.023	.672		
C.ali.	----	.881	.024	.039	.673		
All	sun	.610	.027	.049	.785		
------	shade	.859	.029	.025	.312		

For details of the species or light conditions see text.

O.- Mean value of convexity parameter (dimentionless).
a.- Mean apparent Quantum efficiency (dimentionless).
gm.- Mean mesophyll conductance (mol m^{-2} s^{-1}).
Rd.- Mean dark respiration rate (µmol m^{-2} s^{-1}).
RSS.- Residual sum of squares.
DF.- Degrees of freedom.

Table 3.14. Estimated light compensation point, Qc, maximum assimilation rate, Am, and light saturation rate, Qs. Units are in μmol m^{-2} s^{-1}.

species	Light	Qc	Qm	Anm
B.ali	sun	25	755	7.0
------	shade	9	280	4.9
S.mac	sun	34	745	6.2
------	shade	16	606	4.6
C.odo	sun	22	780	7.8
------	shade	12	394	5.2
C.all	sun	50	769	8.8
------	shade	12	294	5.3
B.ali	s & sh	17	517	5.9
S.mac	------	21	675	5.4
C.odo	------	17	587	6.5
C.all	------	31	531	7.0
All	sun	33	762	7.4
---	shade	13	393	5.0

3.4.3. Growth.

B.alicastrum (primary-forest species) differs markedly from the other species. It has lower height, number of leaves and leaf area growth rates than the other species (Fig. 3.16). Its sensitivity to shade is lower, i.e. their rates and ratios displayed small changes in shade conditions. In general, shade causes an increase in height but in *B.alicastrum* it causes a small reduction. Although leaf number is slightly reduced by shade in all species, differences are not significant. Leaf area was increased by shade in *B.alicastrum* and *S.macrophylla* but greatly reduced in *C.odorata*.

Similar specific responses were observed with derived ratios (Fig. 3.17): *B.alicastrum* displays lower RGRs and sensitivity to shade than the rest of the species. In general, RGRs and NARs were higher in open conditions, the opposite trend is displayed by LAR, SLA and LWR, with the exception of LWR in *C.odorata*. In all cases *B.alicastrum* (shade-tolerant) had lower values and sensitivity than the other species (shade-intolerants), with the exception of LAR where *C.odorata* showed similar values than *B.alicastrum*. SWR and RWR (Fig.

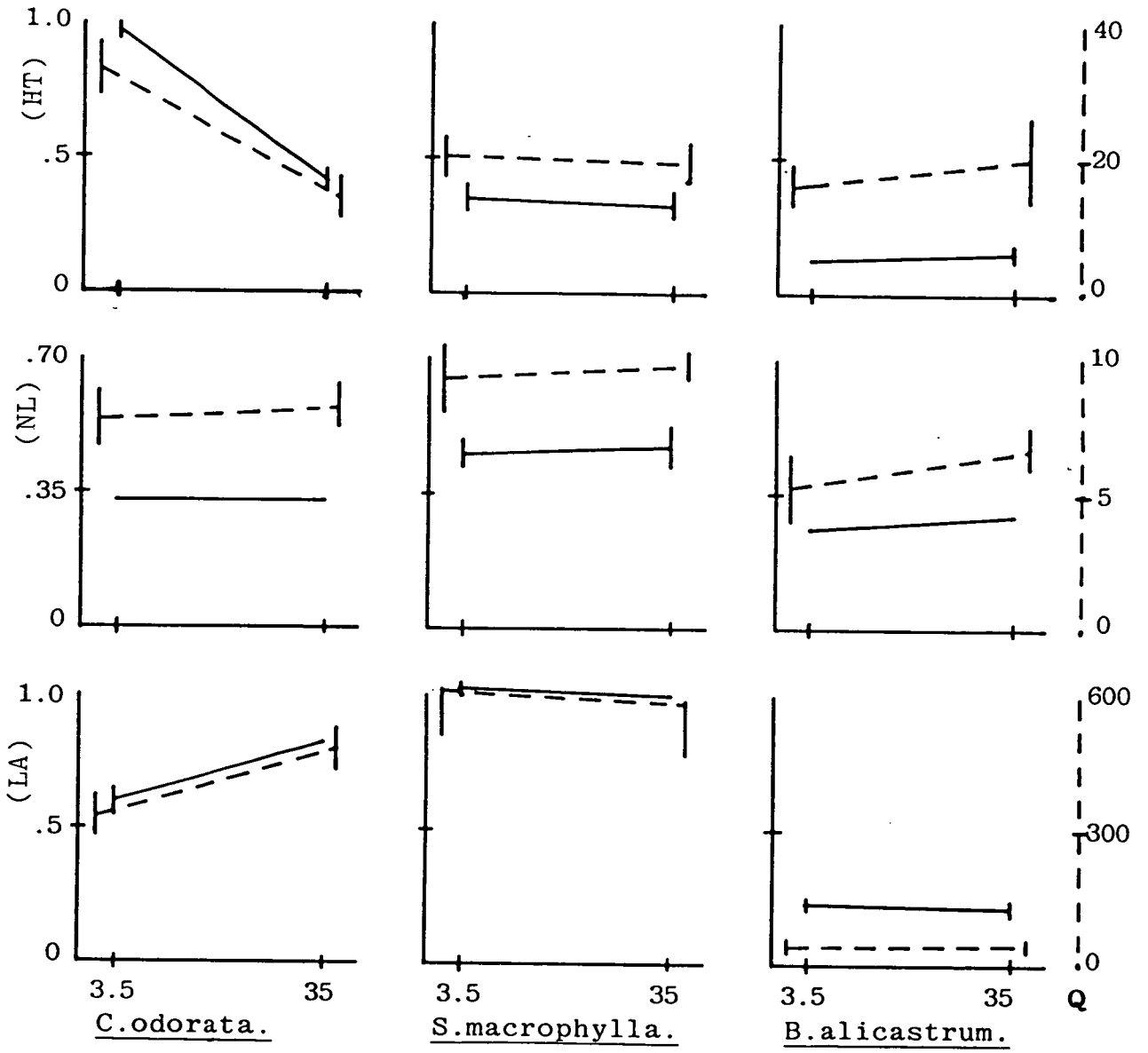


Fig. 3.16 Mean relative growth rates (solid line) and mean absolute growth rates (broken line) of height (HT), number of leaves (NL) and leaf area (LA) under 'sun' (35) and 'shade' (3.5 mol m^{-2} day) conditions.

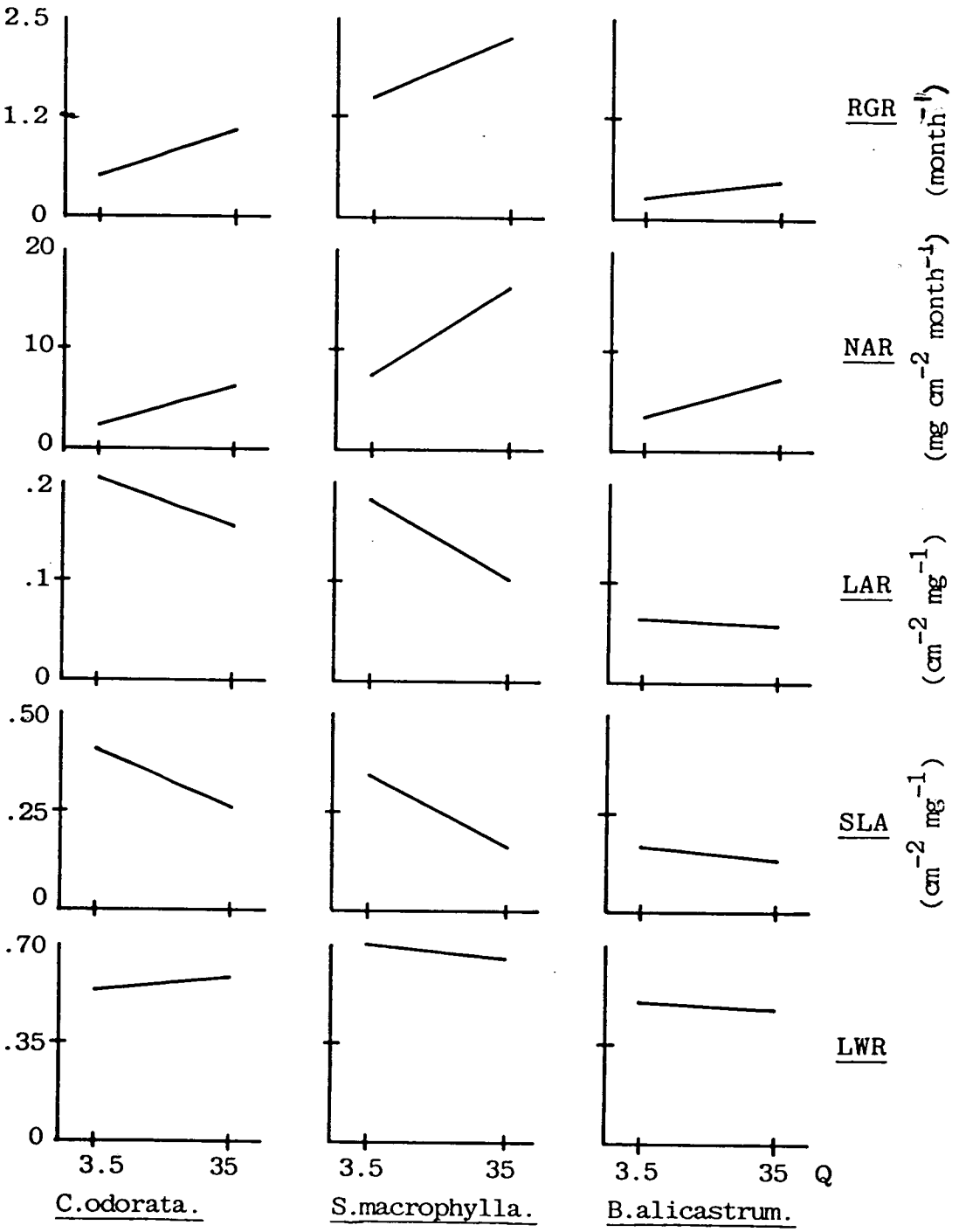


Fig. 3.17 Relative growth rate (RGR), net assimilation rate (NAR), leaf area ratio (LAR), specific leaf area (SLA) and leaf weight ratio (LWR) for different species and treatments; open (35) and shade (3.5 mol m^{-2} day).

3.18) do not follow any pattern under shade conditions. *B.alicastrum* allocates more dry matter into stem than roots; *S.macrophylla* diminishes the amount of matter in both stem and roots, increasing leaf weight; *C.odorata* increases both stem and root weight at the expense of leaf dry matter.

3.4.4. Nitrogen content.

Although in most cases differences are not statistically significant, there is a constant trend of higher N content (on a dry matter basis) in the 'sun' treatment and in the secondary-forest species (Fig. 3.18). When expressed on a leaf area basis the 'sun' treatment maintains its trend but displays larger differences (more than twice) than for the 'shade' treatment. However species patterns are inverted with the 'shade-tolerant' *B.alicastrum* displaying higher values, with the exception of *C.alliodora* with very high values (Table 3.21).

3.5. Discussion.

Both stomatal and assimilation responses to increasing Q levels showed an aberrant behaviour, at Q values above 400 µmol m^{-2} s^{-1} for *B.alicastrum* and *C.odorata* An and g_s fell instead of reaching an asymptotic level as theoretical models suggest (Figs. 3.6-3.9 & 3.12-3.15). Similar behaviour has been observed in other light response curves, especially in shade adapted leaves (Bazzaz 1979, Kwesiga et.al. 1986), but this has not been fully explained. Photoinhibition may be the cause of the drop in the response in some cases but this needs further investigation. Chlorophyll destruction may be one of the factors involved (Langenheim et.al. 1984), which might be an irreversible effect. Other factors not involving photosynthesis may explain stomatal closure a rise in SVPD values due to the radiation load on the leaf may be one of them. If leaf temperature rises then an increment in the leaf-air vapour pressure deficit is expected, with consequent stomatal closure. More complex irradiance and temperature effects may be expected through their effect on respiration and photorespiration, altering internal values of CO_2 concentration which in turn may affect the stomatal and assimilation responses.

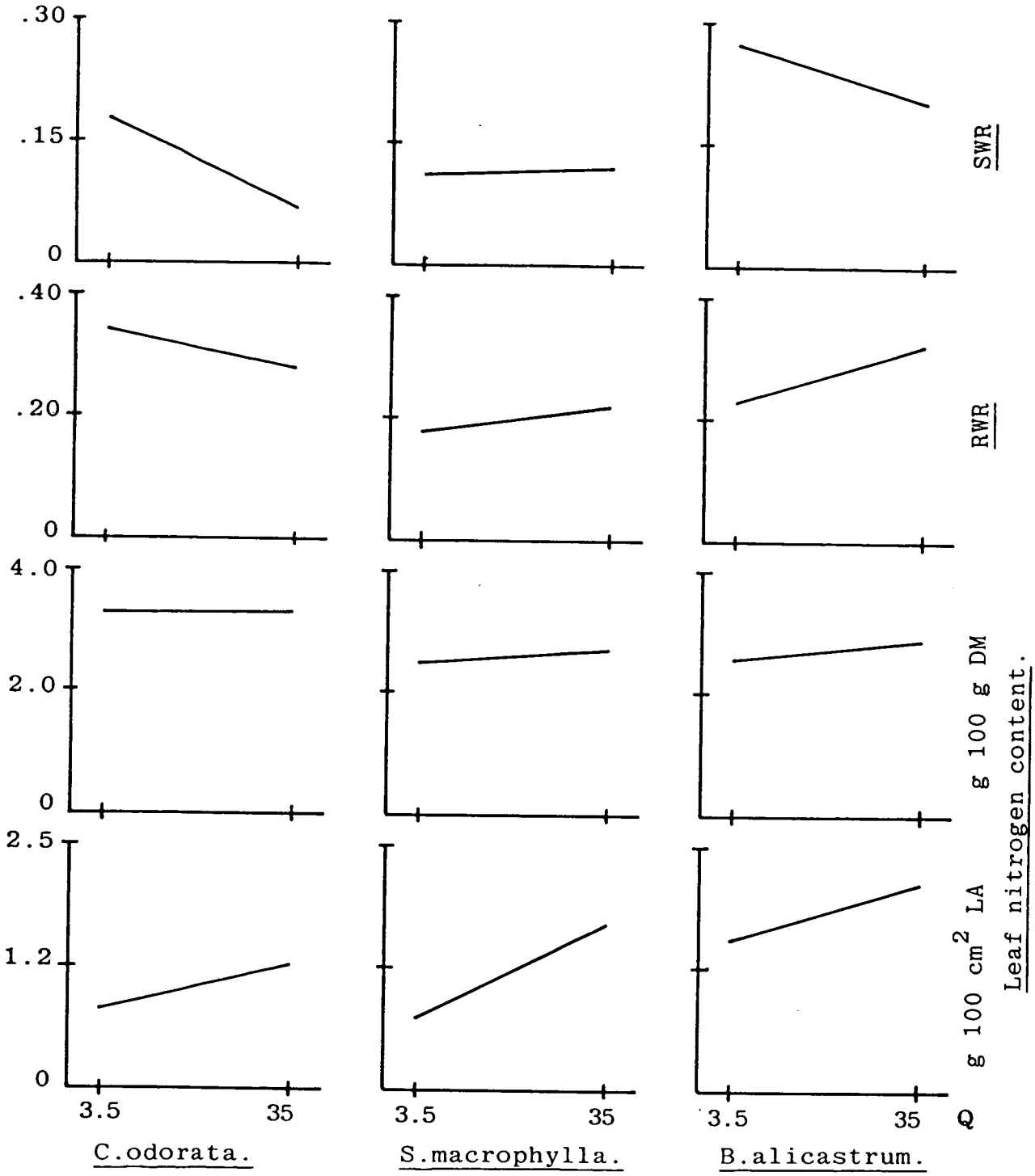


Fig. 3.18 Stem weight ratio (SWR), root weight ratio (RWR) and leaf nitrogen content; on dry weight basis (above) and leaf area basis (below) for different species and treatments; open (35) and shade (3.5 mol m^{-2} day).

3.5.1. Stomatal conductance.

3.5.1.1. Photon flux density.

Differences between g_s in the dark (g_{sd}), initial slope (α) and maximum g_s (g_{sm}) were found between the treatments and between species. In general, g_{sd} and g_{sm} were higher in the sun treatment and in the secondary-forest species; α is steeper in the shade treatment and in the primary-forest species (Table 3.10). Although the differences seem to be significant, it is important to remember that standard errors in non-linear regression need to be taken with caution and also that the high variability of the data, especially at high Q levels may affect the accuracy of the parameters (Figs. 3.6-9).

These results agree with the expected behaviour of primary-forest and secondary-forest species when subjected to high and low Q (Bazzaz & Pickett 1980). Parameter estimates are lower than values found in field conditions (Chariello 1984, Grace et.al. 1982, Mooney et.al. 1984) but are within the range of values found in growth-room conditions (Langenheim et.al. 1984, Kwesiga et.al. 1986).

g_{sd}.

The opening of stomata in the dark is not fully understood or explained but it seems clear that 'sun' adapted leaves or species display higher g_{sd} values than 'shade' adapted ones. The relevance of this fact is worth more investigation. Air in the moist tropics is often saturated with water vapour at dawn; if leaf water potentials are low then it is possible that some water intake at leaf level may occur, with obvious advantages. Alternatively, it is possible that the cuticle of wet tropical species is permeable to water vapour.

α.

The initial slope, indicating the amount of water transpired in relation to the amount of incident quanta, is higher for leaves and species adapted to shade. This faster response, at low Q levels, may give them an advantage when sunflecks illuminate those leaves.

g_{sm}.

Maximum conductance values are higher for shade intolerants and under sun conditions where higher transpiration and photosynthetic rates are expected. The values found in this work are rather low compared with other experiments, especially with values obtained in natural conditions but similar to the ones found under growth-room conditions. Plants grown under environmental controlled conditions tend to be underdeveloped in relation to the ones grown outside. Poor root systems, due to the pot space, composts used, and adaption to low and continuous wind in growth-rooms may be some of the causes which determine this weakness.

Qs.

The light saturation levels for stomatal aperture are lower than the values found for An (between about 250-650 µmol m^{-2} s^{-1}). In addition, the 'sun' adapted leaves and the secondary-forest species tend to saturate at higher levels than the 'shade' adapted leaves and primary-forest species. If light saturation levels in the field are about these values then stomata may be partially closed when shaded, even for 'shade tolerants', the same may be true for 'shade intolerants' when in full sun, because of the drop in conductance at high irradiances. Hence, such plants spend most of the time under g_{sm} with consequent gas exchange limitations.

Variability.

The high variation of the data, at low light levels, may be caused by the faster closure compared to opening of stomata (hysteresis). Although, time was allowed for acclimatization (1 hour), it is possible that when opening and closing the growth-cabinet, the stomata would be disturbed. More controlled experimental conditions or different experimental design may result in better results. Variability between saplings is better observed at high Q levels.

3.5.1.2. Vapour pressure deficit.

It is clear that, in addition to light, water use is related to the environment which the particular species is adapted to. Higher rates of transpiration are expected to help early successional species when subjected to high irradiance

and temperature. Stomata of these species need to respond to VPD levels arising from these conditions, without greatly upsetting photosynthesis; nonetheless, when radiation loads are high, leaf water potential may decrease and if water is not replenished stomatal closure is expected. Small saplings in pots are very likely to suffer from this effect thus, showing the responses seen in Figs. 3.6-3.9.

All species except *C.odorata* show the trend that is expected for an ecological gradient from secondary-forest to primary-forest species i.e. the more secondary-forest the larger the g_{sm} and the more sensitive to VPD changes (Chariello 1984, Mooney et.al. 1984). As mentioned before, *C.odorata* has shown an atypical behaviour as an early successional species, having in this case a similar response to that of *B.alicastrum* primary-forest. It may be possible that the insect attack suffered by this species during growth is the cause of this behaviour. If true, this could lead to important considerations about the deviations of "normal-optimal" conditions to field conditions where diseases and other factors could affect the physiology of a species and hence its ability to compete. Further research on this field is thus important.

In general, although g_{sm} is within the range of values obtained in other studies, they are still rather low compared with values obtained in the field but within the range of values obtained in similar growth room experiments (Kwesiga et.al. 1986). An important point is that, these values represent means from a sample; thus, higher and lower absolute values are expected.

3.5.1.3. Temperature.

Few attempts have been made to fit temperature response models to tropical tree species. Whitehead (1981) mentions that: "Responses to temperature were not clear although there is some indication that conductances were higher at temperatures between 20-28 °C and 27-31 °C for Gmelina and Teak, respectively." Furthermore, interactions of temperature and air saturation deficit on stomatal conductance have been shown to occur in Scots pine (Ng 1978, in the same paper). It seems that although temperature of the leaf is an important factor in the leaf energy balance and on stomatal behaviour (Chariello 1984) it does not show a clear relationship with g_s and that it is a second order environmental variable in dominating stomatal

conductance (Whitehead et.al. 1981).

It is still important however to analyse the response of stomata to temperature and to identify interactions with other environmental variables. This can only be achieved by extensive measurements in controlled environmental conditions, where special attention should be taken in the experimental design. It is clear that the design used in this work was inadequate and that alternative methods should be used which avoid confounding effects. Irradiance and VPD response curves, as used in this work, may be done at several temperature levels. Providing that same temperature levels are used in both responses and that irradiance and VPD levels are measured accurately, it may then be possible to override the problems mentioned above.

3.5.2. Photosynthesis.

3.5.2.1. Photon flux density.

In general, differences in the parameters defining the An - Q model were found both between growing conditions and between species (Tables 3.13, 3.14). They show the expected trends for species found along the successional gradient (Bazzaz 1979, Bazzaz & Pickett 1980). Rates of Am and Rd decrease with succession as well as mesophyll and stomatal conductance. Within species the same trend along the successional gradient can be seen between "sun" and "shade" leaves or for plants growth under high and low Q (Kwesiga et.al. 1986, Langenheim et.al. 1984). Similarly to g_s values, An values are lower than the ones found in the field but similar to the ones found in green-houses and growth-rooms (Mooney et.al. 1984, Oberbauer & Strain 1984).

Due to the lack of studies in which the light response of the trees is fitted to a non-rectangular hyperbola, the parameters of this model will be mainly compared with Kwesiga's (1986) parameters (Tables 3.22 and 3.23).

Table 3.22 Estimated light compensation points, Qc, maximum photosynthetic rate, Amax, and light saturation point, Qmax, for two tropical tree species (seedlings of five weeks). All units are μmol m^{-2} s^{-1}. 'sun' and 'shade' conditions are Q=1000 μmol m^{-2} s^{-1}, R:FR=1.7, VPD=0.62 kPa and Q=40 μmol m^{-2} s^{-1}, R:FR=0.28, VPD=49 kPa respectively. (Kwesiga *et. al. 1986*).

species	Terminalia ivorensis (shade-intolerant)		Khaya senegalensis (shade-tolerant)	
light	'sun'	'shade'	'sun'	'shade'
Qc	25	8	15	6
Qmax	560	430	280	510
Amax	7.6	5.3	4.4	6.5

Dark respiration rate.- Values of Rd for the "sun" treatment are more than twice ~~that of~~ the "shade" treatment. Although, slightly lower than other people's results (Tables 3.13 and 3.22) they show the same trend. Comparisons between early and late successional species show that Rd values increase from the primary-forest to the secondary-forest species consistent with expected successional trends and with other studies (Bazzaz & Pickett 1980, Mooney et.al. 1984). Low Rd rates may be caused by low mitochondrial activity, which can be an advantage in low Q level conditions, where less energy is expended in the synthetic machinery.

Apparent quantum efficiency (α).- Although, no significant differences were found between treatments or species, higher values were found for the shade treatment and for the shade-tolerant species. Hence, a faster response to low Q level changes is expected from these leaves and species. Kwesiga et.al. (1986) found higher α in the shade-tolerant *K.senegalensis* ('sun') but, as expected, α of the shade-tolerant species was higher. This means better use of the light at low Q, i.e. lower compensation and saturation points.

Light compensation point.- Lower values of Qc were found for both shade conditions and shade tolerant species. This estimated parameter is influenced by both Rd and α where low values of Rd and high values of α result in low values of Qc. This means a positive carbon balance at low values of Q, thus, an advantage when growing shaded.

Table 3.23 Summary of photosynthetic and stomatal parameters for tropical tree seedlings at two different light regimes: a) High Q (1000 umol m^{-2} s^{-1}) and high R:FR (1.7), 'sun', and b) Low Q (125 umol m^{-2} s^{-1}) and low R:FR (0.28), 'shade', (Kwesiga et.al. 1986).

Species	Light	Θ	α	g_m	R_d	g_{sm}	g_{sd}
Khaya senegalensis	'sun'	.00	.100(.001)	.018(.002)	1.53(.37)	.14(.02)	.07(.01)
	'shade'	.00	.093(.020)	.035(.002)	.56(.30)	.16(.03)	.04(.01)
Terminalia ivorensis	'sun'	.72(.39)	.038(.014)	.360(.005)	.95(.53)	.38(.01)	.04(.01)
	'shade	.26(.22)	.094(.042)	.027(.003)	.72(.31)	.18(.03)	.05(.01)

The asymptotic standard deviation is quoted between parenthesis.

Θ.- Convexity parameter of the non-rectangular hyperbola.

α.- Initial slope of the photosynthetic response curve.

g_m.- Mesophyll conductance (mol m^{-2} s^{-1}).

R_d.- Dark respiration (umol m^{-2} s^{-1}).

g_{sm}.- Maximum stomatal conductance (mol m^{-2} s^{-1}).

g_{sd}.- Stomatal conductance in the dark (mol m^{-2} s^{-1}).

Convexity coefficient (θ).- This describes the "shoulder" of the response, i.e. the transition from light limitation to light saturation. In general, this parameter shows no significant differences between treatments and species. Nevertheless, some species show significant higher θ in the shade treatment excepting, *S.macrophylla* which shows the opposite behaviour. A trend of higher θ values is seen among the secondary-forest species. In Kwesiga's study, θ was considerably higher in the low Q treatments and also in the secondary-forest species.

Mesophyll conductance.- High Q treatments show larger values (about twice) of g_m in both this and Kwesiga's work, they also were within the same range. This intracellular conductance includes an enzyme component. High values could be related to greater biochemical and photochemical activity due to higher enzyme concentrations which may be correlated with leaf N content (in an area basis). Although no definite trend was found between species in both works it appears that primary-forest species display higher values (with the exception of *C.alliodora*).

Maximum assimilation rate.- Estimated values of A_{nm} show higher values for the 'sun' treatments and for secondary-forest species. Values for shade-tolerant species are within ranges found in other works, for shade-intolerants, values are rather low. There are many environmental factors which could be the cause but, the most important is the fact that plants grown within controlled-environment chambers are often underdeveloped in relation to plants grown in the field.

Light saturation point.- It has been used to categorize plants as shade-tolerant or intolerant. As with many other parameters two characteristics are important; first, the value of this point in relation to other species growing under the same conditions and second, the plasticity or level of change when the plant grows under different light conditions. In general, the Qs for the sun treatments is about twice the value for the shade treatments. Although there are differences between the most primary-forest and secondary-forest species, *B.alicastrum* and *C.alliodora* respectively, there is no clear trend between the other two species.

Shade tolerance.- From this work and other similar it is difficult to assess the shade tolerance of a species from just one or two parameters, for example Am or Qs, specially when the stage of development, light and other environmental conditions are not equivalent. A set of physiological parameters compared in a relative basis could be more helpful. That is, their relative changes (plasticity) in relation to changes in environmental conditions such as, light quality and quantity. With this information it will be easier to analyse and predict performance of those species under such light conditions and allocate them within a continuum of light requirements such as a successional gradient.

3.5.3. Growth.

In general, shade causes an increase in height, however in *B.alicastrum* a reduction in height is not significant, a similar response was found by Fetcher et.al. (1983) for the pioneer *Heliocarpus appendiculatus* and the shade-tolerant *Dipterix panamensis*. Leaf number is slightly reduced by shade in all species but the effect is not significant. Leaf area is slightly increased by shade in *B.alicastrum* and *S.macrophylla* but greatly reduced in *C.odorata* (Fig. 3.16). Differences between species and experimental conditions, in particular light, make generalizations difficult. The same trend between species when shaded was found by Kwesiga & Grace (1986) for number of leaves but different for height and leaf area (Table 3.24). However the 'sun' and 'shade' Q values that they used were considerably lower than the ones used in this work. Both factors, height and leaf area, are very important when dealing with light competition but, it seems that the different species present different strategies. at one extreme *B.alicastrum* is tolerant to light competition; at the other, *C.odorata* may represent a strategy of escape from shade.

Growth analysis has seldom been used in tropical tree seedlings, thus comparisons are made mainly with Kwesiga & Grace's (1986) paper. RGR and NAR, assessing the assimilatory capacity of the plant in a dry weight and leaf area basis respectively, show the same pattern between species and light conditions. Similar behaviour were displayed by *T.ivorensis* and *K.senegalensis* (Table 3.24). The very high RGR of *S.macrophylla* is due to its high NAR and LAR, similarly the low RGR of *B.alicastrum* is due to low values of NAR and LAR. *C.odorata* displayed a relatively high RGR which is caused by its very high LAR, since its NAR is as low as for *B.alicastrum*. It is interesting to note that

RGR is more affected by NAR than by LAR, since both RGR and NAR show an opposite response to that of LAR.

LAR and SLA were higher in shade, that is, an increase in leaf area in relation to total and leaf dry weight respectively. These ratios are also higher for the shade-intolerant species (Fig. 3.17). Similar responses and values than *C.odorata* were displayed by *T.ivorensis* (Table 3.24), both shade-intolerants. The shade-tolerant *K.senegalensis* showed similar values as *B.alicastrum* but the response to shade was opposite i.e. with higher values in the 'sun' (same table). These two ratios seems to behave very similar in their responses to shade for a particular species, suggesting that SLA rather than LWR determine the response of LAR. Alternatively, may be due to the similar values of LWR between species and treatment. Unfortunately there are very few studies to compare with.

Similar SLA values and trends have been reported for other tropical trees (Langenheim et.al. 1984, Fetcher et.al. 1983). It appears that the red to far-red ratio (R:FR) is the main factor affecting SLA changes, in particular in shade-intolerant species, shade-tolerant species seem insensitive to this factor (Kwesiga & Grace 1986). Nevertheless, changes in SLA have been observed under 'shade' with high R:FR (Fetcher et.al. 1983, Langenheim et.al. 1984). Hence, careful control and description of light quality and quantity is essential for the correct interpretation of growth analysis. This is a tedious but potentially productive research area, since little is known regarding the factors and conditions which affect and control partitioning and morphogenesis in tropical trees.

When the different parts of the plant are then taken into account a more specific response is seen: *B.alicastrum* allocates more resources to stem than to the roots when shaded, *S.macrophylla* increases leaf dry weight at the expenses of both stem and roots and *C.odorata* allocates more to stem at the expense of root. In contrast to the other species, *B.alicastrum* increases stem density instead of increasing stem height, the same pattern of resource allocation in response to shade, from roots to stem, can be used in a completely different way. It seems that in shade-tolerant species RGR drops slightly and dry matter is stored in the stem while in shade-intolerant species, RGR drops substantially and either increase in leaf area or stem height results.

Table 3.24. Some characteristics of seedlings of two tropical tree species after five weeks of growth under two light regimes: a) 'sun', Q=610 µmol m^{-2} s^{-1} and R:FR=1.7 and, b) 'shade', Q=125 µmol m^{-2} s^{-1} and R:FR=0.28 (Kwesiga & Grace 1986).

species	Terminalia ivorensis (shade-intolerant)		Khaya senegalensis (shade-tolerant)	
light	'sun'	'shade'	'sun'	'shade'
Num. leaves	15.9	12.1	7.1	5.1
Stem height (cm)	14.9	13.8	15.6	15.0
leaf area (cm^3)	130.7	54.7	77.6	14.7
		Dry weights (g)		
leaves	.518	.154	.634	.161
stem	.169	.054	.266	.071
roots	.150	.039	.288	.048
total	.837	.247	1.188	.280
leaf weight ratio	.620	.620	.530	.575
stem weight ratio	.200	.220	.220	.250
root weight ratio	.180	.160	.240	.170
RGR (week)	.75	.39	.58	.20
NAR (g m^{-2} week)	100	16	90	38
LAR (m^2 kg^{-1})	19	22	9	5
LWR	.65	.62	.50	.69
SLA (m^2 kg^{-1})	25	32	12	9

Values quoted are means.

3.5.4. Nitrogen content.

Most of the N of a leaf is contained in the enzymatic machinery, most of it is shared by the carboxylating enzyme. The total amount of N therefore reflects the ability to photosynthetize as well as the ability to use this energy

In general values obtained (Fig. 3.18) are slightly higher than average values for tropical trees (1.5%) on volcanic soils (Mooney et.al. 1984). It seems that secondary-forest species have inherently high leaf N contents, irrespective of the light conditions. It is also clear that under open conditions leaf N content is higher, Similar values and trends were obtained with three Amazonian tree seedlings (Langenheim et.al. 1984). Nevertheless when N content is compared

On an area basis the relation between species is inverted and it appears that although 'primary'-forest species have less nitrogen per dry weight, they 'display' it more efficiently. It is important to note that the only species which presents significant response to shade is *B.alicastrum* and that even its highest level is lower than the lowest values of the other two species when shaded. Shade adapted species appear to be the most sensitive to shade in relation to N content; opposite behaviour when comparing physiological parameters and growth analysis results where secondary-forest species were the most sensitive.

3.6. Conclusions.

1.- Secondary-forest species displayed higher values of g_s, An, RGR and NAR than those from primary-forests. They were more sensitive to shade, i.e. these values were greatly modified when grown in shade.

2.- Plants grown under 'sun' conditions displayed higher values of g_s, An, RGR and NAR than plants grown in 'shade' but they seem to be less sensitive to environmental changes, i.e. Q and SVPD.

3.- Nitrogen accumulates in leaves of secondary-forest species but is more efficiently displayed by primary-forest species. This pattern of investment could allow them to exploit contrasting environments.

4.- Partitioning of dry matter follows patterns which allocate more dry matter to leaves or stem when shaded; this dry matter is used in different ways either by increasing height, leaf area or just stem density. Research on this field seems very productive.

5.- Responses to the environment can be modelled and the parameters obtained used to compare species adapted to different environmental conditions.

6.- Absolute and relative values of a set of fitted physiological parameters and their relative changes (plasticity) describe better plant responses to their environment than the absolute value of one or two parameters. This is particularly true when a group of parameters are compared for contrasting species and growth conditions.

7.- Physiological, partitioning and morphogenetic processes determine the light requirements of species. The position of any species within a successional stage requires the evaluation and understanding of these processes.

CHAPTER 4

MODELLING ASSIMILATION AND GROWTH

4.1. Introduction

Forests are complex systems with many interactions and their growth is the integration of factors and processes over long periods of time. The analysis of tree growth, and the effects of environmental factors and management, is possible through a quantitative approach to whole-plant physiology and some knowledge of the physics of plant environments (Landsberg 1986). Ecophysiological models allow exploration of the consequences of varying the rates of various processes, and the sensitivity of the system to changes. They provide means of integrating knowledge about processes in quantitative form and hence a framework for research, improving the accuracy of predicting the consequences of management.

In this chapter the results of the previous experiments are integrated into a theoretical framework, a model, which simulates the CO_2 assimilation and growth of both shade-tolerant and shade-intolerant tree species under field conditions, i.e. the prediction of changes in dry matter and leaf area with time. To achieve this aim it is necessary to describe the weather conditions, the stand structure and its microclimate, the parameters which define the photosynthetic and stomatal responses to the environment, and the partitioning of assimilates.

4.2. Model description.

Light will be considered as the only resource for which trees compete, and the sole interaction between them is assumed to be mutual shading. All other factors i.e. water and nutritional status will be assumed optimum and without interaction. A single tree model is the starting point and the growth of the stand will be modelled by 'growing' individual trees which shade each other. The model consist of a number of submodels which describe the environmental conditions, the interception of light and photosynthesis by individual tree crowns, the respiration and allocation of fixed CO_2 of various plant parts and the subsequent change in dry matter. The submodels are interdependent and

outputs from one will be used as inputs for another. The equations used within the model are either theoretical (with reference to the underlying physical or physiological processes), or empirical (based on observations and measurements).

4.2.1. Environmental conditions.

Hourly values of radiation, temperature and humidity will be used as inputs for the absorption of radiation and photosynthesis model.

Light.- From daily integrals (Ch. 2), daily courses of photosynthetic photon flux density (Q) were estimated. Three 'typical' days were simulated: clear, cloudy and overcast. It was assumed that the daily course of Q can be approximated by a sinusoidal curve (Monteith 1973). The expression that describes this pattern is as follows:

$$Q_t = Q_{tm} \sin (\Pi * [t/n])$$

Where:

Q_t.- Q at t hours.
t.- Hours after sunrise.
Q_{tm}.- Maximum Q at solar noon.
n.- Daylength in hours.

Q_{tm} can be calculated from an approximation of the daily integral (loc.cit.):

$$Q_{tm} \simeq [\int_0^n Q_t \, d_t] / [2n / \Pi]$$

Temperature.- The daily cycle of temperature was simulated from maximum and minimum values for each 'typical' day (Ch. 2). A sine-exponential model was used to generate hourly values: a truncated sine function is used for the day temperatures and a negative exponential for the night (Wann et.al. 1985). The following expression was used to calculate the cycle:

$$T_t = \begin{cases} Tn + (Tx + Tn)\sin\dfrac{\Pi\,(t - tr - \beta)}{n + 2(\alpha - \beta)} & tn < t < ts \\ T'n + (T(ts) - T'n)\exp -\dfrac{\alpha\,(t - ts)}{24 - n + \beta} & ts < t < t'n \end{cases}$$

Where:

T_t.- Temperature at time (t).
Tx.- Maximum temperature.
Tn.- Minimum temperature.
T'n.- Minimum temperature for the next day.
t'n.- Time of minimum temperature for the next day.
tr.- Time of sunrise.
ts.- Time of sunset.
n.- Daylength.
tx.- Time of maximum temperature:

$$tx = 1/2\,(tr + ts) + \alpha$$

tn.- Time of minimum temperature:

$$tn = tr + \beta$$

α.- Time difference between tx and midday.
β.- Time difference between tn and sunrise time (tr).
γ.- Decay parameter (rate of temperature change).

Humidity.- The daily cycle of relative humidity or saturated vapour pressure deficit (SVPD) can be calculated for a given temperature (T) at any time (Landsberg 1986). It is assumed that vapour pressure (e_a) does not change during the day and that the dew point temperature is equal to the minimum temperature (Tn). The expression used to calculate SVPD is as follows:

$$SVPD = e_s(T) - e_a.$$

where:

$e_a = e_s(Tn)$, and

$$e_s(T) = 0.61078 \exp [(17.269 * T) / (T + 237.3)].$$

4.2.2. Radiation interception, and photosynthesis.

The rate of dry matter production by forests depends on the interception of radiant energy by leaves and the conversion of this energy into carbohydrate. The proportion of incident energy intercepted and absorbed by forest canopies depends on the leaf area of the stand and the way foliage is distributed. The efficiency with which radiant energy is converted to chemical form depends on the photosynthetic properties of leaves (Landsberg 1986). Modelling radiation penetration and absorption by trees in non-continuous canopies involves a complex model with provision for tree geometry (height, leaf area density, shape and spacing) and the time course of solar elevation, as well as information about the relevant amounts of direct and diffuse radiation (Landsberg 1986). It has been customary to use projections of various opaque shapes such as trapezoids, cylinders and cones (Monteith 1973). Another way is to assume a random distribution of the foliage within a regular geometric shape, 'the weighted random' approach (Norman 1978). Ellipsoid models with randomly distributed foliage have been used to simulate the interception of radiation by isolated plants as well as by groups of plants (Charles-Edwards & Thornley 1973, Thorpe et.al. 1978 and Norman & Wells 1983).

A modified version of Norman & Wells' model was used to simulate the interception of radiation of individual crowns and to calculate the amount of photosynthesis and transpiration. This model was developed by Jenny Grace*

* Grace, J.C; Norman, J.M. & Jarvis, P.G. (in press). Description, sensitivity analysis and field test of a radiative transfer model for widely spaced plants. Agriculture and forest Meteorology. (see also Rook et.al. 1985)

(Forestry Research Institute, New Zealand) and has been updated and improved by Y.P. Wang (Ph.D. student in this Department). The program 'MAESTRO' calculates hourly radiation regime, photosynthesis and transpiration of an individual tree crown in a plant stand. Although it is very sophisticated and allows for changes in the environmental inputs as well as in crown structure characteristics it was necessary to customize it: input routines were modified to fit particular data sets from previous experiments while photosynthesis and stomatal response models were modified to those used in chapter 3.

Results from the enrichment planting and from the response to shade experiments (chapters 2 & 3) were used as inputs and the model was run for two species; *B.alicastrum* (shade-tolerant) and *C.alliodora* (shade-intolerant). Two canopy conditions were simulated: 'open' and 'shade' (100% and 40% light transmittance respectively) and three 'typical' days were considered: clear, cloudy and overcast. Details of the stand structure can be seen in chapter 2. The two species differ in size and leaf area whose mean values were:

	height	crown radii	leaf area
B.alicastrum	1.24	.42	0.3
C.alliodora	2.30	.91	3.0
	(m)	(m)	(m^2)

Due to the small tree size, crowns touched the ground with a depth corresponding to the height. The optical properties of leaves and soil were obtained from the literature (Monteith 1973, Jones 1983) and are as follows:

	PAR	NIR	Thermal
Leaf transmittance	0.1	0.4	0.025
Leaf reflectance	0.1	0.4	0.025
Soil reflectance	0.15	0.35	0.050

PAR.- Photosynthetic active radiation.
NIR.- Near infrared.

Physiological parameters of the stomatal and photosynthetic responses to

the environment are those obtained in the controlled environment experiment (Chapter 3).

Assumptions for the model are given in appendix III.

Calculations were carried out every hour for a single tree during one day after which the integral was estimated. The reason for this approach using 'average' days instead of a whole season of varying days was simple expediency: the model is large and takes a long time to run on the mainframe computer (1 day for one tree takes about 200 sec. of CPU time).

4.2.3. Dry matter distribution and growth.

Total annual values for photosynthesis and transpiration were obtained from the daily totals which were multiplied by their annual frequency. Total annual net photosynthesis was converted to dry matter by assuming a ratio of 0.65 g of dry matter per g of CO_2 (Jones 1983). The total amount of dry matter (in one year) was then allocated into roots, stem and leaves, respiration losses were calculated and the gain in dry weight by each plant compartment was estimated. Growth analysis was carried out with the simulated gain in dry matter and compared with results from the field and controlled environment experiments.

Due to the lack of a mechanistic approach to calculate dry matter partitioning, empirical ratios were used (Landsberg 1986). If calculated dry matter production $d(\sum W) / d_t$ is partitioned into leaf, stem and root growth over a year we have:

$$\Delta W_f = \eta_f \Delta W$$

$$\Delta W_r = \eta_r \Delta W (1 - \gamma_r)$$

$$\Delta W_s = \eta_s \Delta W (1 - \gamma_s)$$

where:

ΔW.- Total annual dry matter production.
ΔW_i.- Total annual dry matter production for the i part.
η_i.- Partitioning coefficient for each plant part.
γ_i.- Fraction of the assimilate respired by each part.
f.- Leaf compartment.
r.- Root compartment.
s.- Stem + branches compartment.

Results of dry matter allocation from the destructive sampling which has been described in previous chapters were used to estimate the partition coefficients used in this section.

Respiration.- Our knowledge of tree respiration is incomplete and inadequate and is an area of uncertainty in the simulation of carbon balance of trees (Landsberg 1986). Total respiration losses from branches, stem and roots appear to range from about 25 to 50% of assimilated carbon. Estimation of the fraction of assimilate respired by stem and roots (γ_i) is difficult but both were set to 0.3 as a fair assumption (Loc.cit.). Values for tropical trees are scarce and difficult to incorporate in a model because they change depending on the species, growing conditions and weather (Lugo 1970, Odum et.al. 1970 who quoted values within the above range).

Growth.- After allocating the annual gross photosynthesis and calculating respiratory losses, the performance of the trees was estimated. The annual net dry matter production together with the initial values of total dry matter were used to carry out standard growth analysis. Details of the equations can be seen in chapter 2. Comparisions between model results and those calculated from real plants in the field and in the growth rooms were used to validate the model.

4.3. Results.

4.3.1. Sensitivity analysis.

Preliminary runs with the model showed the effect of leaf angle distribution (LAD) on daily photosynthesis. The effect of horizontal and spherical LAD was tested for different species, leaf area indices (LAI) and solar altitudes. An increase of about 3 to 12% (for LAI 0.3 and 3.0 respectively) was obtained when LAD was changed from spherical to horizontal. The effect was lower at low solar elevations and below 30° was negligible. The shade-tolerant species *B.alicastrum* was about 70% less sensitive to changes in LAD than the shade-intolerant *C.alliodora*.

The effects of changes in temperature were small and symmetrical, with a 5% change in photosynthesis for a 10 °C change in temperature. Both species were affected similarly at low solar altitudes the effect was negligible. The temperature range covered was 15 to 35 °C.

Sensitivity to saturated vapour pressure deficit (SVPD) was greater than to temperature and the response was asymmetrical. A change in SVPD from 0.1 to 1.0 kPa caused a 12% decrease in photosynthesis for *C.alliodora* and from 1.0 to 2.0 kPa the drop was about 22%. These changes were 50% lower for the shade-tolerant *B.alicastrum*. Similar responses were recorded in relation to solar altitude.

4.3.2. Environment.

Simulated hourly values of Q, temperature and humidity follow the trends observed in other tropical locations, especially when mean hourly values were compared (Fetcher et.al. 1985, Shuttleworth et.al. 1985). For a clear day (open canopy), Q values increased to a peak of about 1200 µmol m^{-2} s^{-1} at noon and then they fell (Fig. 4.1). Early morning temperatures were about 20 °C, rose to about 35 °C in the afternoon and then fell slowly until the next morning. Humidity followed the opposite trend to temperature and fell from near 100% in the early morning to about 45% in the afternoon. Cloudy and overcast days followed the same pattern as the clear day with lower radiation and temperature values but higher humidity. Under 'shade', trends were similar but

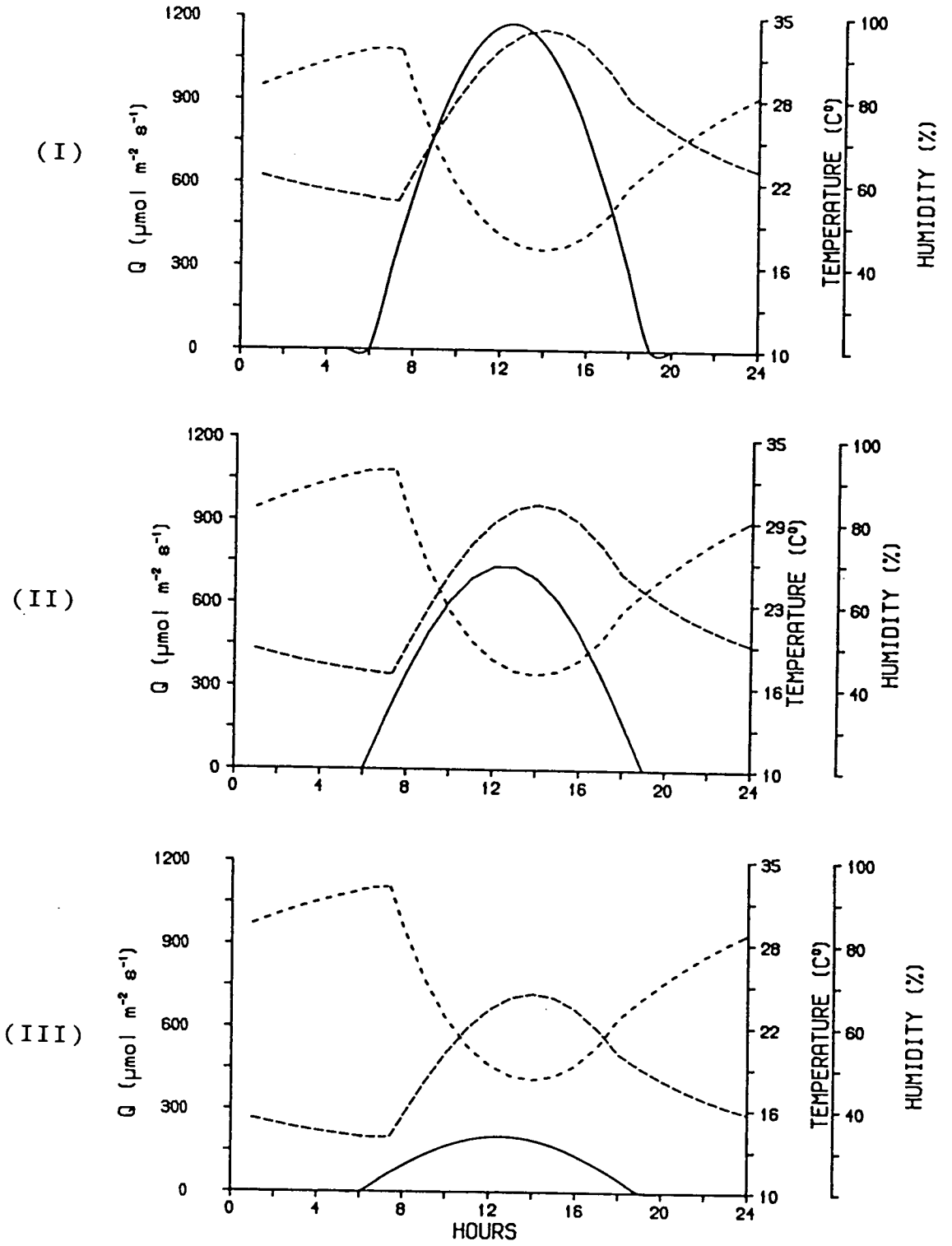


Fig. 4.1 Simulated daily course of radiation (Q), (continuous line), temperature (dashed line) and humidity (dotted line) for 'open' canopy conditions. Average days: clear (I), cloudy (II) and overcast (III) are shown.

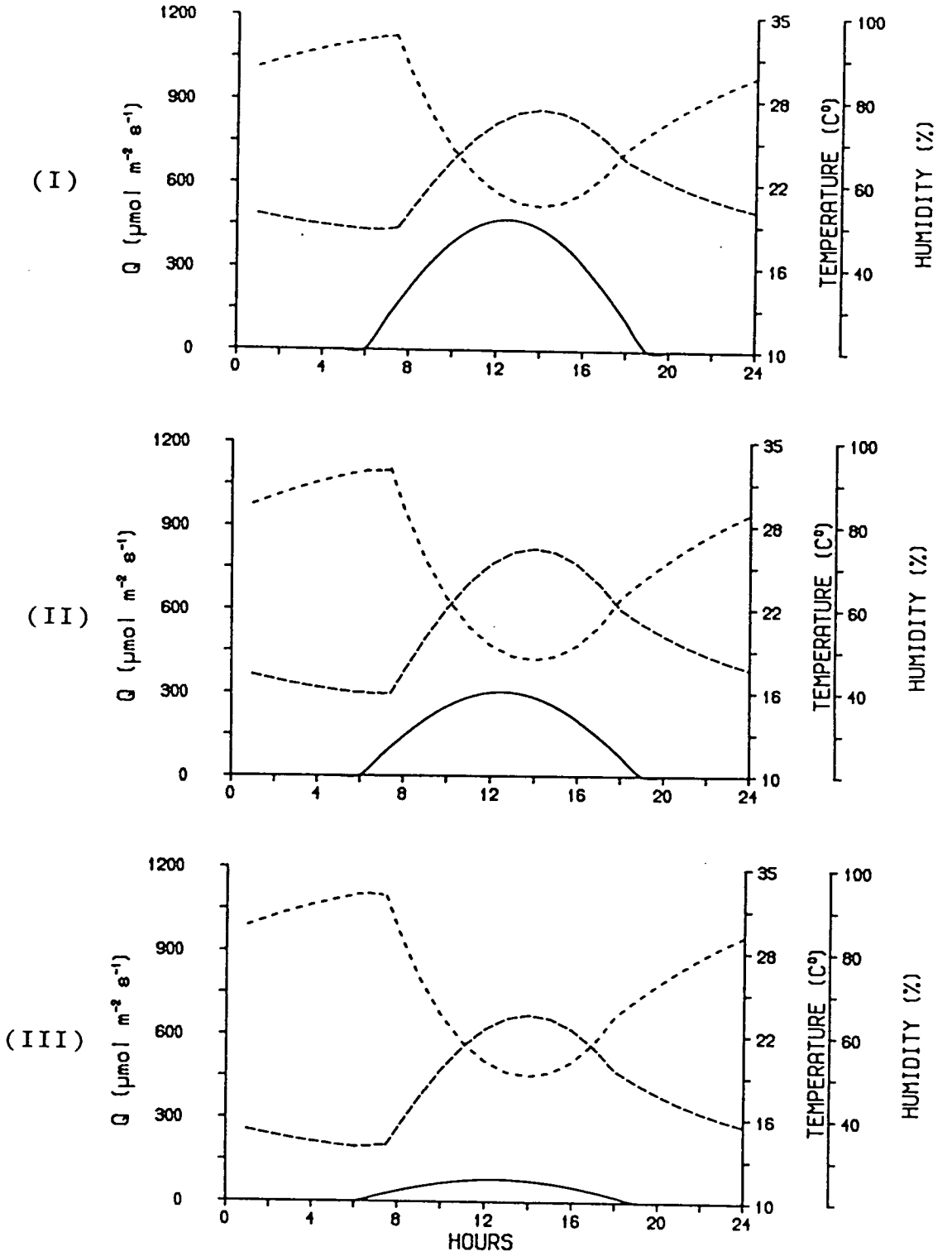


Fig. 4.2 Simulated daily course of radiation, Q, (continuous line). temperature (dashed line) and humidity (dotted line) for 'shade' conditions. Average days: clear (I), cloudy (II) and overcast (III) are shown.

values of radiation and temperature were still lower while for humidity they were higher (Fig. 4.2). It is important to note that the difference between minimum and maximum temperatures were lower under shade, leading to higher humidity levels throughout the day.

4.3.3. Photosynthesis and transpiration

In general, simulated photosynthesis and transpiration followed the pattern observed in the diurnal course of radiation. In the open (clear day) photosynthesis and transpiration rose sharply to reach a maximum before noon, then fell to a minimum in the afternoon followed by another increase just before the sunset, after which values decreased rapidly to very low levels (Figs. 4.3, 4.5). On cloudy and overcast days, and under shade (40% transmittance), there is no afternoon minimum and responses are smoother (Figs. 4.4, 4.6). Maximum values of photosynthesis (clear day, open canopy) were about 4 and 6 μmol m^{-2} s^{-1}, and for transpiration 0.002 and 0.001 mol m^{-2} s^{-1}, for *B.alicastrum* (shade-tolerant) and *C.alliodora* (shade-intolerant) respectively.

The amount of daily photosynthesis (Table 4.1) for a whole tree was highest for clear days followed by cloudy and overcast days, with the exception of *C.alliodora* in the open where the maximum assimilation was on cloudy days. *B.alicastrum* displayed lower daily assimilation values per tree, about 15% of the amount fixed by *C.alliodora*, but when compared on a leaf area basis the relation was reversed and *B.alicastrum* exceeded *C.alliodora* by about 40%. Maximum values were about 0.06 and 0.34 mol day^{-1} $tree^{-1}$ (open) and about 0.04 and 0.27 (shade) for *B.alicastrum* and *C.alliodora* respectively. Transpiration rates (Table 4.1) followed the same patterns as photosynthesis, with higher values in the open canopy and clear day conditions. Maximum values (open) were about 21 and 100 mol day^{-1} $tree^{-1}$, but under shade transpiration was 9 and 53 mol day^{-1} $tree^{-1}$ for *B.alicastrum* and *C.alliodora* respectively. When expressed on a leaf area basis the situation was reversed with maximum values around 71 and 32 mol m^{-2} day^{-1} respectively. Water use efficiency was highest under shade and during cloudy days, with the exception of *B.alicastrum* whose highest value was in the open on clear days. Maximum values were 3.0 and 4.2 (open) and 4.4 and 5.5 (shade) for *C.alliodora* and *B.alicastrum* respectively, *in units of m mole per mole*.

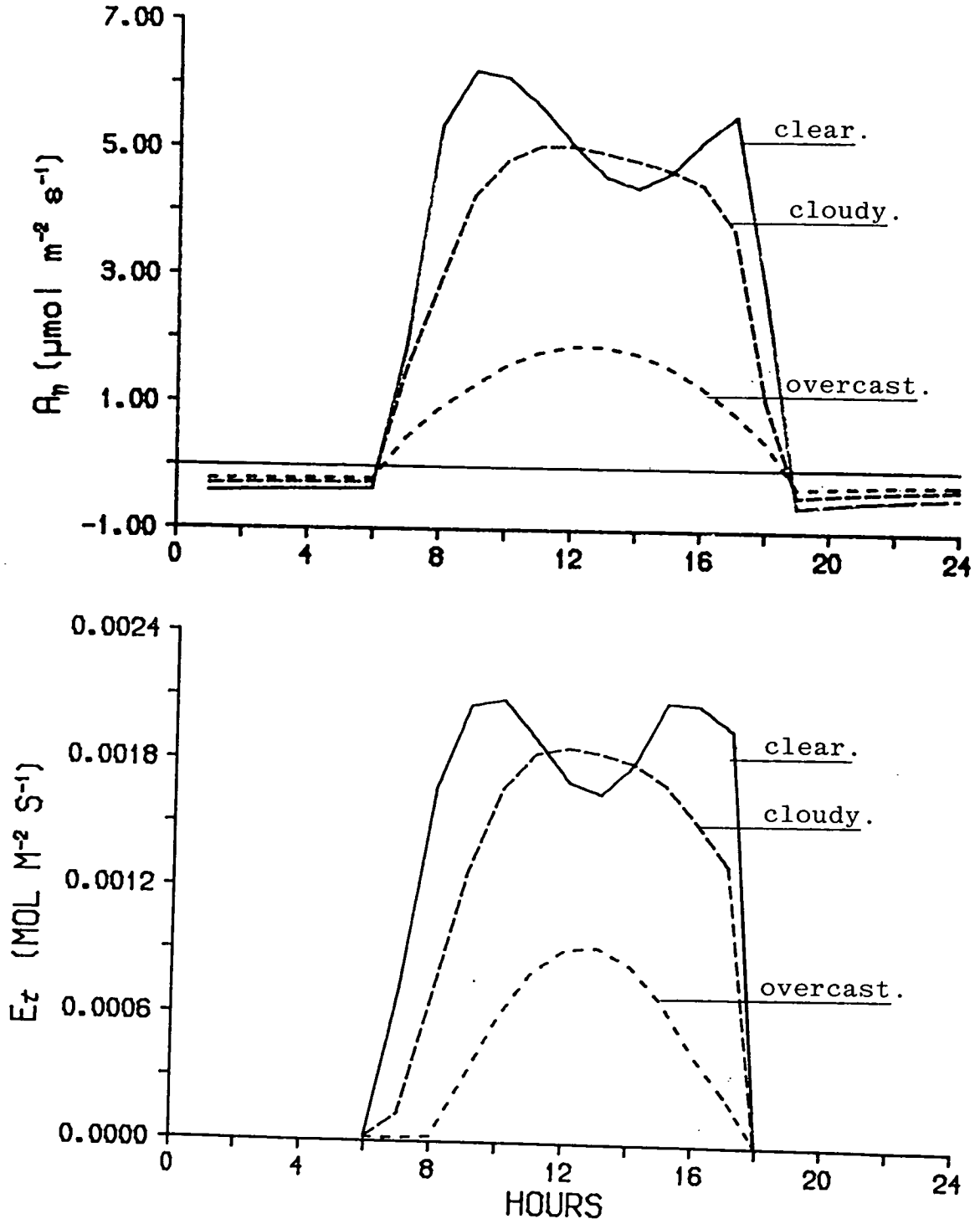


Fig. 4.3 Simulated diurnal course of net assimilation (above) and transpiration (below) for B.alicastrum (shade-tolerant) in 'open' conditions. Mean hourly values are displayed for three average days.

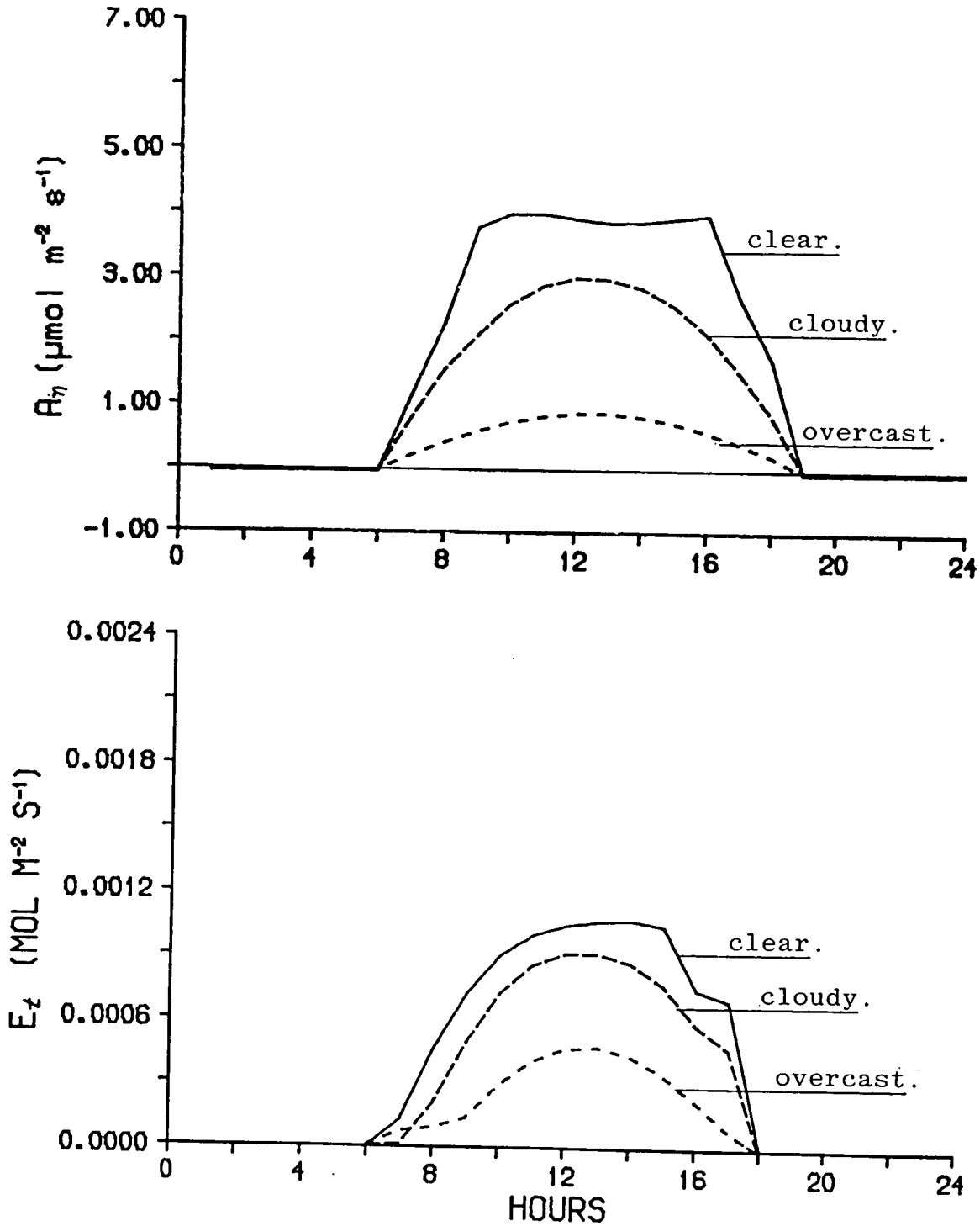


Fig. 4.4 Simulated diurnal course of net assimilation (above) and transpiration (below) for B.alicastrum (shade-tolerant) under 'shade' (40% transmittance) conditions. Mean hourly values are displayed for three average days.

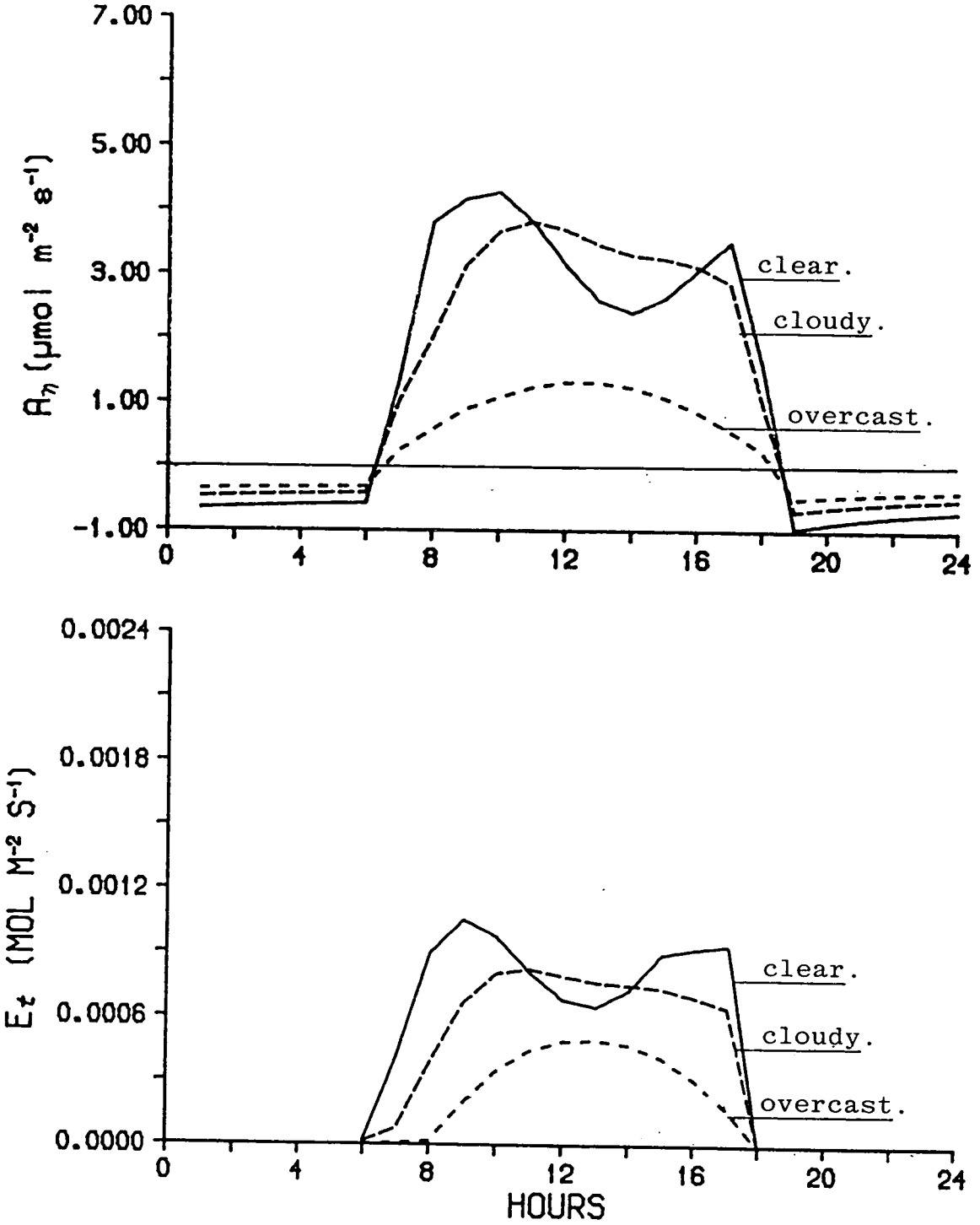


Fig. 4.5 Simulated course of net assimilation (above) and transpiration (below) for C.alliodora (shade-intolerant) in 'open' conditions. Mean hourly values are displayed for three average days.

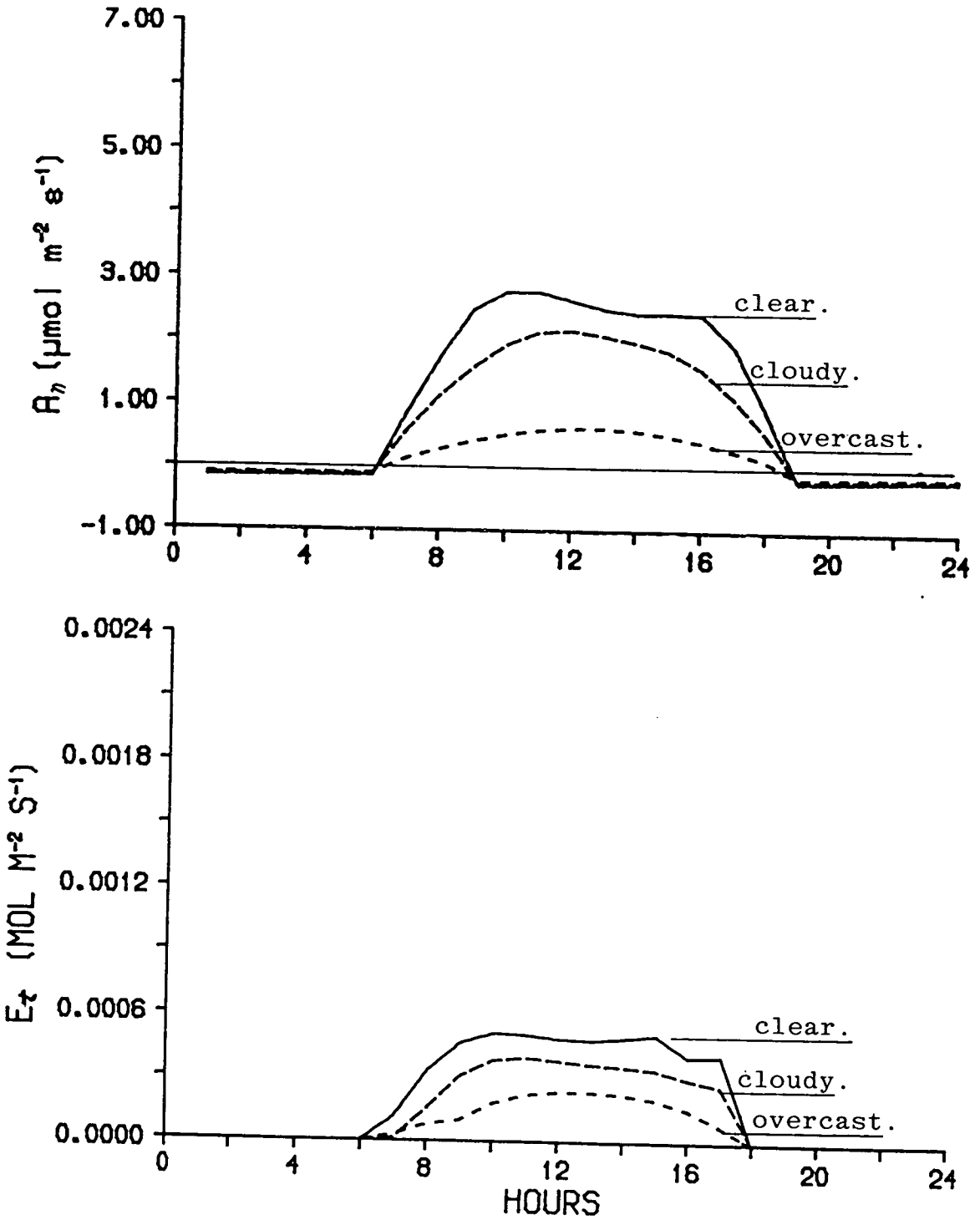


Fig. 4.6 Simulated course of net assimilation (above) and transpiration (below) for C.alliodora (shade-intolerant) under 'shade' (40% transmittance) conditions. Mean hourly values are displayed for three average days.

Table 4.1 Simulated daily net assimilation, transpiration and water use efficiency of two species under two different canopy conditions, open (100%) and shade (40%). Values are displayed for three types of day: clear, cloudy and overcast. Units are mol day^{-1} $tree^{-1}$ for photosynthesis and transpiration; water use efficiency is in CO_2 mol H_2O mol^{-1}, leaf area (LA) is in m^2 and light is in relative units.

Species	Canopy transmittance	day clear	cloudy	overcast	LA
		Photosynthesis.			
B.alicastrum	100%	.058 (.20)	.051 (.17)	.014 (.05)	0.3
	40%	.042 (.14)	.028 (.10)	.007 (.02)	0.3
C.alliodora	100%	.332 (.11)	.336 (.11)	.070 (.02)	3.0
	40%	.272 (.09)	.198 (.06)	.041 (.01)	3.0
		Transpiration.			
B.alicastrum	100%	21 (71)	17 (57)	6 (20)	0.3
	40%	9 (32)	7 (24)	3 (10)	0.3
C.alliodora	100%	100 (32)	80 (26)	36 (12)	3.0
	40%	53 (17)	36 (12)	17 (5)	3.0
		Water use efficiency. (mmol mol^{-1})			
B.alicastrum	100%	2.7	3.0	2.2	0.3
	40%	4.4	4.0	2.4	0.3
C.alliodora	100%	3.3	4.2	1.8	3.0
	40%	5.1	5.5	2.4	3.0

In general, higher dry matter production was achieved in open conditions and by the shade-intolerant *C.alliodora* (Table 4.2). The same trend was observed for all plant compartments except leaf dry matter of *C.alliodora* with higher values under shade, which lead to higher total leaf area values. Values as high as 2 kg $year^{-1}$ of net production (dry matter) were achieved by *C.alliodora* while *B.alicastrum* reached values around 0.3 kg.

Table 4.2 Simulated gross and (net) annual dry matter production for two species under two different canopy conditions. Dry matter is in grams, leaf area in m^2 and light in relative units.

Species	Canopy	leaf	stem	roots	LA	total
B.alicastrum	100%	(95)	189 (132)	146 (102)	1.15	430 (329)
	40%	(57)	99 (69)	110 (77)	0.70	261 (203)
C.alliodora	100%	(526)	1261 (883)	841 (589)	6.94	2629 (1998)
	40%	(557)	540 (378)	644 (451)	7.35	1741 (1386)

4.3.4. Growth analysis.

Simulated RGRs in the open were higher than under shade for both species, in the open *B.alicastrum* showed a higher value than *C.alliodora*, under shade both species displayed the similar values (Table 4.3 and Fig. 4.7). Similarly NARs were higher in the open and for *B.alicastrum*, but they showed larger differences. LARs were higher for *C.alliodora* (particularly under shade) than for *B.alicastrum*, which showed similar values for both canopy conditions.

Table 4.3 Simulated plant performance under 'optimum' conditions. Units are: RGR ($year^{-1}$), NAR (kg m^{-2} $year^{-1}$), SLA (m^2 kg $^{-1}$) and light is in relative units, LAR ($m^2 kg^{-1}$), LWR (kg leaf / kg plant).

Species	Canopy	RGR	NAR	LAR	SLA	LWR
B.alicastrum	100%	1.4	.45	3.0	12	.22
	40%	1.0	.36	2.9	13	.20
C.alliodora	100%	1.2	.34	3.6	13	.20
	40%	1.0	.23	4.3	21	.32

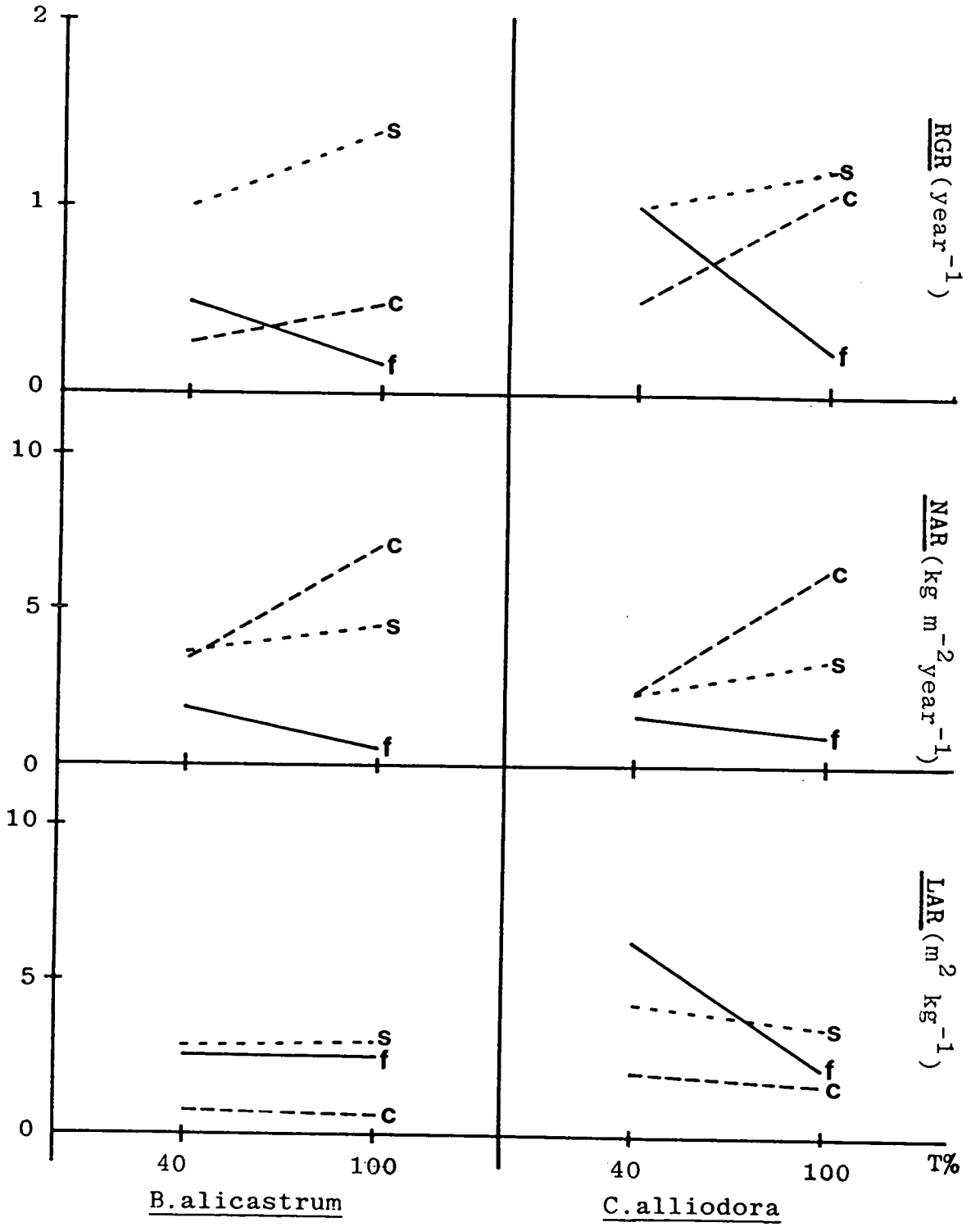


Fig 4.7 Relative growth rate (RGR), net assimilation rate (NAR), and leaf area ratio (LAR) for two different species and two light conditions: 'open' (100% transmittance) and 'shade'(40%). Simulated values (S) are compared with values under controlled environment (C) and field (F) conditions.

4.4. Discussion.

4.4.1. Sensitivity analysis.

The amount of radiation intercepted by a canopy is affected, among other factors, by the inclination of leaves (Ross 1981). However, results in the present work suggest differences of only up to 13% between spherical and horizontal distributions around noon. At low solar elevation the effect is negligible and consequently overall differences, when daily photosynthesis is compared, are rather small. The average inclination of the leaves for the species used in this work is not known, and thus a spherical leaf angle distribution was assumed. They do not present a clear planophile or erectophile distribution, thus they are unlikely to differ significantly from the spherical case.

The effects of changes in temperature and VPD reflect the shape of the functions which describe the responses of stomata to these variables (Ch. 3). Differences between species are the result of differences in the parameters of the fitted functions.

4.4.2. Environmental factors.

Clear days are easy to simulate accurately; cloudy and overcast days deviate sometimes from the real situation and are only adequate when comparing daily integral and average trends (Fetcher et.al. 1985). The problem arises when rapid changes are involved which would affect photosynthetic and stomatal mechanisms. These rapid environmental changes are common in tropical moist-forest for example, sunflecks and rainstorms (Shuttleworth et.al. 1985). Under natural light regimes, between 40% and 60% of the carbon gain in two tropical species was attributable to sunflecks (Pearcy & Calkin 1983). The mechanisms by which understorey plants utilize sunflecks may be as important as those that increase photosynthetic performance in diffuse light (loc.cit.). The ability to utilize sunflecks depends on other factors in addition to photosynthetic capacity, e.g. changes in pool sizes of photosynthesis intermediates or activation of enzymes (Pearcy et.al. 1985). It seems that steady state values of stomatal conductance and photosynthesis (as the ones in chapter 3) are inadequate for use in simulating naturally fluctuating environments, in particular under low light conditions. Thus, models of dynamic

responses to understorey light regimes need to be modified to take into account induction effects and post illumination CO_2 fixation (Pearcy et.al. 1985). Other effects not taken into account are the feedback between evapo-transpiration and air humidity which may have strong consequences. However, simulated hourly average values follow the trends and are close to values obtained in natural conditions (Shuttleworth et.al. 1985).

4.4.3. Photosynthesis and transpiration.

Very few studies exist on the daily course of photosynthesis for tropical species in natural conditions. Field measurements of assimilation with small enclosures for several tropical tree species are described by Lugo (1970), he found values between 1.4 and 9 µmol m^{-2} s^{-1} in *Sloanea berteriana* seedlings for overcast and clear days respectively and values around 2.1 for *Dacryodes excelsa* seedlings irrespective of the day. Both are shade-tolerant species. Total average net photosynthesis and night respiration (mol m^{-2} day^{-1}) were .038 and .037, respectively, for *S.berteriana*, .015 and .017 for *D.excelsa* and, .064 and .014 for *Cecropia peltata* (shade-intolerant) (loc.cit.). Simulated net photosynthetic rates (between 1 to 7 µmol m^{-2} s^{-1}) are within the range found in natural conditions; however, simulated daily totals are rather high, about 0.1 and 0.03 mol m^{-2} day^{-1} for clear and overcast days respectively. It is important to note that Lugo's values were obtained during several different days and that the shade-tolerant species were under natural canopy where transmittance is very low. The drop in the photosynthetic response during clear days is not documented for tropical plants but is a stomatal effect and the transpiration rate shows the same behaviour.

Transpiration studies on moist-forest species leaves are scarce, in particular under natural conditions. Whitehead et.al. (1981) and Grace et.al. (1982) studied transpiration rates for two tropical species Gmelina and Tectona during the dry and wet season respectively. They found a strong correlation between transpiration and radiation but not with stomatal conductance. Nevertheless, the drop in conductance at noon was observed and associated with the increasing air saturation deficit. Simulated average maximum hourly transpiration rates (0.001 to 0.002 mol m^{-2} s^{-1}) are lower than those recorded by Whitehead et.al. (1981) but within the range found by Grace et.al. (1982) in field conditions. Daily totals are quite similar to values found in natural

conditions, Odum et.al. (1970) mention average values between 6 and 30 mol m^{-2} day^{-1}, for average days, and around 6 or less for the night. Nevertheless, values as high as 75 mol m^{-2} day^{-1} were found in dry clear days. These are very similar to the simulated values whose maxima for clear days range between 30 and 70 mol m^{-2} day^{-1} and for overcast days between 5 and 20 mol m^{-2} day^{-1} respectively.

Data on water use efficiency are not available for tropical trees. Mooney et.al. (1984) mention that this did not vary much between sites although it did between genera; however there are no figures to which comparisons can be made. Averages for potted C_3 plants are given by Jones (1983) and range between 0.88 and 2.65mmol mol^{-1}). He also mentions values for wheat under natural conditions, ranging from about 1.74 to 4.22 for different regions and years. Simulated values range from 1.79 to 5.52 for overcast and cloudy days respectively. These values seem slightly high but well within normal ranges. Differences between species are consistent and are related to the photosynthetic pathways (Jones 1983). In these simulations, *C.alliodora* (shade-intolerant) displays higher values than the shade-tolerant *B.alicastrum*, suggesting better water control mechanisms in the former species i.e. higher quantum saturation levels and greater sensitivity to VPD changes. Differences between canopy conditions show that both species are less efficient in the open for similar days, but this effect is mainly caused by the lower transpiration rates under the canopy, where photosynthesis is also diminished, which could be not advantageous when water is not limiting. Jones (1983) mentions that 'optimization' of WUE is more desirable than 'maximization', as a result other factors i.e. water availability and respiratory losses, should be taken into account.

4.4.4. Growth.

The shade-tolerant *B.alicastrum* displayed lower values of simulated dry matter production in a year than the shade-intolerant *C.alliodora*. However, when compared on a leaf area basis the inverse is true. This behaviour is not expected since higher maximum assimilation rates and stomatal conductance were found in *C.alliodora* when the species were compared in a controlled environment room (Ch. 3). Two factors may explain these results:

a) stomatal conductance in *C.alliodora* is more sensitive to VPD changes, which limit gas exchange when humidity is low, e.g. in the field and in simulated conditions.

b) the greater amount of leaf area in this species may cause selfshading on the lower part of the canopy and hence limiting the light available for photosynthesis. This effect is greater in the field and in the model than in the growth room.

After allocating the annual dry matter production, the respiratory losses were calculated. Lugo (1970) presents some data on respiration: in the open, from 20% to 30% of net photosynthesis is used in respiration by shade-intolerant and shade-tolerant species respectively, under shade these values are much higher, ranging from about 22% to 110%. Although simulated shade conditions are not as in the understorey of a tropical-moist forest, the assumption that respiration is the same and does not change through the year for different species and canopies is rather naive. Leaf respiration changes during development and the ratio photosynthesis/respiration (P/R) is not always positive. The parameters used for calculating photosynthesis were obtained from mature leaves, hence probably overestimating assimilation during the whole period. However, these parameters were obtained under controlled conditions and tend to be lower than parameters obtained in the field. As a result, errors derived from these differences cannot be large. Respiration rates were higher for the shade-intolerant species but photosynthetic rates were also high (in high light levels); hence they display high P/R under sunny conditions (Odum 1970). As we lack information regarding the respiration rates for the species used and their response to environmental and physiological variables no attempt was made to simulate them; instead, a fixed value was used within the range found in natural conditions.

Simulated values of total dry matter production (Table 4.2) are about one order of magnitude larger than the average sampled in the field (Fig. 4.7). Differences between simulated RGR, NAR and LAR and observed values are smaller than total dry matter and in some cases very similar. In general, simulated RGRs and NARs are higher in open conditions; the same trend is observed in the values obtained under controlled environmental conditions but opposite to the values in the field, probably due to different initial sizes of the plants in the field and inaccuracies in estimating leaf dry weight (Ch. 2).

Simulated LARs show the same trend as LARs observed in controlled and field conditions. In *B.alicastrum* values are very similar, but a very high value is displayed by *C.alliodora* under shade.

Assuming that plants would exhibit optimum growth in a controlled environment compared to field conditions, differences should arise from those environmental factors which were held constant and in 'optimum' conditions i.e. water, nutrients supply and protection from pests and diseases. Following the same argument the differences between the 'optimum' observed values and the output of the model could arise from other factors or from inadequacy of the model. Although respiration is not adequately modelled and sampling methods in the field were also inadequate (Ch.2), differences between the observed values (in the field and under controlled conditions) and the simulated values are too large in some cases to be explained for these variations i.e. in the parameters assumed and sampling errors. Validation of this part of the model is not possible due to the poor understanding and lack of data on dry matter allocation and respiration.

4.5. Conclusions.

1.- Environmental variables can be simulated fairly well, that is, they follow the average trends found in natural conditions; simulated values for photosynthesis and transpiration are within the range found under controlled and field conditions.

2.- The radiation model gave reasonable results on a daily basis; simulated photosynthetic and transpiration rates were well within the range found for similar species and locations. It is necessary to define the canopy in terms of sun and shade leaves so as to avoid underestimation of photosynthesis in the lower portions of the crowns. Leaf area changes with time are also very important.

3.- Modelling growth needs much effort to get sound results and adequate predictions. Although empirical allocation ratios were useful and give a good idea of the effect of light, it is necessary to obtain a set of surface responses in relation to other environmental factors, so that interactions can be modelled. Respiration is inadequately studied and the model would benefit from research in this area, in particular under controlled and field conditions.

4.- Although the trends of light competition between species with different adaptations is somehow 'predicted' the most important results of the simulations are the comparisons with theoretical results and those obtained in previous studies. More research is needed before this kind of model can be used for the management of tropical trees.

CHAPTER 5

GENERAL DISCUSSION.

In general, the results from both the natural and the controlled environment experiments agree with the patterns and trends mentioned in the literature regarding the response of tropical trees to different light environments. The field experiment was particularly helpful in assessing the possibility of manipulating secondary forest canopies to optimize growth and mortality of enrichment planting schemes. The controlled environment experiment allowed mathematical models to be fitted which describe physiological responses to environmental variables. These models and their parameters were very useful in the comparision of the species when grown at different light conditions, they were also important constituents of the simulation model of tree growth. Although the performance of the species in the field was inadequately predicted, the simulation model was an invaluable tool for synthetizing the information collected, it was also helpful in defining areas for further research.

Modern research on photosynthesis of tropical plants began with the classical approach of sun and shade plants, trying to detect genetically and environmentally determined adaptations of the photosynthetic apparatus (Medina 1986). This subject has lead to the comparision of secondary-forest species with primary-forest species. However, this dichotomy of rainforest trees into two exclusive groups of species, which underlies the analysis made throughout this study, hides an underlying complexity. Denslow (1980) recognized three groups: understorey, small gap and large gap species. Whitmore (1982) went further in identifying four responses to gaps amongst twelve tropical tree species. The response of tree species to gaps has also been linked to whether the species of all successional stages start simultaneously or establish sequentially (Whitmore 1983). In the literature dealing with secondary succession in tropical forests, it is easy to find lists of characteristics which species should have. However, there are few experimental data either to support or to reject those suggestions dealing with species physiology. The need for detailed studies to understand and predict forest growth is evident. The appreciation of the variation in adaptive strategies of the species involved is essential to understand the processes of secondary succession (Denslow 1978). These studies must be based on the quantitative

understanding of the physiological processes contributing to the forest growth and on the responses of these processes to changes in the environmental conditions (Landsberg 1986).

Following this ecophysiological approach, species were analysed in relation to their tolerance to shade. Their responses were found, in general, to be as expected for secondary-forest and primary-forest species: primary-forest and late-secondary forest species, *B.alicastrum* and *S.macrophylla* respectively, displayed lower growth rates, and lower photosynthetic and transpiration rates than the secondary-forest species, *C.alliodora* and *C.odorata*. Secondary-forest species were more plastic in their responses i.e. they displayed larger changes when shaded. Dry matter allocation patterns were complex and generalizations were difficult to draw. Nevertheless, all species tended to allocate more dry matter to stem and leaves when shaded. Secondary-forest species tended to favour leaf area and stem height while primary-forest species increased stem density.

5.1. Natural environment.

Frequency distributions of height and mortality (Figs. 2.15, 2.16) were very useful in assessing growth and shade tolerance in the field. However, very few studies have used these techniques with trees (Ford 1975, Cannell et.al.1984). These frequency distributions also showed the vulnerability of secondary-forest species to competition and density dependant mortality (Harper 1977). Growth analysis and dry matter partitioning (Figs. 2.17, 2.18), though very powerful, have not been used to study shade tolerance in the field for tropical trees. The results obtained in this study showed some ambiguity due to problems with the sampling techniques. Specific leaf area and leaf nitrogen content (Fig. 2.18) are very good indicators of shade tolerance and plasticity, they also provide information regarding the photosynthetic capacity of the leaves. Values in the field are not directly comparable with other studies because of the different light conditions and age of the saplings. Detailed description of the environmental variables, in particular light quality and quantity, and age of saplings and leaves, are necessary to make comparisions possible. The effect of nutrient and water status on the growth and dry matter partitioning need to be evaluated since these factors can affect the assimilatory capacity of the plants. This represents an important research area for future studies.

Two groups of species are clearly seen: those with higher growth rates and lower mortality in full sun conditions (shade-intolerants), and those with higher growth and lower mortality under moderate shade (shade-tolerants). All species displayed low growth rates and high mortality under deep-shade conditions. Due to density dependant competition, groups of 'dominants' and 'suppressed' individuals re formed, especially amongst the secondary-forest species, which ha important consequences regarding their shade tolerance. These groups need to be taken into account when manipulating the system e.g. thinning the suppressed individuals so as to liberate the rest. Specific leaf area (SLA) increases when shaded and is higher for secondary-forest species. Values are similar to other studies but before drawing final conclusions more attention to the light quality should be taken. For example, red to far-red ratio (R:FR) during growth conditions affects SLA (Kwesiga & Grace 1986). Hence, care should be taken in the absence of information on the R/FR.

The distribution of environmental variables through the year, their ranges and averages are important factors that determine floristic composition, species distribution and forest dynamics (Medina 1986). The regimes of average temperature and rainfall can be graphically characterized by climate diagrams (Fig. 2.2). They are particularly useful for assessing the length and severity of potential dry seasons. Daily integrals of radiation and weekly minimum and maximum temperatures (Fig. 2.10) are very helpful when modelling daily courses of: radiation, temperature and humidity (Fig. 4.1). The interplay between microclimate and vegetation creates vertical gradients of leaf microclimates. Hence, vertical profiles of light intensity, air temperature and humidity, and wind speed can be correlated to forest structure (Chariello 1984). Hemispherical photographs can be used to estimate the transmissivity of canopy layers (Fig. 2.11) which together with temperature (maximum-minimum) can be used to simulate daily courses and vertical gradients of microclimate (Fig. 4.2).

The climate of the area is typical of a seasonal moist forest (Walter 1979) with a dry season lasting four months. Temperature and radiation displayed differences between seasons, with higher values during the dry season. Canopy transmissivity of the secondary forest is slightly higher than the values obtained for primary forests (Pearcy 1983, Chazdon & Fetcher 1984). Transmissivity of the different canopy layers, which helps to describe the forest canopy structure, has not been studied in tropical forest. In this study the middle canopy layer intercepted more radiation than the top layer, 80% and

60% respectively. Hemispherical photographs offer a possibility of assessing these canopy properties, which could be used in the management of these forests by controlling light intensity at the forest floor.

5.2. Controlled environment.

Controlled environment conditions permit comparative studies of carbon balance without the problem of high variability and the confounding effect of environmental factors associated with field studies (Whitehead et.al. 1981, Grace et.al. 1982). The carbon balance of plants is related to survival and reproductive success. This balance depends on adjustments in the CO_2 exchange capacity of plants which is genetically determined for each species. Plant-water relations are closely associated with CO_2 exchange. As a result, the carbon balance and the water relations of tropical trees requires special attention and further investigation. Results obtained under controlled environmental conditions follow the patterns observed in other studies and although they are lower than values obtained in field conditions they are within values obtained in other works under controlled environmental conditions Kwesiga et.al. 1986). This suggests that values obtained under controlled conditions should be used with caution when simulating field conditions or comparing with field data. This is particularly important when considering rapid fluctuations of the environment, in particular sunflecks, wind and rain. Sunflecks are extremely important for plants growing under shade since a substantial amount of photosynthesis is obtained from them (Pearcy et.al. 1985). These factors are inadequately modelled and should be taken into account when analysing the results from simulations. Fitting models of photosynthesis and stomatal conductance to experimental data was successful and the physiological parameters obtained were used to compare species and treatments. These parameters described the leaf response to light and humidity, but not to temperature. They agree with the results and conclusions obtained through growth analysis and were used in the simulation of plants performance in the field.

This work indicates that secondary-forest species have higher mesophyll and stomatal conductances which confer a higher photosynthetic capacity per area of leaf than primary-forest species (Figs. 3.10, 3.13); they are also more sensitive to shade and show greater reductions when shaded. This sensitivity

to shade suggests that secondary-forest species present an effective shade-sensing mechanism e.g. phytochrome (Smith 1981). Their high stomatal conductance implies high transpiration rates, which may be an adaptation for heat dissipation (Chariello 1984). Secondary-forest species also showed higher RGR and NAR than primary-forest species, mainly due to their high SLA. Under 'sun' conditions all species displayed higher values of photosynthesis and stomatal conductance, RGR and NAR but, they were less sensitive to environmental changes (Figs. 3.10-3.13). Dry matter partitioning, under shade, favours leaves and stem at the expenses of roots. However, species used the dry matter in different ways, either for height, leaf expansion or stem density (Figs. 3.17, 3.18). Nitrogen leaf content is higher in secondary-forest species and under sun conditions but is more efficiently displayed by primary-forest species (Fig. 3.18).

5.3. Simulation.

The simulation of environmental variables was adequate for the purposes of this work. However, the effect of rapid microclimatic changes, such as sunflecks, was not attempted and their effect not estimated. The physiological parameters can be similarly criticized, since they were obtained under controlled and constant conditions. The effect of these sudden changes seem to be important in natural conditions and should really be investigated so that the results can be incorporated into the model (Mooney et.al. 1984, Pearcy et.al. 1985). Most other workers have also dealt with steady-state responses, and perhaps the time has now come for studies of the dynamic responses of e.g. stomata in relation to the natural fluctuation in light climate. The radiation model gave reasonable results on daily courses and although it was not formally tested, e.g. with radiation measurements at the site, simulated values of photosynthesis and transpiration were within the range of values obtained under similar conditions (Lugo 1970, Grace et.al. 1982). The relationships between leaf structure, leaf span and photosynthesis were assumed constant through the year. This assumption is not adequate when photosynthesis is modelled for long periods of time e.g. months, since photosynthetic and stomatal characteristics change as the leaves age (Ticha 1985). Sun and shade-leaf area distributions were assumed homogeneously distributed but, they may have consequences on radiation interception (Ross 1981). To improve the model in this area, canopy characteristics, e.g. spatial distribution of leaf area

density and its phenology need to be investigated. Dry matter allocation was crudely simulated and although the effect of shade was taken into account, the effect of nutrition and water status on partitioning was neglected. There are very few studies of dry matter allocation in tropical trees, thus it is not possible to predict the effects of the interaction of environmental variables on dry matter allocation. Respiration is probably the least known and the weakest part of the model. Stem and root respiration is an area of speculation and suggestions but, very few data can support these ideas (Lugo 1970, Odum 1970). Much research is needed before these areas can be properly modelled and consequently field performance predicted.

5.4. Further research.

Although it is possible to predict the potential success of the species studied in the field, providing environmental conditions are similar, the model did not predict accurately the performance of these species in natural conditions. Thus, extrapolations for conditions outside the range tested are unreliable. After identifying some general trends and research priorities, it is worth mentioning the importance of coupling field work with controlled environment studies. The feedback of information in this dual approach makes it easier to pinpoint weak areas and wrong conclusions; it also makes it easier to identify general patterns and trends. Techniques in ecophysiology and modelling are very powerful and give a deep insight into the processes and mechanisms by which species use in adapting to the environment, their tolerance ranges and their responses to the environment. However, these techniques need to be used cautiously, in particular when predicting field performance. This is because of the static, steady-state conditions of controlled environments in which these responses were measured. Frequency distributions of height, mortality rates and growth analysis, although not as sophisticated as ecophysiology and modelling, provide us with a good set of tools which can be used when the other techniques are not available. Alternatively, when used in conjunction with them, they can help to interprate the results of ecophysiological an modelling exercises. It is clear that data on the physiological properties of leaves of tropical trees is scanty and in many cases difficult to compare. Many of these properties are dependent on leaf age, nutrition and water status and yet these parameters are not often specified. Measurements of responses reported utilize a variety of techniques under

different conditions and the precise environmental and soil conditions are often not specified and making comparisions difficult to interpret.

It seems feasible and advisable to manipulate secondary-forests for management purposes. For example, their canopies can be used to control light intensity, temperature and humidity in the first stages of enrichment planting. Growth and mortality can be optimized in this way. Later, these canopies may be opened and allow more light to reach the plants. The effect of the canopy on the development and control of weeds and on nutrient cycles are other areas worth investigating, since canopy manipulation could be easier and cheaper than conventional fertilizers and herbicides.

5.5. Concluding remarks.

1.- Secondary-forest species (*C.odorata & C.alliodora*) can be regarded as shade-intolerant. They grow faster and survive better under full sun conditions. They are very sensitive to competition, in particular for light, and as a result they developed skewed and bimodal frequency distributions. This behaviour may be explained by their high photosynthetic and stomatal capacity, together with their higher sensitivity to shade (plasticity). Their dry matter allocation patterns also reflect this shade-intolerance, increasing height or leaf area when shaded.

2.- The primary-forest species *B.alicastrum* is shade-tolerant. It survives better under moderate shade and growth is similar in full sun and under moderate shade. Partitioning of dry matter reflects this tolerance and stem density increases slightly with shade without much change in height or leaf area. Photosynthetic and stomatal capacity are low and their sensitivity to shade is also low.

3.- *S.macrophylla* displayed an intermediate behaviour, with moderate values and plasticity. These facts support the idea of a continuum of requirements and tolerances among species and that although the dichotomy of primary and secondary-forest species is useful, it could be misleading. Growth rates, mortality rates, allocation patterns and physiological parameters can help in building a framework within which species could be allocated, so that their responses to the environment could be better described.

4.- Secondary forests seem to be suitable and versatile environments for ecophysiological and management experiments. They are widely distributed, present similar characteristics and are relatively easy to modify, e.g. gaps can be opened, canopy layers can be removed and species can be introduced or removed. The effect of the canopy structure on the vertical profiles of environmental variables e.g. light transmittance, will help in describing growing conditions and could be used to make decisions regarding their modification.

5.- Controlled environment studies are invaluable tools for isolating environmental factors. Data collected under these studies are ideal for fitting exercises. The physiological parameters obtained help to compare species and their responses to particular conditions. In this work they displayed specific differences as well as environmental modifications (plasticity). It was clear that photosynthetic and stomatal capacity differ between species and that the different light conditions modified this capacity and its sensitivity.

6.- Growth analysis and dry matter allocation were very helpful in describing species responses to the growing conditions. Height frequency distributions and mortality were particularly useful in the field. Growth analysis in the field was not adequate but reasonable results were obtained under controlled environmental conditions. Specific leaf area is a very good index of shade-tolerance and plasticity. It gave very good results in both natural and controlled environments and is suggested as a first hand tool for assessing and comparing species responses to light. Care should be taken when describing the light conditions and the R/FR should be included. Nitrogen content of the leaves is also a good index and can be used to asses the assimilatory capacity of leaves under different growing conditions.

7.- Gas exchange measurements are a powerful technique for analysing the potential that a species has for producing dry matter. Under controlled environmental conditions the responses were good enough to be used for fitting models and obtaining physiological parameters. The steady-state conditions of controlled environment experiments limit the application of the parameters found when simulating or comparing with natural conditions. Parallel studies under field conditions can complement the information obtained under controlled conditions and give more confidence in extrapolations.

8.- Simulation models were very useful in synthetizing the information

obtained during the experiments and in comparing this with ecophysiological theory. Simulation of weather variables was adequate: daily courses of photosynthesis and transpiration were within the range obtained under similar conditions. The simulation of growth in one year was inadequate, mainly due to the lack of knowledge regarding dry matter allocation patterns and respiratory losses. The distribution of leaf area in space and time may also have influenced the results.

I. Summary of results and statistical analysis.

I.I. Enrichment planting experiment.

Environment.-

Q.- mol m^{-2} day^{-1}

Minimum	3.0	
Mean	24.3	(Dry season)
Maximum	37.4	
Minimum	2.4	
Mean	18.7	(Wet season).
Maximum	41.1	

Temperature.-

Minimum	27.0	
Mean	32.2	Dry season (maximum temperatures).
Maximum	36.0	
Minimum	12.0	
Mean	17.6	Dry season (minimum temperatures).
Maximum	20.0	
Minimum	20.0	
Mean	30.3	Wet season (maximum temperatures).
Maximum	38.0	
Minimum	11.0	
Mean	19.5	Wet season (minimum temperatures).
Maximum	23.0	

Growth.-

Non-destructive sampling.-

Table 2.6 Height (log-transformed data) and height relative growth rates (HRGR), means and (s.e.) are shown.

Height.-

Species	Year 1983	1984	1985	Canopy
B.alicastrum	4.39 (.27)	4.82 (.33)	5.14 (.34)	open
----------	4.44 (.22)	4.56 (.27)	4.86 (.26)	shade
----------	4.50 (.23)	4.70 (.27)	4.95 (.25)	deep-sh
S.macrophylla	3.93 (.58)	5.10 (.48)	5.81 (.44)	open
----------	3.82 (.57)	4.18 (.46)	5.02 (.36)	shade
----------	3.85 (.66)	4.46 (.60)	5.15 (.46)	deep-sh
C .odorata	3.29 (.57)	4.72 (.70)	5.27 (.62)	open
---------	2.89 (.40)	3.55 (.37)	4.16 (.42)	shade
---------	2.92 (.56)	4.14 (.66)	4.82 (.55)	deep-sh
C.alliodora	4.04 (.73)	5.44 (.61)	6.08 (.59)	open
----------	3.62 (.47)	4.30 (.56)	4.79 (.58)	shade
----------	3.78 (.76)	4.59 (.85)	5.13 (.65)	deep-sh

HRGR.-

Species	Year First	Second	Mean	Canopy
B.alicastrum	0.43 (.06)	0.32 (.01)	0.37 (.04)	open
----------	0.12 (.05)	0.30 (.01)	0.21 (.02)	shade
----------	0.20 (.04)	0.25 (.02)	0.22 (.01)	deep-sh
S.macrophylla	1.17 (.10)	0.71 (.04)	0.94 (.07)	open
----------	0.36 (.11)	0.84 (.10)	0.60 (.10)	shade
----------	0.61 (.06)	0.69 (.14)	0.65 (.10)	deep-sh
C.odorata	1.43 (.13)	0.55 (.08)	0.99 (.03)	open
--------	0.66 (.03)	0.61 (.05)	0.63 (.01)	shade
--------	1.22 (.10)	0.68 (.11)	0.95 (.01)	deep-sh
C.alliodora	1.40 (.12)	0.64 (.02)	1.02 (.07)	open
----------	0.68 (.09)	0.49 (.02)	0.58 (.06)	shade
----------	0.81 (.09)	0.54 (.20)	0.67 (.06)	deep-sh

Table 2.7 Mortality (%) and change of mortality of saplings during the first three years of growth. Average for each plot.

Mortality.-

Species	YEAR 1983	1984	1985	Canopy
B.alicastrum	8.5	29.5	39.0	open
----------	8.5	23.0	32.5	shade
----------	3.0	19.0	35.5	deep-sh
S.macrophylla	54.5	67.5	70.5	open
----------	25.0	36.5	39.5	shade
----------	30.5	51.5	66.5	deep-sh
C.odorata	35.0	50.0	57.0	open
--------	26.0	64.5	73.5	shade
--------	22.0	74.5	89.0	deep-sh
C.alliodora	13.0	16.5	24.0	open
----------	9.5	17.5	27.5	shade
----------	2.0	28.0	55.0	deep-sh

RMR.-

Species	83-84	84-85	Mean	Canopy
B.alicastrum	21.0	9.5	15.2	open
----------	14.5	9.5	12.0	shade
----------	16.0	16.5	16.2	deep-sh
S.macrophylla	13.0	30.0	21.5	open
----------	11.5	3.0	7.2	shade
----------	21.0	15.0	18.0	deep-sh
C.odorata	15.0	7.0	11.0	open
--------	38.5	9.0	24.7	shade
--------	52.5	14.5	33.5	deep-sh
C.alliodora	3.5	7.5	5.5	open
----------	8.0	10.0	9.0	shade
----------	26.0	27.0	26.5	deep-sh

Destructive sampling (harvest)

Table 2.8 Means and s.e. of logarithm transformed data.

Year	1984			1985		
Canopy	Open	shade	deep-sh	Open	shade	deep-sh
Species						
Crown depth.-	s.e. 0.15 (1984), 0.23 (1985)					
B.ali.	4.66	4.26	4.42	4.65	4.45	4.64
S.mac.	4.38	4.23	4.12	4.61	4.43	4.48
C.odo.	4.47	2.72	3.74	4.05	4.14	3.31
C.all.	5.30	4.13	3.87	5.56	4.47	4.76
Crown diameter.-	s.e. 0.18 (1984), 0.26 (1985)					
B.ali.	4.11	4.01	4.02	4.48	4.13	4.37
S.mac.	4.22	3.98	4.00	4.51	4.24	4.23
C.odo.	4.20	1.72	3.34	3.64	3.54	3.00
C.all.	5.10	4.02	3.69	5.26	4.24	4.61
Leaf fresh weight.-	s.e. 0.31 (1984), 0.36 (1985)					
B.ali.	4.32	3.72	4.03	4.18	3.74	4.01
S.mac.	4.34	3.62	3.59	5.35	3.53	3.52
C.odo.	3.52	1.50	2.47	3.58	2.45	2.06
C.all.	6.67	3.86	3.73	5.72	4.44	4.41
Leaf dry weight.-	s.e. 0.29 (1984), 0.38 (1985)					
B.ali.	3.16	2.34	2.62	3.24	2.56	3.05
S.mac.	3.12	2.22	2.16	4.30	2.84	2.65
C.odo.	1.87	0.32	0.38	1.91	1.24	0.79
C.all.	5.31	2.28	2.13	4.50	3.32	2.84
Stem length.-	s.e. 0.19 (1984), 0.22 (1985)					
B.ali.	5.01	4.61	4.72	4.99	4.71	4.92
S.mac.	4.33	3.97	4.20	5.09	4.37	4.66
C.odo.	4.84	3.40	3.95	4.96	3.94	4.25
C.all.	5.38	4.25	4.51	5.58	4.51	5.08
Stem perimeter.-	s.e. 0.14 (1984), 0.19 (1985)					
B.ali.	1.22	1.33	1.01	2.56	2.61	2.67
S.mac.	1.56	1.13	0.99	2.45	2.69	2.63
C.odo.	2.02	1.47	0.90	3.08	2.28	2.12
C.all.	2.12	1.40	1.10	3.20	2.59	2.50

continue

Stem fresh weight.- s.e. 0.41 (1984), 0.42 (1985)						
B.ali.	4.52	3.53	3.38	5.12	4.16	4.32
S.mac.	4.38	3.23	3.20	6.04	3.94	4.45
C.odo.	5.96	1.90	2.44	5.85	3.47	3.80
C.all.	6.58	2.94	3.15	7.16	4.06	4.12
Stem dry weight.- s.e. 0.47 (1984), 0.40 (1985)						
B.ali.	3.83	3.17	2.79	3.94	3.66	3.61
S.mac.	3.71	2.41	2.51	5.00	2.97	3.73
C.odo.	5.13	1.01	1.38	4.87	2.16	2.98
C.all.	5.65	2.14	2.09	6.30	3.20	3.50
Roots length.- s.e. 0.17 (1984)						
B.ali.	3.57	3.34	3.46	----------		
S.mac.	3.72	3.32	3.39	There are no data for		
C.odo.	3.91	3.01	2.80	this year.		
C.all.	4.32	3.54	3.46	----------		
Root fresh weight.- s.e. 0.36 (1984), 0.34 (1985)						
B.ali.	4.41	4.04	3.74	4.97	4.12	4.10
S.mac.	4.32	2.82	2.98	5.75	3.65	3.22
C.odo.	5.56	1.83	2.25	5.80	3.52	2.97
C.all.	6.34	3.66	2.77	6.84	4.10	4.91
Root dry weight.- s.e. 0.34 (1984), 0.40 (1985)						
B.ali.	3.68	3.26	3.13	3.58	3.65	2.84
S.mac.	3.26	1.94	2.01	4.60	3.01	2.67
C.odo.	4.25	0.78	0.98	4.51	2.55	2.08
C.all.	5.22	2.64	2.11	5.88	3.60	3.41
Total dry weight.- s.e. 1.0 (1984), 0.97 (1985)						
B.ali.	4.72	4.06	4.16	4.86	4.55	4.44
S.mac.	5.06	3.71	3.71	5.98	4.14	4.36
C.odo.	5.94	2.48	2.08	5.96	3.43	3.99
C.all.	6.73	3.55	3.69	6.97	4.57	5.29

Table 2.9 Summary of plant performance during one year (1984-1985): relative growth rate (RGR), net assimilation rate (NAR), leaf area ratio (LAR), specific leaf area (SLA), leaf weight ratio (LWR), stem weight ratio (SWR) and root weight ratio (RWR).

Species Canopy	RGR	NAR	LAR	SLA	LWR	SWR	RWR
B.ali.							
open	0.14	.053	2.63	12.2	.22	.43	.34
shade	0.49	.185	2.65	13.3	.20	.38	.42
deep-sh	0.28	.089	3.14	15.3	.22	.42	.36
S.mac.							
open	0.91	.290	3.71	13.7	.24	.45	.30
shade	0.42	.084	5.02	19.3	.30	.39	.31
deep-sh	0.64	.087	7.39	28.9	.27	.50	.23
C.odo.							
open	0.01	.016	0.64	20.3	.04	.62	.34
shade	0.94	.190	4.83	40.8	.17	.43	.39
deep-sh	1.91	.467	4.08	50.8	.15	.54	.31
C.all.							
open	0.24	.110	2.18	13.2	.20	.48	.32
shade	1.02	.160	6.38	21.1	.32	.31	.37
deep-sh	1.60	.204	7.85	29.8	.27	.30	.43

Table 2.10 Mean nitrogen content of leaves for different species and treatments. Percentages of nitrogen in a dry weight basis.

Canopy Species	open	shade	deep-sh	all
B.alicastrum	2.58	2.39	3.23	2.73
S.macrophylla	2.23	1.99	2.26	2.16
C.odorata	3.79	4.18	4.80	4.26
C.alliodora	3.96	3.61	3.76	3.51
All	3.14	3.04	3.51	
	(per unit area, g 100 cm^{-2})			
B.alicastrum	2.11	1.80	2.11	2.01
S.macrophylla	1.63	1.03	0.78	1.15
C.odorata	1.87	1.02	0.94	1.28
C.alliodora	3.00	1.71	1.26	1.99
All	2.15	1.39	1.27	(s.e.= 0.1,n= 3)

I.II. Response to shade experiment.

Fitting procedures.-

An example of the "F" test carried out with both complete and truncated data (due to aberrant points) for the fitted models is shown. The 'lack of fit' of the models is tested against the experimental error.

Variate: Net assimilation, species: *B.alicastrum*, Treatment: 'sun'.

SOURCE OF VARIATION	DEGREE OF FREEDOM	SUM OF SQUARES	MEAN SQUARE	VARIANCE RATIO	P
Q	6	296.0938	49.3490	215.284	.01
Residual(error)	35	8.0230	0.2292		
Model(fitting)	38	9.1140			
Lack of fit	3	1.0910	0.3636	1.58	n.s.
TOTAL	41				

This analysis shows that the "lack of fit" term is "not significant" and we can say therefore that the model fits the data reasonably well.

The next example shows a "bad fit".
Variate: Stomatal conductance, species: *B.alicastrum*, Treatment: 'sun'.

SOURCE OF VARIATION	DEGREE OF FREEDOM	SUM OF SQUARES	MEAN SQUARE	VARIANCE RATIO	P
Q	6	8965			
Model	39	1638			
Lack of fit	4	377	94	2.618	.1
TOTAL	41	10266			

As the term 'lack of fit' is significant at P=0.1, we can say that the model does not represent (fit) the data.

After removing the aberrant data the results are as follow:

SOURCE OF VARIATION	DEGREE OF FREEDOM	SUM OF SQUARES	MEAN SQUARE	VARIANCE RATIO	P
Q	5	8055			
Residual	30	951	32		
Model	33	1019			
Lack of fit	3	68	22	0.71	n.s.
TOTAL	35	9006			

Although it uses less degrees of freedom, this method improves the fitting procedures.

Light response.-

The anovar results and the 'lack of fit' test done for the non-linear models (N-L-M) fitted to the light responses data are shown in Table 3.7. Values refer to the percentage points of the 'F' distribution and n.s. refers to 'non-significant'. The 'sun' and 'shade' conditions are described in Ch.3. Net assimilation, An, and stomatal conductance, g_s, are both analysed. The whole (full) and the truncated (trunc) set of data are shown.

Table 3.7 Anovar and 'lack of fit' test for An and g_s.

species	growth conditions	variate	anovar (full)	N-L-M (full)	anovar (trunc)	N-L-M (trunc)
Brosimum	'sun'	An	.01	n.s.	.01	.1
alicastrum	---	gs	.01	.1	.01	n.s.
--------	'shade'	An	.01	n.s.	.01	n.s.
--------	-----	gs	.01	.01	.01	n.s.
Swietenia	'sun'	An	.01	n.s.	.01	n.s.
macrophylla	---	gs	.01	n.s.	.01	n.s.
--------	'shade'	An	.01	n.s.	.01	n.s.
--------	-----	gs	.01	n.s.	.01	n.s.
Cedrela	'sun'	An	.01	n.s.	.01	n.s.
odorata	---	gs	.01	n.s.	.01	n.s.
-------	'shade'	An	.01	.01	.01	.05
-------	-----	gs	.01	.01	.01	.1
Cordia	'sun'	An	.01	n.s.	.01	n.s.
alliodora	---	gs	.01	n.s.	.01	n.s.
------	'shade'	An	.01	.1	.01	.1
-------	-----	gs	.01	.1	.01	.05

Although the variance analysis shows highly significant differences between light levels in both An and g_s, the g_s variance ratio is about 2-5 times higher than the An variance ratio. This fact shows the higher variability of the stomatal values during the light response (Figs. 3.6a - 3.13a).

As we can see in the above table, aberrant data affect the fitting procedures with better fits using truncated data sets, thus improving the estimation of the parameters and their description of the responses. Parameters from the models fitted to the truncated data sets are therefore assumed as the true values of the parameters and used as appropriate in the following sections.

VPD response.-

The following table (3.8) shows the anovar results and the "lack of fit" test of the linear and negative exponential models used to describe the g_s - VPD relationship. The values refer to the 10, 5 and 1% probability points for the "F" distribution, (variance ratio test).

Table 3.8 anovar and 'lack of fit' test for g_s-VPD models.

species	Growth cond.	anovar	LINEAR REG.	NEG-EXP. MODEL
B.ali	sun	0.01	0.1	0.1
	shade	0.01	n.s.	n.s.
S.mac	sun	0.01	0.05	n.s.
	shade	0.01	n.s.	n.s.
C.odo	sun	0.05	n.s.	n.s.
	shade	0.01	n.s.	n.s.
C.ali	sun	0.01	n.s.	n.s.
	shade	0.01	0.01	0.01

As the anovar shows, the response of all species at both growing conditions to the changes of leaf-air VPD were very significant. It is also clear that both models describe the relationship between g*s* and VPD fairly well, with the exception of 2-3 cases (*B.alicastrum* (sun) *S.macrophylla* (sun) and *C.alliodora* (shade)). Although there were no significant differences between the linear and non-linear models, the negative exponential model showed lower residual mean square than the linear regression. This fact, together with the case in which only the non-linear model showed a "good fit", *S.macrophylla* (sun), suggest that the negative-exponential model describes this set of data better than the linear one.

As a result, the negative-exponential model parameters and their standard errors (s.e.) were assumed to describe this response better. Although two cases showed a lack of fit to the model, reflecting the data variability rather than a "bad model", their parameters are assumed to be appropriate, table 3.11.

Temperature.-

Although, there were significant effects of temperature on g_s, it was impossible to obtain a set of parameters which could represent the temperature response. Most of the cases show a 'lack of fit' significant, table 3.9. Others cases show an unsuccessful optimization, i.e. the parameters have values lower or higher than the limits which reasonable may have. Some show good fit but, the anovar in this cases is not significative thus, invalidating the regression. The only good fit result is from *S.macrophylla* 'shade', with an

optium temperature of 26 °C, about 6 °C lower than expected (growing temperature was 28 °C).

Table 3.9 anovar results and the "lack of fit" test of g_s - temperature non-linear model.

species	Light	anovar	N-L-R
B.ali	sun	0.01	0.01
	shade	0.01	0.05
S.mac	sun	0.01	0.01 *
	shade	0.05	n.s.
C.odo	sun	n.s.	n.s. *
	shade	0.01	0.01
C.all	sun	n.s.	n.s.
	shade	0.01	0.05

* Unsuccessful optimization: a parameter has gone out of bounds!

Growth analysis.-

The following tables summarize the results obtained in order to carry out the growth analysis.

Table 3.15. Mean and (s.e.) of the loge transformed data at the start of the experiment. Number of replicates is the same for all species (5).

species VARIATE	B.ali	S.mac	C.odo	C.all
NL	1.273(.154)	1.458(.266)	2.377(.035)	
HT mm	5.679(.059)	5.051(.272)	5.104(.033)	
LFW mg	7.159(.179)	7.144(.237)	8.722(.074)	
SFW	7.072(.059)	6.695(.211)	7.674(.087)	
RFW	6.858(.348)	6.626(.427)	8.290(.212)	
LDW mg	6.153(.192)	5.794(.226)	7.015(.060)	
SDW	5.683(.252)	5.202(.198)	5.743(.108)	
RDW	5.546(.207)	4.891(.332)	6.045(.193)	
LA cm2	4.155(.190)	4.474(.216)	5.902(.046)	
TDW	6.93	6.47	7.52	

* As cuttings of *C.alliodora* where used and enough material for this determination was unavailable, this set of data is lacking. See discussion for more details.

NL.- Number of leaves.
HT.- Height.
LFW.- Leaf fresh weight.
SFW.- Stem fresh weight.
RFW.- Root fresh weight.
LDW.- Leaf dry weight.
SDW.- Stem dry weight.
RDW.- Root dry weight.
LA.- Leaf area.
TFW.- Total fresh weight.
TDW.- Total dry weight.

Table 3.16. Mean and (s.e.) of the loge transformed data at the end of the experiment. Treatments, growth period and number of replicates is also shown. Variates notation is the same as the previous table. Results have been normalized for one month.

TREATMENT SUN GP (weeks)	B.ali n=5 10	S.mac n=6 8	C.odo n=6 4	C.all n=3 * 4
NL	2.298(.123)	2.707(.042)	2.820(.031)	4.314(.045)
HT	6.079(.154)	5.704(.088)	5.531(.061)	5.641(.060)
LFW	7.797(.326)	9.631(.132)	9.538(.048)	9.551(.102)
SFW	7.190(.318)	8.116(.258)	7.768(.119)	8.996(.121)
RFW	7.414(.966)	9.031(.158)	9.387(.098)	-----
LDW	6.665(.480)	8.310(.141)	8.075(.082)	8.165(.107)
SDW	5.761(.344)	6.643(.247)	5.935(.089)	7.448(.109)
RDW	6.241(.844)	7.206(.133)	7.535(.139)	-----
LA	4.683(.303)	6.500(.206)	6.732(.050)	6.464(.108)
TDW	7.39	8.73	8.61	5.61
SHADE				
NL	2.146(.133)	2.671(.095)	2.813(.037)	3.828(.132)
HT	6.009(.080)	5.764(.111)	6.082(.053)	5.209(.186)
LFW	7.586(.275)	9.091(.179)	8.982(.104)	8.181(.589)
SFW	7.344(.084)	7.454(.238)	8.485(.098)	7.493(.578)
RFW	6.958(.411)	8.220(.167)	8.494(.074)	-----
LDW	6.487(.264)	7.618(.151)	7.404(.095)	6.603(.515)
SDW	5.878(.087)	5.765(.239)	6.320(.110)	5.450(.697)
RDW	5.719(.303)	6.218(.194)	6.733(.008)	-----
LA	4.710(.292)	6.544(.122)	6.510(.082)	5.331(.676)
TDW	7.18	7.96	8.02	12.05

* Root biomass estimation was not done. See text for explanation.

GP.- Growth period (see text).
The rest of the variables are the same as the previous table.

Table 3.17. Mean relative growth rates and (s.d.). Expressed in a monthly basis.

species	B.ali	S.mac	C.odo	C.all
SUN				
NL	.410(.007)	.624(.065)	.442(.005)	
HT	.160(.022)	.327(.053)	.427(.036)	
LFW	.255(.034)	1.244(.030)	.816(.034)	
SFW	.068(.042)	.710(.014)	.094(.041)	
RFW	.242(.125)	1.202(.078)	1.118(.148)	
LDW	.205(.067)	1.258(.024)	1.060(.028)	
SDW	.034(.019)	.721(.014)	.192(.024)	
RDW	.280(.145)	1.157(.057)	1.490(.069)	
LA	.211(.026)	1.013(.003)	.830(.005)	
SHADE				
NL	.349(.005)	.606(.049)	.436(.002)	
HT	.132(.005)	.357(.046)	.978(.026)	
LFW	.171(.022)	.974(.017)	.260(.039)	
SFW	.109(.006)	.380(.008)	.811(.014)	
RFW	.040(.015)	.797(.075)	.241(.167)	
LDW	.134(.017)	.912(.022)	.389(.045)	
SDW	.078(.038)	.282(.012)	.577(.004)	
RDW	.069(.022)	.663(.040)	.687(.137)	
LA	.222(.023)	1.035(.027)	.608(.048)	

* s.e.

Table 3.19. Mean and (s.d.) of derived ratios for some plant compartments.

species	B.ali.	S.mac.	C.odo.	C.all.
SUN				
LFWR	.302 (.085)	.268 (.049)	.275 (.040)	.251 (.057)
SFWR	.548 (.126)	.230 (.052)	.135 (.029)	.212 (.053)
RFWR	.319 (.155)	.159 (.040)	.194 (.063)	----------
LWR	.405 (.131)	.674 (.131)	.542 (.109)	.672 (.158)
SWR	.187 (.054)	.107 (.023)	.085 (.020)	.328 (.078)
RWR	.407 (.158)	.218 (.047)	.373 (.110)	----------
SLA	126.4 (35.1)	155.8 (30.2)	222.9 (29.4)	182.6 (42.9)
TFWR	.337 (.111)	.334 (.073)	.253 (.058)	.236 (.056)
SHADE				
LFWR	.272 (.060)	.223 (.044)	.286 (.053)	.190 (.157)
SFWR	.412 (.065)	.150 (.033)	.090 (.019)	.149 (.130)
RFWR	.450 (.136)	.125 (.034)	.579 (.171)	----------
LWR	.331 (.072)	.770 (.156)	.476 (.096)	.719 (.596)
SWR	.578 (.112)	.063 (.014)	.191 (.044)	.281 (.245)
RWR	.093 (.021)	.166 (.039)	.333 (.086)	----------
SLA	253.6 (58.2)	355.1 (62.6)	604.2 (94.8)	337.9 (288.)
TFWR	.354 (.078)	.192 (.042)	.229 (.053)	.176 (.147)

* *C.alliodora* ratios are not based in total dry weight but, in shoot dry weight.

LFWR.- Leaf fresh to dry weight ratio (gm/gm).
SFWR.- Stem fresh to dry weight ratio.
RFWR.- Root fresh to dry weight ratio.
LWR.- Leaf weight (dry) ratio.
SWR.- Stem weight ratio.
RWR.- Root weight ratio.
SLA.- Specific leaf area (cm^2/gm).
TFWR.- Total fresh to dry weight ratio.

Table 3.20. Contribution of NAR and LAR to the RGR and, of SLA and LWR to the LAR.

Species	Light	RGR	NAR	LAR	SLA	LWR	SWR	RWR
B.ali.	sun	.459	7.14	.064	.138	.48	.20	.32
------	shade	.256	3.52	.073	.169	.50	.27	.23
S.mac.	sun	2.26	19.44	.116	.164	.66	.12	.22
------	shade	1.49	7.54	.197	.342	.71	.11	.18
C.odo.	sun	1.08	6.35	.170	.261	.59	.07	.34
------	shade	0.50	2.36	.211	.409	.54	.18	.28
B.ali.	s & sh	.357	5.33	.068	.153	.49	.23	.27
S.mac.	------	1.87	13.49	.156	.253	.68	.11	.20
C.odo.	------	0.79	4.35	.190	.335	.56	.12	.31
All	sun	1.27	10.98	.117	.188	.58	.13	.29
---	shade	0.75	4.47	.160	.307	.58	.19	.23

RGR.- Relative growth rate ($month^{-1}$).
NAR.- Net assimilation rate ($mg\ cm^{-2}\ month^{-1}$).
LAR.- Leaf area ratio ($cm^{-2}\ mg^{-1}$).
SLA.- Specific leaf area ($cm^2\ mg^{-1}$.

Nitrogen content.-

Table 3.21 Leaf nitrogent content (g N / 100g dry matter and g N / 100 cm^2), means and (s.e.).

Species Light	B.ali	S.mac	C.odo	C.all	All
		(dry weight basis)			
start	2.64 (.01)	2.78 (.11)	3.24 (.06)	----------	
sun	2.91 (.07)	2.72 (.11)	3.33 (.07)	3.46 (.06)	3.10
shade	2.63 (.09)	2.54 (.08)	3.30 (.02)	3.37 (.02)	2.96
s & sh	2.77	2.63	3.31	3.41	
		(leaf area basis)			
sun	2.11	1.66	1.28	1.90	
shade	1.56	0.74	0.81	1.20	

II. Equipment manufacturers and addresses.

Area meter, (LI-3100) LI-COR, Inc. Lincoln, Nebraska USA.

Bio-liquid feed, N/K fertilizer, Panbritanica Ind. Ltd. Herts, England.

Drierite with indicator, (anhidrous Ca SO_4) W.A. Hammond, drierite Co. Ohio, USA.

Fisons Fi-totron, (growth cabinet) 2340 G3, Fisons Sci. Apparatus, Loughborough, England.

Filters, 'Cinemoid' No. 22 (moss green) Northern light, Edinburgh.

Filters, 'Rosco' 50% (3402), 25% (3403), 12% (3404), 69/71 upper ground, London, England.

Gas exchange analyser system, ADC (LCA-2, ASU-MF, PLC-BL, DL-1) The analytical development Co. Ltd., Hoddesdon, England.

Millivolt integrator, (MVI) Delta-T, Delta-T Devices Ltd., 128 Low Rd., Burwell, Cambridge CB5 0EJ, England.

Millivolt meter, (DVM-IC) Ferranti, 2N451E/CJ. Ferranti Electronic Ltd. Fields New Rd., Chadderton, Oldham OL9 8NP, England.

Pynosect 30 (insecticide), Mitchell Cotts Chem. Ltd., Westyorkshire, England.

Quantum sensor, (SD101QV) MACAM Photometrics Ltd., 10 Kelwin Square, Livingston EH 54 5DG, Scotland.

Quantum spectroradiometer, (QSM-2500) Techtum Instruments, Kungsgatan 145, 5-90245 Umea, Sweden.

Rotaire dehumidifier, (M120) Rotaire Driers Ltd., Huntingdon, England.

III Assumptions of the model.

Environment.

- Sinusoidal distribution of Q.

- Q, near infrared and thermal radiation treated separately.

- Beam and diffuse radiation treated separately.

- Isotropic sky for diffuse radiation.

- Sine-exponential distribution of temperature and VPD during the day.

- 'Typical' days and their annual frequency distribution represent one year.

- Wind and rain effects were neglected.

Plot and crown structure

- Trees for each species have the same dimensions within the plot.

- Crowns described as half ellipsoids.

- Foliage is grouped into crowns, leaf area density uniform within crowns.

- Spherical leaf angle distribution.

- Only one type of leaf was considered ('sun' or 'shade') depending on the treatment.

- Leaf area constant through the year.

- Leaf size was neglected.

- Non-limiting water and nutrient conditions.

Stomatal conductance.

- The general shape and values of parameters of the response function (rectangular hyperbola), measured in controlled environment, applies in the field.

- The main variables affecting g_s are: Q, temperature and VPD.

- There are no interactions between Q, temperature and VPD.

- Leaf temperature and VPD are everywhere equal to the values at the reference level above the canopy.

Net assimilation.

- A_n is related to Q by a non-rectangular hyperbola and the values of parameters of this function, measured in controlled environment, applies in the field.

- A_n is linearly related to C_i over the range of interest.

- C_i depends on the rate of A_n and g_s.

- CO_2 concentrations are everywhere the same within the canopy and equal to the values at the reference level above the canopy.

Dry matter allocation and growth.

- Daily integrals of A_n for typical days multiplied by their frequency represented yearly net assimilation.

- A ratio of 0.65 g of dry matter per g CO_2 was used.

- Empirical ratios of dry matter allocation were used.

- Respiration losses for roots and stem were estimated using a constant ratio of 0.3.

- Respiration losses were constant and equal for different species and days.

III. References

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