TREES AND LIGHT

tree development and morphology in relation to light availability in a tropical rain forest in French Guiana

ARBRES ET LUMIERE

Développement et morphologie de l'arbre en fonction de l'intensité lumineuse dans une forêt tropicale humide de Guyane française
(avec un résumé en français)

BOMEN EN LICHT

De morfologie en ontwikkeling van bomen in relatie tot de lichtbeschikbaarheid in een tropisch regenbos in Frans Guyana.
(met een samenvatting in het Nederlands)

F.J. Sterck

1997

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PROEFSCHRIFT

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STELLINGEN

-1- Bomen in tropisch regenbos produceren relatief platte kronen bij lage en hoge lichtniveaus en relatief smalle kronen bij intermediaire lichtniveaus (dit proefschrift).

-2- Onderzoek naar de effecten van licht op boommorfologie en boomgroei moet het hele scala aan lichtniveaus omvatten om recht te doen aan complexe groeireacties (dit proefschrift)

-3- Pad-analyse kan ons meer inzicht verschaffen over morfologische aanpassingen van bomen aan licht dan meer traditionele methoden (dit proefschrift).

-4- Bomen die groeien volgens hetzelfde architectuurmodel kunnen in veel opzichten morfologisch van elkaar verschillen (dit proefschrift).

-5- Bomen die groeien volgens verschillende architectuurmodellen kunnen in veel opzichten morfologisch op elkaar lijken (Fisher & Hibbs 1982).

-6- In hun strijd om licht nemen bomen grote risico's (dit proefschrift).

-7- Bij het verzamelen van gegevens nemen kronendak-onderzoekers grote risico's.

-8- Het publiceren in identieke tijdschriften zou de communicatie tussen bosbouwers en ecologen vergemakkelijken.

-9- Terwijl miljoenenprojecten het kronendak, uit naam van de wetenschap, bereikbaar hebben gemaakt voor bejaarden, gehandicapten en tv-kijkers, heeft het kronendak-onderzoek meer aan een klimuitrusting ter waarde van enkele honderden guldens.

-10- De beschermers van tropische regenbossen en andere uitgestrekte natuurlijke ecosystemen voeren een verloren strijd indien de wereldbevolking blijft groeien.

-11- Economische modellen zullen de waarde van tropisch regenbossen onderschatten zolang het bos niet wordt erkend als levend kunstwerk.

-12- De antirook-lobby dient het algemeen belang beter als ze haar aandacht meer op auto's richt en minder op sigaretten.

-13- Internationale computernetwerken maken het samenwerken binnen bestaande instituten minder belangrijk.

-14- Het hondje van Obelix is een vijand van onderzoekers.

Pour Desmo en Wemo Betian

Contents

Preface / Voorwoord

Dit proefschrift gaat over de wijze waarop bomen groeien in tropisch regenbos, en over de invloed van licht op deze groei. In de inleiding (hoofdstuk 1) beschrijf ik enkele onderzoeksbenaderingen die hierop betrekking hebben, en presenteer de centrale vraagstelling van mijn eigen onderzoek. In de vijf volgende hoofdstukken bespreek ik enkele studies. Tenslotte, in hoofdstuk 7, worden de resultaten van deze studies samen besproken en vergeleken met andere studies. Ik hoop van harte dat ik er met dit schrijven in ben geslaagd de lezers, op zijn minst zo nu dan, te boeien.

Bij het tot stand komen van dit proefschrift heb ik veel hulp gehad van vrienden en collega's. Hierbij wil ik als eerste de samenwerking met Frans Bongers, mijn begeleider, noemen. Zijn inzet, enthousiasme en wetenschappelijke scherpte zijn gedurende de afgelopen vijf jaren een blijvende bron van inspiratie geweest. Ook is de samenwerking met Herbert Prins, mijn promotor, en Jan van Groenendael, mijn externe begeleider van de onderzoeksschool Functionele Ecologie, uitstekend verlopen. Hun commentaren op manuscripten waren vaak origineel en verrijkend. Een rode draad is de samenwerking geweest met de collega-ecologen en meestal collega-AIO's en OIO's Hank Bartelink, Kunfang Cao, Patrick Jansen, Peter van der Meer, Jan den Ouden, Marc Parren, Rob Peters, Lourens Poorter, Renaat Van Rompaey en Toon Rijkers. Hierbij denk ik aan de vele besprekingen op de zolder van Hinkeloord waarbij mijn manuscripten op de korrel werden genomen. Voorts heb ik veel hulp gehad van Toon, Lourens en Peter tijdens het veldwerk in Frans Guyana. Gedurende tijden van tegenspoed (geknakte enkels en dergelijke) hebben zij en Frans mij geholpen met het klimmen en opmeten van bomen om cruciale veldgegevens te verzamelen. Ook heb ik veel van mijn tijd samengewerkt met verschillende studenten, zowel in Wageningen als in Frans Guyana. Het was vaak leerzaam, inspirerend en bovendien gezellig om met Yonke van Geloven, Jan Willem Gunnink, Andreas Hofmann, Jan Jansen, Marten Karelse, Kees Konings, Peter Kremer, Annemarie Marttin, Arjen Mulder, Rutger van Heck en Marc Smeenge te werken.

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Marga Born, Eveline Desperrière, Reinier Hille Ris Lambers, Patrick Jansen, en Sara Otterloo Butler hebben in een laat stadium het proefschrift gelezen en mij voorzien van vele textuele commentaren.

Je voudrais exprimer ma gratitude a tous mes amis et collègues qui m'ont aidé avec mon travaille du terrain en Guyane, en particulier les équipes de C.N.R.S. - Brunoy, du Laboratoire Botanique de l'O.R.S.T.O.M. et de l'Institut Botanique de Montpellier. Je remercie M. Rocheteau et

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Frank Sterck
Wageningen, januari 1997.

1

GENERAL INTRODUCTION

Trees in tropical rain forests live in a heterogeneous light environment. The actual amount of available light that a tree receives is of great importance for the establishment, growth, survival, and reproduction of the tree. The influence of light availability on tree growth is complex because light affects many different aspects of tree growth. So far, these influences have been shown for tree seedlings and saplings, but rarely for older and taller trees in tropical rain forest (e.g. Zagt & Werger in press). In this thesis, the focus is on the influence of light availability on two aspects of tree growth, namely tree development and morphology. Both tree development and morphology are investigated for trees in different phases of ontogeny (including individuals taller and older than saplings), and are related to the light availability in tropical rain forest.

1.1 Heterogeneous light environments: theory

The influence of a heterogeneous light environment on tree growth is a matter of scale. Following the theoretical arguments of MacArthur & Levins (1964), Levins (1968), and Ackerly (in press), trees may be subject to two scales of variation in light availability, both in space and time. In a coarse grain environment, trees of the same population (of one species) are exposed to different light levels, and may differ in their growth responses. In a fine grain environment, parts of individual trees (branches, leaves, leaflets, Chazdon 1988) are exposed to different light levels, and may exhibit different traits. While these two 'grains' refer to different scales of spatial variation in the light environment, the same terms are used to refer to different scales of temporal changes in the light environment. In a (temporal) coarse grain environment, trees are exposed to the same light level during their life. In a fine grain environment, they are subject to successive changes in light levels, and may change their growth responses during their life.

Gross (1986) elaborated on the temporal changes in the light environment, and related time scales of environmental change to different types of plant responses. On an evolutionary scale, environmental changes may produce genetic changes in populations over several generations. On a scale of weeks to years, the environmental changes may lead to differences in tree performance. Finally, changes on a scale of seconds to hours may provoke physiological responses, for example a change in the rate of photosynthesis (see also Chazdon 1988).

Trees in tropical rain forests may be exposed to light variation at each of these theoretical scales (e.g. Terborgh 1992). The focus in this thesis is on the scales that have major influence on the growth of tropical rain forest trees. The first scale is the spatial coarse grain environment. This concerns trees of the same population that are exposed to different light levels, and the ways in which they differ in growth. The second scale is the (temporal) fine grain environment and, more particularly, the changes in light levels that occur on a scale of months to years. This scale refers to trees that are subject to different light levels during their life, and the way they grow under these light levels. The first scale depends largely on the forest structure, and the second scale on the dynamics in the forest structure.

1.2 Tropical rain forests and variation in light availability

A wide range of light levels occurs in tropical rain forests. These light levels depend largely on the forest structure. Closed canopies may intercept up to 99% of the incident light, and thus may reduce light levels to as low as 1% relative to the light level in the open sky. In places, light penetrates directly through large holes in the canopy ('gaps'), and light levels may reach up to 50% of the light level in the open sky (e.g. Chazdon & Fetcher 1984). In addition to this overall variation in light, the light levels increase gradually with increasing height in the forest (Yoda 1974, Koop & Sterck 1994), due to a concurrent increase in gap size (Hubbell & Foster 1986, Van der Meer *et al.* 1994). Above the highest canopy layer, there is an abrupt change to the higher light levels of the open sky. This change occurred at 48 m in a forest transect in Malaysia (Yoda 1974), and at 30 m in forest transect in French Guiana (Koop & Sterck 1994). Below the highest canopy layer, trees may be exposed to a wide range of light levels, but in general they grow gradually from low to higher light levels (e.g. Clark & Clark 1992).

The temporal variation in light availability is caused by changes in forest structure. Large tree falls change the canopy structure most abruptly. They create canopy gaps and a concurrent rise in light levels. These canopy gaps gradually close because the remaining trees and newly established seedlings grow rapidly at these high light levels. As the canopy gap closes, the light levels gradually decrease. In many tropical rain forests, about 1-2% of the forest area is transformed annually into a canopy gap (e.g. Hartshorn 1991, Jans *et al.* 1993, Van der Meer & Bongers 1996), but light levels increase over considerably larger areas (Popma *et al.* 1988, Van der Meer *et al.* 1994). Moreover, light levels vary both within canopy gaps and below a closed canopy (Lieberman *et al.* 1989, Brown 1993). Given a usual life span of hundreds of years (e.g. Condit *et al.* 1995), it is no surprise that tropical rain forest trees are subject to different light levels during their life (e.g. Clark & Clark 1992).

1.3 Tree growth and light availability

1.3.1 The role of meristems

Tree growth is for a large part accommodated by meristems. Meristems produce new cells by cell division; these cells then enlarge and differentiate into one of the many cell types that make up a tree. Apical meristems at the tip of the shoots and roots produce cells for axis elongation. Above ground, some of these cells differentiate into leaves. The apical meristems also produce new meristems: both axillary and cambial meristems. Axillary meristems become apical meristems when they start to produce cells for the extension of a new axis. Cambial meristems are located between wood and bark (and cork cambium within the bark), and they produce cells for axis thickening. Thus, apical meristems (together with axillary meristems which turn into apical meristems) produce the expanding stature and increasingly complex branched structure of trees, and cambial meristems accommodate stem and branch thickening (e.g. Wilson 1984).

1.3.2 Carbon fixation and growth rates

Meristems use carbohydrates (i.e. carbon) to produce new cells. Carbon is supplied to the meristems through the process of photosynthesis. This process takes place in the leaves. Leaves use the energy from sunlight, carbon dioxide from the air, and water from the soil to make carbon. New carbon may be translocated through the phloem from one of the carbon sinks to the meristems (e.g. ray parenchyma, a carbon storage tissue in roots, branches, and stem, see Cannell & Dewar 1994). The carbon that arrives at the meristems may be used for growth.

The light environment of tropical rain forests is highly variable and trees respond to different light levels by changing their rate of photosynthesis. At higher light availability, they have higher photosynthetic rates, fix more carbon, and may use the increasing amount of fixed carbon for faster growth (e.g. Fetcher *et al.* 1994). With increasing light levels the apical meristems produce more leaves (Bentley 1979, Tinoco-Oranjuren & Vasquez-Yanes 1983, Langenheim *et al.* 1984, Meave del Castillo 1987, Bongers & Popma 1989), internodes (Sasaki & Mori 1981, King 1991c, King 1994), or shoots (Fisher 1986). These apical meristems also produce larger internodes and shoots, but not leaves (same references). Simultaneously, the cambial meristems may produce more rapid thickness growth (e.g. Turner 1989, Welden *et al.* 1991). The increase in (meristematic) growth with light availability results in increases in relative growth (or RGR, biomass increment/initial biomass ratio, for seedlings only, e.g. Augspurger 1984, Bongers *et al.* 1988a, Popma & Bongers 1988), increments in absolute height and diameter (for seedlings, e.g. Turner 1989, Van der Meer 1995; for saplings, e.g. King 1991c, Welden *et al.* 1991; for taller juveniles, e.g. Primack *et al.* 1985, Clark & Clark 1992), and total leaf area (for seedlings, e.g. Bongers *et al.* 1988a, Osunkoya *et al.* 1993; for saplings, e.g. Oberbauer *et al.* 1993, Cornelissen 1993).

1.3.3 Carbon allocation

However, the growth responses of trees to different light levels depend not only on photosynthesis and the level of carbon fixation. The allocation of carbon among the meristems (and the other carbon sinks, Cannell & Dewar 1994) may also change in response to different light levels. At the meristems, the allocation of carbon among different cell types may also change. These changes in carbon allocation as a result of light availability may affect tree development and morphology.

The carbon allocation in trees is often expressed as biomass allocation. Biomass allocation is usually assessed by harvesting plants and determining the masses of different parts (e.g. roots, shoots, leaves). For practical reasons seedlings were used in biomass allocation experiments, and above ground allocation was assessed for 1-2 m tall saplings only (King 1991c, 1994). Heavily shaded trees usually display greater biomass allocation to above ground parts, in particular to the leaves. This is expressed by their lower root/shoot ratios (root mass/shoot mass ratio), higher leaf weight ratio (LWR, leaf mass/total biomass ratio), and higher leaf area ratio (LAR, total leaf area/total biomass ratio). The shaded trees increase their light interception per carbon investment (for seedlings, e.g. Bongers *et al.* 1988a, for saplings, e.g. King 1991c, 1994, see also Givnish 1988). Thus, in general, tropical rain forest trees adjust their growth rates and carbon allocation in relation to the given level of light availability. In this way, they tune their development and morphology to ambient light levels. In this introduction, tree development and morphology, and their relation to light availability, are discussed from four perspectives: architectural tree models, leaf display, allometry, and mechanical design.

Table 1.1. Definitions of the above-ground components of individual plants in order of increasing size (partly adapted from Room et al. *1994). Underlined components receive major attention in this thesis.*

Component	Definition
Node	The most distal point of the junction between a stem and a leaf, just proximal to any subtended axillary bud(s) (Kurihara *et al.* 1978).
<u>Meristem</u>	A cell or group of cells, specialised for mitosis, initiating or at the apex of the shoot. An axillary meristem becomes an apical meristem as soon as it starts to produce a shoot.
Bud	An unextended, partly developed shoot with at its summit the apical meristem which produces it; an unexpanded metamer or group of metamers (Bell 1991).
Internode	A portion of stem between nodes, i.e. from immediately distal to the junction of a leaf with the stem to the same position with respect to the next most distal leaf. The basal internode of a branch starts at the node of the leaf from whose axil the branch grew.
<u>Metamer</u>	An internode and the leaf or leaves and the axillary bud(s) at its distal end, but not a shoot resulting from growth of axillary buds.
<u>Unit of extension</u>[1]	A morphologically discrete growth increment, the result of one episode of rhythmic growth by a sympodial unit, i.e. extension of the preformed contents of a previously dormant apical bud followed by growth of neoformed leaves (if any) and formation of a new, dormant apical bud (Hallé *et al.* 1978)
Shoot	A young stem which has grown from a single meristem and the leaves and buds which it carries; the young portion of a sympodial unit.
<u>Sympodial unit</u>[2]	The product of one meristem
Axis	A sequence of units of extension in the same general direction from one (monopodial) or more (sympodial) meristems
Branch	An axis other than the main stem plus any subordinate axes it bears.
Architectural unit	The complete set of axis types and their relative arrangements found in a species. It cannot be seen until an individual is old enough to have expressed its architectural model(s) in full (Barthélémy 1991).

1) Unit of extension instead of unit of growth, as the term <u>growth unit</u> is used as a general term for metamers and units of extension in this thesis.

2) Sympodial unit instead of module, as module is also used as a general term for different types of components (e.g. Bell 1991).

1.3.4 Architectural tree models

Architectural tree models are descriptions of qualitative changes in tree development. They provide a model of how the above-ground apical meristems produce plant components (see Table 1.1, and also White 1979, 1984, Barthélémy 1991, Bell 1991, Room *et al.* 1994), and how these plant components are arranged in space (Hallé & Oldeman 1970, Hallé *et al.* 1978). For tree species of tropical rain forests, a given model may describe early tree development, but not the development in older and larger trees (e.g. Edelin 1991). The development in the larger trees can be described as reiteration (Oldeman 1974, 1990) or metamorphosis (Edelin 1984) in some but not all cases. Reiteration and metamorphosis refer to development of architectural model-like branch structures at various locations in the crown. However, recent studies suggest that the development of tropical rain forest trees is too complex to be described by architectural tree models, reiteration and metamorphosis alone (e.g. Edelin 1984, 1991, Loubry 1994, Drénou 1994, Loup 1994).

Thus, for the smaller and younger trees of a given tree species at least, architectural tree models formalise the way trees produce their plant components at apical meristems (e.g. Barthélémy 1991). Trees of the same species grow in accordance with the same model in different light habitats, but exhibit different crown shape and leaf display (Fisher & Hibbs 1982, Borchert & Tomlinson 1984, Shukla & Ramakrishnan 1986). However, the same crown shape and leaf display may also arise in trees of different species which grow according to different models. Boojh & Ramakrishnan (1982) and Foresta (1983) found that early successional tree species tend to grow in accordance with models which are different from those for late successional tree species (but see Vester & Saldarriaga 1993). Oldeman & Van Dijk (1991) relate architectural tree models to different growth strategies with respect to light. However, they do not provide data which confirm that such a relationship actually exists. In fact, tree species that occur in contrasting light habitats (e.g. early versus late successional species) may grow in accordance with the same model (Ashton 1978, Tomlinson 1987). Thus, in general, trees do not change their architectural model in response to different light levels, and their growth responses are not very closely related to their architectural model.

1.3.5 Leaf display

Leaf display is needed to fix the carbon that can be used for growth at the meristems. Conversely, the leaves are produced by meristems, and leaf display depends on the growth rates and the allocation of carbon in response to the given light levels. Horn (1971) relates various aspects of leaf display to light availability in one coherent ecological theory. He presents two theoretical strategies of leaf display with respect to light availability: under low light levels, the optimal display of leaves is a single layer (mono-layer) of large leaves which do not shade one another. Self-shading would result in light levels that are below the photosynthetic light compensation point, and self-shaded leaves would be of more cost than benefit to the tree (see also Givnish 1988). The mono-layer leaf display, however, involves high costs to support a given amount of leaf area, as branches have to grow out horizontally to avoid self-shading of the leaves. Under high light levels, a diffuse distribution of small leaves over more than one layer (multi-layer) is more beneficial. The costs of supporting a given amount of total leaf area are relatively low, and the leaves in each layer receive enough light to be of benefit to the tree (above the light compensation point).

Horn's model may be applied for a comparison of the leaf display between individuals of the same species, and between species. Leopold (1971) and Borchert & Tomlinson (1984) argue that trees of the same species produce narrow crowns (with higher leaf packing) at high light availability, because this reduces the cost of leaf support. In contrast, these trees produce more planar crowns at low light availability, so as to avoid self-shading of the leaves (see Horns' predictions). They used either simulations (Leopold 1971) or compared forest trees (low light) with 'urban' trees (high light) outside their natural habitat (Borchert & Tomlinson 1984). They do not indicate whether such a response in leaf display is exhibited by trees that occur at different light levels in tropical rain forest. Between tree species, the early and late successional tree species in temperate forest display their leaves as predicted by Horn, but not in tropical rain forest (Bazzaz & Pickett 1980, Givnish 1984). Thus, there is little evidence that Horn's model applies to trees in tropical rain forests.

1.3.6 Allometry

Tree allometry refers to relations between different size variables within a tree. On the basis of harvest experiments, various variables of allometry were determined for seedlings and related to the light environment. In general, the heavily shaded seedlings produced a larger leaf area ratio, a higher specific leaf area (SLA, leaf area/leaf mass ratio), and a lower root/shoot ratio than seedlings at sites with higher illumination levels. This indicates that heavily shaded seedlings invest more in leaf area per unit carbon investment, and thus increase light interception at low light availability (e.g. Givnish 1988). These measures of allometry are often used as measures of carbon allocation between different plant parts (see also 1.3.3, carbon allocation).

Shukla & Ramakrishnan (1986) report on small saplings that change their crown shape in relation to light. They and others (Kohyama & Hotta 1990) found more columnar shapes in fast-growing and light demanding species, in contrast to the more planar shaped crown shapes of slower growing and more shade-tolerant species. King (1991a, 1996) found that overstorey species tend to have more columnar shaped crowns than understorey species. They argued that these allometries (crown length relative to width) may reflect an exploring strategy (columnar crown, more height gain) in open conditions, and an exploiting strategy (planar crown, more light interception) in more shaded sites. Within species, trees also produced more columnar shaped crowns at higher light availability (Fisher & Hibbs 1982, Borchert & Tomlinson 1984). In these latter studies, a comparison was made between trees in forest and open 'urban' conditions, but not between trees growing in different light conditions within tropical rain forest.

1.3.7 Mechanical design

So far the major focus has been on the growth pattern that results from the apical meristems above-ground. Clearly, these meristems accommodate the development and morphology of a tree. In general, they account for the increasing tree stature during ontogeny, and thus also for increasing self-loading (tree mass) and wind stress. The cambial meristems accommodate the girth increment of stem and branches. These girth increments increase self-loading stress, but also enable a tree carry its own increasing mass and to resist the increasing wind stress during ontogeny.

Trees carry their own mass and resist wind forces by virtue of an adequate mechanical design. Models were developed to quantify the mechanical design on the basis of size, allometry, and wood properties (e.g. McMahon 1973, King & Loucks 1978, Waller 1986, Holbrook & Putz 1989, Niklas 1992, 1994a, 1994b). In these models, the self-loading and wind stress increase with increasing overall tree stature, and the resistance against stress increases with stem and branch thickness. The mechanical design of trees may change with ontogeny, and may differ between species (e.g. Rich *et al.* 1986, O'Brien *et al.* 1995). The more shaded trees may invest more in increasing stature than in girth increment per carbon investment than trees which grow in the open (Holbrook & Putz 1989). As such, they may be able to compete for light with their neighbours, but this will be at the cost of mechanical safety.

1.4 Objectives

From the above, it appears that the functional relationships between tropical rain forest trees and their light environments are rather complex. Tropical rain forest trees respond to light availability by changing their morphology and development (growth rates, allocation, leaf display, allometry, and mechanical design), but not their 'qualitative' development as described in the architectural tree models. These changes in morphology and development are accommodated by changes in photosynthesis in response to different light levels. The photosynthetic rates determine the amount of carbon that is fixed, allocated to meristems, and used for growth at the meristems. This thesis does not directly address the photosynthesis, carbon allocation or meristem activity (in terms of cell production, and so forth), nor does it address the responses to different levels of light availability. Instead, the focus is on the consequences of these processes for tree development and morphology at different levels of light availability.

In the literature, individual studies usually include small sets of plant traits on morphology or development. Moreover, many changes in morphology and development in response to light availability are only assessed for the smaller individuals. For the larger individuals, only rough growth responses (diameter and height increments) are assessed in relation to light availability, but not, or rarely, the responses in leaf display, allometry, or mechanical design. In some cases, these latter responses are compared between taller trees in forest and open 'urban' sites, but not between trees growing under different light levels in the forest. Thus, for tropical rain forest trees, many facets of their morphology and development in relation to light availability remain unexplored. This is particularly true for trees older and larger than 2-m tall saplings.

There are three possible reasons for this lack of data on growth responses to light in these larger individuals. Firstly, these trees are too large for easy handling in controlled light experiments. Secondly, they may not respond as rapidly as tree seedlings (Zagt & Werger in press). Thirdly, because of their size they are difficult to approach for making field observations. In order to overcome these problems, long term studies are needed on large numbers of trees in their natural habitat. These trees have to be climbed in order to measure and monitor their morphology, development, and light environment, using the appropriate techniques (e.g. Moffet & Lowman 1995).

The central theme of this thesis is the morphology and development of trees in relation to a natural range of light availability in tropical rain forest. *Morphology* refers to plant traits at a given moment, i.e. tree size, tree mass, tree allometry, leaf display, mechanical design, and also the masses, sizes, and numbers of different components (Table 1.1), or other plant parts (e.g. roots, shoots, leaves). *Development* refers to the temporal changes in these morphological plant traits. Light availability, development, and morphology are investigated for trees of different size, ranging from small saplings to trees of adult stature. By putting trees in order of increasing size, an exploration is made of how morphology and development, as well as responses to light, change with ontogeny. *Ontogeny* refers here to the overall growth and development pattern during tree life, both for individual trees and, in more general, for a given tree species.

Thus, tree morphology and development are compared for trees that are exposed to different light levels. This refers to the spatial light variation of a coarse- grain environment. However, by investigating trees of increasing size, the data is interpreted as indicating changes in morphology and development with ontogeny. Given that light levels change with ontogeny, the data is used to interpret how trees develop in relation to different light levels during their life. This refers to the temporal light variation of a fine grain environment. In this thesis, the following two main questions are addressed:

1 How are tree development and morphology affected by light availability in tropical rain forest?
2 What are the ecological consequences of different traits of morphology and development for trees in tropical rain forest?

1.5 Study sites

Most of the field work for this study was carried out in French Guiana. This country in the north-east of South America covers an area of 83.000 km^2 and is situated on the Pre-Cambrian Guiana Shield (Lindeman & Mori 1989). About 98% of the area is covered by evergreen tropical rain forest (Groene 1989). Annual rainfall is usually between 3.000 and 4.000 mm, but may be lower than 2.000 mm in some parts of the South (De Granville 1982). Near the coast, rainfall is usually high throughout the year, but is less than 100 mm/month in September and October (long dry season) and, in some years, in March as well (short dry season).

Two biological stations were used for the field work. The 'Piste St. Elie' station (5° 14'N, 53° 03'W) of the O.R.S.T.O.M. de Cayenne is located 30 km from the coast, south of the town of Sinnamary. The area directly around the station is covered with undisturbed tropical rain forest, but most of the remaining area has been logged during the past 15 years. Annual rainfall is around 2.900 mm. Rainfall is usually less than 100 mm per month in September and October (dry season), and sometimes also in March (short dry season). The most dominant families of tree species in the forest are the Lecythidaceae, Caesalpiniaceae, Sapotaceae, Chrysobalanaceae, Burseraceae and Mimosaceae (Sabatier & Prévost 1989).

The biological station 'Les Nouragues' of the C.N.R.S. is located about 100 km from the coast, south of Cayenne (4° 05' N, 52° 40' W). The forest around the station has been free of human disturbance for at least two centuries, but it was inhabited by Nouragues Indians before the eighteenth century. Annual rain fall is around 3.000 mm. Rainfall is usually less than 100 mm/month in September and October (dry season), and sometimes in March as well (short dry season). This forest is dominated by the same families of tree species as the Piste forest (Sabatier & Prévost 1989). The area is covered by well-drained, clayey to sandy-clayey ferralitic soils on weathered granite parent material.

1.6 Study species

Two canopy tree species were selected for this study, namely *Dicorynia guianensis* Amshoff. (Caesalpiniaceae) and *Vouacapoua americana* Aubl. (Caesalpiniaceae, Figure 1.1). Both are common species in the forests of French Guiana, and are considered late successionals or shade-tolerant species (Schulz 1960). In Chapters 2 and 6, both species are compared with an early successional species, namely *Goupia glabra* Aubl. (Celastraceae, Figure 1.1). Trees of these three species are harvested for their timber in both French Guiana and surrounding countries.

1.7 Thesis outline

The work is presented as a series of independent studies (Chapters 2 to 6), and the major results are integrated and discussed in the synthesis (Chapter 7). In Chapter 2, the development and morphology

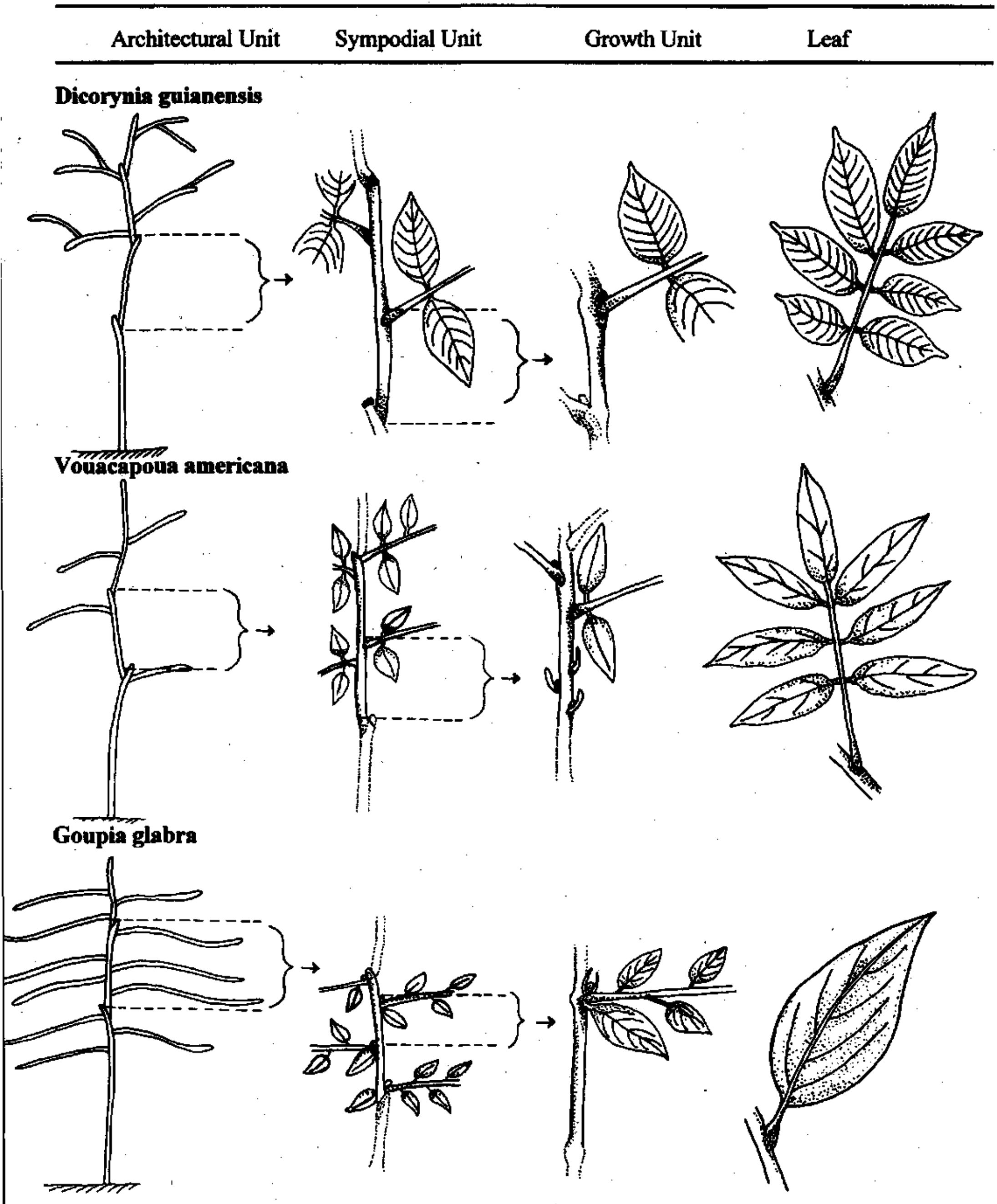


*Figure 1.1 Illustration of plant components of three tropical rain forest tree species (not in scale). *Growth Unit is metamer for* Dicorynia *and* Goupia, *and unit of extension for* Vouacapoua.

of 1 m tall saplings is compared between individuals in the forest (low-light levels) and in a clearing (high-light levels). The differences between forest and clearing are discussed in terms of strategies adapted to tolerate shade and to compete for light. In Chapter 3, the focus is on larger sized individuals. The development and morphology of 4-10 m tall trees are compared for trees growing in large gaps (high-light levels) and in closed forest (low-light levels). For these trees, the influence of their development on their morphology is addressed explicitly. Until this point the focus is on individuals of a given size class, and on their responses to contrasting light environments. In Chapter 4, morphology and development are investigated for trees of different sizes (0-40 m), occurring under a range of light levels in the forest. In this part of the study, the focus is on changes in morphology and development with ontogeny. The relative importance of light availability and height on ontogenetic changes in morphology and development are weighted. In Chapter 5, the individuals from Chapters 3 and 4 are used to compare height growth of trees in contrasting light environments (data from Chapter 3), and along a whole range of light levels (data from Chapter 4). Height growth is assessed from the extension growth of the leader shoot. Changes in height growth with ontogeny are related to tree height and light levels, and are also used to estimate the time trees spend on growing through successive height classes. In Chapter 6, the morphological changes with ontogeny are investigated, but not directly related to the light environment. Instead, the focus is on the ontogenetic changes in mechanical tree design, using two theoretical models. Finally, in Chapter 7, the results of these chapters are summarised, and compared with the literature. Similarities and differences between tree species of tropical rain forests, as well as between tropical and temperate tree species, are further discussed.

2

THE GROWTH HISTORY AND MORPHOLOGY OF SAPLINGS: FOREST UNDERSTOREY VERSUS CLEARING

with Annemarie Marttin, Toon Rijkers en Frans Bongers

Abstract

1. The morphology and modular structure of 1-m tall saplings were compared for two light environments, a tropical rain forest understorey and an adjacent clearing, in French Guiana. Three species were studied, the pioneer *Goupia glabra* and the shade-tolerants *Dicorynia guianensis* and *Vouacapoua americana*. Light was expected to limit sapling growth in the forest understorey, but not in the clearing. Growth histories of saplings were inferred from the modular structure of the stem, and were related to current sapling morphology.

2. Saplings in the clearing had greater root, shoot, and leaf dry weights, higher total leaf area, higher leaf weight ratio (LWR, leaf mass/plant mass ratio), lower specific leaf area (SLA, leaf area/leaf mass ratio), and they supported more and heavier leaves, than saplings in the forest. The leaf area ratio (LAR, leaf area/plant mass ratio) and root/shoot ratio did not differ between the two environments.

3. Forest - and clearing saplings of *Goupia* produced similar numbers of growth units to reach a given height. Forest saplings of this species produced fewer leaves than clearing saplings to reach the same height. In contrast, forest saplings of *Dicorynia* and *Vouacapoua* produced more (and shorter) growth units, and more leaves to reach a given height than clearing individuals. Thus, in the forest, *Dicorynia* and *Vouacapoua* individuals allocate more resources to leaves, but not *Goupia*.

4. Forest saplings grew slower in height than clearing saplings. In the forest, *Dicorynia* and *Vouacapoua* had reduced height growth due to the production of shorter growth units at a slower rate, whereas *Goupia* had reduced height growth due only to a slower production of units.

5. Forest saplings had a higher SLA than clearing saplings, but did not have a higher LAR than clearing saplings. This is because forest saplings were older, had shed far more leaves than the younger clearing saplings, and thus had a lower LAR than was expected.

2.1 Introduction

Trees in the tropical rain forest understorey live in an environment that is dominated by very low levels of light (e.g. Swaine & Lieberman 1987, Fetcher *et al.* 1994). Trees of the same species have higher growth rates in clearings (e.g. Augspurger 1984, Bongers & Popma 1988) because light levels do not limit growth in these open spots. Also, trees of different species may differ in their growth and morphology in these two light habitats (e.g. King 1991c).

Tree morphology can be expressed in terms of size (e.g. height, total leaf area), biomass distribution (e.g. root/shoot ratio, leaf weight ratio), and allometric relationships (e.g. leaf area ratio, specific leaf area). The relationships between these morphological characters and growth are two-fold: Firstly, the morphological characters affect the acquisition of the carbon that can be used for growth. However, growth responses of trees to light cannot be predicted from these characters, as they depend on complex interactions between various environmental factors and different plant traits (e.g. Bazzaz & Wayne 1994). These relationships fall beyond the scope of this chapter.

Secondly, morphological characters result from a particular growth history under given ambient conditions (e.g. Augspurger 1984, Popma & Bongers 1988). Trees can be monitored for their growth, and their growth can then be related to their newly established morphology. This method extends over years when it is applied to slow-growing trees in the forest understorey. A less time-consuming method has been explored by King (1991c, 1993, 1994). King inferred growth histories of trees from their modular structure. In this way, he was able to relate tree growth to post-growth morphology by taking measurements at one point in time. This latter approach is used in this chapter.

The modular structure of a tree can be expressed by the sizes or numbers of plant components. Examples of components are leaves, internodes, metamers, growth units, sympodial units, and architectural models (Table 1.1, see also Hallé *et al.* 1978, White 1979, Barthélémy 1991, Bell 1991, Room *et al.* 1994). The successive production and extension of plant components is reflected by the sequences of these components, or scars left by lost components, along the stem. This approach has been used to infer the growth histories of trees in relation to light environments in the past (King 1993).

In this chapter, the morphology and modular structure of saplings (approximately 1 m tall) are described for three tree species in French Guiana. Saplings were compared between two light environments, forest understorey and clearing. Levels of available light were measured per environment. Growth histories of saplings were inferred from the modular structure of the stem. The ecological significance of the sapling growth and - morphology in these two habitats is discussed.

2.2 Methods

2.2.1 Site and species

The study was carried out at the research station 'La Piste St. Elie', (5 14'N, 53 03'W) of the O.R.S.T.O.M. (Cayenne), French Guiana. The three study tree species were *Goupia glabra* Aubl. (Celastraceae), *Dicorynia guianensis* Amshoff. (Caesalpiniaceae), and *Vouacapoua americana* Aubl. (Caesalpiniaceae). For site and species information, see Chapter 1. Henceforth, the species are referred to by their generic names only.

2.2.2 Selection of individuals

Fifteen saplings were randomly selected per species in the rain forest understorey, as well as on an adjacent 3-yr old clearing. Saplings were selected for this study on the basis of their height (115-130 cm). This height was measured along the stem, even when the stem was curved along its length.

2.2.3 Light availability

Light levels over saplings were compared between the two environments, as they were expected to have affected the modular structure and morphologies of saplings. Therefore, hemispherical photographs were taken over the apices of selected saplings. For each hemispherical photograph, the camera was mounted on a tripod just over the apex of a selected sapling, levelled horizontally, and with the top directed to the north. The black and white photographs were scanned and digitised with DeskScann II and analysed with PPFDCALC-2 (Ter Steege 1992). The canopy openness, direct photosynthetic photon flux density (direct PPFD) on a cloudless day, and diffuse PPFD were estimated for each selected sapling. The levels of canopy openness, direct PPFD, and diffuse PPFD were compared between the two environments, and between the study species (two-way ANOVA, Tukey HSD for pair-wise comparisons).

2.2.4 Modular structure

The modular structure of saplings was determined by measurements on components along the stem. For *Goupia* and *Dicorynia*, the metamer was chosen as the focal component (see also Figure 1.1). For *Goupia*, the metamer consists of an internode, the node supported by that internode, a simple leaf and a bud which directly develops into a horizontal branch (Edelin 1991). For *Dicorynia*, it consists of an internode, the node supported by that internode, a compound leaf, and a bud which normally remains dormant. For *Vouacapoua*, two distinct types of metamers exist, one with a (normally) dormant bud and a scale leaf, and one with a (normally) dormant bud and a photosynthetic (compound) leaf (e.g. Loubry 1994). Therefore, for this latter species, the unit of extension (after Hallé & Martin 1968, Hallé *et al.* 1978, Bell 1991) was chosen as the focal component. A unit of extension develops after flushing of a bud and, for *Vouacapoua*, it consists of a number of both types of metamers. Both *Dicorynia* and *Goupia* either did not grow by units of extension, or did not form obvious morphological markers by which units of extension could be delimited. As metamers in *Dicorynia* and *Goupia* and units of extension in *Vouacapoua* are the smallest repetitive woody units produced by the apical meristems, they are further referred to by the same term, the *growth unit* (GU). This contrasts with other researchers, who used the term *growth unit* as a synonym of the unit of extension (Barthélémy 1991, amongst others).

Stems were marked at 65, 90 and 115 cm above-ground to indicate three height ranges (from 40 to 65 cm, 65 to 90 cm, and 90 to 115 cm) which represent successive steps in sapling growth. Height ranges were measured along the stem, even when the stem was curved. For each sapling, one height range was selected at random for further study. The growth units with their bases within the selected height ranges were counted (N_1) and were measured for their length using specific morphological markers (as mentioned before). For *Vouacapoua*, leaves and leaf scars were counted for each of these growth units. For *Dicorynia* and *Goupia*, the number of growth units per height range is equal to either the number or leaves and leaf scars (*Dicorynia*) or the number of branches and branch scars (*Goupia*).

These counts were made to assess the number of leaves or branches that saplings had to produce to grow through the height ranges.

The mean GU length and the number of produced leaves (*Dicorynia* and *Vouacapoua*) or branches (*Goupia*) were compared between the three height ranges and between the two environments (two-way ANOVA, and Tukey-HSD test for paired comparisons). A comparison between species was not made, as growth units differed between species. For the statistical analysis, GU length was log transformed and count data were root transformed as to equalise variances within different groups.

2.2.5 Morphology

Plant height (at apex) and diameter (at 10 cm) were measured, and the number of leaves was counted per plant. Plants were harvested and divided into root, leaf and stem/branch fractions. For determination of the leaf surface variables, all leaves (*Dicorynia* and *Vouacapoua*), or a sample of 40 leaves (*Goupia*), of each individual plant were spread out on a white paper, and black and white photographs were made of them. These photographs were scanned to calculate the average leaf size (cm^2), and average leaflet size (cm^2, only for *Dicorynia* and *Vouacapoua*), using a Digital Image Analysis System (Eijkelkamp 1991). Total leaf area was then calculated as average leaf size times the number of leaves per sapling. Roots, stems and leaves were oven dried at 70° C, and weighed separately. From this the following characters were derived: total dry weight (g), leaf dry weight (g), shoot dry weight (g), root dry weight (g), root/shoot ratio (g/g), leaf area ratio (LAR, total leaf area/total plant dry weight in m^2g^{-1}), leaf weight ratio (LWR, leaf dry weight/total dry weight in g/g), specific leaf area (SLA, total leaf area/leaf dry weight in m^2g^{-1}), and leaf weight (g). The morphological characters were compared between the two environments, and between the species (two-way ANOVA, and Tukey-HSD for comparison of pairs). For LAR, LWR, SLA, leaf size, and total leaf area, log-transformed data were used in the analysis as to equalise the variances among different groups.

2.3 Results

2.3.1 Light

The incident light level and crown cover over individual saplings differed significantly between environments and between species (Table 2.1). As expected, individuals in the forest understorey received less light than in the clearing, although the variation was quite large among individuals. In the forest, canopy openness and incident light levels did not differ between species. In the clearing, however, saplings of *Goupia* and *Dicorynia* received more light than saplings of *Vouacapoua*. Apparently, the clearing saplings of *Vouacapoua* were overgrown to a higher extent than those of both other species. Canopy openness and diffuse PPFD showed a larger variation in the forest understorey than in the clearing. This is probably because the micro-sites of forest individuals varied from closed forest to canopy gaps, whereas the micro-sites of clearing individuals were always relatively open. Conversely, direct PPFD showed greater variation in the clearing than in the forest understorey. This can only be explained by the fact that the fortuitous position of the large canopy openings over clearing individuals determined whether or not direct sunlight was intercepted before it reached the sapling.

Table 2.1. Light conditions over saplings of the tree species Dicorynia guianensis, Goupia glabra *and* Vouacapoua americana *in two environments in French Guiana, i.e. a tropical rain forest and a clearing. Light values (and standard deviations) are given as percentages from the light values in the open sky.*

Light factor	Site	*Goupia*	*Dicorynia*	*Vouacapoua*	N
diffuse	forest	7 ± 13 a	7 ± 12 a	9 ± 8 a	15
PPFD (%)	clearing	45 ± 4 c	43 ± 3 c	27 ± 6 b	15
direct	forest	14 ± 9 a	8 ± 5 a	13 ± 9 a	15
PPFD (%)	clearing	67 ± 16 c	64 ± 20 c	42 ± 15 b	15
canopy	forest	12 ± 14 a	7 ± 16 a	10 ± 12 a	15
openness(%)	clearing	57 ± 6 c	53 ± 4 c	36 ± 7 b	15

-Differences between environments and species were tested (two-way ANOVA). Significant differences ($p<0.05$) between species and sites are indicated by different letters (Tukey-HSD, $P<0.05$).
-PPFD stands for photosynthetic photon flux density.

2.3.2 Modular structure

The influence of the environment on modular characters differed between species (Figure 2.1). For *Dicorynia* and *Vouacapoua*, forest saplings produced shorter growth units, and thus had to produce more growth units to grow through a height range than clearing saplings. In both species, this was only

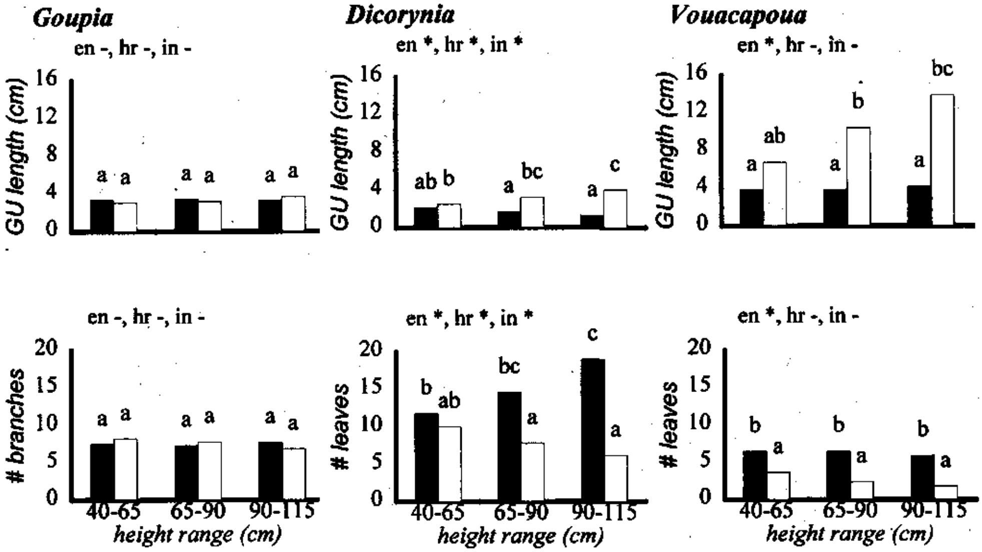


Figure 2.1. Modular characters for saplings of the tree species Goupia glabra, Dicorynia guianensis *and* Vouacapoua americana *in two environments in French Guiana, i.e. a tropical rain forest (black bars) and a clearing (white bars). Mean growth unit length and mean number of branches or leaves per height range are given (N=5). Significant relationships of the environment (en), height range (hr), and interaction term (in) with the modular character are indicated by an asterix *, and pair-wise differences are indicated with different letters (Tukey-HSD test).*

Table 2.2. Morphological traits for saplings of three tree species in two environments in French Guiana, i.e. a tropical rain forest and clearing. Values are means of 15 saplings.

Site	Trait	*Goupia*	*Dicorynia*	*Vouacapoua*	Significant differences		
<u>Size, biomass and biomass distribution</u>					<u>sp</u>	<u>en</u>	<u>in</u>
forest	diameter	0.71 a	0.95 b	1.16 c	*	*	-
clearing		1.00 bc	1.31 c	1.32 c			
forest	total dry weight	35.8 a	46.7 a	80.7 b	*	*	*
clearing		85.1 b	123.3 c	13.6 bc			
forest	leaf dry weight	7.8 ab	7.6 a	9.1 ab	*	*	*
clearing		29.3 cd	35.0 d	19.0 bc			
forest	shoot dry weight	21.1 a	29.0 a	56.6 b	*	*	-
clearing		34.4 a	60.8 bc	78.6 c			
forest	root dry weight	6.9 a	10.1 a	15.0 ab	-	*	*
clearing		21.4 bc	27.5 c	16.0 ab			
forest	root/shoot ratio	0.33	0.35	0.26	-	-	-
clearing		0.62	0.45	0.20			
forest	leaf weight ratio	0.22 bc	0.16 a	0.11 a	*	*	-
clearing		0.34 d	0.28 c	0.17 a			
<u>Allometry</u>							
forest	leaf area ratio	65.10^{-4}c	40.10^{-4}b	22.10^{-4}a	*	-	-
clearing		64.10^{-4}c	33.10^{-4}ab	24.10^{-4}ab			
forest	specific leaf area	30.10^{-3}e	24.10^{-3}d	19.10^{-3}c	*	*	*
clearing		19.10^{-3}bc	12.10^{-3}a	14.10^{-3}ab			
<u>Leaf display</u>							
forest	total leaf area	23.10^{2}ab	19.10^{2}a	17.10^{2}a	*	*	-
clearing		54.10^{2}c	40.10^{2}bc	27.10^{2}a			
forest	number of leaves	155 c	7 a	7 a	*	*	*
clearing		301 d	16 b	13 b			
forest	leaf size	15 a	265 b	249 b	*	-	-
clearing		18 a	252 b	209 b			
forest	leaf weight	0.05 a	1.09 c	1.33 c	*	*	*
clearing		0.10 b	2.19 d	1.46 c			

-Effects of species (sp), environment (en), and interactions on traits were tested for significance (two-way ANOVA); Significant effects ($p<0.05$) were indicated by '*' and significant differences among groups by different letters (Tukey-HSD, $p<0.05$); Diameter is given in cm, weights in grams, biomass distribution in g/g, allometry in m^2/g, areas in cm^2

significant in the upper two height ranges. For *Dicorynia*, this means that forest saplings produced more leaves as they grew through these height ranges than clearing saplings. The same is true for *Vouacapoua*, as appeared from counts of leaves and leaf scars along height ranges (Sterck, non published data). For *Goupia*, GU length and the number of branches produced did not differ between height ranges or environments (Figure 2.1). However, branches of clearing individuals were much longer and supported more leaves than branches of forest individuals (Sterck, unpublished data). Thus, in contrast to both other species, the clearing saplings of *Goupia* produced more leaves per height range than forest saplings.

2.3.3 Morphology

Sapling morphology differed between species and environments (Table 2.2). The low total dry weight for *Goupia* compared with *Dicorynia* and *Vouacapoua* was mainly due to the low shoot dry weight, although *Goupia* had many horizontal branches whereas both other species had not. *Goupia* had highest, *Dicorynia* intermediate, and *Vouacapoua* lowest total leaf area, LAR, and LWR. *Goupia* greatly contrasted with both *Dicorynia* and *Vouacapoua* in leaf display, as it supported more and smaller (simple) leaves along the lateral branches (data not shown) while both other species supported relatively low numbers of large sized (compound) leaves. The species did not differ in root/shoot ratio.

Where the influence of light environment on modular characters differed between species, the influence of the light environment on morphological characters was similar for the three species (Table 2.2). Species showed similar changes in biomass, biomass distribution, allometric relationships, and leaf display with respect to the environment. The saplings and their parts, i.e. roots, shoots and leaves, all weighted more in the clearing than in the forest understorey, although this was not significant for shoots in saplings of *Goupia*, nor for leaves or roots in saplings of *Vouacapoua*. The higher mass of shoots in the clearing was due to the greater diameter for clearing saplings. In the clearing, saplings had a higher total leaf area, a higher LWR (not significant for *Vouacapoua*), a lower SLA, and they supported more and heavier (only for *Goupia* and *Dicorynia*) leaves than saplings in the forest. LAR and root/shoot ratio did not differ between the two environments.

2.4 Discussion

2.4.1 Light environments

Light was expected to limit sapling growth in the forest, but not in the clearing. But what evidence is there for this given the light measurements? Firstly, saplings were on average exposed to diffuse light levels of 7-9% in the forest, and to levels of 27-45% in the clearing. Since understorey light levels of 1.5 % correspond with a PPFD of around 10 mmol m^{-2}s^{-1} in a tropical rain forest understorey (Chazdon & Fetcher 1984, Fetcher *et al.* 1994), the forest saplings are expected to have received between 46 and 60 mmol m^{-2}s^{-1} diffuse PPFD, and the clearing saplings between 180 and 300 m^{-2}s^{-1} diffuse PPFD. It has been shown that photosynthetic rates increase steeply at a PPFD of 46-60 mmol m^{-2}s^{-1}, and that they are at maximum level at a PPFD of 180-300 mmol m^{-2}s^{-1}, for the three study species (Rijkers, unpublished data) as well as for other tropical tree species (e.g. Fetcher *et al.* 1987).

Secondly, saplings were exposed to direct light levels of 7-12% in the forest, and to levels of 36-57% in the clearing. Direct site factors refer to the time periods during which saplings are exposed to sunbeams that penetrate canopy holes and shine directly on them. In these periods, light does generally not limit growth (e.g. Chazdon & Fetcher 1984, Chazdon 1988), although it may take leaves tens of minutes to reach maximum photosynthesis during high light periods (Fetcher *et al.* 1987, Poorter & Oberbauer 1993, amongst others). Direct site factors indicate that forest individuals are exposed to these high light levels for a shorter time than clearing individuals. Moreover, forest saplings may profit less from the relatively short periods of direct light, as it takes leaves several minutes to reach maximum photosynthetic rates. Thus, both the diffuse and direct light factor give evidence that forest saplings were exposed to more light-stressed conditions than clearing saplings.

2.4.2 Growth histories, allocation and height growth

Growth histories differed between the shade tolerant species (*Dicorynia* and *Vouacapoua*) and the pioneer species (*Goupia*, e.g. Schulz 1960). Forest saplings of *Dicorynia* and *Vouacapoua* produced more (and shorter) growth units, and more leaves, to grow through the successive height ranges than clearing saplings. In contrast, forest saplings of *Goupia* produced similar numbers of growth units (of the same length), and less leaves, to grow through the successive height ranges than clearing saplings. These results are consistent with King (1991c). King found that saplings of shade-tolerant species allocated more organic matter to leaves when exposed to light-suppressed conditions, whereas he did not observe this pattern in saplings of pioneer species. The saplings of shade-tolerant species increase their light interception in light suppressed conditions, lower their whole plant compensation point, and thus increase their ability to survive in the shade. In contrast, saplings of pioneer species seem to be constrained to allocate a given fraction of fixed carbon to stem growth. As they cannot increase their amount of light interception in light suppressed conditions, they may have a lower capacity to survive in the shade (see also Givnish 1988).

Each species produced its growth units faster in the clearing than in the forest (Sterck, unpublished data). Thus, all three species had reduced height growth in the forest. The shade-tolerant species *Dicorynia* and *Vouacapoua* had reduced investments by producing shorter growth units *and* by a slower production rate of these units, whereas the pioneer species *Goupia* had reduced investments by a slower production rate only. Because forest and clearing saplings had a similar height, it follows that forest individuals were older than the clearing individuals for each of the study species.

2.4.3 Growth history and morphology

The influence of light environments on the morphology and growth of tropical rain forest trees has been studied for seedlings (e.g. Augspurger 1984, Bongers *et al.* 1988a, Popma & Bongers 1988, Ter Steege *et al.* 1994) and for saplings (Kohyama 1991, King 1991c, 1994). While the studies on seedlings used harvest experiments in order to determine relative growth rates, biomass distributions, and allometric relationships (e.g. LWR, LAR), the studies on saplings were based on non-destructive measurements of growth (height gain or diameter extension) and size characters (e.g. total leaf area). Where biomass distributions and allometric relationships were calculated for saplings (King 1991c, 1994), they only referred to above-ground plant parts and neglected the roots. In the present study, the morphological characters of saplings were based on harvests of whole plants (shoots, leaves, and roots) and, thus, the calculated biomass distributions and allometric relationships included both above and below ground plant parts.

Plants with a typical shade plant morphology have higher SLA, higher LAR, and lower root/shoot ratio, than plants with a typical sun plant morphology. A shade plant morphology permits a plant to grow more efficiently under light-stressed conditions (Givnish 1988), because similar biomass investments would result in higher amounts of light interception. As expected, forest saplings had a higher SLA than clearing saplings. However, forest saplings did not differ from clearing saplings in their root/shoot ratio or LAR. This contrasts with studies on tree seedlings (e.g. Augspurger 1984, Popma & Bongers 1988). The root/shoot ratio is not further discussed here because soil properties were not controlled nor investigated. The lack of differences in LAR between clearing and forest saplings is further discussed below.

LAR is the net result of the production of new parts (roots, shoots, leaves) minus losses of older parts over the life of a plant. While shoots and roots may be permanent parts of a tree, individual leaves are transient. Consequently, leaf losses are expected to be relatively greater than root or shoot losses. If the production and losses of plant parts continue over time, older individuals are expected to have a lower LAR than younger individuals. This explains why the older forest saplings had a LAR similar to that of the younger clearing saplings. In forest saplings of *Dicorynia* and *Vouacapoua*, the higher investments in leaves were compensated by higher numbers of leaves that were shed already. In contrast, the number of produced and shed leaves was not assessed in saplings of *Goupia*. Thus, at least for *Dicorynia* and *Vouacapoua*, forest and clearing saplings grew as shade- and sun-plants, but this was not expressed in LAR due to the age difference.

It can be concluded that modular and morphological characters provide supplementary information about the functioning of trees in their habitat. In part of this discussion, however, reference was made to the production rate of growth units. Thus, for good interpretations of growth histories on the basis of modular and morphological characters, accompanying monitoring studies supply significant information. Monitoring studies on both morphological and modular characters are particularly relevant to the understanding of the functioning of trees in their habitat.

3

CROWN DEVELOPMENT IN GAPS AND UNDERSTOREY

Abstract

1. Crown development was monitored for juvenile trees (4-10 m) of the canopy tree species *Dicorynia guianensis* and *Vouacapoua americana* in a tropical rain forest in French Guiana. Crown development was compared between trees in canopy gaps (high light) and forest understorey (low light), and was expressed in terms of component traits (production rate, size, and structure of different plant components) and crown traits (crown characters and growth).

2. Gap individuals developed their crowns more extensively than understorey individuals, both in terms of crown and component traits. (1) *Crown traits*: Gap individuals produced more branch length, more leader length, and they produced their leaves further apart from each other. At the end of the experiment, they had a larger total leaf area, a larger LAI, and a larger crown cover. In gap individuals, the leader grew more in extension than other axes in the crown. In contrast, in understorey individuals, the leader and the other axes grew a similar amount in extension. (2) *Component traits*: Gap individuals produced more sympodial units (by branching more frequently), more growth units, and more leaves. They also produced longer growth units, but their leaves were neither larger nor smaller. In *Vouacapoua*, gap individuals produced and lost more leaves per growth unit. In *Dicorynia*, trees produced one leaf per growth unit, and gap and understorey individuals dropped a similar number of leaves per growth unit.

3. Path-analysis was used to show the influence of the light environment (gap versus understorey) on crown traits through the influence of the light environment on different component traits. As such, it revealed that gap individuals increased their total leaf area, LAI, and branch length mainly by producing more growth units (which resulted from an increase in branching frequency). For *Vouacapoua*, gap individuals increased their leader growth mainly by increasing their growth unit production rate. They also spaced their leaves further apart by producing longer growth units. Gap individuals of *Dicorynia* also tended to produce longer leaders and to space their leaves further apart, but this was not significant.

4. The ecological consequences of differential crown development in gaps versus understorey individuals is discussed and compared with other tree species, both in tropical rain forest as well as in temperate forest.

3.1 Introduction

Juvenile tropical rain forest trees grow in an environment that is dominated by low light levels. Temporarily, juveniles may occur in canopy gaps, where they are exposed to higher light levels. The crown development in juveniles varies with light, but factual evidence for this is mainly restricted to seedlings (e.g. Augspurger 1984, Bongers & Popma 1988) and 1-2 m tall saplings (e.g. Shukla & Ramakrishnan 1986, Kohyama & Hotta 1990, King 1991c, 1994). Taller juveniles are hard to study with respect to crown development because their structural complexity and large stature complicate measurements.

Crown development in juveniles may be described by one of 23 architectural models (Hallé & Oldeman 1970, Hallé *et al.* 1978), or by a combination of these models (Borchert & Tomlinson 1984, Edelin 1991). Each of the models describes a particular developmental sequence, and defines development by a set of growth rules for the production and the spatial arrangement of different components (Table 1.1, Bell 1991, Barthélémy 1991, Room *et al.* 1994, White 1979) in the trunk (monopodial or sympodial, and continuous or rhythmic growth), and in branches (monopodial or sympodial, orthotropic or plagiotropic) (Hallé *et al.* 1978). Thus, the architectural models indicate how different components contribute to crown development, and define limits within which crown development may vary (e.g. Hallé *et al.* 1978).

Because crown growth, crown shape, and leaf display are highly variable within architectural models, these models are of limited value for explaining the functioning of juvenile trees in a variable light environment (Fisher & Hibbs 1982). Within a given model, trees produce components at different rates and of different sizes in contrasting light environments (for shoots e.g. Fisher & Honda 1979, Borchert & Tomlinson 1984, Fisher 1986, for internodes e.g. Kohyama & Hotta 1990, King 1991c, for leaves e.g. Shukla & Ramakrishnan 1984, Bongers & Popma 1989). This may lead to differences in ecologically significant crown characters (e.g. total leaf area, leaf area index) and growth (e.g. Borchert & Tomlinson 1984, Fisher & Hibbs 1982, Canham 1988).

In this chapter, crown development is described for juvenile trees (4-10 m) of two canopy tree species in a tropical rain forest in French Guiana. Crown development was expressed by the production rates and sizes of different components of these juveniles in two contrasting light environments: canopy gap versus forest understorey. The objectives were, (1), to compare crown development between these two light environments and, (2), to relate the production rates and sizes of different components to crown characters and growth. In the discussion, the ecological significance of differential crown development in gap versus understorey is evaluated. Changes in crown development with ontogeny are addressed in Chapter 4.

3.2 Methods

3.2.1 Site and species

The study was carried out at the research station 'La Piste St. Elie', (5 14'N, 53 03'W) of O.R.S.T.O.M. (Cayenne), French Guiana. Two canopy tree species were selected for study, namely *Dicorynia guianensis* Amshoff. (Caesalpiniaceae) and *Vouacapoua americana* Aubl. (Caesalpiniaceae). For information about site and species, see Chapter 1. Henceforth, the species are referred to by generic names only.

3.2.2 Selection of individuals

Juveniles were inventoried in the understorey and in treefall gaps in November 1991. Gaps were large (>200 m^2 *sensu* Brokaw 1982) and fresh (<3 months). For each species, five individuals were selected in the understorey (understorey individuals), and five individuals of similar height were selected in gaps (gap individuals). Understorey and gap individuals were matched as to differ no more than 20 % in height at the start of the experiment. Height ranged from 4 to 10 m, except for one pair of *Vouacapoua* (15-18 m).

3.2.3 Light measurements

The light environment was characterised for each individual using two methods. Visual estimates of light were made on an annual basis, using the Crown Position Index (Table 3.1). At the end of the experiment, hemispherical photographs were made over the individuals in order to calculate canopy openness (Ter Steege 1992).

Table 3.1. Crown position index values and definitions (Adapted from Clark & Clark 1992).

Index value	Definition
5	Crown completely exposed (to vertical light and to lateral light within the 90° inverted cone encompassing the crown).
4	Full overhead light (>90% of the vertical projection of the crown exposed to vertical light; lateral light blocked within some or all of the 90° inverted cone encompassing the crown).
3	Some overhead light (10-90% of the vertical projection of the crown exposed to vertical light).
2.5	High lateral light
2.0	Medium lateral light
1.5	Low lateral light
1	No direct light (crown not lit directly either vertically or laterally).

3.2.4 Crown development

In November 1991, trees were coded and drawn to scale. Neighbouring trees were climbed using spikes or alpinist ropes in order to tag and code all branches and their apical meristems, and to count the number of apical meristems. For individuals taller than 7 m, an at random sample of 5 to 10 branches plus their apical meristems, and the potential leader branch(es) and their apical meristems, were tagged and coded. The leader was defined as the sequence of growth units responsible for the height growth between 1991 and 1994 (potential prolongation of the stem), and equivalent sequences of growth units at other crown locations are further referred to as axes. In November 1994, trees were climbed again to measure the production, the sizes of the components that were produced during three years (1991-1994).

The components that contribute to the crown development of juveniles are meristems, leaves, metamers, units of extension, and sympodial units. The juvenile tree as a whole is considered equivalent to the architectural unit (Table 1.1, Figure 1.1). For *Vouacapoua*, metamers were not considered because these differ structurally, i.e. metamers at the basis of the unit of extension always have scale leaves, while those at the distal end have compound, and photosynthetically active, leaves. Metamers were thus used as morphological markers to distinguish between units of extension. For *Dicorynia*, metamers are structurally equivalent, i.e. each of them consists of a compound, and photosynthetically active, leaf. Therefore, its units of extension cannot always be distinguished unambiguously (but see Drénou 1994). As units of extension in *Vouacapoua* and metamers in *Dicorynia* are the smallest repetitive woody units produced by the meristems, they are further referred to by the same term: growth unit (or GU).

3.2.4.1 component traits

The term 'component traits' is further used to refer to the production rates and sizes of components (Table 1.1). The production of different components was assessed by counting leaves, leaf scars, growth units, and sympodial units that were produced during a 3-yr period (1991-1994). Leaf production is equal to the sum of leaves plus leaf scars (for *Vouacapoua*, only the large scars which referred to the loss of a compound leaf). The leaves that were still present since the start of the experiment were counted as well. GU production was measured for the whole crown, as well as for the leader and other axes and branches separately. Sympodial unit production is by definition equal to apical meristem production, and is similar to the rate of branching. It was not determined in its narrow sense, but was based on counts of the apical meristems on top of leaf supporting growth units at the end of the experiment. Thus, it is the sum of sympodial units that remained active since the start of experiment, plus the sympodial units that were produced during the 3-yr experiment (branching rate), minus the sympodial units that died during the same period (loss rate).

Sizes and other traits were determined for a sample of 20 leaves, and for the growth units that were produced during the 3-yr period (1991-1994). Similar traits were not measured for sympodial units, because the majority of sympodial units had a living apical meristem and may thus change in size and other traits after the experiment.

Leaves: For each leaf sample, leaf surfaces were measured using DIAS (Eijkelkamp 1991). Mean leaf size (cm^2) was obtained by averaging leaf surfaces. Leaves were oven dried at 70° C for 48 hours and weighed (g). The specific leaf area (SLA) was calculated as the ratio of mean leaf size/mean leaf dry weight (cm^2/g).

Growth units: Lengths of growth units were measured with a folding ruler and mean GU length was calculated from these values. The leaf production per GU was calculated as the (total) leaf production divided by (total) GU production. For *Dicorynia*, this is 1 by definition. The number of fallen leaves per GU was calculated as the number of leaf scars divided by the GU production.

Growth units along leader: GU production was determined by counting the growth units along the leader. Mean GU length was obtained by averaging the lengths of the growth units along the leader.

3.2.4.2 Crown traits

Crown traits refer to crown growth between 1991-1994, and to the crown characters in 1994. The three measures of crown growth were calculated as follows:

leader growth = mean GU length x GU production (both along leader) (1)
axis growth = mean GU length x GU production (per axis) (2)
branch growth = mean GU length x GU production (per branch) (3)
total branch growth = branch growth x no. of branches (4)

Leader growth is presented as a crown trait because it enables the crown (and whole tree) to achieve height gain. For the sake of comparison, length increments were calculated for individual axes in the same way. Branches are the structures that are produced by apical meristems after 1991. Unlike axes, branches may be branched (see Table 1.1). Total branch growth is the summed length of all the produced growth units.

Four crown characters were determined. Crown cover was based on measurements of the longest crown width D_1 and the crown width D_2 perpendicular to D_1 as measured with a folding ruler.

crown cover = 0.25 x D_1 x D_2 x π (5)
total leaf area = mean leaf size x number of supported leaves (6)
leaf area index (LAI)= total leaf area/crown cover (7)
leaf spacing = mean GU length (*Dicorynia*) (8a)
= total branch growth/leaf production (*Vouacapoua*) (8b)

3.2.5 Hypotheses and statistical analyses

Crown development was compared between understorey and gap individuals, on the basis of the following hypothesis:

H_0: component traits and crown traits do not differ between gap and understorey.
H_1 : As crown development is less limited by light in gaps, gap individuals produce more and larger components (component traits), and have faster expanding and larger crowns (crown traits), than understorey individuals.

Understorey and gap individuals were compared using the Wilcoxon-matched pair test (one-tailed). Because 5 matched pairs were used per species, the individuals of each pair had to differ in the same direction (conform H_1) in order to obtain a significant result ($P<0.05$, Sokal & Rohlf 1981).

Within individuals, leader development was compared with axis development on the basis of the following hypothesis:

H_0: Leader growth does not differ from axis growth.
H_1: The leader grows more in extension than an individual axis.

The comparison was made for gap and understorey individuals separately. The Wilcoxon-matched pair test was used to test for differences in leader growth, mean GU length (along the leader), and GU production (along the leader), by matching the leader to an average axis. For the average axis, values were obtained by averaging the development variables of selected axes. Because the sample size was 5, significant results were only obtained if each leader differed from the average axis in the same direction (conform H_1, see above).

In fact, the crown traits integrate different component traits. Path-analyses were used to quantify the effects of different component traits (predictors) on crown traits (criterion variable, e.g. Wright 1934, Sokal & Rohlf 1981, Kingsolver & Schemske 1991, and see Figure 3.1). In path-analysis, the path-diagrams formalise the hypothesised direct and indirect effects (respectively causal and non-causal effects) of predictors on a criterion variable. The direct effects of a predictor is indicated by a path-coefficient (or standard partial regression coefficient), and an arrow which indicates the direction of the causal connection between predictor and criterion variable. The indirect effect occurs when the given predictor is correlated with another predictor which has a direct effect on the criterion variable. It is calculated as the correlation coefficient times the path-coefficient for the direct effect of the correlated predictor. Thus, path-analysis indicates the change in the criterion variable (expressed in

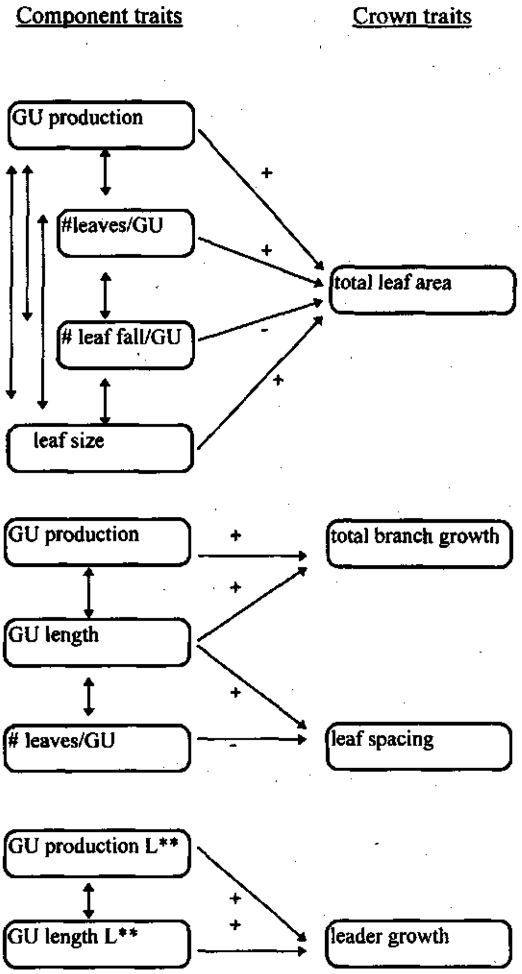


Figure 3.1 Hypotheses for the influence of component traits on crown traits, presented as path-models. Single headed arrows refer to the direct effects of different component traits, and the signs refer to the expected direction of the effect, either positive (+) or negative (-). For Dicorynia*, the effects of leaf production per GU (# leaves/GU) are excluded. Double headed arrows refer to correlations among component traits. L refers to traits of the leader (for further explanation, see text).*

units standard deviation) as a result of a change of one unit standard deviation in each of its predictors, both direct and indirect (for calculations of direct and indirect effects, see Sokal & Rohlf 1981).

For the path-analyses of this study, it is hypothesised that component traits affect crown traits as follows: Increases in GU production, leaf production per GU (#leaves/GU), leaf size, and a decrease in the leaf fall per GU (#leaf fall/GU), will cause an increase in the total leaf area (Figure 3.1). An increase in the GU length and a decrease in the leaf production per GU cause an increase in leaf spacing, but not for *Dicorynia* because its distance between leaves is equal to its GU length by definition. Increases in GU production and GU length cause an increase in the total branch growth. And finally, increases in GU production and GU length along the leader cause an increase in the leader growth. Thus, the hypotheses give the component traits that are expected to have direct effect on the focal crown trait, and define the directions (either positive or negative) of these direct effects (Figure 3.1). No predictions are made for either the positive or negative correlations among component traits, nor for the magnitudes of correlations or direct effects.

Table 3.2. Site conditions for individuals of the canopy tree species Dicorynia guianensis *and* Vouacapoua americana *in the Piste St. Elie forest in French Guiana. Height was measured at the start of the experiment (1991). The light environment over trees was quantified by annual estimations of the crown position index (1991-1994), and by canopy openness estimates from hemispherical photographs made at the end of the experiment (1994).*

Matched Pair	Understorey individuals			Gap individuals		
	Height (m)	CPI range	Canopy openness (%)	Height (m)	CPI range	Canopy openness (%)
Dicorynia						
1	4.1	1.0-1.5	5	4.5	3.0-4.0	18
2	5.0	1.5-2.0	19	4.8	2.5-4.0	16
3	5.1	1.0-1.5	2	5.6	3.0-4.0	23
4	6.7	1.5-2.0	15	6.6	2.5-2.5	27
5	8.9	1.0-1.5	2	7.8	3.0-4.0	31
Vouacapoua						
1	4.9	1.5-1.5	1	4.9	2.5-4.0	20
2	6.1	1.0-1.5	1	6.1	2.5-2.5	27
3	6.4	1.0-1.5	1	6.3	3.0-4.0	15
4	7.8	1.0-1.5	2	8.2	2.5-3.0	22
5	18.2	1.5-1.5	2	15.6	2.5-2.5	20

3.3 Results

3.3.1 Light and crown development

Gap individuals had higher values of both CPI (>2.5) and canopy openness (15-31%) than understorey individuals (CPI=1.0-1.5, canopy openness; 1-5%), except for two understorey individuals of *Dicorynia* (Table 3.2). These two individuals (pair 2 and 4, Table 3.2) grew near treefall gaps that were created between the censuses in 1991 and 1992, and thus had a higher CPI (2.0, between 1992 and 1994) and canopy openness than the other understorey individuals.

As expected, gap individuals developed more extensively than understorey individuals with regard to both crown and component traits (Table 3.3). For most traits, this was significant for *Vouacapoua*, but not for *Dicorynia*. In *Vouacapoua*, gap individuals produced more branch length, longer leaders, and spaced their leaves further apart from each other. At the end of the experiment, they had more total leaf area and larger crown cover. The same patterns were found in *Dicorynia*, but were only significant for total branch growth and total leaf area. Gap individuals of both species had a larger LAI, but this was not significant for *Vouacapoua*.

Table 3.3. Crown development and morphology for gap individuals and understorey individuals of two canopy tree species, Dicorynia guianensis *and* Vouacapoua americana, *in the Piste St. Elie forest, French Guiana, during a 3-yr period (1991-1994). Median values are given per trait (N=5).*

Traits	*Dicorynia*			*Vouacapoua*		
	Understorey	Gap		Understorey	Gap	
Crown traits						
Characters:						
total leaf area (m^2)	1.8	7.1	*	5.2	9.9	*
leaf spacing (cm)	3.4	4.0	ns	1.4	4.8	*
leaf area index	1.3	2.3	*	1.0	2.0	ns
crown cover	1.2	3.6	ns	2.9	6.4	*
Growth (m):						
leader growth	0.2	0.6	ns	0.0	1.1	*
total branch growth	3.1	10.7	*	0.9	9.8	*
Component traits						
#sympodial units!!	19	37	*	19	34	*
GU production	88	300	*	22	58	*
GU production leader	5	40	*	1	12	*
leaf production	30	130	*	93	230	*
GU length (cm)	3.4	4.0	ns	4.1	12.1	*
GU length leader (cm)	3.2	7.3	ns	5.0	32.0	*
#leaves/GU	1	1	-!	2.6	4.3	*
#leaf fall/GU	0.4	0.5	ns	0.2	1.1	*
leaf size (cm^2)	413	545	ns	441	489	ns
SLA (cm^2/g)	205	128	*	191	156	*

- The Wilcoxon-matched pair sample test was used to test for differences between gap and understorey individuals. Significance differences are indicated by * ($P<0.05$); ns means not significant.
- ! No test was performed as *Dicorynia* cannot differ by its leaf production per GU, see text.
- !! The number of apical meristems is given as a measure of the sympodial unit production, see text.

Parallel to this, gap individuals produced more sympodial units (by branching more frequently, data not shown), growth units, and leaves (Table 3.3). In *Vouacapoua*, they produced longer growth units, produced more leaves per growth unit, but also lost more leaves per growth unit. In *Dicorynia*, however, gap and understorey individuals produced growth units of similar length, produced one leaf per growth unit by definition, and lost the same number of leaves per growth unit. Leaf size did not differ between gap and understorey individuals, but SLA was, as expected, lower in gap individuals.

Gap individuals produced more, and longer (not significant for *Dicorynia*), growth units along their leader than understorey individuals. In gap individuals, the leader produced longer (only significant for *Vouacapoua*) and more growth units than other axes (Table 3.4), and thus produced more extension growth than an average axis. In understorey individuals, the leader and other axes produced growth units of similar length, and at a similar rate. Consequently, in understorey individuals, the leader did not differ from an average axis with regard to extension growth.

3.3.2 Components related to crown traits.

The effects of sizes and production rates of different plant components (predictors) on crown characters (total leaf area and leaf spacing) and crown growth (leader growth, total branch growth) are shown by path-analysis (Figure 3.2, Table 3.5). Path-diagrams explained more than 90 % of the observed variation in crown traits, except for leader growth in *Dicorynia* (29%) and total leaf area in *Vouacapoua* (24%). Per path-diagram, predictors contrasted more for their direct effect than for their total effect (Table 3.5), because predictors were usually highly correlated. A high correlation indicates that two predictors varied in response to the same common cause(s) (Sokal & Rohlf 1981). Amongst other factors, light (gap versus understorey) may be one of these common causes. For purpose of illustration, the influence of light (gap versus understorey) on predictors was shown in the path-diagrams, but this influence was based on the Wilcoxon-matched pair test (see Table 3.3) and not on path-analysis.

The total effects (Table 3.5) indicate that total leaf area was positively correlated with GU production, leaf production per GU (only for *Vouacapoua*), leaf fall per GU, and leaf size (only for

Table 3.4. Leader and axis development (1991-1994) compared for two tropical rain forest tree species in French Guiana. GU length (len), GU production (prod), and total increment (incr) are presented for the leader and for an average axis.

	Dicorynia						Vouacapoua					
	Understorey			Gap			Understorey			Gap		
	AX[1]	LE[2]	s[3]	AX	LE	s	AX	LE	s	AX	LE	s
len	3.4	3.2	ns	4.0	7.3	ns	4.1	5.0	ns	21.0	32.0	*
prod	3.3	5.0	ns	13.0	40.0	*	1.4	1.0	ns	3.7	12.0	*
incr	9.4	19.5	ns	43.4	218.0	*	6.1	7.0	ns	67.6	316.0	*

-Axis values were obtained by averaging the values of measured axes (excluding the leader) per tree.

-Medians of five individuals are presented, both for leader and average axis.

[1] AX stands for axis.

[2] LE stands for leader.

[3] s gives significance level, using the Wilcoxon-matched pair test (1-tailed): * for $P < 0.05$, ns for $P >= 0.05$.

Table 3.5. The effects of component traits (predictor variable) on crown traits (criterion variable). Effects are split into direct, indirect, and total effects, following path-analysis (see text).

Predictor Variables	Effects on criterion variables:											
	total leaf area			leaf spacing			leader growth			total branch growth		
	dir	ind	tot	dir	ind	tot	dir	ind	tot	dir	ind	tot
Dicorynia												
GU production	0.71	0.06	0.77	-	-	-	-	-	-	0.91	0.02	0.93
GU production L	-	-	-	-	-	-	0.59	-0.06	0.53	-	-	-
GU length	-	-	-	-	-	-	-	-	-	0.34	0.05	0.39
GU length L	-	-	-	-	-	-	-0.11	0.33	0.22	-	-	-
#leaf fall/GU	-0.09	0.50	0.41	-	-	-	-	-	-	-	-	-
leaf size	0.58	0.16	0.74	-	-	-	-	-	-	-	-	-
R^2 for model	*0.92*						*0.29*			*0.97*		
Vouacapoua												
GU production	0.70	-0.07	0.63	-	-	-	-	-	-	0.52	0.22	0.74
GU production L	-	-	-	-	-	-	0.42	0.31	0.73	-	-	-
GU length	-	-	-	0.91	0.07	0.98	-	-	-	0.66	0.18	0.84
GU length L	-	-	-	-	-	-	0.61	0.21	0.82	-	-	-
#leaves/GU	-0.18	0.63	0.45	0.07	0.86	0.93	-	-	-	-	-	-
#leaf fall/GU	0.34	0.16	0.50	-	-	-	-	-	-	-	-	-
leaf size	-0.40	0.19	-0.21	-	-	-	-	-	-	-	-	-
R^2 for model	*0.24*			*0.95*			*0.91*			*0.94*		

- L, for leader traits.
- R^2 of path-models were calculated after Sokal & Rohlf (1981).
- '-' means that effects were not part of the path-model (see Figure 3.1).
- for direct effects: underlined means significant, P<0.05 (single line), P<0.01 (double line).
- for indirect and total effects: significant levels were not calculated (see Sokal & Rohlf 1981).

Dicorynia). In both species, these total effects were largely due to the direct effect of GU production (Figure 3.2). An increase in the GU production caused an increase in total leaf area, although this was not significant for *Vouacapoua* (P=0.06). Interestingly, if branching rate instead of GU production was incorporated in the path-analysis (data not shown), similar results were obtained in both species. Moreover, this branching rate is highly correlated with GU production (r = 0.91 for *Dicorynia*, r =0.86 for *Vouacapoua*, both P<0.000). Apparently, GU production increased in gap individuals by a more frequent release of axillary meristems (branching rates). In *Dicorynia*, leaf size also had positive direct effect on total leaf area, but leaf fall per growth unit had no significant direct effect. Its high coefficient of determination (92%) indicates that the path-diagram largely explains the effects of component traits on total leaf area. In *Vouacapoua*, the effects of the other components were not significant. The path model of this species had a low coefficient of determination (24%) and a low significance level (P=0.07).

In *Vouacapoua*, the space between leaves was positively correlated (total effects) with GU length and leaf production per GU (Table 3.5). Path-coefficients indicate a strong direct effect for GU length. Thus, leaves were placed further apart from each other by producing longer growth units, rather than by producing less leaves per GU. The strong correlation between the two predictors indicates that long growth units produced more leaves, which caused the high total effect of leaf production per GU on

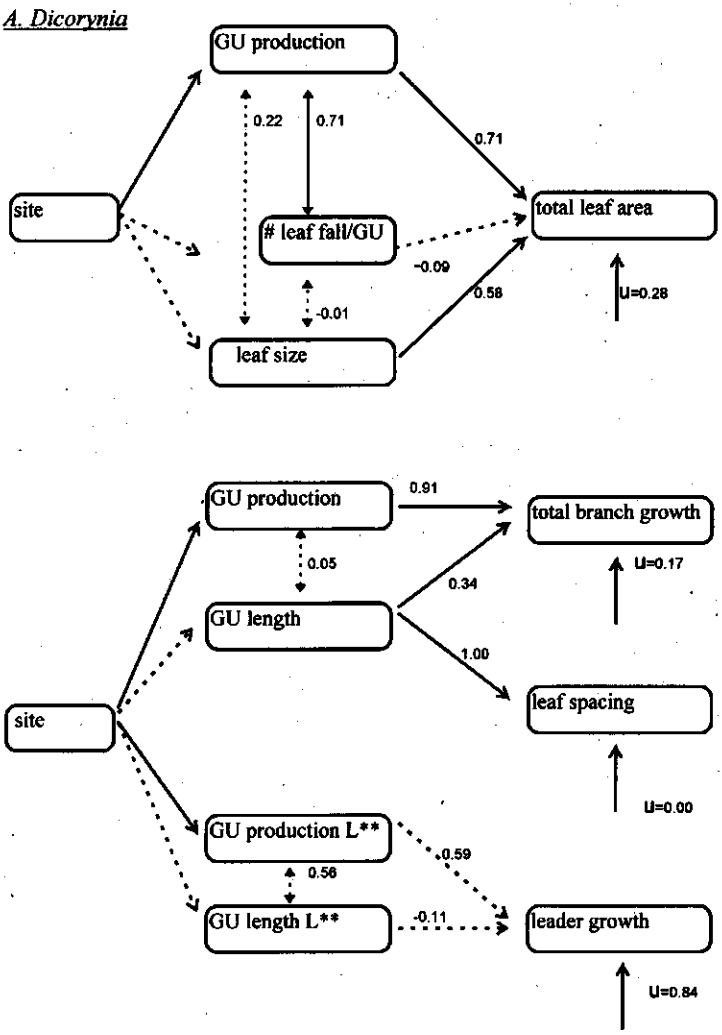
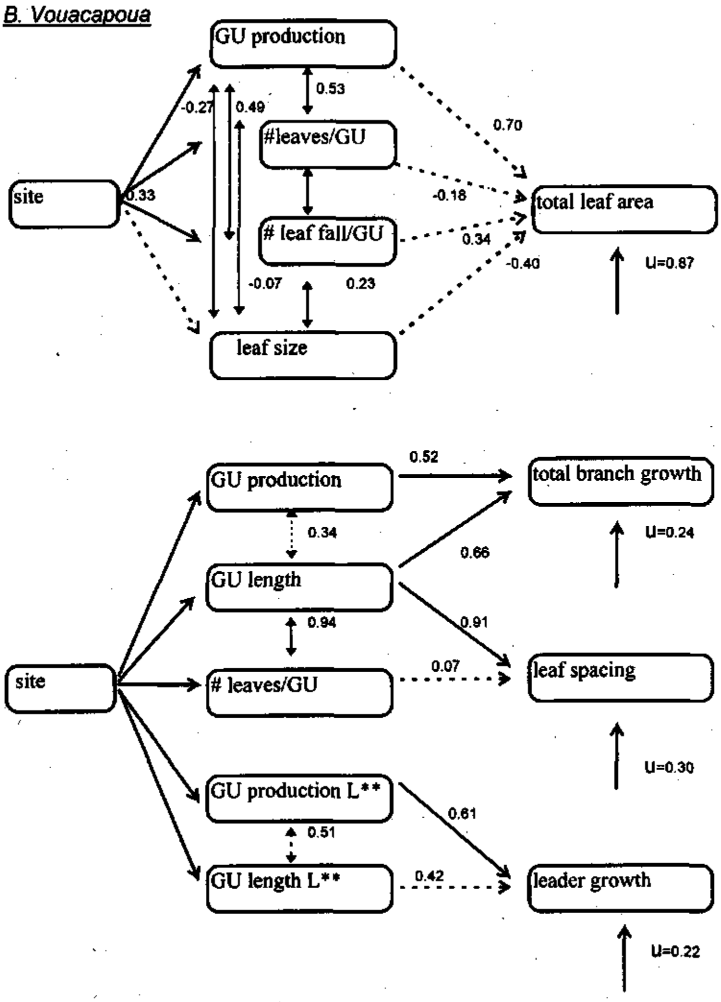


Figure 3.2 The effects of component traits on crown traits presented in path-models. Effects are presented as path-coefficients along the single headed arrows. For purpose of illustration, the effect of the site (gap versus understorey) on component traits is given by single headed arrows as well (see Table 3.3). A. Models for Dicorynia. *B. Models for* Vouacapoua. *Significant effects (P<0.05) are given by non-disrupted arrows, non-significant relationships (P>=0.05) are given by dotted arrows. U stands for the effects of unknown sources which cause the unexplained variation. Correlations among component traits are expressed as Pearson correlation coefficients along double headed arrows. (further explanation, see text).*

the space between leaves. The path-diagram explains 95 % of the observed variation. In *Dicorynia*, the space between leaves is completely determined by GU length by definition.

Total branch growth was positively correlated (total effects) with the GU production and GU



B. Vouacapoua

Figure 3.2(B). For explanation, see previous page.

length. In *Dicorynia*, GU production had a stronger direct effect on total branch growth than GU length. In *Vouacapoua*, the two predictors had a similar direct effect on total branch growth. In both species, the path-model explained more than 90 % of the observed variation.

Leader growth was positively correlated (total effects) with the GU production and GU length of the leader. In *Vouacapoua*, both GU production and GU length positively affected leader growth (direct effects), but the effect of GU length was not significant. The path-diagram explained 91% of the observed variation for this species. In *Dicorynia*, only the GU production had a positive effect, but this was not significant. The path-diagram only explained 29% of the observed variation for this species.

3.4 Discussion

Gap individuals developed more extensively than understorey individuals, both for their component and crown traits (Table 3.3). This indicates that crown development was limited by low light levels in the understorey. For most traits, the results were significant for *Vouacapoua*, but not for *Dicorynia*. Two understorey individuals of *Dicorynia* grew near gaps and were thus exposed to higher light levels, but did not cause the lower number of significant results of *Dicorynia*. Probably, the low sample sizes accounted for the lack of significant results for some traits in *Dicorynia* and for the LAI in *Vouacapoua*. If the data of both species were pooled, the results were significant for all traits but leaf size (data not shown).

The light environment may affect crown traits through its effects on different component traits. Such a chain of effects, i.e. the influence of light on component traits followed by the influence of component traits on crown trait(s), may be analysed by path-analysis (e.g. Sokal & Rohlf 1981). In this study, the influence of light on component traits was not included in the path-analysis, because the effects of two light environments (gap versus understorey) cannot be expressed by path-coefficients. Instead, the influence of light on component traits was indicated to be significant or not (Wilcoxon-matched pair test). The effects of component traits on crown traits were investigated using path-analysis. Although the effects of light on component traits were not quantified by path-analysis, the diagrams (Figure 3.2) indicate how gap and understorey individuals produced different crown traits by their differentiation in different component traits.

3.4.1 Competition for light and space

Gap individuals developed their crowns more extensively than understorey individuals by producing more and longer growth units. Consequently, gap individuals produced more branch length and leader length (height gain), and they had larger crowns by the end of the experiment. These findings are in agreement with studies on other shade tolerant species. For temperate forest trees, the same type of response to gaps were found for 1-2 m tall saplings (Canham 1988) and seedlings (Sipe & Bazzaz 1994). Clark & Clark (1992) found higher height growth rates under increasing light availability for 1-16 m tall juveniles of tree species in a Costa Rican rain forest, but they did not assess other measures of crown expansion. In general, trees of these shade tolerant species may reduce their crown growth because of low light availability. In contrast, trees of some light demanding species may have high growth rates, irrespective of the light environment. Trees of these latter species however die more rapidly under dark conditions (e.g. Alvarez-Buylla & Martinez-Ramos 1992).

Gap individuals had faster growing leaders because they produced more, and taller, growth units. Moreover, gap individuals showed preferential growth of the leader, i.e. their leaders grew even faster than equivalent axes in the crown. In contrast, understorey individuals did not show preferential growth of their leader. From this it is inferred that juveniles increase their height growth in canopy gaps by faster crown growth, as well as by preferential growth of their leader. The increasing height growth rates in canopy gaps may enable these juveniles to compete for light and space with neighbouring trees of similar size, and to occupy more favourable sites (more open, more light) at higher locations in the forest. Thus, canopy gaps may increase the chances of a tree to reach adult stature and reproductive status (Kohyama 1991, Küppers 1989, 1994).

Steingraeber *et al.* (1979) found the same growth habit in 'forest' and 'open grown' saplings of *Acer saccharum*. The open grown individuals had extensive leader growth relative to lateral axes, while this was not so in forest individuals. For the same species, however, Bonser & Aarssen (1994) showed that vertical (leader) growth was larger relative to lateral (axis) growth at lower light levels in temperate forest. They suggested that this allowed trees to minimise the chances of being overgrown at low light availability and, conversely, to maximise light interception at higher light availability. These contrasting growth habits may result from different ranges of light availability that were under investigation, but also from different growth habits of *Dicorynia* and *Vouacapoua* as compared with *Acer* (see Chapter 4).

3.4.2 Leaf display

Gap individuals had more total leaf area than understorey individuals, because they branched more frequently and produced more growth units. For shade tolerant tree species in temperate forests, Horn (1971) and Canham (1988) also observed that gap individuals had a greater total leaf area than understorey individuals. As gap individuals were still exposed to higher light availability at the end of the experiment, the large total leaf area may permit gap individuals to acquire and use more carbon for future growth than understorey individuals.

Gap individuals had a larger LAI than understorey individuals, but this was not significant for *Vouacapoua*. Because LAI largely depends on total leaf area, gap individuals increased their LAI with increasing branching rates and GU production (not shown in path-analysis). Similarly, Horn (1971) and Canham (1988) found trees with a higher LAI in gaps than in the dark understorey. Horn (1971) argued that this variation in LAI was of adaptive value. The leaves in understorey individuals can only fix enough energy if they do not overlap (low LAI). The leaves in gap individuals may overlap (high LAI) until the light levels reach the leaf compensation point, where the cost of adding a leaf just balances the energetic profit it earns (see also Givnish 1984). In addition, a high LAI reduces the cost of supporting a given amount of leaf area, but a low LAI implies high cost of leaf area support (Leopold 1971, Borchert & Tomlinson 1984). In the present study, the understorey and gap individuals were exposed to persisting low and high light levels, respectively. Thus, the understorey individuals with a low LAI may indeed avoid self-shading and have higher support costs, whereas gap individuals with a high LAI may reduce their costs of leaf display as predicted by Horn, Leopold, and Borchert & Tomlinson. However, the LAI as an estimate of support costs of leaf display refers to the production costs of the whole crown (during the whole life-history of the tree), and not to the production costs of the amount of supported leaf area. This latter cost of producing leaf area can be estimated from the space between leaves.

Understorey individuals set leaves less apart from one another than gap individuals by producing shorter growth units. Even the understorey individuals of *Vouacapoua*, which produced less leaves per growth unit, packed their leaves more closely. The space between leaves, i.e. the average size of the woody unit that supported one leaf, may be used to infer the relative costs of displaying leaf area (e.g. Canham 1988, King 1991c). These costs were not affected by leaf size, as leaf size was similar for gap and understorey individuals. Thus, the understorey individuals had lower costs of displaying a unit leaf area than gap individuals. King (1991c) found the same for 1-2 m tall saplings of shade tolerant tree species in a tropical forest, but found no such pattern for saplings of light demanding tree species. Following Givnish (1988) and King (1991c), the ability to display their leaf area more economically in a light limited environment allows trees to lower their whole plant compensation point, and this may contribute to their ability to tolerate shade (Givnish 1988, King 1991c). In contrast, for two shade tolerant species in temperate forest, Canham (1988) did not find differences in the costs of displaying leaf area (*Fagus grandiflora*) in two contrasting light environments, or lower costs in the least light limited environment (*Acer saccharum*). In *Acer*, these low costs may explain the large increase in growth rates in gaps (Canham 1988). As similar patterns were found in the light demanders of a tropical rain forest (King 1991c), this may indicate that trees of these temperate species are exposed to higher light levels than the two study species in tropical rain forest. Then, trees of these temperate species may not need to reduce their costs of leaf display for their survival in the shaded understorey. Indeed, Canham *et al.* (1990) found higher levels of light availability (per time unit in the growing season) in the temperate *Fagus-Acer* forest than in a tropical rain forest of Costa Rica. However, there are no measures to compare the light environments of *Acer* and *Fagus* with the light environments of *Dicorynia* and *Vouacapoua* directly (see also Chapter 4).

It is concluded that gap individuals had more extensive crown development than understorey individuals. So far, this comparison of species was mainly restricted to juveniles in the post-seedling phase. Tree seedlings also develop more extensively in gaps, but their crown development is usually expressed by biomass (of leaves and shoots) or size increments (e.g. Augspurger 1984, Popma & Bongers 1988) and not by the presented component and crown traits (but see Sipe & Bazzaz 1994). Apart from interspecific similarities, gap individuals spaced their leaves at longer distances and had preferential growth of leader in the two study species, but not in some temperate tree species. The hypothesis has been put forward that tropical rain forest trees differ from temperate trees with regard to these development traits because they are subject to more reduced light levels.

4

CROWN DEVELOPMENT: THE INFLUENCE OF TREE HEIGHT AND LIGHT

with Frans Bongers

Abstract

1. Crown development was monitored for the canopy tree species *Dicorynia guianensis* and *Vouacapoua americana* in a tropical rain forest in French Guiana. The trees studied ranged in height between 0.5 m and 37 m, and were used to assess the influences of tree height and light availability on crown development. For individuals shorter than 5 m, height and crown development were measured from the ground. Taller individuals were climbed in order to make these measurements. The estimate of light availability was canopy openness, using hemispherical photographs.

2. The changes with tree height and light availability were studied for six crown traits: leader growth, total branch growth, crown shape (length/width ratio), total leaf area, leaf area index (LAI), and leaf spacing. These traits integrate the production rates and sizes of various plant components (leaves, metamers, units of extension, meristems). The production rates and sizes of these plant components are referred to as component traits. Using path-analysis, the influence of height and light on the crown traits (except crown shape) were assessed through their effects on component traits. For this analysis, only trees within the 0.5 to 20 m range were used.

3. Total leaf area, LAI and total branch growth increased with height because taller trees supported more apical meristems, and (except for total branch growth) indirectly, because they had larger leaves. Crown shape also increased with height, but was not related to component traits. Leader growth and the space between leaves did not differ with tree height.

4. In *Vouacapoua*, total leaf area, LAI and total branch growth also increased with canopy openness because the individuals which grew in more open spaces branched more frequently (and thus produced more apical meristems), produced longer growth units, and, indirectly, also because they produced larger leaves. In this species, leader growth also tended to increase with canopy openness, but not significantly. Crown shape also increased with increasing canopy openness. In *Dicorynia*, total branch and leader growth increased with canopy openness because the individuals growing in more open spaces produced longer growth units. The other crown traits did not change with canopy openness.

5. Trees taller than 26 m produced more total leaf area and had more total branch growth. They also had smaller crown shapes because horizontal crown growth was not further limited by light or space. Their LAI did not further increase, and leader growth and leaf spacing decreased.

6. In general, for (0-20 m tall) trees of both species, the crown traits change in the same direction with light availability, but they may differ in terms of the range of light levels to which they respond. The taller (26-37 m) trees seem to change some of their crown traits in the opposite direction, which may be a response to the much higher light levels to which they are exposed.

4.1 Introduction

Trees of tropical rain forests live in a variable light environment (e.g. Chazdon & Fetcher 1984, Terborgh 1985, Clark *et al.* 1996). Trees may encounter many different light environments during ontogeny, but generally they will occupy more favourable sites, i.e. a higher light and space availability as they grow taller (Clark & Clark 1992, Bongers & Sterck in press). Before trees reach their adult stature and become reproductive, they compete with neighbouring trees for these scarce resources. In trees competing for light, crown development plays a crucial role. It determines the interception of light, shading effects on neighbouring trees, and further expansion, both in horizontal and vertical direction (e.g. Hallé *et al.* 1978, Givnish 1984, Shukla & Ramakrishnan 1986, Kohyama & Hotta 1990).

Trees undergo many changes in structure when they grow up in the forest. They usually start their development as pole seedlings which support their leaves along a vertical axis. After this pole phase, axillary meristems become active and an increasingly branched, and thus more complex, crown structure develops. The changes in crown structure during ontogeny may be described on the basis of qualitative and quantitative criteria. The qualitative changes in branching patterns early in ontogeny are usually nicely described by one of the architectural models of Hallé and Oldeman (1970, see also, Hallé *et al.* 1978, Barthélémy 1991, Edelin 1991). These models define the spatial arrangement of different plant components during tree life (see Table 1.1). They give most emphasis to two components, i.e. units of extension (product of one bud) and sympodial units (product of one meristem, Table 1.1, see also White 1979, Bell 1991, Barthélémy 1991, Room *et al.* 1994). These models describe the overall development in some tree species (e.g. some palm species). For other tree species, however, adult trees usually produce crown structures which cannot be described by one of the models only (e.g. Borchert & Tomlinson 1984, Edelin 1991).

The quantitative changes in branching patterns may be described as increases in the production of apical meristems (Alvarez-Buylla & Martinez-Ramos 1992), buds (Maillette 1982), leaves (Boojh & Ramakrishnan 1982), shoots (Jones 1985), and other plant components (Table 1.1, see also Room *et al.* 1994). The combined effect of the production of these plant components and their positions within the crown determine the overall crown expansion (Shukla & Ramakrishnan 1986, Kohyama & Hotta 1990), crown form (Horn 1971, Brunig 1976, Givnish 1984), crown size (O'Brien *et al.* 1995, O'Brien *et al.* 1996, King 1991a, 1996), crown symmetry (O'Brien *et al.* 1995), crown allometry (King 1996), and leaf display (Canham 1988, Borchert & Tomlinson 1984) during ontogeny. These crown traits determine how trees compete for light (Shukla & Ramakrishnan 1986, Kohyama & Hotta 1990, King 1991a, 1996) and intercept light (e.g. Leopold 1971, Horn 1971, O'Brien *et al.* 1995, Ackerly in press).

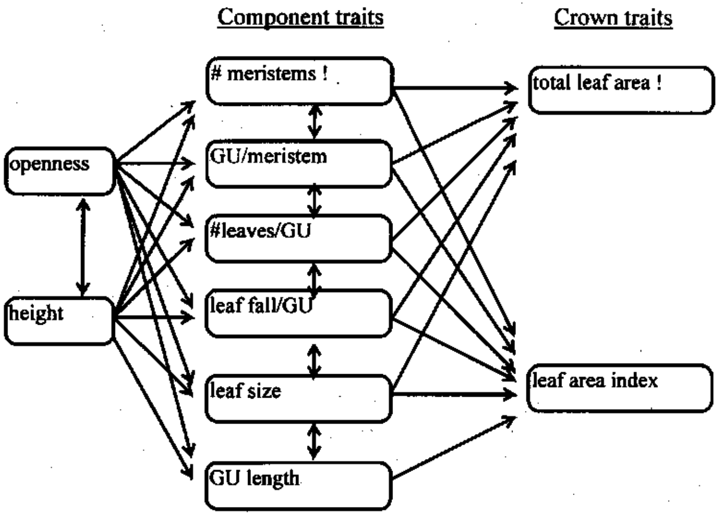
Most studies on crown development have focused on a few aspects of crown structure. Inspired by the work of Hallé and Oldeman, a number of studies were carried out to describe the qualitative changes with ontogeny for tree species of, for example, Malaysia (Edelin 1984), French Guiana (Loubry 1994, Loup 1994), Mali (Sterck *et al.* 1991), and France (Drénou 1994). Oldeman and van Dijk (1991) assigned different architectural tree models to six different growth strategies with respect to the light environment. They lack however the data to support these highly hypothetical relationships. Other researchers related model-conform tree development to leaf display and crown shape (Fisher & Hibbs 1982, Borchert & Tomlinson 1984, Ramakrishnan *et al.* 1982, Shukla & Ramakrishnan 1986). They showed that the same architectural model gave rise to different crown shapes and leaf display in different light environments (see also Loup 1994). Conversely, different architectural models may produce similar crown shapes and leaf display (Fisher & Hibbs 1982). Thus, the qualitative criteria of tree development, as used in these architectural tree models, seem to be of limited ecological value for the way trees grow up in a heterogeneous light environment (Ramakrishnan *et al.* 1982, Shukla & Ramakrishnan 1986, Fisher 1986).

Studies on quantitative changes with ontogeny have mainly been restricted to tree seedlings and 1-2 m tall saplings grown at different levels of light availability. At the higher light levels, these individuals grew more rapidly as was expressed by faster relative growth rates or absolute increases in biomass (e.g. Popma & Bongers 1988) or size (e.g. Welden *et al.* 1991); had faster production rates of leaves, internodes and shoots (e.g. Fisher 1986); allocated less organic matter to the leaves (e.g. King 1991c); produced more leaf layers (e.g. Canham 1988); had higher bifurcation ratios (e.g. Shukla & Ramakrishnan 1986); produced more columnar shaped crowns (e.g. Steingraeber *et al.* 1979); and produced sun adapted leaves (e.g. Givnish 1988). Taller juveniles were compared between completely open 'urban' sites and forest sites (Fisher & Hibbs 1982, Borchert & Tomlinson 1984, Roloff 1989). Open grown individuals usually reached their maximum size at lower stature, and produced more planar shaped crowns. Within forests, taller juveniles were investigated with respect to their crown size, allometry, and symmetry (King 1991a, King 1994, 1996, O'Brien *et al.* 1995, 1996), but not in direct relation to different light environments. Clark and Clark (1992) related height and diameter increments to light availability in taller juveniles, but did not assess crown traits.

Thus, the changes in crown structure during ontogeny are at least partly affected by the light environment. The influence of light availability on the qualitative changes in crown structure seem to be of minor importance however (Hallé *et al.* 1978, Edelin 1984, Loubry 1994). In contrast, the quantitative changes in crown structure were usually assessed for trees of a given size or age, and related to variation in light availability. However, apart from the influence of light, these quantitative traits are likely to undergo large changes during ontogeny. Few if any studies focused on the influence of light availability on the changes in crown structure and development during ontogeny.

The changes in crown structure can be expressed by different plant traits. Most studies focused on small sub-sets of plant traits, and evaluated their specific role in the development of tree crowns. In real, crown development consists of many correlated changes in different plant traits. Here, two types of traits are defined for crown development; crown traits and component traits (see also Chapter 3). The crown traits refer to overall crown expansion and overall crown characters. These crown traits integrate the production rates and sizes of various plant components. These production rates and sizes of components are further referred to as component traits.

In the present study, the major focus is on five crown traits (Figure 4.1). These traits are thought to be of ecological significance. Leader growth permits a tree to gain height (Chapter 5), and thus to compete with its neighbours for higher light availability at higher levels in the forest (e.g. Tilman 1988). Total branch growth is a measure of overall crown expansion. The tree with the higher branch growth is able to occupy more space, to space its leaves over a larger volume for light interception, and to increase shading over its lower neighbours. Leaf spacing is the above ground equivalent of the leaf area/plant mass ratio or LAR (Zagt & Werger in press). It expresses the size of the woody unit which supports one leaf. The further apart the leaves are spaced, the higher the costs to display one leaf (e.g. Canham 1988, King 1991c) if twig thickness and leaf size are constant. The total leaf area determines the area over which light can be intercepted. Its role in the acquisition of carbon was shown by Oberbauer *et al.* (1993). For small saplings, they observed that the individuals with the larger total leaf area grew fastest. Finally, the leaf area index (LAI) is used to evaluate the model of Horn (1971) and related models. Horn distinguished two opposing growth strategies: multi-layer (high LAI) versus mono-layer (low LAI). A high LAI is expected to occur at high light availability, as every leaf is above its light compensation point, and the support costs of the total leaf area are kept low (Leopold 1971,



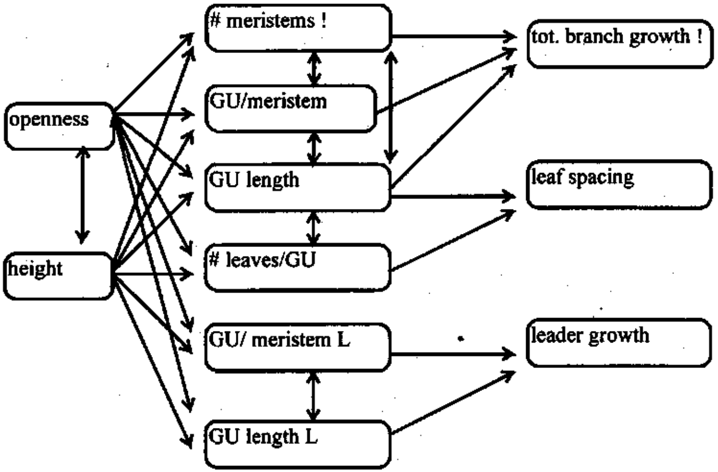


Figure 4.1. Two path-diagrams presenting the expected influences of tree height and light availability (estimated as canopy openness) on crown traits by two successive steps: (1), the influence of light availability and tree height on different component traits; (2), the influence of component traits on crown traits. Single headed arrows indicate the direct effects of tree height and light availability on component traits, and of component traits on crown traits. Double headed arrows indicate the correlations between height and openness, and between the component traits that are expected to influence the same crown trait. For the sake of clarity, some but not all correlations among component traits were presented in the first diagram. The path-diagrams represent the expected relationships for both Dicorynia guianensis *and* Vouacapoua americana, *but # leaves/GU was equal to 1 for* Dicorynia *and thus excluded for this species. ! means that log transformed values were used. L refers to component traits of the leader.*

Borchert & Tomlinson 1984). In contrast, a low LAI is expected to be beneficial at low light availability because it permits trees to avoid self-shading of its leaves, although this implies higher support costs of the total leaf area. As shown by Figure 4.1, each of these crown traits is expected to integrate various component traits. In the presented models, height and light may cause a change in each of the component traits, and the combined effects of such component traits determine the crown traits.

In this chapter, crown development is described for trees of two canopy tree species in a tropical rain forest in French Guiana. The focus is on changes in both component traits and crown traits with ontogeny, and in more particular, in relation to tree height and light availability. The whole height range of trees is considered (0-37 m), but the emphasise was on 0-20 m tall trees which are still growing towards the upper canopy. Crown development and light environments were assessed for the whole height range of trees, using appropriate climbing techniques. The following questions are addressed:

(1) How do component traits and crown traits change with tree height and light availability?

(2) How does the influence of tree height and light availability on the different component traits cause changes in crown traits?

4.2 Methods

4.2.1 Site and species

Field work was carried out in a lowland tropical rain forest at the Biological field station 'les Nouragues' (4°05'N; 52°40'W), French Guiana. Two canopy tree species were selected, namely *Dicorynia guianensis* Amshoff. (Caesalpiniaceae) and *Vouacapoua americana* Aubl. (Caesalpiniaceae). They are further referred to by their generic names only. For general site and species information, see Chapter 1.

4.2.2 Selection of individuals

Populations of both species were inventoried in October 1992, as part of a long-term study on the vegetative growth of these tree species. A 12-ha plot was searched for trees with a stem diameter >=10 cm at 1.30 m (DBH). A central 1.5-ha plot was searched for trees with a stem diameter <10 cm, but with a height above 50 cm.

For each species, individuals shorter than 5 m tall (N=20 per species) were selected so as to occur along the whole range of observed light levels in the population. Crown development in these individuals was measured from the ground, in some cases by bending the stem, or by climbing a natural elevation. The crown development in taller individuals could not be measured from the forest floor, but only by climbing neighbouring trees (using spikes or alpinist ropes). Because few of the inventoried individuals were accessible in this way, such taller individuals were searched for outside the inventoried plots as well and included in this study. On the basis of light estimates calculated from the crown position index (e.g. Clark & Clark 1992, Chapter 3), the 5-20 m tall trees selected for this study (N=13 for *Dicorynia*, N=20 for *Vouacapoua*) occurred at a smaller range of light habitats than the individuals of the same height in the population (see also Chapter 5). For trees taller than 20 m, five individuals were accessible, three for *Vouacapoua* (27, 35, and 37 m) and two for *Dicorynia* (26, 35 m). For all selected trees, the study on crown development was initiated in November 1992, and crown development was measured during two later censuses in November 1993 and November 1994.

4.2.3 Light measurements

The light environment was characterised using hemispherical photographs. These photographs were made during a second census in November 1993 (half-way through). A Canon Ti 70 body and Canon lens 7.5 mm/5.6 were fixed in a leveller, which was mounted on telescopic poles (up to 6 m long). The camera automatically levelled horizontally, and black and white pictures were made over each of the selected individuals, including the taller ones. Photographs were scanned and digitised with DeskScann II so as to calculate canopy openness as a percentage from the open sky, using PPFD-CALC-2 (Ter Steege 1992). Canopy openness is further used as an estimate of light availability.

4.2.4 Crown development measurements

In November 1992, trees were coded and drawn to scale. For individuals shorter than 5 m, all branches and their apical meristems were tagged and coded. For individuals taller than 5 m, a selection of branches plus their apical meristems (N (meristems) = 10-45) in the top of the crown were tagged and coded. At later censuses in 1993 and 1994, the trees were climbed again to measure the sizes and production rates of components (see below for details). In the present study, the focus is on the overall crown development between the first and the last census (1992-1994).

The components that contribute to crown development in juveniles of these tree species are meristems, leaves, metamers, units of extension, and sympodial units (Table 1.1, Figure 1.1). For *Vouacapoua*, metamers were not considered because they are structurally variable. A scale leaf is produced within each metamer at the base of the unit of extension, while a compound photosynthetically active leaf is produced within each metamer at the distal end of the unit of extension. Thus, metamers were used as morphological markers to distinguish between units of extension. For *Dicorynia*, metamers are structurally equivalent. One compound leaf is produced within each metamer. Its units of extension cannot always be distinguished unambiguously (but see Drénou 1994). As units of extension in *Vouacapoua* and metamers in *Dicorynia* are the smallest repetitive woody units produced by meristems, they are further referred to by the same term: growth unit (GU).

4.2.5 Component traits

In November 1994, the production of different components was assessed by counting leaves, leaf scars, growth units, and apical meristems (or active sympodial units) that were produced on top of tagged apical meristems. For *Vouacapoua*, the photosynthetic leaves and their (large) scars were counted, but not the scale leaves and their (smaller) scars. For trees shorter than 5 m tall, these counts reflect the total numbers of components produced within their crowns. For trees more than 5 m tall, these counts were made for a selection of apical meristems. However, by climbing slowly along the whole length of these taller trees, the total numbers of leaves and apical meristems were counted for these taller individuals as well. In each individual, one axis (linear sequence of growth units) was defined as the leader. This leader supported the upper most apical meristem of the crown in 1994. These measurements were used to calculate the following variables based on a 2 year interval of growth (unit of each variable = yr^{-1}):

GU production per meristem = ½ x number of GU's / numbers of monitored meristems (1)
leaf production per GU = (½ x number of (leaves+scars))/ number of GU's (2)
leaf fall per GU = ½ x number of scars / number of GU's (3)
GU production (per tree) = ½ x GU production per meristem x number of meristems (4)
leaf production (per tree) = ½ x GU production x leaf production per GU (5)
GU production (leader) = ½ x number of GU's along leader (6)

Mean sizes were measured for the leaves and growth units, but not for sympodial units. Many of the sympodial units had a living apical meristem and may thus have continued to grow after the last census in November 1994. Mean leaf size was determined from a sample of 20 leaves, taken from random positions in the crown. Surface area of each leaf was measured using a Digital Image Analysis System (Eijkelkamp 1991). Lengths were measured for all growth units produced on top of monitored meristems, using a folding ruler. Mean GU length (cm) was obtained by averaging these individual GU length values. For the leader, the mean GU length was calculated separately.

4.2.6 Crown traits

Crown traits refer to overall crown expansion during 1992-1994, and to crown characters in 1994. Two measures of overall crown expansion were calculated, as follows:

total branch growth = ½ x mean GU length x GU production (per tree) (7)
leader growth = ½ x mean GU length (leader) x GU production (leader) (8)

Five crown characters were determined in November 1994. The longest crown width D_1, the crown width D_2 (perpendicular to D_1) and crown length L, i.e. the distance between upper most leaf and bottom leaf along the vertical, were measured. Crown length was measured using a folding ruler. In trees shorter than 5 m, crown widths were measured using a folding ruler as well. In the 5-20 m tall trees, crown widths were measured either by using a folding ruler or by extending telescopic poles from the crown centre to crown sides. In the 35-37 m tall trees, crown widths were assessed from the ground, using a Suunto clino-measurer to locate crown sides, and a folding ruler to measure the distance between opposite crown sides. The crown characters were then calculated as follows:

crown cover = $0.25 \times D_1 \times D_2 \times \pi$ (9)
crown shape = $L / (½ D_1 + ½ D_2)$ (10)
total leaf area = mean leaf size x total number of leaves (11)
leaf area index (LAI) = total leaf area / crown cover (12)
leaf spacing = mean GU length (*Dicorynia*) (13)
= leaf production per GU / mean GU length (*Vouacapoua*) (14)

4.2.7 Analysis

Firstly, crown traits and component traits were plotted against height to show the overall changes in these traits with increasing height. Correlations between these traits and height were calculated for the trees shorter than 20 m, mainly because these trees were still growing towards the canopy (and thus the light environment is highly variable) while the taller trees were already in the more open canopy. Additionally, the sample sizes were small for trees taller than 20 m. The number of meristems, the

Additionally, the sample sizes were small for trees taller than 20 m. The number of meristems, the total leaf area, and branch growth increased exponentially with height and were log-transformed.

Secondly, a multiple linear regression was used to assess the relative importance of height and canopy openness in determining crown traits. Non-transformed values of LAI, leaf spacing, and leader growth, and log-transformed values of total leaf area and total branch growth, were used as they did approach a normal distribution. The following regression model was used:

$$\text{crown trait} = c + (b_1 \times \text{height}) + (b_2 \times \text{openness}) + (b_3 \times \text{height} \times \text{openness}) + e \qquad (15)$$

Here, c is the constant (intercept), the b's represent the regression coefficients, and e is the error term. The constant was not set to 0, because individuals with no height (seeds that start to germinate, not included in this study) may still produce crown traits over the study period of two years.

Thirdly, by means of path-analysis (e.g. Wright 1934, Kingsolver & Schemske 1991) the mechanisms were evaluated by which height and canopy openness influence crown traits. Path-models show the possible influences of height and canopy openness on component traits, and the influences of these component traits on crown traits (Figure 4.1). In path-analysis, these two relationships are referred to as direct (or causal) effects of predictors on criterion variables, and they are indicated by single headed arrows. Direct effects are expressed as path-coefficients (or standard partial regression coefficients). Other relations among traits are expected to be without any causal effect, and they are indicated by double headed arrows. These relations are expressed as correlations, using the Pearson product moment correlation coefficient. Indirect effects occur when a predictor (e.g. height) is correlated with another predictor (e.g. canopy openness), which itself has a direct effect on the criterion variable (e.g. a component trait). Similarly, the component traits (as predictors) may directly and indirectly affect crown traits (criterion variable). Indirect effects are calculated as the product of the correlation coefficient times the path-coefficient for the direct effect of the correlated predictor. Total effects of predictors on criterion variables are calculated as the sum of direct and indirect effects. Finally, compound effects are calculated as the direct effect of either height or canopy openness on one component trait, multiplied by the direct effect of this component trait on the focal crown trait. Thus, path-analysis indicates the change in a criterion variable (expressed in units standard deviation) as a result of a change of one unit standard deviation in each of its predictors, both direct and indirect (for calculations, Sokal & Rohlf 1981). Non-transformed values of component traits, except for the number of meristems (log transformation), were used as they did approach a normal distribution.

Finally, the influence of height and canopy openness on the production of new apical meristems (through the release of axillary meristems) was assessed, because this was expected to be the basic mechanism by which trees modify their number of apical meristems (see component trait in Figure 4.1). The origin was assessed for the apical meristems of 1994 relative to the monitored apical meristems of 1992. There were two possibilities: either the apical meristem was one of the apical meristems of 1992 ('apical origin'), or it originated from an activated axillary meristem ('axillary origin'). For each tree, the 'apical' or 'axillary' origin of the apical meristems (in 1994) was expressed as a percentage (the sum of them being equal to 100%). Multiple linear regression analysis was used to test whether origins changed with tree height, canopy openness, or their mutual interaction. The following model was used:

$$\text{apical origin (\%)} = c + (b_1 \times \text{height}) + (b_2 \times \text{openness}) + (b_3 \times \text{interaction}) + e \qquad (16)$$

Here, c is the constant (intercept), the b's represent the regression coefficients, and e is the error term.

4.3 Results

Crown development was related to tree height and canopy openness. Tree height and canopy openness were modestly (*Dicorynia*) to strongly (*Vouacapoua*) correlated with each other (Figure 4.2). Canopy openness varied between 0.8% and 11% in individuals shorter than 4 m, and between 4.8 and 30% in individuals from 4 to 20 m. In the few individuals taller than 20 m, canopy openness varied between 12% and 80%. In general, the taller trees were more exposed than the shorter ones, but the variation in canopy openness was large at a given height. Thus, the changes in crown development with increasing height may be the result of height, but also of an increase in canopy openness.

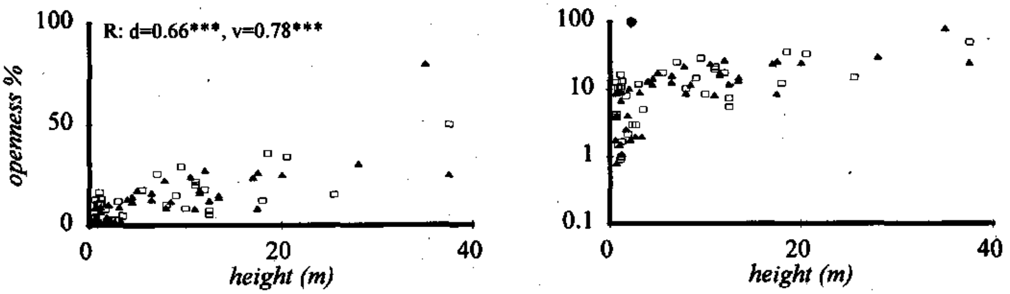


Figure 4.2. Canopy openness over trees of increasing height for Dicorynia guianensis *(d, open squares) and* Vouacapoua americana *(v, black triangles) in a tropical rain forest, French Guiana. The correlation between height and canopy openness is expressed by Spearmans' correlation coefficient R (two-tailed test, * = P<0.05; ** = P<0.01; *** = P<0.001), and was only calculated for trees shorter than 20 m. A plot with a log transformed Y axis is also given to show changes in canopy openness at lower heights.*

4.3.1 Component and crown traits related to tree height

Most of the component and crown traits were significantly correlated with tree height in the range of 0 to 20 m (Figure 4.3 & 4.4). Clearly, taller trees supported more apical meristems than shorter ones. In *Vouacapoua*, taller individuals produced fewer GU's per meristem. The shorter trees produced between 1 and 5 GU's per meristem in 2 years, while the taller trees produced only 1 GU per meristem in this period. In *Dicorynia*, there was no such relationship. Taller trees produced longer GU's (both species) and more leaves per GU (only for *Vouacapoua*), but the very tallest trees of *Vouacapoua* (35 and 37 m) produced shorter GU's and fewer leaves per GU. Both GU length and the number of leaves produced per GU varied considerably between trees of similar height. Trees of different height dropped a similar number of leaves per GU (both species). Up to 20 m, taller trees of both species had larger leaves. This correlation was weak, however, mainly because leaf size varied by an order of 10 in trees shorter than 10 m. In *Vouacapoua*, leaf size showed a maximum at intermediate tree height, as leaf size decreased in the tallest trees (27-37 m).

Crown traits were usually significantly correlated with tree height (Figure 4.4). Up to 20 m, taller trees supported more total leaf area, had a higher LAI, and spaced their leaves at increasing distance from each other (but not significantly for *Vouacapoua*). In the very tallest trees of *Vouacapoua* (27-37

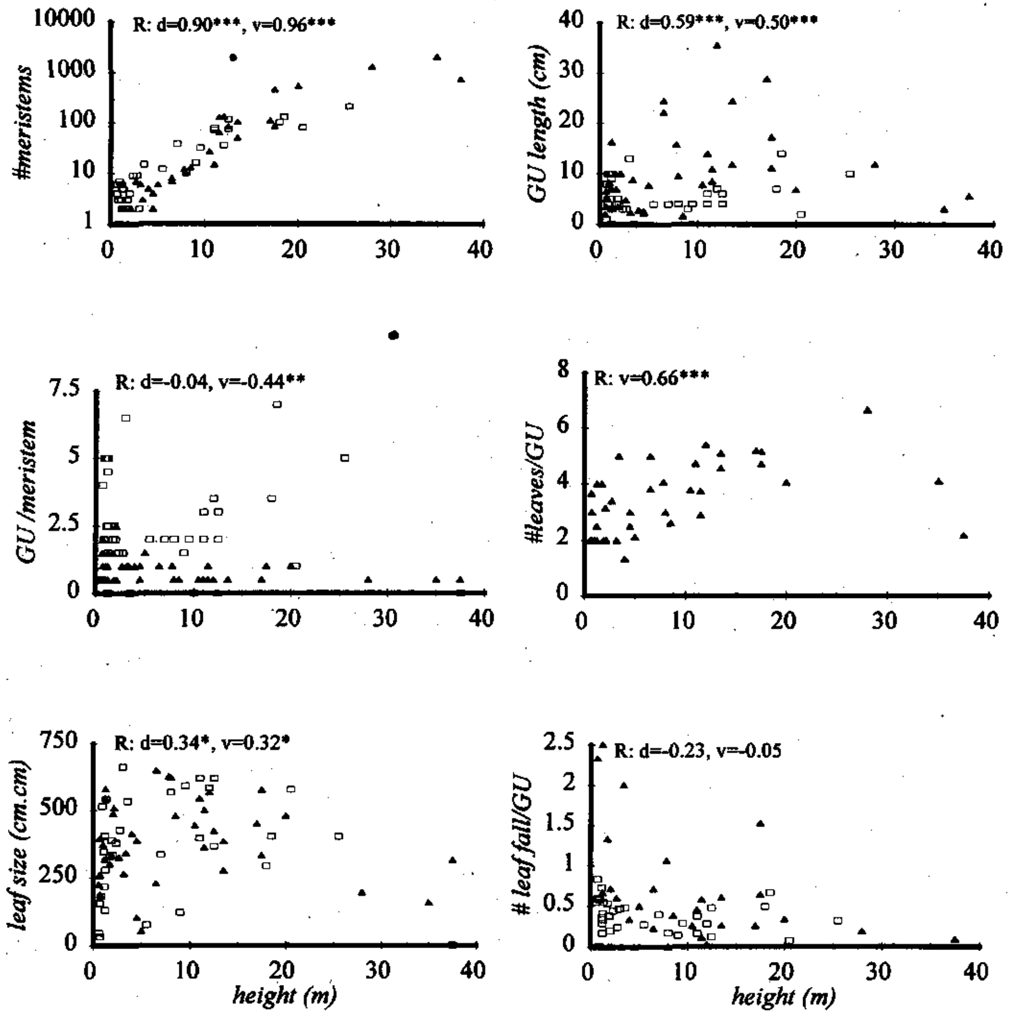


Figure 4.3. Component traits in trees of increasing height for Dicorynia guianensis *(d, open squares) and* Vouacapoua americana *(v, black triangles) in a tropical rain forest, French Guiana. Spearmans' correlation coefficients (R) were calculated to express the correlations between height and the component traits (two-tailed test, * = $P<0.05$; ** = $P<0.01$; *** = $P<0.001$), and were only calculated for trees shorter than 20 m. The number of produced leaves per GU (#leaves/GU) is not presented for* Dicorynia, *because it is 1 by definition.*

m), the total leaf area further increased, the LAI stabilised at 2.3-2.5, and the spacing between leaves decreased. Up to 20 m, taller individuals also produced more branch length and a longer leader than the shorter ones, but the very tallest individuals of *Vouacapoua* (35-37 m) did not further increase total branch growth and tended to produce shorter leaders. Finally, up to 20 m, taller trees produced

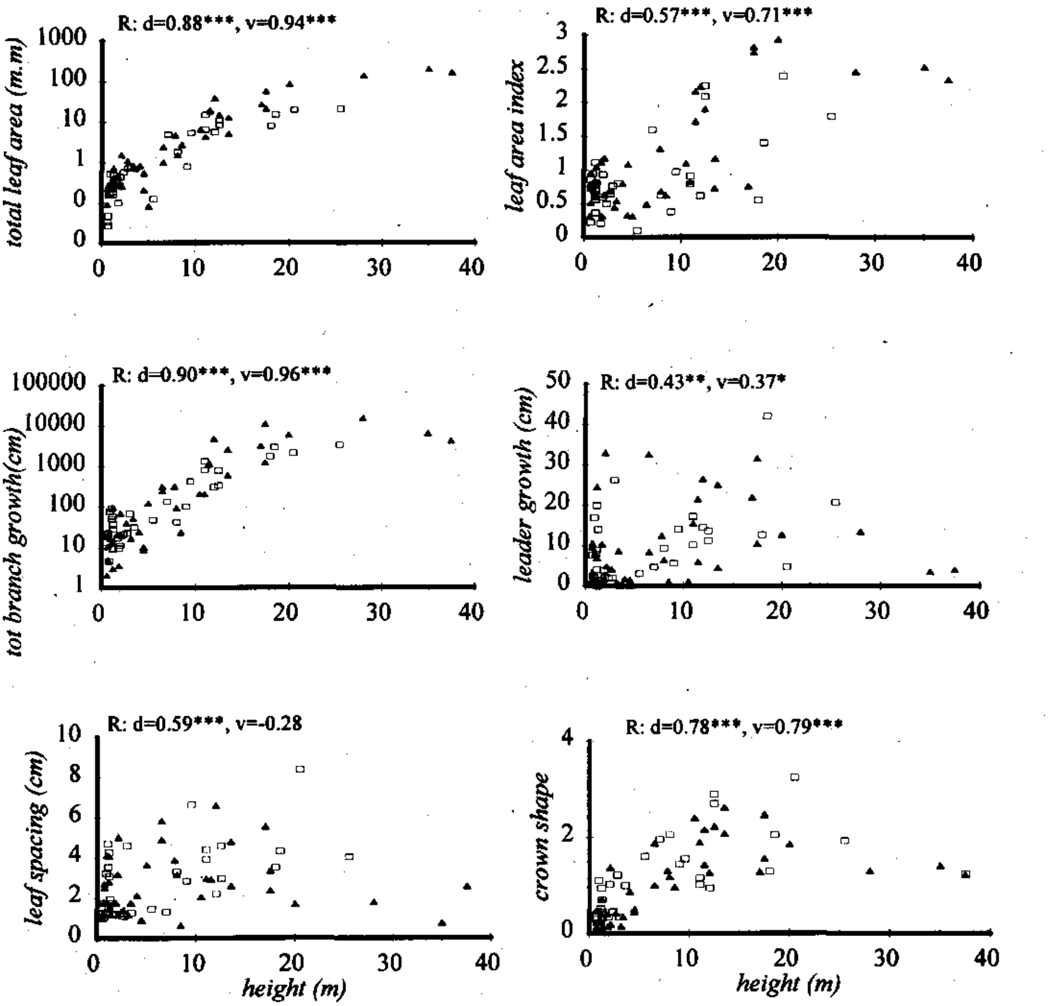


Figure 4.4. Crown traits in trees of increasing height for Dicorynia guianensis *(d, open squares) and* Vouacapoua americana *(v, black triangles) in a tropical rain forest, French Guiana. Spearmans' correlation coefficients (R) were calculated to express relations between height and crown traits (two-tailed test, * = $P<0.05$; ** = $P<0.01$; *** = $P<0.001$), and were only calculated for trees shorter than 20 m.*

more columnar shaped crowns than shorter trees. In the very tallest trees of *Vouacapoua* (27-37 m), crown shape became more planar.

4.3.2 Crown traits related to both height and canopy openness.

Multiple regressions of tree height and canopy openness on crown traits were all significant (Table 4.1), except the regression on leader growth of *Vouacapoua*. This analysis again shows that trees increased their total leaf area, total branch growth and the crown shape with increasing height. Trees of *Vouacapoua* also increased their total leaf area, branch growth, and crown shape under a more open canopy, but trees of *Dicorynia* increased only their total branch growth under a more open canopy. In *Vouacapoua*, trees increased their LAI by increasing in height, but the level of significance was low. Also, the LAI changed with the interaction term, suggesting that LAI increased with concurrent increases in tree height and light levels. In *Dicorynia*, trees did not significantly change their LAI in relation to height or canopy openness. Trees of both species spaced their leaves further apart from each other along the twigs under the more open conditions, while tree height did not significantly affect leaf spacing. Thus, the taller individuals of *Dicorynia* spaced their leaves further apart from each other (see correlation coefficient, Figure 4.4) because they were exposed to more open conditions, and not because they were taller. In both species, leader growth did not significantly increase with height or canopy openness, but the increases with canopy openness were close to significance (P values between 0.05 and 0.10 for both species).

Table 4.1. Multiple regressions of tree height (m) and canopy openness (%) on crown traits for juvenile trees (0.5-20 m tall) of two canopy tree species, Dicorynia guianensis *(N=33)and* Vouacapoua americana *(n=40), in a tropical rain forest, French Guiana. F-value of the regression (!!) and partial regression coefficients are shown.*

		Partial regression coefficients			
	F-value	Constant	Height (m)	Openness (%)	Interaction
Dicorynia					
10log total leaf area(m^2)	32.5 ***	-0.94 ***	0.140 ***	0.0181	-0.00162
leaf area index (m^2/m^2)	4.2 *	0.59 **	0.043	-0.0054	0.00064
leaf spacing (cm)	6.5 **	1.78 **	0.056	0.0392 *	0.00304
10log branch growth!(m)	52.0 ***	1.01 ***	0.116 ***	0.0340 **	-0.00155
leader growth (cm)	3.2 *	3.31	0.259	0.373	-0.00047
crown shape (m/m)	14.5 ***	0.26	0.130 ***	0.013	-0.00138
Vouacapoua					
10log total leaf area(m^2)	93.1 ***	-0.74 ***	0.111 ***	0.021 *	-0.00002
leaf area index (m^2/m^2)	12.6 ***	0.55 **	0.052 *	0.000	0.00115 *
leaf spacing (cm)	3.5 *	1.73 ***	0.046	0.096 *	-0.00240
10log branch growth!(m)	50.6 ***	0.74 ***	0.127 ***	0.036 *	-0.00026
leader growth (cm)	2.6	3.94	0.299	0.500	-0.00569
crown shape (m/m)	39.5 ***	-0.15	0.186 ***	0.056 **	-0.00627**

- ! total branch growth
-!! regression model, with regression coefficients b and error term e:
crown trait = constant + (b_1 x height) + b_2 x (openness) + (b_3 x (height x openness)) + e.
\- significance levels: * = $P<0.05$; ** = $P<0.01$; *** = $P<0.001$.

4.2.3 Path-analysis

Path-analysis quantifies the influences of tree height and canopy openness on the crown traits through their effects on different component traits. The significant effects, both direct and indirect, are illustrated by path-models (Figure 4.5). All the significant and non-significant relationship are presented in tables: the correlations among component traits (Table 4.2); the direct, indirect, and total effects of height and canopy openness on component traits (Table 4.3); the direct, indirect, and total effects of component traits on the crown traits (Table 4.4); and the compound effects of height and canopy openness on the crown traits (Table 4.5). The focus is further on the significant direct, indirect, and compound effects (Figure 4.5).

Table 4.2. Correlations among component traits of juveniles trees (0.5-20.0 m tall) of two canopy tree species, Dicorynia guianensis *and* Vouacapoua americana, *French Guiana. Pearsons' correlation coefficients were calculated.*

	<u>Component traits</u> (corresponding with numbers in left column)							
Component traits	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
<u>*Dicorynia*</u>								
(1) 10log (# meristems)	-							
(2) GU/meristem	-0.23	-						
(3) #leaves/GU								
(4) leaf fall/GU	-0.14	0.35 *		-				
(5) leaf size	0.31 *	0.01		0.01	-			
(6) GU-length	0.53**	0.11		-0.18	0.45**	-		
(7) GU/meristem leader	0.00	0.43**		0.42**	0.30	0.25	-	
(8) GU-length leader	0.68**	-0.05		-0.13	0.51**	0.72**	0.41*	-
<u>*Vouacapoua*</u>								
(1) 10log (# meristems)	-							
(2) GU/meristem	-0.44**	-						
(3) #leaves/GU	0.64**	-0.08	-					
(4) leaf fall/GU	-0.10	0.35*	0.33*	-				
(5) leaf size	0.29*	-0.21	0.19	-0.07	-			
(6) GU-length	0.53**	-0.14	0.75**	-0.02	0.36*	-		
(7) GU/meristem leader	-0.28	0.92**	-0.03	0.37*	-0.03	-0.09	-	
(8) GU-length leader	0.59**	-0.20	0.70**	-0.09	0.37*	0.91**	-0.12	-

- significance levels: * = $p<0.05$, ** = $p<0.01$ (two-tailed test).

Taller trees had more total leaf area mainly because they supported more apical meristems (Tables 4.3, 4.4 & 4.5, Figure 4.5). Indirectly, they also increased their total leaf area because they had larger leaves. The taller trees of *Vouacapoua* produced less GU's per meristem, but the negative effect of this on total leaf area was of minor strength. Trees of *Vouacapoua* also produced more total leaf area under more open conditions, mainly through the positive effect of canopy openness on the number of apical meristems, and indirectly by a larger leaf size. In *Dicorynia*, canopy openness did not affect total leaf area through any of the paths. Because LAI was calculated as the ratio of total leaf area over crown cover, the path-model of LAI was very similar to the path-model of total leaf area. In order to account for a change in crown cover, GU length was included in the set of component traits (Figure 4.5). In both species, taller trees produced a higher LAI because they supported more apical meristems (and thus more total leaf area, see above). In *Dicorynia*, this was the only path by which height affected

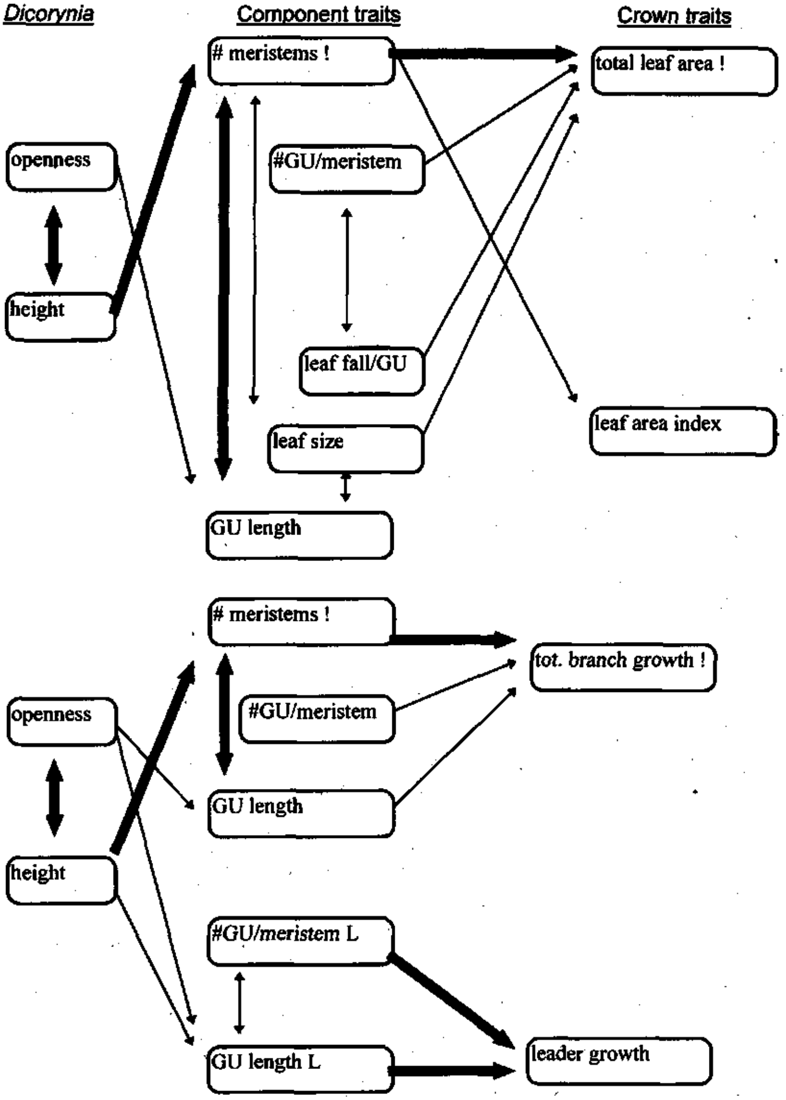


Figure 4.5. Path-diagrams presenting the effects of height and canopy openness on crown traits for the canopy tree species Dicorynia guianensis *and* Vouacapoua americana *in a tropical rain forest in French Guiana. The effects are split into two successive steps: (1), the effects of canopy openness and height on component traits; (2), the effects of component traits on crown traits. The significant correlations and effects are indicated by double - and single headed arrows, respectively (* for $P<0.05$, ** for $P<0.01$). Thick lined arrows indicate the stronger effects and correlations (b or r > 0.5), and thin lined arrows the weaker effects and correlations (b or r ≤ 0.5). Relationships were usually positive, and in case of a negative relationship a -sign is given. The non-significant relationships are not shown (see Figure 4.1). Significance levels for correlations are presented in Table 4.2, and for direct effects are presented in Tables 4.3 & 4.4.*

Vouacapoua

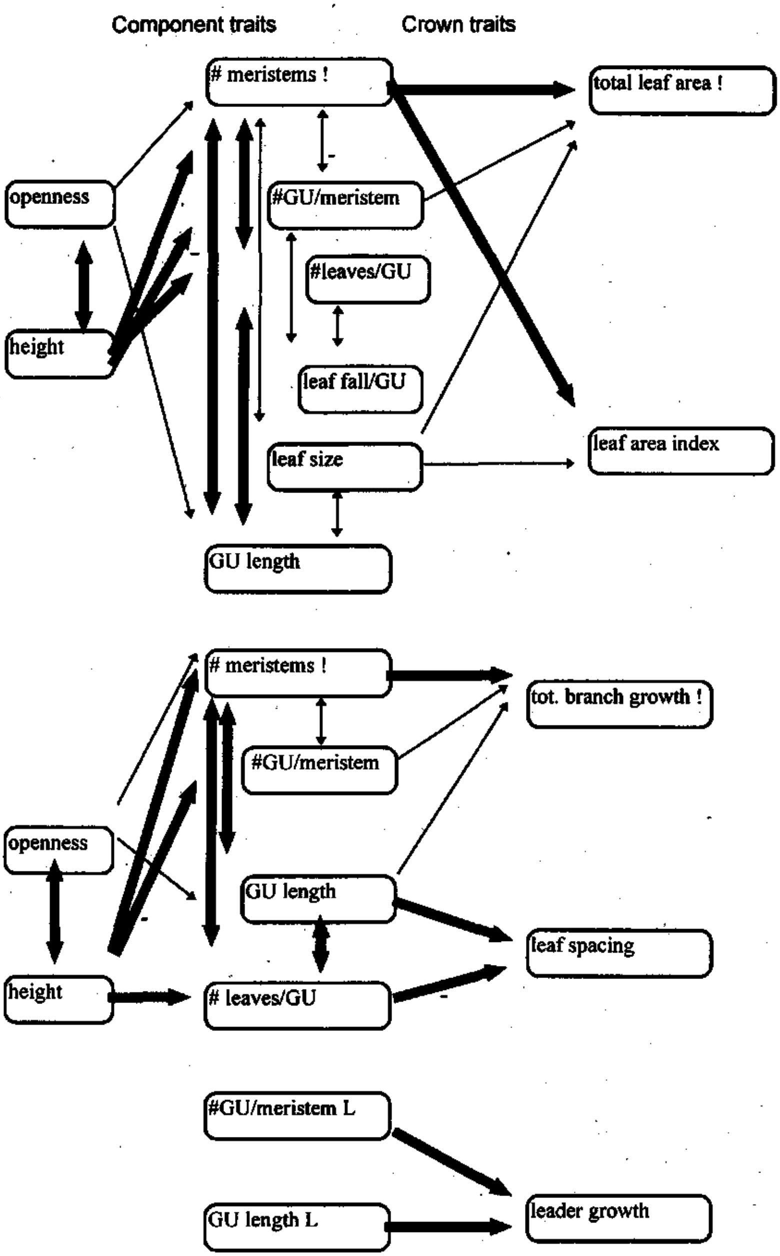


Figure 4.5 (second part).

Table 4.3. Effects of height and canopy openness on component traits for two canopy tree species, Dicorynia guianensis *and* Vouacapoua americana, *French Guiana. Direct, indirect, and total effects are presented.*

EFFECTS OF :	height on component traits:			openness on component traits		
	DIR	IND	TOT	DIR	IND	TOT
Dicorynia						
10log # meristems	0.89	0.01	0.90	0.03	0.58	0.61
GU/meristem	-0.27	0.23	-0.04	0.37	-0.19	0.18
#leaves/GU						
leaf fall/GU	-0.43	0.20	-0.23	0.27	-0.26	0.01
leaf size	0.35	-0.01	0.34	0.03	0.20	0.23
GU-length	0.35	0.24	0.59	0.37	0.22	0.59
GU/meristem (leader)	-0.07	0.15	0.08	0.28	-0.08	0.20
GU-length (leader)	0.47	0.22	0.69	0.34	0.31	0.65
Vouacapoua						
10log #meristems	0.84	0.12	0.96	0.17	0.64	0.81
GU/meristem	-0.60	0.16	-0.44	0.22	-0.49	-0.27
#leaves/GU	0.62	0.04	0.66	0.05	0.51	0.56
leaf fall/GU	0.02	-0.07	-0.05	-0.08	0.02	-0.06
leaf size	0.43	-0.11	0.32	-0.16	0.40	0.24
GU-length	0.19	0.31	0.50	0.41	0.17	0.58
GU/meristem (leader)	-0.42	0.15	-0.27	0.19	-0.32	-0.13
GU-length (leader)	0.36	0.20	0.56	0.27	0.27	0.54

- DIR is direct effect, IND is indirect effect, and TOT is total effect.
- for direct effects: underlined means significant, $P<0.05$ (single line), $P<0.01$ (double line)
- for indirect and total effects: significance levels cannot be calculated (see Sokal & Rohlf 1981)

LAI, and there was no path by which canopy openness affected LAI. Indirectly, the taller trees of *Vouacapoua* also had a larger LAI by their larger leaf size. Also, trees of *Vouacapoua* increased their LAI under the more open conditions through an increase in the number of apical meristems and, indirectly, by increasing their leaf size. The other paths did not cause significant changes in LAI.

In *Vouacapoua*, the taller trees did not space their leaves at shorter distances (see also regression analysis, Table 4.1). Apparently, the higher leaf production per GU was compensated by the larger GU length. In *Dicorynia*, leaf spacing is equal to GU length. For this species, the multiple regression shows that taller trees spaced their leaves at similar distances as shorter trees. Both species produced their leaves further apart from each other by producing longer GU's under more open conditions but, for *Vouacapoua*, this was partly compensated by the negative indirect effect of an increase in the leaf production per GU (Figure 4.5).

Taller trees produced more branch length because they supported more apical meristems. In *Vouacapoua*, taller trees produced less GU's per meristem, but the negative effect of this on total branch growth was of minor strength. Trees also produced more branch length at more open sites because they had more apical meristems (only for *Vouacapoua*) and produced longer GU's (both species). These findings parallel the results of the regression analysis, which showed positive effects of

Table 4.4. Effects of component traits on crown traits for two canopy tree species, Dicorynia guianensis *and* Vouacapoua americana, *French Guiana. Direct, indirect, and total effects are given.*

EFFECTS ON:

	total leaf area!			leaf area index			leaf spacing			total branch growth!			leader growth		
	DIR	IND	TOT	DIR	IND	TOT	DIR	IND	TOT	DIR	IND	TOT	DIR	IND	TOT
Dicorynia															
#meristems!	0.73	0.15	0.88	0.39	0.21	0.60				0.81	0.08	0.89			
GU/meristem	0.15	-0.28	-0.09	-0.13	-0.03	-0.16				0.28	-0.15	0.13			
#leaves/GU															
leaf fall/GU	-0.22	-0.04	-0.26	0.00	-0.13	-0.13									
leaf size	0.40	0.23	0.63	0.15	0.26	0.41									
GU-length				0.30	0.24	0.54			1.00	0.30	0.40	0.70			
GU/meristem L													0.65	0.19	0.84
GU-length L													0.45	0.26	0.71
Vouacapoua															
#meristems!	0.85	0.11	0.96	0.93	-0.20	0.73				0.88	0.05	0.93			
GU/meristem	0.11	-0.42	-0.31	0.35	-0.40	-0.05				0.24	-0.43	-0.19			
#leaves/GU	0.09	0.59	0.68	-0.02	0.47	0.45	-0.54	0.98	0.44						
leaf fall/GU	0.01	-0.03	-0.02	0.10	0.01	0.11									
leaf size	0.26	0.18	0.44	0.32	0.03	0.35									
GU-length				-0.24	0.54	0.30	1.29	-0.40	0.89	0.30	0.42	0.72			
GU/meristem L													0.53	-0.09	0.44
GU-length L													0.84	-0.06	0.78

- ! means that log transformed values were used.
- DIR is direct effect, IND is indirect effect, and TOT is total effect.
- for direct effects: underlined means significant, P<0.05 (single line), P<0.01 (double line)
- for indirect and total effects: significance levels were not calculated (see Sokal & Rohlf 1981)
-L, for leader traits

both height and canopy openness on total branch growth (Table 4.1).

Trees of *Dicorynia* produced more leader growth when they were taller, as well as when they grew under more open conditions, mainly by producing longer GU's. Trees of *Vouacapoua* showed the same trends with respect to canopy openness, but these trends were not significant (effect of canopy openness on GU length, P=0.06).

4.3.4 Height, light and apical meristem production

The compound effects (Table 4.5) indicate that trees of *Vouacapoua* changed their total leaf area, LAI, and branch growth mainly through the effects of both height and canopy openness on the number of apical meristems. The influence of canopy openness can only be explained by an increase in axillary meristem release (axillary meristems start to develop and turn into apical meristems) at more open conditions. In *Dicorynia*, there was no significant effect of canopy openness via this component trait, and axillary meristem release was therefore not expected to change with canopy openness.

Multiple linear regression analysis was used to show whether tree height and/or canopy openness affect the rate of branching (and thus the rate of apical meristem production) in either of the two

Table 4.5. Compound effects of height and canopy openness on crown traits for two canopy tree species, Dicorynia guianensis *and* Vouacapoua americana, *French Guiana. The compound effects are the effects of height and canopy openness, through component traits (in rows), on crown traits (in columns).*

EFFECTS ON:	total leaf area		leaf area index		leaf spacing		tot branch growth		leader growth	
EFFECTS OF:	height	openness	height	openness	height	openness	height	openness	height	openness
Dicorynia										
#meristems!	0.65	0.02	0.35	0.01			0.72	0.02		
GU/meristem	-0.04	0.06	0.04	-0.05			-0.08	0.10		
#leaves/GU										
leaf fall/GU	0.09	-0.06	-0.00	0.00						
leaf size	0.14	0.01	0.05	0.00						
GU-length			0.11	0.11			0.11	0.11		
GU/meristem L									-0.05	0.18
GU-length L									0.21	0.15
Vouacapoua										
# meristems!	0.71	0.14	0.78	0.16			0.74	0.15		
GU/meristem	-0.07	0.02	-0.21	0.08			-0.14	0.05		
#leaves/GU	0.06	0.00	-0.01	-0.00	-0.33	-0.03				
leaf fall/GU	0.00	-0.00	0.00	-0.01						
leaf size	0.11	-0.04	0.14	-0.05						
GU-length			-0.06	-0.10	0.25	0.53	0.06	0.12		
GU/meristem L									-0.22	0.10
GU-length L									0.30	0.23

- ! means that log transformed values were used.
- L for leader traits

Table 4.6. Multiple regressions of the apical origin of the apical meristems in 1994 (%) on tree height (m), canopy openness (%) and their interaction. The apical meristems (in 1994) originated either from apical meristems in 1992 (apical origin), or from axillary meristems which started to develop between 1992 and 1994 (axillary origin, see text).

		PARTIAL REGRESSION COEFFICIENTS			
Apical origin (%)	F-value	Constant	Height (m)	Openness (%)	Interaction
Dicorynia	9.1**	69.7***	0.88 **	ns	ns
Vouacapoua	7.6**	88.8***	ns	-1.39 **	ns

- !! regression model, with regression coefficients b and error term e:
  apical origin = constant + (b_1 x height) + b_2 x (openness) + (b_3 x (height x openness)) + e.
- asterices indicate significance levels: * for $P<0.05$; ** for $P<0.01$; *** for $P<0.001$.

species (Table 4.6). In *Dicorynia*, the taller trees have a smaller fraction of apical meristems that originated from axillary meristem release than shorter trees. Thus, the taller trees of this species branched less frequently, and increased their number of apical meristems only because they were older (and branched over a longer time span). The fraction of apical meristems that resulted from axillary meristems was not affected by canopy openness. In *Vouacapoua*, however, the fraction of apical meristems that originated from axillary meristems did not change with tree height. Thus, the taller trees of *Vouacapoua* had more apical meristems because they were larger, and not because they branched more (or less) frequently. As expected, trees of *Vouacapoua* branched more frequently under more open conditions. This is consistent with the positive effect of canopy openness on the number of apical meristems, as was shown by the path-analysis (Figure 4.5, also Table 4.3).

4.4 Discussion

Crown development in juvenile trees changed both with height and canopy openness. These changes are further discussed from four major perspectives. Firstly, these changes are discussed for juveniles from 0-20 m, emphasising the mechanisms of crown development on the basis of path-analysis. Secondly, the crown development of the taller individuals (26-37 m) is compared with these 0-20 m tall juveniles. Thirdly, the present study is compared with a study in which the crown development of juveniles of the same species was compared between two contrasting light environments (Chapter 3), instead of in relation to a gradient of light availability (this chapter). The implications of these and related approaches are further discussed. Finally, the benefits and short-comings of path-analysis as a tool to study crown development during ontogeny are briefly evaluated.

4.4.1 Changes in crown development with height

The changes in crown development with height were similar in both species. In general, total leaf area, LAI, total branch growth, and crown shape increased with tree height, as was shown by highly significant correlations and multiple-regression analyses (but significance was low for LAI in *Dicorynia*). Leaf spacing (only *Dicorynia*) and leader growth were also positively correlated with tree height, but the regression analysis did not show a significant influence of height on these crown traits.

Using path-analysis it was shown that the taller trees had a higher total leaf area and larger LAI than shorter trees because they had more apical meristems and also, but indirectly, because they had larger leaves. The increase in LAI with tree height was found for other species as well (Fisher & Hibbs 1982, Borchert & Tomlinson 1984). Other studies reported on LAI's of various tree species, but did not relate LAI to tree height (e.g. Ashton 1978, Honda & Fisher 1979, Canham 1988). Alvarez-Buylla and Martinez-Ramos (1992) reported increasing total leaf area with tree height for the pioneer tree *Cecropia obtusifolia* in a Mexican rain forest. Similar to *Dicorynia* and *Vouacapoua, Cecropia* increased its total leaf area exponentially with tree height. The < 2 m and 10-20 m tall *Cecropia* trees had similar amounts of total leaf area as *Dicorynia* - and *Vouacapoua* trees of the same height. The 2-10 m tall *Cecropia* trees had a larger total leaf area. When growing from seedling to 10 m tall tree, *Cecropia* increased its total leaf area by increasing its leaf size by more than 100-fold, while *Dicorynia* and *Vouacapoua* showed a very minor increase in leaf size. Instead, *Dicorynia* and *Vouacapoua* increased their total leaf area by growing from pole saplings (1 meristem) to branched trees with around 20 living apical meristems. Conversely, *Cecropia* usually had only one apical meristem within this height range. Above 10 m, *Dicorynia* and *Vouacapoua* further increased their total leaf area by producing more apical meristems. At the same height, *Cecropia* also started to increase its total leaf area by producing more apical meristems (or branches, *sensu* Alvarez-Buylla & Martinez-Ramos 1992), and not by a further increase in its leaf size. These interspecific differences in the ways trees produce total leaf area may result from differences in qualitative growth patterns. *Dicorynia* and

Vouacapoua branch early during ontogeny as described by Troll's model. In contrast, *Cecropia* starts as one long pole axis, and is described by Rauh's model (Alvarez-Buylla & Martinez-Ramos 1992).

Taller trees also produced more branch length because they had more apical meristems. We are not aware of any other study on changes in total branch growth with tree height. Crown shape was not related to component traits, but increased with tree height. In contrast, on the basis of profile diagrams, Givnish (1984) hypothesised that trees decreased their crown shape with height. However, these profile diagrams do not distinguish between different species, and they include trees taller than 20 m in the overstorey.

Leaf spacing and leader growth did not change with tree height when canopy openness is held constant. We are not aware of other studies on changes in leaf spacing with height. The lack of change in leader growth with height contrasts with an increase in median leader growth with increasing height class of these species (Chapter 5). For height growth, which is expected to be correlated with leader growth, Clark and Clark (1992) found increasing median growth with increasing size class in six Costa Rican tree species. The variation in leader growth in the present study was too large to show any significant increase in leader growth on the basis of multiple regression analysis.

4.4.2 Crown development in relation to canopy openness

Trees of *Dicorynia* did not change their total leaf area, crown shape, or LAI in response to light availability. In contrast, trees of *Vouacapoua* produced greater total leaf areas, more columnar shaped crowns, and larger LAI, at higher light availability. These responses in *Vouacapoua* occurred by enhanced axillary meristem release at higher light availability. Although the bifurcation ratio was not directly measured for our species, *Vouacapoua* is likely to increase its bifurcation ratio through axillary meristem release (see Canham 1988). Thus, in contrast to *Dicorynia*, *Vouacapoua* displayed its leaves consistent to the arguments of Leopold (1971), Horn (1971), Whitney (1976), and Borchert and Tomlinson (1984). Leopold (1971) and Whitney (1976) argued that high bifurcation ratios should be more efficient (in terms of stem tissue used for leaf display) for columnar crowns (high crown shape) in the higher light environment, while low bifurcation ratios should be more efficient for planar crowns (low crown shape) at lower light levels. Indeed, higher bifurcation ratios were found in trees growing at higher light availability, both in tropical forest tree species (Shukla & Ramakrishnan 1986) and in temperate forest tree species (Steingraeber *et al*. 1979). Horn (1971) stated that trees with more columnar crowns and a higher LAI may have functionally efficient leaves (above light compensation point) and reduce their costs to support a given total leaf area (see also Borchert & Tomlinson 1984) under high light levels. In contrast, trees with more planar crowns and a lower LAI may avoid self-shading of leaves under low light levels, but are subject to higher support costs. However, this measure of support costs for leaf display refers to the construction of the crown (cost of support over the whole tree life-history), and not to the production costs of the amount of supported leaf area (costs of support during latest period of tree life-history).

While in the present study *Dicorynia* did not show significant changes in total leaf area, crown shape, and LAI to light, the 4-10 m tall trees of *Dicorynia* (and of *Vouacapoua* as well) were found to have larger total leaf areas and larger LAI's in very large gaps (>200 m^2) rather than below a closed canopy (Chapter 3). Thus, including the high light levels associated with these large gaps, *Dicorynia* trees may exhibit the same direction of response as was found for *Vouacapoua* in the present study. Similar to *Dicorynia*, *Acer saccharum*, a temperate tree species, did not show this direction of response when fully exposed sites (highest light levels) were not included (Canham 1988, Bonser & Aarssen 1994), while it showed a response when individuals in deep shade were compared with individuals in full-sun sites (Steingraeber *et al.* 1979). In fact, each of these species show the same direction of response when deep shaded individuals are compared with open grown trees, but some species may not show this response at the more common, but smaller, ranges of light availability in the forest. In case a response would only occur outside the range of light levels in the forest, the ecological value is nil for the species in its natural habitat. Conversely, if the response is within the range of light levels in the forest, it is expected to be of ecological value.

Trees of *Dicorynia* and *Vouacapoua* spaced their leaves at shorter distances at decreasing light availability. This was also found by King (1991c, 1993, 1994) in 1-2 m tall saplings (see also the Chapters 2 & 3). The space between leaves represents the average size of the woody unit that supports one leaf, and may be used to infer relative costs of displaying leaf area (e.g. Canham 1988, King 1991c). These costs were not affected by leaf size, as leaf size did not change in relation to light (see also Chapter 3). As trees displayed their leaf area more economically in a light limited environment, they increased their light interception per carbon investment and lowered their whole plant compensation point. It follows that they may therefore be better able to survive in the shade (Givnish 1988, King 1991c). Thus, whereas Horns' (1971) and Borchert and Tomlinsons' arguments (1984) suggest higher support costs for leaf display at lower light availability, trees produced their leaves at lower costs at low light availability.

Canham (1988) calculated costs of leaf display for two shade tolerant species of temperate forests, using the same criterion of leaf spacing. He found no differences in the costs of displaying leaf area (*Fagus grandiflora*) between gaps and understorey, or even lower costs at the higher light availability in gaps (*Acer saccharum*). These temperate trees may not space their leaves at shorter distances in shaded conditions as *Dicorynia* and *Vouacapoua* because they occur at higher light levels. Unfortunately, there is no data to compare the light environments of *Dicorynia* and *Vouacapoua* directly with the light environments of *Acer* and *Fagus*. In general, however, tropical rain forest trees may occur at lower light levels due to a larger vertical gradient in light availability (Terborgh 1985), if this gradient would reduce light availability to lower levels in tropical rain forest than in temperate forest. Indeed, Canham *et al.* (1990) found lower PAR transmission in a tropical rain forest site than in four temperate forest sites, including Northern hardwoods with *Acer saccharum* and *Fagus grandiflora*. As these sites were exposed to similar open sky PAR levels during the growth season (calculated from potential PAR data and growth season length), light levels may indeed be further reduced in the tropical rain forest site.

Height growth enables trees to reach adult stature and reproductive status. Leader growth in juvenile trees is expected to be highly correlated with height growth, as the leader may be a part of the future stem (Chapter 5). In both species, leader growth was not significantly affected by canopy openness (P=0.06 for both species). In contrast, it was shown that 4-10 m tall gap trees had more than 10 fold higher leader growth than understorey trees (Chapters 3 & 5). Thus, despite the lack of significant results in this study, both species seem to respond to high light levels associated with large gaps by more extensive leader growth. As such, large gaps may enable trees of both species to reach reproductive status more rapidly, given that the onset of reproduction is related to tree height (see Thomas 1996b). Moreover, the leaders in gap individuals grew faster than other equivalent axes in the crown, while there was no difference between leader and axes in understorey individuals (Chapter 3). Although this growth pattern could not be shown from the data in the present study, such a growth pattern may account for the more columnar shaped crowns of *Vouacapoua* trees in more open conditions.

4.4.3 Juveniles up to 20 m compared with taller (26-37 m) individuals

As expected, the taller trees had higher total leaf areas and more branch growth than juvenile trees. This was paralleled by higher numbers of apical meristems (see also, Alvarez-Buylla & Martinez-Ramos 1992). At the same time, these trees seemed to have smaller leaves. Similarly, Thomas (1995) found that adults of most canopy tree species had smaller leaves than juveniles of the same species, probably because the adults were exposed to full sun. In the 35-37 m tall trees (N=3), leader growth was very low (4 cm per year). This indicates that these tall trees had fully expanded vertically. Their leaders may not account for significant (vegetative) height growth, but rather for the production of new leaves, flowers, and fruits. As such, their leaders were functionally equivalent to other shoots in the crown (see also Chapter 5).

Whereas crown shape and LAI increased with tree height in juvenile trees, crowns were of more planar shape (lower crown shape) and LAI did not further increase in taller trees. These patterns may result from a shift to a much larger crown width in these taller trees (Bongers & Sterck in press). Similarly, Bongers *et al.* (1988b) and King (1991a, 1996) found extensively increasing crown widths in the taller trees in a Mexican and Costa Rican rain forest, respectively. These increasing crown widths in taller trees may account for a decrease in the crown shape, and correspond with the increasingly open canopy at these height levels in the Nouragues forest (Koop & Sterck 1994). This parallels the decrease in crown shape with increasing height in the forest, as depicted from profile diagrams (e.g. Givnish 1984, Richards 1952, 1983). Given that open grown *Dicorynia* and *Vouacapoua* trees in plantations increase their crown width at lower stature (personal observation Sterck), these shifts to wider crowns are likely to be caused by the increasing light (and space) availability, and not by the increase in height. The large increase in crown width under open, well-illuminated conditions, may help these trees to shade shorter tree neighbours and to occupy the space before neighbours of similar stature grow in.

The LAI did not further increase, and remained below 3, with increasing tree height in these > 26 m tall trees. Following Horns' arguments (1971), the LAI may increase with increasing sun exposure as long as the most shaded leaves at the bottom of the crown remain above the compensation point. Thus, because light levels still increased between 20 and 35 m (see also, Koop & Sterck 1994, Chapter 5), Horns' hypothesis would predict a further increase in the LAI. As this is not the case, other constraints than the light availability seem to limit a further increase in the LAI. Possibly, the large increase in crown width in combination with constraints on leaf production limit further increase in the LAI.

4.4.4 Methodological constraints on the study of growth responses to light availability

As mentioned earlier, crown development was compared between 4-10 m tall gap (>20% canopy openness) and understorey individuals (1-5% canopy openness) in Chapter 3. Gap individuals had larger total leaf area, LAI, and branch growth in both species. Thus, under extreme light conditions, both species showed the same direction of response. In the present study, *Vouacapoua* showed the same direction of response to an increase in light availability. The lack of significant results for *Dicorynia* (it tended to follow the same direction of response as *Vouacapoua*) may partly result from errors in estimating light availability: Firstly, canopy openness estimates below 10 % are less accurate due to the halo-effect (Whitmore *et al.* 1993). Secondly, canopy openness may not be a good estimate of the light environment of the whole crown, as light levels vary considerably within crowns, especially in the understorey of the forest (Oberbauer *et al.* 1988, Chazdon *et al.* 1988). Consequently, individuals with the same canopy openness value may in fact be exposed to different levels of light availability. Thirdly, estimations of the light environment were based on values at one point in time. However, the light environments of trees may fluctuate in time, both on a scale of months (Clark *et al.* 1996) and years (unpublished data, Sterck). Thus, the crown traits may not reflect a response to the measured estimate of light availability, but rather reflect an integrated response to successive light environments in time (see, e.g. Ackerly in press). These confounding factors do not occur when individuals are compared between contrasting light environments (Chapter 3), but are likely to result in under-estimation of the responses to light availability in the present study.

In general, the different results between these two studies, as well as between studies on other species (see example below), depend on the light ranges that are considered, as well as on the response type of the species. For example, in saplings of *Acer saccharum*, Canham (1988) did not find a change to more columnar shaped crowns at higher light availability. In contrast, Steingraeber *et al.* (1979) found more columnar shaped crowns for saplings of the same species in open grown saplings as compared with forest grown saplings. It is probable that trees only respond to full sunlight with the more columnar crown shapes, but not to a light range up to approximately 25% of full sunlight as was considered by Canham. Thus, the studied light range in combination with the type of response determine whether any response is observed or not.

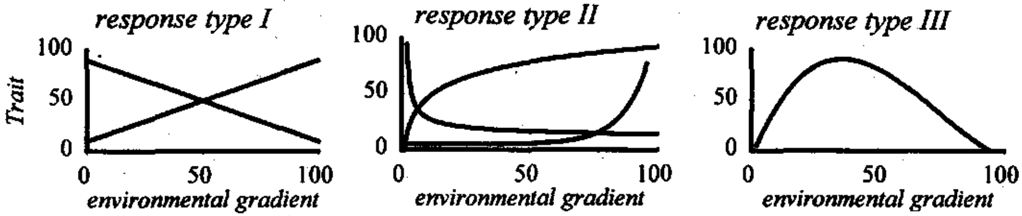


Figure 4.6. Three possible types of response in a plant trait to an environmental gradient (e.g. light availability in percentages from the open sky). The response type I is linear, either increasing or decreasing; The response type II is curved (three examples are given), either increasing or decreasing; The response type III is a bell shaped curve, with an increase followed by a decrease (see graph), or vice versa (not shown). A fourth possibility would be no response at all (not shown).

The influence of the response type in relation to changes in light availability may be complex. This is illustrated by the effects of three hypothetical response types (Figure 4.6). In case of response type (I), a linear response, different ranges of light availability do not affect the observed direction of morphological response, but the larger the light range the easier the response is demonstrated at a given level of variation. In case of response type (II), a curved response, different ranges do not affect the direction of response, but may affect the magnitude of response. Some light ranges cause a large response, while other ranges cause only a minor response which is harder to demonstrate at a given level of variation. In case of response type (III), a bell shaped response, different light ranges may result in responses of the same direction, in responses of opposite direction, or in no response at all. In general, the problems of conflicting results, as shown by the example of *Acer*, can be overcome by observing morphological responses of trees at many different light levels in controlled experiments (e.g. Veenendaal *et al.* 1996, Ducrey 1992). The taller individuals, however, are hard to grow under controlled conditions, and their responses should be observed along the whole gradient of light levels in the forest. These responses may be subject to large variation, because individuals differ in growth history and current environment. Individuals under extremely (and relatively rare) high light levels should be searched for in large gaps in order to cover the whole range of light availability.

Thus, apart from the difficulties to measure canopy openness accurately, this reasoning provides new arguments to explain the differences in responses between the two study species. *Vouacapoua* responded to a lower range of light availability than *Dicorynia*, the latter of which showed the same direction of response at extremely high light levels only. This indicates that most of these responses are of type II in *Dicorynia* and of type I or II in *Vouacapoua.*

4.4.5 Path-analysis: the general issue

Path-analysis may cause some difficulty in the interpretation of the results. On the basis of the present study and another study on the same species (Chapter 3), it is shown that non-significant paths do not mean that these relationships do not exist. Moreover, path-analysis describes linear relationships, but relationships between height or canopy openness with plant traits may not be linear. Transformations of plant trait values may help to make relationships linear, but not in all cases.

Path-analysis has some advantages over multiple regression analysis. In this study, it enabled us to determine the major paths by which the trees changed their crown traits with height and light availability. Moreover, path-analysis quantifies the effects of a given component trait on different crown traits, and thus indicates the various ecological consequences of a change in one component trait. We think that, in general, path-analysis is a very useful tool to understand crown development.

On the basis of this study, it is concluded that changes in crown development and morphology during the ontogeny of tropical rain forest trees depend on height and light environment. The influence of light may be underestimated (relative to the influence of height) because of measurement errors, light variation in space and time, and the small range of light availability that was considered. Interestingly, both species showed the same direction of response to light availability, but may respond to different ranges of light availability. Moreover, these species may respond differently to fluctuations in the light environment, as was shown for tree species in other tropical rain forests (e.g. Ackerly in press). Long-term observations are needed to show how crown development is affected by light availability in the long run. Accompanying observations on fitness components of individual trees, i.e. vegetative growth, survival, and the onset and amount of reproduction, may then provide information on the ultimate ecological consequences of crown development. Such observations are currently carried out for these two species in the Nouragues rain forest in French Guiana.

5

HEIGHT GROWTH, LIGHT, AND TREE AGE

with Frans Bongers

Abstract

1. The growth of the leader shoot was investigated for 0-37 m tall trees of two canopy tree species in the 'Nouragues' tropical rain forest in French Guiana. For trees less than 20 m tall, leader growth was related to tree height and light availability. Light availability was estimated on the basis of two methods: the visual crown position index, and canopy openness (%) as assessed from hemispherical photographs. Leader growth was used to calculate the ages for trees up to 20 m tall.

2. For the same species, leader growth of 4-10 m tall trees was compared between large gaps and the understorey in the 'Piste' forest in French Guiana. Levels of light availability were assessed for these trees, using the same two methods already described above. The results of this study were referred to only briefly.

3. Although light levels varied widely at a given tree height, the taller trees occurred in more open conditions than shorter individuals. The taller trees had higher leader growth than the shorter individuals, mainly because they were exposed to higher levels of light availability, and not because they were taller. On the basis of the Piste study, it was shown that leader growth was approximately ten times larger in gap individuals than in understorey individuals. Thus, the leader growth in the more shaded trees was limited by light availability.

4. Similarly, the median leader growth rates increased gradually with height because of increasing light levels. Maximum leader growth increased with height in the lower height classes, but stabilised in the height classes above 1 to 2 m. It is hypothesised that this early cease in maximum leader growth resulted from reduced apical dominance of the leader over other meristems. Consequently, a larger part of fixed carbon was directed towards axillary meristems, and not to one single leader.

5. A 20 m tall tree was estimated to have a minimum age of 68 (*Vouacapoua*) or 84 years (*Dicorynia*), and a median age of 235 (*Vouacapoua*) or 288 years (*Dicorynia*). The age estimates of *Dicorynia* and *Vouacapoua* were low compared with such figures of species at other tropical rain forest sites. This was either due to less favourable growth conditions in the Nouragues forest, or to the use of different estimates for tree age.

5.1 Introduction

In tropical rain forests, height growth rates have great impact on the ability of trees to compete for light (e.g. Kohyama & Hotta 1990), and on the time by which trees become reproductive (e.g. Thomas 1996b). Trees gradually cease height growth late in ontogeny (e.g. Hallé *et al.* 1978, Thomas 1996a). Besides, trees also have different height growth rates at different levels of light in the forest understorey (Clark & Clark 1992). The availability of light is highly variable in this habitat, both in space and time (Chazdon & Fetcher 1984). Consequently, height growth varies between trees of the same species, and between life time periods of the same tree (Clark & Clark 1992).

Changes in the growth of tropical rain forest trees with ontogeny are usually presented by diameter growth rates (e.g. Lang & Knight 1983, Primack *et al.* 1985, Lieberman & Lieberman 1985, Lieberman *et al.* 1994, Welden *et al.* 1991), and only scarcely by height growth rates (e.g. Alvarez-Buylla & Martinez-Ramos 1992, Clark & Clark 1992). This lack of height growth data is due to the difficulty to measure height growth properly for tropical rain forest trees. In temperate zone trees, height growth curves are used to assess height growth rates through ontogeny. Tree height is plotted against age, and the slope of the curve represents the height growth rate. Unfortunately, such curves are hard to construct for trees in tropical rain forests, because these trees lack age markers in the form of growth rings (Bormann & Berlyn 1981, Baas & Vetter 1989). Other age markers of trees are usually hard to obtain (e.g. Jacoby 1989, Worbes & Junk 1989).

Therefore, alternative methods were used to assess height growth in tropical rain forest trees. Height growth was assessed by making measurements on height at successive censuses in time (Martinez-Ramos *et al.* 1989, Alvarez-Buylla & Martinez-Ramos 1992, Clark & Clark 1992). O'Brien *et al.* (1995) estimated age at a given diameter on the basis of mean diameter growth in successive diameter classes (see also Lieberman & Lieberman 1985). They correlated height with stem diameter and the corresponding tree age. As such, they provided the data to construct height growth curves. In general, data on height growth of tropical rain forest trees remains scarce however.

In this chapter, an alternative method is presented to estimate height growth in trees. The method is applied to two canopy tree species of a tropical rain forest in French Guiana. Height growth of both species is expected to be determined by the length increment of the leader (leader growth), i.e. the shoot by which a tree achieves height gain. Leader growth was assessed for trees of different height (up to 37 m), and was related to estimates of light availability. In addition, this data was used to estimate ages for trees of different height.

5.2 Methods

5.2.1 Site and species

Field work was carried out in lowland tropical rain forests at two biological field stations in French Guiana; 'les Nouragues' of C.N.R.S. and 'Piste St. Elie' of the O.R.S.T.O.M. de Cayenne. The study species were the two canopy tree species *Dicorynia guianensis* Amshoff. (Caesalpiniaceae) and *Vouacapoua americana* Aubl. (Caesalpiniaceae). They are further referred to by their generic names only. For site and species description, see Chapter 1.

5.2.2 Selection of individuals

At the Nouragues forest site, tree populations of both species were inventoried in October 1992, as part of a long-term study on the vegetative growth of these tree species (see also Chapter 4). A 12-ha plot was searched for trees with a stem diameter >=10 cm at 1.30 m (DBH). A central 1.5-ha plot was searched for trees with a trunk diameter <10 cm, but with a height above 50 cm. The central 0.5-ha strip was inventoried for individuals <=50 cm tall.

Individuals were selected in order to make detailed observations on their light environment, height, and leader growth. Of the population, all individuals shorter than 5 m were selected (N=101 for *Dicorynia*, and N=49 for *Vouacapoua*), and were measured from ground-level. For trees taller than 5 m, tree neighbours were climbed (using spikes or alpinist ropes) to make measurements. Because few inventoried individuals could be measured as such, accessible trees taller than 5 m were searched outside the inventoried plots and added to the study. Most of these individuals were between 5-20 m tall (N=13 for *Dicorynia*, and N=20 for *Vouacapoua*). Only five trees greater than 20 m were found to be accessible, three for *Vouacapoua* (27, 35, and 37 m) and two for *Dicorynia* (26, 35 m). Three of these trees were measured by climbing alpinist ropes, and the two others from aerial walkways. Thus, leader growth was compared among trees which occurred along a 'continuous' range of light availability in the Nouragues forest.

At the Piste St Elie forest site, juveniles were inventoried in the understorey (understorey individuals) and in treefall gaps (gap individuals) in November 1991 (see also Chapter 3). Gaps were large (>200 m^2 *sensu* Brokaw 1982) and fresh (<3 months). For each species, five individuals were selected in the understorey, and five individuals of similar height were selected in gaps. Understorey and gap individuals were matched as to differ no more than 20% in height at the start of the experiment. Heights ranged from 4 to 10 m, except for one pair of *Vouacapoua* (15-18 m). Thus, at the Piste forest site, leader growth was compared between juvenile trees in highly contrasting light environments.

5.2.3 Field measurements

Tree height was measured in 1992 (Nouragues site) or 1991 (Piste site), using a folding ruler. Tree height was measured as the vertical distance between the stem base and the base of the upper most apical meristem in the crown.

Light availability was estimated using two different methods. Light was visually estimated on an annual basis between 1992 and 1994 (Nouragues) and between 1991 and 1994 (Piste), using the Crown Position Index (CPI) of Clark & Clark (1987, 1992, adapted from Dawkins & Field 1978). The index was based on the vegetation structure around and above the focal tree: 1= no direct light; 2= crown lit only from the side; 3= partial (10-90%) vertical illumination; 4= full vertical illumination; and 5= fully exposed to vertical and lateral light. The category 2 was subdivided into high (= 2.5, exposed to at least one major or multiple medium-sized openings), low (= 1.5, no large or medium openings), and intermediate categories (= 2, see also Clark & Clark 1987, 1992, and Chapter 3). The CPI-value of each tree was calculated as the average of the estimates in 1992 and 1994 (Nouragues trees) or in 1991 and 1994 (Piste trees). The CPI was measured for all trees of the population inventory in the Nouragues forest, but not for the individuals shorter than 50 cm tall.

Light availability was also assessed as canopy openness (%), using hemispherical photographs. These photographs were made over each tree in 1993 (Nouragues) and 1994 (Piste). Hemispherical photographs were scanned and digitised with DeskScann II and analysed with PPFDCALC-2 (Ter Steege 1992) in order to calculate canopy openness (%).

Leader growth was measured over a period of 2 (Nouragues, 1992-1994) or 3 years (Piste, 1991-1994). Potential leaders (axes in the top of the crown) were coded and tagged at the start of the experiment, and were drawn to scale. Lengths of growth units (metamers for *Dicorynia* and units of extension for *Vouacapoua*, Table 1.1., see also e.g. Bell 1991, Room *et al.* 1994, Loubry 1994) along potential leaders were measured (see Chapters 3 & 4). In 1994, length increment was measured for the leader, i.e. the axis with the upper most apical meristem in 1994. Leader growth was measured as the distance from the base of its apical meristem at the start of the experiment to the base of its upper most apical meristem in 1994, using a folding ruler. Measurements were made along the leader, even when it was curved along its length. This leader growth measure is likely to reflect height growth, because curved leaders straighten afterwards towards the vertical if they become part of the future stem (pers. observation). In case the leader was broken or partly dead, negative leader growth was measured by summing the lengths of its fallen or dead growth units. Leader growth was expressed by cm increment per year.

5.2.4 Leader growth related to tree size and light

For the Nouragues individuals shorter than 20 m, leader growth was related to the light environment. These trees may be subject to highly variable light levels, and may still grow towards the canopy. On the basis of their height in 1992, trees were assigned to one of six height classes: (1) 0 - 0.5 m; (2) 0.5 - 1 m; (3) 1-2 m; (4) 2-5 m; (5) 5-10 m; (6) 10-20 m. Spearmans' correlations between leader growth and CPI-values were calculated per height class. Multiple regressions of leader growth (cm) on light and height (m) were calculated, using the model:

$$\text{leader growth} \quad = \quad c + (b_1 \text{ x light}) + (b_2 \text{ x height}) + (b_3 \text{ x light x height}) + e. \qquad (1)$$

Here, c is a constant, b's indicate partial regression coefficients, and e is the error term. Two multiple regressions were calculated per species, using either CPI or canopy openness as the estimate of light availability. For the calculation of both correlation coefficients and partial regression coefficients, leader growth was set to 0 in case of leader die-back or leader death.

For the matched Piste individuals, leader growth was compared between gap and understorey individuals, using the Wilcoxon test for matched pairs.

5.2.5 Tree age

On the basis of the leader growth (cm/yr) in the Nouragues trees, tree ages were calculated using annual increment data analysis (e.g. Lieberman & Lieberman 1985). Using the median and the maximum leader growth (L, cm) in each of the six height classes (see above), the time (T, yr) trees spent in successive height classes was calculated, after equation:

$$T_n = E_n/L_n \qquad (2)$$

Here, n indicates a given height class n, and E is the extension (cm) between the bottom and upper bound of height class n. In the lowest height class (0-0.5 m), the seedling height after establishment (3 months after germination) was taken as the bottom bound. In these 3 months, *Dicorynia* and

Vouacapoua on average established as individuals of 8 and 38 cm tall, respectively. Thus, for this height class, E was only 42 cm for *Dicorynia* (from 8 to 50 cm) and 12 cm for *Vouacapoua* (from 38 to 50 cm).

Tree age (years) was estimated for six height levels (m), i.e. the upper bounds of height classes. Age estimates are here given as six {height, age}- coordinates, as follows:

$$\{0.5,T_1\};\{1,\Sigma_{n=1}^{n=2}(T_n)\};\{2,\Sigma_{n=1}^{n=3}(T_n)\};\{5,\Sigma_{n=1}^{n=4}(T_n)\};\{10,\Sigma_{n=1}^{n=5}(T_n)\};\{20,\Sigma_{n=1}^{n=6}(T_n)\} \quad (3)$$

Thus, median tree ages (using median growth) and minimum tree ages (using maximum growth) were calculated for trees of different height.

5.3 Results

For both species, the results refer to three samples of trees. CPI was measured as an estimate of light availability for populations of the study species in the Nouragues forest. From this population inventory, a sub-sample of trees was selected to measure leader growth and canopy openness, including some trees taller than 5 m outside the inventory plot. These individuals are further referred to as the *Nouragues trees*. Similarly, leader growth, canopy openness, and CPI's were assessed for trees that grew in gaps or dark understorey in the Piste forest. These latter trees are referred to as *Piste trees*.

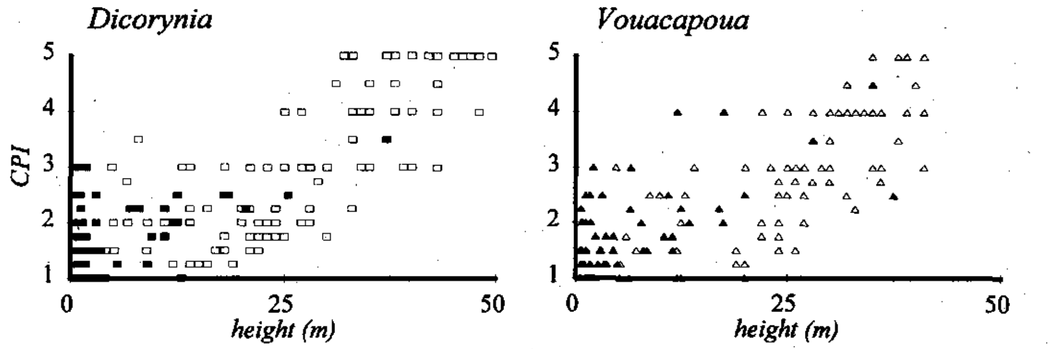


Figure 5.1. Crown position index values (CPI) in populations of two canopy tree species, Dicorynia guianensis *and* Vouacapoua americana, *in the Nouragues forest in French Guiana. Selected individuals for leader growth measurements are indicated by the marks filled with black, and those not selected for these measurements by open marks. The selected individuals less than 5 m tall are the same as the inventoried population individuals, but selected individuals taller than 5 m were usually not part of the population inventory (see text).*

5.3.1 Light

In the populations of *Dicorynia* and *Vouacapoua* in the Nouragues forest, crown position index (CPI-) values followed the same overall pattern. CPI varied between 1 and 3 (with few outliers) for trees

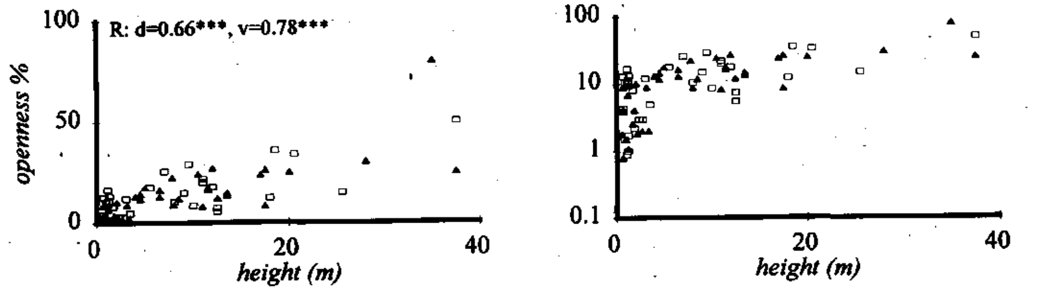


Figure 5.2. Canopy openness (%) over selected trees of two canopy species, Dicorynia guianensis *(open squares, D) and* Vouacapoua americana *(black triangles, V), in the Nouragues forest in French Guiana. Correlation coefficients between canopy openness and tree height are given for both species, using Spearmans correlation rank test, and were highly significant (***=P<0.001).*

shorter than 20 m, gradually increased for trees between 20 and 35 m, and stabilised between 3 and 5 for trees taller than 35 m (Figure 5.1). Leader growth was determined for all individuals up to 5 m tall, and for a sub-sample of individuals more than 5 m tall (Figure 5.1, see method section). These individuals taller than 5 m occurred at a smaller range of CPI- values than individuals of the same size in the whole population, but one 12 m tall individual of *Vouacapoua* had a higher CPI (4) than any of the population individuals of similar height.

Canopy openness followed another pattern with increasing height than CPI. For the selected individuals, individuals shorter than 4 m tall had a lower canopy openness (0.8-11%) than the 4-20 m tall individuals (4.8-30%, Figure 5.2). Such a trend was not found for CPI, but the individuals shorter than 4 m more frequently had low CPI's (1 to 1.5) than the 4-20 m tall individuals. The five selected individuals that were between 26 and 37 m tall had CPI's greater than or equal to 2.5, and their canopy openness was between 12 and 80% (see also Chapter 4).

At the Piste site, the gap and understorey individuals were exposed to contrasting light conditions (Table 5.1). Understorey individuals had low CPI's (1-1.5) and low canopy openness (1-5%), except for two individuals of *Dicorynia* which were close to gaps that were created between the censuses in 1991 and 1992 (CPI 1.5-2.0, canopy openness 15-19%, pairs 2 and 4). In contrast, gap individuals had higher CPI's (2.5-4.0) and canopy openness (15-31%). Thus, on the basis of both CPI and canopy openness, the Piste trees grew at extremely low (understorey) and high (gap) light levels as compared with the Nouragues trees. Some of the Piste trees in gaps had a higher CPI and/or canopy openness than the most open grown Nouragues trees of similar size.

5.3.2 Leader growth and light

In the Nouragues trees, CPI was positively correlated with leader growth in most height classes (Table 5.2). Correlations were weak to modest, except for the 5-10 m height class in *Vouacapoua* (strong correlation) and the 10-20 m height class in *Dicorynia* (no correlation). The lack of correlation in this latter class may have resulted from both the low sample size (N=7), and from the low inter-individual variation in CPI (1.75-2.5, Figure 5.1).

Table 5.1. Leader growth for gap and understorey trees of the canopy species Dicorynia guianensis and Vouacapoua americana *in the Piste forest, French Guiana. Trees were matched on the basis of height. Light conditions were quantified by annual estimates of CPI (1991-1994), and by assessing canopy openness from hemispherical photographs that were taken in 1994.*

	Understorey individuals				Gap individuals			
pair no.	tree height (m)	CPI-range	openness (%)	leader-growth (cm/yr)	tree height (m)	CPI-range	openness (%)	leader growth (cm/yr)
Dicorynia								
1	4.1	1.0-1.5	5	6	4.5	3.0-4.0	18	84
2	5.0	1.5-2.0	19	32	4.8	2.5-4.0	16	60
3	5.1	1.0-1.5	2	1	5.6	3.0-4.0	23	37
4	6.7	1.5-2.0	15	3	6.6	2.5-2.5	27	37
5	8.9	1.0-1.5	2	8	7.8	3.0-4.0	31	13
Vouacapoua								
1	4.9	1.5-1.5	1	2	4.9	2.5-4.0	20	41
2	6.1	1.0-1.5	1	2	6.1	2.5-2.5	27	36
3	6.4	1.0-1.5	1	1	6.3	3.0-4.0	15	46
4	7.8	1.0-1.5	2	4	8.2	2.5-3.0	22	39
5	18.2	1.5-1.5	2	4	15.6	2.5-2.5	20	36

- In both species, leader growth was significantly higher in gap trees ($P<0.05$, one-tailed, Match-pair test of Wilcoxon).

For the same set of trees, leader growth increased with light availability but not with tree height (Table 5.3). These results were highly significant if CPI was used as the measure of light availability, but only slightly significant if canopy openness was used.

Table 5.2. Correlations between CPI and leader growth for the canopy tree species Dicorynia guianensis *and* Vouacapoua americana *in the Nouragues forest, French Guiana. Spearman's rank correlation coefficients (r_C) were calculated per height class.*

	Spearman correlation coefficients					
height class	*Dicorynia*			*Vouacapoua*		
	r_C	Sig	N	r_C	Sig	N
0.5 -1 m	0.41	**	39	0.28	ns	20
1 -2 m	0.33	*	39	0.54	*	15
2 -5 m	0.44	*	23	0.14	ns	14
5 -10 m	0.32	ns	6	0.93	**	7
10 -20 m	0.00	ns	7	0.50	*	13

- Significance levels (Sig) are indicated as 'ns' ($p>=0.05$), as '*' ($p<0.05$), or as '**' ($p<0.01$) (two-tailed test).
-N gives the sample size per height class.

Table 5.3. Linear multiple regressions of leader growth (cm/yr) on light availability, tree height (m), and the interaction term for the tree species Dicorynia guianensis *(N=114) and* Vouacapoua americana *(N=69) in the Nouragues forest, French Guiana. Light availability was estimated as CPI and canopy openness, and these estimates were used in two separate regressions per species.*

Species		Partial regression coefficients			
	F-value	CPI	openness	height	interaction
Dicorynia	22.3***	15.42***		- 3.86*	1.72
	2.5(*)		0.55(*)	0.13	-0.0037
Vouacapoua	21.9***	10.85***		0.14	0.03
	3.6*		0.40(*)	0.30	-0.0023

- Significance levels are indicated for the F-value and partial regression coefficients: (*) for $P<0.1$, * for $P<0.05$, ** for $P<0.01$, *** for $P<0.001$.

Table 5.4. Leader growth for two tree species in the Nouragues forest in French Guiana. Median -, minimum -, and maximum growth per year are shown per height class. Negative growth is given as a '-'sign. For trees >20m, leader growth is given individually (ind).

	leader growth (cm/yr)										
	Dicorynia					*Vouacapoua*					
	Ind	Med.	Min.	Max.	N	Ind.	Med.	Min.	Max.	N	sig
height class											
0- 0.5 m		2	-	6	20		1	-	5	20	ns
0.5- 1.0 m		2	-	17	39		3	-	11	20	ns
1.0- 2.0 m		4	0	25	39		4	-	25	15	ns
2.0- 5.0 m		4	0	26	23		7	0	33	14	ns
5.0-10.0 m		9	1	13	6		8	0	33	7	ns
10.0-20.0 m		12	5	42	7		14	0	32	13	ns
height											
26 m	21										
27 m						14					
35 m	5					4					
37 m						4					

- sig: leader growth compared between species per height class, using Mann-Whitney U test (* for $P<0.05$, ns means non-significant).

In Piste trees, the gap individuals had more extensive leader growth than the understorey individuals (Table 5.1). In 8 of the 10 matched pairs, leader growth was approximately 10 (or more) times more extensive in the gap individuals. These high leader growth rates in gap trees exceeded the growth rates of the most rapidly growing Nouragues trees of the same height (Table 5.4, see below).

5.3.3 Height and leader growth

In Nouragues trees, leader growth varied among the six height classes, and ranged from negative growth to 42 cm (*Dicorynia*) or 33 cm extension growth (*Vouacapoua*, Table 5.4, Figure 5.3). Negative growth was due to die-back of the leader or to physical damage of the tree. Minimum growth was negative in the lowest size classes, 0 cm in the intermediate classes, and 0 cm (*Vouacapoua*) or between 1 to 5 cm (*Dicorynia*) in the two upper classes (Table 5.4). Median growth gradually increased from 1-2 cm in the lowest class to 12-14 cm in the upper class. Maximum growth increased in the two lower classes, but stabilised from the third height class (1-2 m, Table 5.4, Figure 5.3). Apart from the height classes, an individual of 26 m (*Dicorynia*) grew 21 cm, an individual of 27 m (*Vouacapoua*) grew 14 cm, and individuals of 35-38 m (N=1 for *Dicorynia*, and N=2 for *Vouacapoua*) grew only 4-5 cm (Table 5.4).

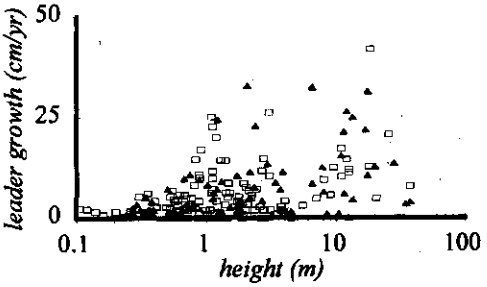


Figure 5.3. Leader growth for two canopy tree species, Dicorynia guianensis *(open squares) and* Vouacapoua americana *(black triangles), in the Nouragues forest in French Guiana.*

Table 5.5. Tree age at successive tree heights for two species in tropical rain forest in French Guiana. Median and minimal ages were calculated on the basis of median and maximum leader growth. For calculations, see text.

	Age (years)						
	Dicorynia			*Vouacapoua*			
height	Med.	Min.	(N)	Med.	Min.	(N)	sig
0.5 m	24	6	15	13	3	19	***
1 m	46	9	29	30	7	13	ns
2 m	71	13	29	57	12	14	ns
5 m	149	22	20	97	21	13	ns
10 m	207	61	6	164	36	5	ns
20 m	288	84	7	235	68	11	ns

- time to grow through height classes compared between species (Mann-Whitney U test, *** for $P<0.001$, ns if $P>0.05$)
- individuals with negative or nil leader growth were omitted from analysis

5.3.4 Age

Age estimates at successive height levels were lower for *Vouacapoua* than for *Dicorynia* (Table 5.5). A height of 0.5 m was more rapidly reached by *Vouacapoua* than by *Dicorynia*, mainly because *Vouacapoua* seedlings were taller after establishment. Above 0.5 m, *Dicorynia* and *Vouacapoua* spent similar amounts of time growing through successive height classes, as both species had similar median and maximum growth rates (Table 5.4). A 20 m tall tree was estimated to be 235 (*Vouacapoua*) or 288 (*Dicorynia*) years old on the basis of median growth, and 68 (*Vouacapoua*) or 84 (*Dicorynia*) years old on the basis of maximum growth.

5.4 Discussion

5.4.1 Two study approaches compared

The studies in the Piste forest and in the Nouragues forest represent two different study approaches. In the Piste forest, growth was compared between individuals of similar height which grew either in a gap or in the understorey. Gap and understorey represent two extremes along the spatial gradient of light variation in the forest. Under these contrasting conditions, leader growth was usually 10 or more times as large in gap individuals. This indicates that higher light levels may permit trees of these species to reach the canopy more rapidly, because leader growth is not, or less, limited. However, the impact of these light levels for the populations of both species remains unknown on the basis of this approach.

In the Nouragues forest, leader growth was related to light levels for population samples of both species. This approach permitted us to assess the range of light levels these trees encountered most frequently, to relate leader growth to these light levels and tree height (ontogenetic change) and, finally, to calculate tree ages at successive height levels. These issues are here further discussed on the basis of the Nouragues forest study, and compared with the results of the Piste study and other studies. The comparison mainly focuses on a study of six canopy and emergent tree species in a Costa Rican rain forest (Clark & Clark 1992). This is one of the few studies in which researchers report on ontogenetic changes in median and maximum height growth of tropical rain forest trees.

5.4.2 Light environment

In both study species, trees shorter than 20 m were exposed to CPI-values between 1 and 3. However, taller individuals were more frequently exposed to higher CPI-values than shorter individuals. Moreover, tall individuals may be exposed to higher light levels than shorter individuals that have the same CPI- value, because CPI values are relative to the (crown) size of trees (Sterck, unpublished data). Indeed, trees taller than 4 m had their crowns exposed to more open conditions than shorter individuals (see canopy openness values). In fact, taller individuals have higher chances on more light exposure because gap areas increase with height in the Nouragues forest (Van der Meer *et al.* 1994), as well as in other tropical rain forests (Hubbell & Foster 1986).

In the Piste study, understorey trees had CPI's between 1.0-1.5 and gap individuals had CPI's of 2.5-4.0. These 4-10 m tall trees were thus at the very opposite extremes of the encountered CPI's in the population sample. In fact, six out of ten gap individuals were, at least some period, exposed to a CPI of 4, which was higher than for any of the population individuals of the same size. This illustrates that the study trees at the Piste site, and in particular the gap individuals, occurred under light conditions that are rarely encountered by trees of the same species in the Nouragues forest. Conversely, the trees of populations in the Nouragues forest covered a whole range of light levels, but may not include the rare high light levels in large gaps.

5.4.3 Leader growth in relation to tree height and light

In both species, median and maximum leader growth changed with tree height. Median growth rates increased gradually from 1-2 cm/yr in <0.5 m tall trees to 12-14 cm/yr in 10-20 m tall trees. However, the increase in leader growth did not result from the increase in tree height, but from the increase in light levels. This is shown by the significant influence of both CPI and canopy openness on leader growth, while tree height had no direct positive effect on leader growth. Canopy openness had a less significant effect on leader growth than CPI. This may result from the large error in estimates of low canopy openness values (0-10%), using hemispherical photography (Whitmore *et al.* 1993). It is concluded that taller trees had faster growing leaders because they occurred at higher light levels than shorter trees, and not because they were taller. The large influence of light on leader growth is affirmed by the results of the Piste study. Eight out of ten gap individuals had leader growth that was at least 10 times as extensive as understorey individuals of the same height.

These results are in agreement with the results of Clark & Clark (1992). In <16 m tall trees, they found increasing median height (and diameter) growth with increasing diameter class. They showed that median height (and diameter) growth was correlated with light (CPI) for their trees. In other studies on seedlings and saplings, increasing light levels also caused increases in height growth (e.g. Sasaki & Mori 1981, Augspurger 1984, Osunkoya *et al.* 1993, King 1991c, Uhl *et al.* 1988) and diameter growth (e.g. Turner 1989, Welden *et al.* 1991). Thus, for tropical rain forest trees, the higher growth rates in the taller trees may be caused by the less growth limiting light levels, rather than by tree size itself.

In the two individuals of 26 and 27 m, leader growth was similar or even larger (14 and 21 cm/yr) than in the 10-20 m size class. These trees received much direct light, and their strong leader growth indicates that they were still in full vertical expansion. The three trees of 35-38 m received much direct light as well, but had lower leader growth (4-5 cm/yr). It may be that these trees had fully expanded vertically, and showed the typical cease in height growth late in ontogeny (e.g. Hallé *et al.* 1978, Thomas 1996a). Their leaders may not account for significant (vegetative) height growth, but rather for the production of new leaves, flowers, and fruits. As such, their leaders were functionally equivalent to other shoots in the crown.

Maximum leader growth increased steeply in the lowest size classes, but stabilised from the 1-2 m class. These maximum growth rates were lower than the growth rates of nine of the ten gap individuals of the Piste study. This stresses the problem that maximum growth figures of a population sample are correlated with sample size, and that they may underestimate real and rarely occurring maximum growth rates in the population. However, the changes in maximum growth with height occurred in both species, and may be due to some biological process.

The increase in maximum growth at increasing juvenile sizes is common to tree growth. It refers to a higher capacity of the trees to acquire carbon that is used for growth under non-stressed conditions. As, for short trees, the apical meristem of the leader is dominant over other meristems, increasing amounts of fixed carbon may be invested in the apical meristem of the leader. Consequently, leader growth increases with increasing tree height. However, if the apical dominance of the leader weakens and more meristems become active, the fixed carbon has to be distributed over an increasing number of meristems. In fact, there may be no clear leader, as several equivalent shoots in the top of the crown compete for more valuable space by extension growth. In our species, the number of meristems increased from 1 to 2 or more at a height of about 0.5 (*Dicorynia*) and 1.5-2.0 m (*Vouacapoua*), and than continued to increase exponentially with tree height (Chapter 4). Thus, the loss of apical dominance of the leader may, to some extent, explain the decrease in maximum leader growth rates. Apart from this, the decrease in maximum growth may be related to an increasing percentage of fixed carbon that had to be invested in stem thickness growth in order to ensure the mechanical stability of a tree (e.g. McMahon 1973, Niklas 1992, Chapter 6).

Finally, the minimum growth was negative, 0, or close to 0. In the smallest size classes, minimum growth rates were negative because many individuals lost height by die-back, death, or damage of the leader (data not shown). This may, partly, reflect a very light stressed environment and/or, partly, the higher chance of short individuals to be damaged by falling debris (Putz & Brokaw 1989, Clark & Clark 1991, Van der Meer 1995). Minimum growth was 0 or close to 0 in the taller size classes which did not suffer from physical damage. In contrast, studies on tree growth and survival indicate that physical damage still occurred in tall individuals (Van der Meer 1995), but at a lower frequency than in small individuals (Clark & Clark 1992). Thus, the lack of physical damage in the larger height classes seems to be due to the small sample size and the short time span of this study.

5.4.4 Leader growth and tree age

Leader growth and age estimates of the Nouragues trees can be compared with height growth and age estimates of trees in tropical rain forests of Costa Rica (Clark & Clark 1992) and Panama (O'Brien *et al.* 1995). Leader growth rates were lower than height growth rates in juvenile trees of a Costa Rican rain forest (Clark & Clark 1992), on the basis of both median and maximum growth rates. The lower maximum growth rates for *Dicorynia* and *Vouacapoua* were not the result of lower sample sizes, as sample sizes were similar in both studies. Moreover, the extremely high leader growth rates in the gap individuals of the Piste study were lower than the maximum height growth rates in the Costa Rican tree species. Given that leader growth either equals or over-estimates height growth, it can be concluded that our study species grew slower in height than the study species in the Costa Rican rain forest.

Clark & Clark (1992) calculated the median and minimum ages of their tree species on the basis of diameter increments and diameter size. Because 20 m tall trees of *Dicorynia* and *Vouacapoua* had a DBH between 10-12 cm (Chapter 6), their ages may be compared with the 10 cm DBH individuals of Clark & Clark (1992). A 20 m tall tree had a median age of 235 (*Vouacapoua*) and 288 years (*Dicorynia*), and a minimum age of 68 (*Vouacapoua*) and 84 years (*Dicorynia*). Clark & Clark (1992) calculated median ages of 98-183 years, and minimum ages of 17-39 years for 10 cm DBH trees of six canopy and emergent tree species. This supports the idea that *Dicorynia* and *Vouacapoua* grew slower in height than the juveniles of the Costa Rican rain forest tree species. Amongst other factors, these growth differences between the two forest sites may reflect the relatively high soil-fertility (Sollins *et al.* 1994) or high precipitation (on average 3.962 mm per yr, Sanford *et al.* 1994) of the Costa Rican forest site, relative to lower soil fertility or precipitation (on average 2.920 mm per year, Van der Meer 1995) in the Nouragues forest.

O'Brien *et al.* (1995) calculated the ages for trees of eight tree species in a tropical rain forest in Panama, and related tree ages to successive tree heights. Their 20 m tall trees were estimated to be between 66 and 194 years old. O'Brien and co-workers based their age estimates on the mean diameter growth rates of trees which survived all 8 years of study. Consequently, tree height was related to stem diameter and corresponding tree age. Their age estimates are expected to be lower than our age estimates for 20 m tall trees using median growth rates: Firstly, mean growth rates are usually higher than median growth rates (personal observation). And secondly, O'Brien and co-workers excluded slow growers which did not survive all eight years of study. This illustrates that our estimates of median tree age are likely to over-estimate the ages of trees that survive through all size classes, and finally reach adult stature.

The ecological significance of leader growth is mainly through its correlation with height growth. Height growth determines the ability of trees to compete for light and space, and the time by which trees reach reproductive status. However, (leader - and) height growth are only one aspect of tree growth, and its relation to the light environment and tree size may differ from other growth components, for example stem diameter growth, and shoot growth at other crown locations. Such other growth components were addressed for the same species in other studies (Chapters 2, 3, 4 & 6).

6

ONTOGENETIC CHANGES IN SIZE, ALLOMETRY, AND MECHANICAL DESIGN

with Frans Bongers

Abstract

1. Size and allometry were measured for trees of three canopy species in a tropical rain forest in French Guiana, namely *Goupia glabra, Dicorynia guianensis*, and *Vouacapoua americana*. Changes in height, crown width, allometry, and mechanical design with ontogeny (increasing stem diameter) were described by regressions, and compared between species.

2. Height and crown width increased sharply at small diameters, and approached a maximum asymptotically at larger stem diameters. At the smallest diameters, *Dicorynia* increased faster in height than *Goupia*, but later on *Goupia* increased more rapidly in height than both other species. Both *Goupia* and *Vouacapoua* increased their crown width faster than *Dicorynia* at small diameters, but not significantly. *Dicorynia* and *Goupia* became tallest, and *Vouacapoua* and *Dicorynia* had the larger crowns, at large diameters.

3. The height/crown width ratio did not change with ontogeny. Overall, *Vouacapoua* had a higher crown width/height ratio than both other species.

4. Safety margins against mechanical failure decreased to a minimum in trees with a diameter of 15-25 cm, but increased continuously in thicker trees. The minimum safety margins were largest for *Vouacapoua* (1.5), intermediate for *Dicorynia* (1.3), and lowest for *Goupia* (1.0).

5. Safety margins against wind forces increased linearly with increasing diameter, and did not differ between species.

6. A growth model is described, relating size and allometry to allocation between three different growth directions: height growth, lateral crown growth, and stem diameter growth. This model implies trade-offs between these three growth directions. Trees with more height growth compete for the higher light levels in the upper canopy; trees with more lateral crown growth intercept more light and may survive at the lower light levels; and trees with more rapid diameter growth are better able to carry their own weight and resist wind stress. Using this model, the ontogenetic changes in size and allometry are compared for the three species studied, and between tropical rain forest trees and temperate trees in general.

6.1 Introduction

Tree size and allometry vary among tropical rain forest trees, both within and between species. This variation may be related to micro-site (Horn 1971, Bongers & Popma 1988, Clark & Clark 1992), architectural growth patterns (Brunig 1976, Hallé *et al.* 1978, Niklas 1994b), ontogeny (Rich *et al.* 1986, Claussen & Maycock 1995, King 1996), adult tree stature (King 1991a, 1996), and forest type (King 1991a). The changes in size and allometry with ontogeny determine the changes in the abilities of trees to compete for light and space (Küppers 1989, 1994) and to carry their own mass and resist wind stress (Niklas 1992).

Trees compete for light and space by increasing their size (Küppers 1989, 1994) and changing their allometry (King 1991a). Shukla & Ramakrishnan (1986) and others (e.g. Kohyama & Hotta 1990) recognised two distinct growth habits for tropical rain forest tree species: species with wide crowns that increase light interception to survive under persisting dark conditions, and species with narrow crowns that invest in height growth to exploit better-lit conditions in the future. Similarly, these two growth habits may reflect different ways of competing for space in the dense forest understorey, where crown growth may be hampered by (the physical presence of) branches and leaves of neighbouring trees (Küppers 1989, 1994, Lieberman & Lieberman 1994). The competition for light and space by crown growth has to be balanced with stem diameter growth to prevent trees from buckling under their own increasing mass or by increasing wind stress higher up in the canopy (e.g. King 1986, Givnish 1995).

Trees resist their own mass and wind forces by an adequate mechanical design. Models were developed to quantify the mechanical design of trees based on size and allometry (e.g. McMahon 1973, King & Loucks 1978, Waller 1986, Holbrook & Putz 1989, Niklas 1992, 1994b). The *elastic-stability model* emphasizes stress due to static loadings, i.e. self-loading as well as snow or epiphyte loadings (King & Loucks 1978, Niklas 1992). This model is represented by the following equation (after Greenhill 1881):

$$L_{cr} = c_1 \times (E/\rho)^{1/3} \times D^{2/3} \qquad (1)$$

The models express the height at which a tree starts to buckle under its own mass. This critical length (L_{cr}) or buckling height increases with a 2/3 power increase in trunk diameter D, and with a 1/3 power increase in the ratio of the elastic (or Youngs') modulus E (a measure of stiffness of the wood) and wood density ρ. The constant c_1 is a variable of shape, and was modified by various researchers (e.g. McMahon 1973, King & Louks 1978, King 1981, 1986, Holbrook & Putz 1989, Niklas 1994b). On the basis of this model, King (1981, 1986) calculated safety factors of trees as follows:

$$\text{safety factor} = L_{cr}/H \qquad (2)$$

This ratio of buckling height L_{cr} and actual tree height H quantifies the margins of safety against buckling under its own mass.

The *constant-stress model* refers to stress due to dynamic wind forces (e.g. Niklas 1992). This model is represented by:

$$D = c_2 \times (S \times H)^{1/3} \qquad (3)$$

The model expresses the minimum diameter that a tree needs to resist wind forces. These forces are assumed to be proportional to 1/3 power increase in the product of total leaf area (or silhouette area S, Dean & Long 1986) and tree height H. The wind pressure and maximum wind stress are assumed to be constant, and included in the constant c_2 (Niklas 1992). Wood properties such as the elastic modulus and wood density are not taken into account.

The changes in size and allometry with ontogeny follow the elastic-stability model in some (O'Brien *et al.* 1995) but not all tree species (Rich *et al.* 1986, O'Brien *et al.* 1995, Claussen & Maycock 1995, Niklas 1994b, Alvarez-Buylla & Martinez-Ramos 1992), and do not follow the constant-stress model (O'Brien *et al.* 1995, Niklas 1994b, but see Dean & Long 1986 for conifers). In these studies, slopes of double log-transformed height-diameter relationships of tree species were compared with theoretical slope values of the described models. However, this approach does not account for the asymptotic nature of height - diameter relationships (Thomas 1996a), and subtle ontogenetic changes in size and allometry are masked (see Niklas 1994b), and are either not or wrongly interpreted (Thomas 1996a).

The changes in size and allometry with ontogeny, and their consequences for mechanical tree design, were studied for three canopy tree species in a tropical rain forest in French Guiana. Ontogenetic changes further refer to changes with increasing stem diameter. Nonlinear regression models were used to describe the changes in size and allometry with ontogeny, and to compare these changes between the study species. Asymptotic functions were used to described the changes in size. The changes in height and theoretical buckling height with ontogeny were used to calculate the ontogenetic changes in the safety factor. Also, the ontogenetic changes in the resistance against wind stress were calculated. In the discussion, a tree growth model is presented relating different sizes and allometries to different ways of allocating organic matter. On the basis of this tree growth model, the changes in size, allometry and mechanical design with ontogeny are discussed per species, compared between the study species, and finally compared with tree species in temperate forests.

6.2 Methods

6.2.1 Species and site

The study was carried out at the research station La Piste St. Elie, (5 14'N, 53 03'W) of O.R.S.T.O.M. (Cayenne), French Guiana. The species of study were the canopy tree species *Vouacapoua americana* Aubl. (Caesalpiniaceae), *Dicorynia guianensis* Amshoff. (Caesalpiniaceae) and *Goupia glabra* Aubl. (Celastraceae). Henceforth, the species are referred to by their generic names only. For site and species description, see Chapter 1.

6.2.2 Field measurements

An inventory of a 5-ha forest plot in the Piste rain forest was used to make a random selection of individuals between 2 m and maximum stature for *Dicorynia* (N=54), *Goupia* (N=24), and *Vouacapoua* (N=44). Sample size was small for *Goupia*, because this species was rare in the study area. Tree height (H), fork height (Hf), crown cover (C), and stem diameter at 1.3 m (D) were determined for each tree. Fork height was defined as the vertical distance between the stem base and the lowest major branch. Major branches were defined as branches that are at least half as thick as the stem at the same height. Crown cover was calculated from drawings of the vertical crown projection, using a Suunto clino-measurer. Height measures were made using the same Suunto clino-measurer. Crown width (W) and silhouette area (S) were calculated, using the following equations:

$$W = \sqrt{(4 \times C \times \pi^{-1})} \quad (4)$$
$$S = \tfrac{1}{4} \times \pi \times W \times (H - Hf) \quad (5)$$

6.2.3 Size and allometry

The changes in size or allometry with ontogeny were assessed as changes in size and allometry with increasing stem diameter. Regression models were used to describe these changes. The changes in size, i.e. height and crown width, were described by asymptotic sigmoidal curves, using the following regression model:

$$\text{size variable} = \gamma \times (1+e^{\alpha+\beta \times D})^{-1} \quad (6)$$

D is the stem diameter at breast height (1.3 m). The parameters α, β, γ were estimated per species. Within the range of calculated values, a lower (and positive) α indicates a more rapid increase in size with increasing diameter before the bending point, a lower (and negative) parameter β indicates a more rapid increase after the bending point, and parameter γ gives the maximum size at large diameters.

The allometry of trees was expressed as the ratio between crown width and tree height. Scatter plots showed no change with increasing diameter. Therefore, the ratio was compared between species using the Kruskal-Wallis test, and Mann-Whitney U tests for pairwise comparisons.

6.2.4 Mechanical design

The changes in mechanical design were calculated on the basis of the elastic-stability model and the constant-stress model. According to the elastic-stability model, the theoretical buckling height was calculated for each species using the Euler-Greenhill formula (McMahon 1973):

$$L_{cr} = 0.792 \times (E/\rho)^{1/3} \times D^{2/3} \quad (7)$$

Table 6.1. Wood properties for the canopy tree species Dicorynia guianensis, Goupia glabra, *and* Vouacapoua americana, *French Guiana (CIRAD-CTFT 1989).*

	Elastic modulus E ($kg.10^6/m^2$)	Wood density ρ (kg/m^3)	E/ρ (10^3 m)
Dicorynia	1510	780	1936
Goupia	1570	840	1869
Vouacapoua	1650	920	1793

Thus, the constant c_1 of equation (1) is set to 0.792 for all individuals. Theoretical buckling height was plotted per species over the whole range of observed diameters, using fixed values for wood properties (Table 6.1). After King (1981), the mechanical design of trees was expressed by the safety factor, and is derived from equation (2):

$$\text{safety factor} = L_{cr}/(H-1.3) \tag{8}$$

Height was decreased by 1.3 m in order to obtain the actual tree length above breast height (where stem diameter was measured). The ontogenetic changes in the safety factor were plotted for each species. Therefore, the equations 6, with height as the size variable, and 7 were substituted in equation 8, taking the calculated estimates for the parameters and the wood properties per species.

The constant-stress model calculates the minimum stem diameter that is needed to resist wind forces. The wind forces on a tree are a function of tree dimensions (height, crown size) and wind pressure (Dean & Long 1986, Niklas 1992). Equation 3 can be rewritten as:

$$F = D \times (S \times H)^{-1/3} \quad ,(9)$$

The F in this equation is equal to c_2 in equation 3, and is further referred to as *wind safety*. It expresses the wind force resistance of the tree in terms of D, relative to the wind force on the tree in terms of tree size ($(S \times H)^{1/3}$) and at a fixed level of wind pressure (Niklas 1992) . It was calculated for each individual on the basis of its height, silhouette area, and stem diameter. Because the changes in wind safety with ontogeny followed a linear relationship, they were described by a linear regression model.

6.3 Results

6.3.1 Size

The size of trees changed with ontogeny (Table 6.2, Figure 6.1). The asymptotic sigmoidal regression model explained between 85-98 % of the observed variation for height and 54-73% of the variation for crown width (Table 6.2). The major changes in size occurred at stem diameters smaller than 30 cm. In this phase, trees were in full expansion and had not yet reached the upper canopy (Figure 6.1). After this phase, trees approach their adult stature, and most changes in size and allometry were mitigated. The interspecific differences in model parameters were used to compare the ontogenetic changes in size between species.

Figure 6.1 Ontogenetic changes in size for the canopy tree species Dicorynia guianensis *(squares and line),* Goupia glabra *(crosses and dotted line), and* Vouacapoua americana *(triangles and line with interuptions) in a tropical rain forest, French Guiana. For statistics of regressions, see Table 6.2.*

The species differed by their increase in size at small diameters (see parameters α and β), and by their maximum size at large diameters (parameter γ, Table 6.2, Figure 6.1). At the small diameters before the bending point, *Dicorynia* increased faster in height than *Goupia* (see α). After the bending point, *Goupia* increased faster in height than both *Dicorynia* and *Vouacapoua* (see β). *Dicorynia* may increase faster in height than *Vouacapoua*, but this is not shown by the parameters α and β because *Dicorynia* is taller than *Vouacapoua* at larger diameters. After the bending point, both *Goupia* and *Vouacapoua* increased their crown width more rapidly than *Dicorynia* (see β, only slightly significant, P<0.1). At large diameters, *Dicorynia* and *Goupia* were taller than *Vouacapoua*, and *Vouacapoua* and *Dicorynia* had larger crowns than *Goupia* (see γ).

Table 6.2. Regressions and statistical parameters for ontogenetic changes in size and mechanical design of tree species in a tropical rain forest, French Guiana. In the regression models, D = stem diameter at breast height (1.3 m), and α, β, and γ are model parameters. Results of two models are given:
(1) size variable (height or crown width) = $\gamma \times (1+e^{\alpha+\beta \times D})^{-1}$ *; (2) wind safety =* $\alpha + \beta \times D$

Y	R^2 !	Parameters ± standard error of the mean								
		α			β			γ		
<u>Height</u>										
Dicorynia	0.85**	1.43	±0.215	a	-11.7	±1.67	a	39.5	±1.19	b
Goupia	0.98**	2.02	±0.102	b	-19.9	±1.38	b	36.7	±0.86	b
Vouacapoua	0.86**	1.58	±0.256	ab	-12.6	±2.05	a	31.3	±1.14	a
<u>Crown width</u>										
Dicorynia	0.54**	1.52	±0.287	a	-0.082	±0.019	a	9.02	±0.579	b
Goupia	0.62**	1.69	±0.353	a	-0.300	±0.091	a	6.26	±0.421	a
Vouacapoua	0.73**	1.86	±0.301	a	-0.151	±0.024	a	9.44	±0.320	b
<u>Wind safety</u>										
Dicorynia	0.86**	0.94	±0.123	a	0.0556	±0.00314	a			
Goupia	0.98**	0.82	±0.057	a	0.0592	±0.00192	a			
Vouacapoua	0.69**	1.14	±0.162	a	0.0484	±0.00497	a			

-! level of significance is given for F-value of regression; P<0.01 as *, and P<0.001 as **
-Different letters after SE-values indicate interspecific differences for parameter values. For each pair of species, significant differences were calculated from t-values, by equation:
t = (parameter X_{spec1}-parameter X_{spec2})/(SE-parameter $X_{spec1}{}^2$ + SE-parameter $X_{spec2}{}^2$), X stands for a given parameter, SE is the standard error of the mean for the parameter. Spec 1 and spec 2 represent two species that are compared (two-tailed test, significance level per comparison P<0.0167, for df>68, t>2.5, after Fowler & Cohen 1990).

6.3.2 Allometry

The crown width/height ratio did hardly change with ontogeny (Figure 6.2). This ratio was significantly higher for *Vouacapoua*, irrespective of stem diameter (Kruskal- Wallis, P<0.0000, Mann-Whitney U for comparisons with *Dicorynia*, P<0.0000, and with *Goupia* P=0.008). Using the same tests, it was found that *Goupia* and *Dicorynia* did not significantly differ for this ratio.

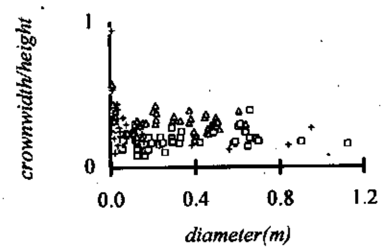


Figure 6.2 Ontogenetic changes in allometry for the canopy tree species Dicorynia guianensis, Goupia glabra, *and* Vouacapoua americana *in a tropical rain forest, French Guiana. For statistics of regressions, see text. For symbols of species, see Figure 6.1.*

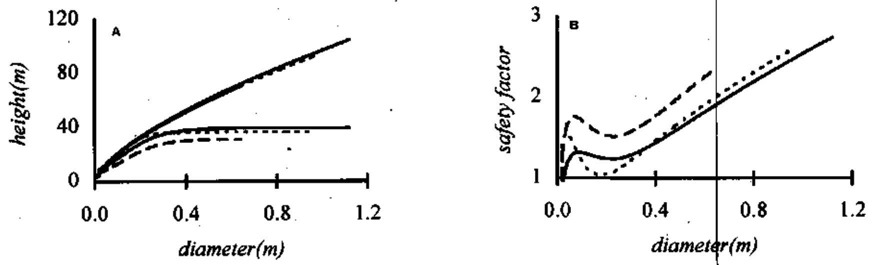


Figure 6.3. Ontogenetic changes in mechanical design for the tree species Dicorynia guianensis, Goupia glabra, *and* Vouacapoua americana *in a tropical rain forest, French Guiana. A. Three top lines give the theoretical buckling height, and the three bottom lines the actual tree height (Figure 6.1). B. Ontogenetic changes in the safety factor. For calculation see text. For symbols of species, see Figure 6.1.*

6.3.3 Mechanical design

The mechanical design of trees changed with ontogeny (Figures 6.3 & 6.4). Three study trees actually exceeded theoretical buckling height, two of *Goupia* and one of *Dicorynia*. The relative distance between actual height and buckling height changed with increasing diameter. At small diameters (<30 cm), trees were close to their theoretical buckling height, and their safety factors ranged between 1 and 1.8 (Figure 6.3). The rise in the safety factor at small diameters (<10 cm) may result from the fact that diameters were always measured at 1.3 m, even in the smallest trees. After this increase, safety factors declined to their minimum between 15 and 25 cm. At a further increase in stem diameters, the safety factors increased continuously as tree height approached its maximum asymptotically while the stem diameter continued to increase.

The safety factor is composed of actual height and theoretical buckling height (see above). At a given diameter, the interspecific differences in theoretical buckling height are small compared with differences in actual tree height (Figure 6.3). The interspecific differences in safety factors are caused by the actual tree heights rather than by the theoretical buckling heights. Over the whole range of diameters, *Vouacapoua* had the highest safety factor because it was less slender (shorter at given diameter) than both other species (Figures 6.1A & 6.3A). The minimum safety margins were largest for *Vouacapoua* (1.5), intermediate for *Dicorynia* (1.3), and lowest for *Goupia* (1.0). Thus, *Goupia* had the most slender habit.

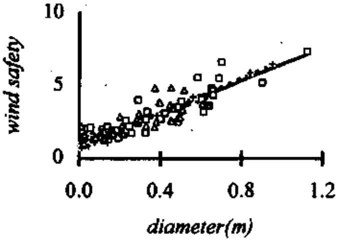


Figure 6.4. Ontogenetic changes in wind safety for the canopy tree species Dicorynia guianensis, Goupia glabra, *and* Vouacapoua americana *in a tropical rain forest, French Guiana. For calculation of wind safety, see text. For statistics of regressions, see Table 6.2. For symbols of species, see Figure 6.1.*

Mechanical design and wind forces were related following the constant stress-model (Figure 6.4). Linear regressions explained 69-98% of the variation of this relationship (Table 6.2). Wind safety increased linearly with increasing diameter for each of the study species. There were no significant interspecific differences in the changes in wind safety with ontogeny (Table 6.2).

6.4 Discussion

6.4.1 A growth strategy model and its consequences

In a growth strategy model for trees, tree size and allometry are related to the allocation of organic matter between three different growth directions above ground: vertical crown growth or height growth, lateral crown growth, and stem diameter growth (Figure 6.5). This model implies trade-offs among these three growth directions. Trees with more height growth compete for the higher light levels in the upper canopy (e.g. Shukla & Ramakrishnan 1986, Tilman 1988), trees with more lateral crown growth intercept more light and may survive at the lower light levels (e.g. Shukla & Ramakrishnan 1986, Kohyama & Hotta 1990), and trees with more rapid diameter growth are better able to carry their own weight and resist wind stress (e.g. King & Loucks 1978, Niklas 1992). Using this model, the overall changes in size and allometry with ontogeny are discussed, compared between the study species and, finally, also compared between the study species and some tree species of temperate forests.

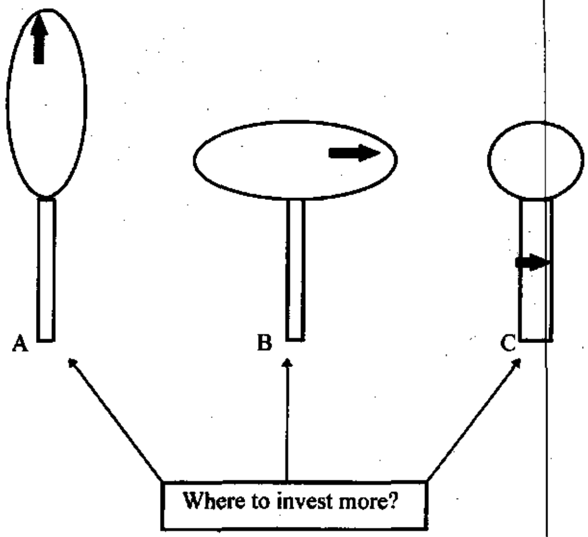


Figure 6.5. A tree growth strategy model. Above-ground tree size and allometry are related to allocation of organic matter between three different growth directions: (A) height growth or vertical crown growth, (B) lateral crown growth, and (C) stem diameter growth. For functional interpretation of the model, see text.

6.4.2 Changes in allocation and allometry

The increases in height and crown width with ontogeny cease at larger diameters. In line of the model, this refers to a shift from high investments in crown growth (both lateral and vertical) and low investments in stem diameter growth to low investments in crown growth and high investments in stem diameter growth. However, the magnitude of crown growth may be underestimated, as size variables do not account for losses by branch and stem die back during the growth history of a tree (Putz & Brokaw 1989, Clark & Clark 1991, 1992, Van der Meer 1995). In contrast, such losses do not exist for stem diameter growth.

The competitive ability for light and space as well as mechanical design are expected to change with the ontogenetic changes in size and allometry. Extensive crown growth early in ontogeny permits trees to compete for light and space by overtopping and shading its neighbours in the understorey of the forest. The trade-off between crown growth and stem diameter growth may explain the low safety margins against mechanical failure early in ontogeny. A decrease in safety margins before trees reach their minimum margins at a stem diameter between 15 and 25 cm was observed in other species as well (King 1981, 1986, Claussen & Maycock 1995). Claussen & Maycock (1995) argued that the higher safety margins at low stature permits these small trees to resist falling debris (Clark & Clark 1991). After trees have reached their minimum safety margins at a stem diameter between 15 and 25 cm, the safety margins increased with larger stem diameters. This pattern was found for tree species in a Costa Rican rain forest (Rich *et al.* 1986, King 1996), and in upland rain forest in Australia (Claussen & Maycock 1995). However, more light demanding species as well as palm species may experience decreasing safety factors at larger diameters (Rich *et al.* 1986, Alvarez-Buylla & Martinez-

Ramos 1992, Claussen & Maycock 1995). Rich *et al.* (1986) argued that mechanical failure may therefore contribute to the early death in trees of light demanding species. Alvarez-Buylla & Martinez-Ramos (1992) suggested that a high risk of mechanical failure at adult stature may be attributed to genetically based high height growth rates of light demanders. In contrast, the light demanding species *Goupia*, as well as other light demanding canopy species (King 1996), had ceased height growth while diameter growth continued. As such, these latter species increased their mechanical stability at adult stature, as was found for the more shade-tolerant species of this and other studies.

6.4.3 Interspecific differences

On the basis of the model, the changes in size and allometry with ontogeny are compared between species. The focus was on trees with a diameter smaller than 30 cm because they were expected to be still in the race for more light and space in the upper canopy. The more light-demanding species *Goupia* differed in some aspects from the more shade tolerant species *Dicorynia* and *Vouacapoua*. *Goupia* had a more slender habit (taller at given diameter) than *Vouacapoua*. At the lowest diameters, *Goupia* had a less slender habit than *Dicorynia*. *Goupia* also tended to have a wider crown than *Dicorynia*. Following the model, this indicates that *Goupia* invested more in height growth than *Vouacapoua*, but less in height growth than *Dicorynia*. Also, *Goupia* invested more in lateral crown growth than *Dicorynia*. These patterns are in disagreement with the argument that light demanding species face a trade-off between inherent high height growth rates and lower margins of mechanical safety (King 1981, 1991a, Alvarez-Buylla & Martinez-Ramos 1992). Only at intermediate stem diameters (approximately 20 cm), *Goupia* tended to have lower margins against mechanical safety than both other species. Also, for *Goupia*, the extensive lateral crown growth is not consistent with the expectations. In line of the model, this would reflect a high tolerance against shaded conditions. This extensive lateral crown growth results from the production of extensive horizontal branches, conforming to the model of Roux (Edelin 1991). Interestingly, the branched growth patterns of the models of Roux and Rauh (Hallé *et al.* 1978) characterise juvenile trees of many light-demanding species (Foresta 1983, but see Oldeman & van Dijk 1991, Vester & Saldarriaga 1993). The more shade-tolerant species *Dicorynia* and *Vouacapoua* grew according to the model of Troll, but not exclusively (Drénou 1988, Loubry 1994). These species develop branches when they are 1-2 m tall (unpublished data), but the branches were not as long as those of *Goupia*. The model of Troll characterises the growth habit of many shade-tolerant tree species in a Neo-tropical rain forest (Foresta 1983). This may reflect the dominance of Leguminoceae in these forests (Oldeman 1989).

Changes in size and allometry with ontogeny are related to the adult stature of the species (King 1991a, 1996, Thomas 1996a). *Vouacapoua* had a lower adult stature than *Dicorynia* and *Goupia*. With *Goupia*, *Vouacapoua* had a wider crown than *Dicorynia* at a given diameter. *Vouacapoua* also had a higher crown width/height ratio at a given diameter than both other species. In line with the model, and following Kings' arguments for species with lower adult stature (1991a, 1996), *Vouacapoua* may increase its capacity of light interception by extensive lateral crown growth at the cost of height growth. Also, lateral crown growth may permit *Vouacapoua* to occupy more space for the establishment of its adult crown in a more space limited environment than both other species. Moreover, *Vouacapoua* had a relatively thick trunk, as is indicated from its higher safety margins. High safety margins enhance its chance to survive falling branches, trees, and epiphytes during its life in the lower strata of the forest. In contrast, the more slender habit and narrower crown (only for *Dicorynia*) may reflect the higher investments in height growth of *Goupia* and *Dicorynia*. In line of the model, such investments would allow these taller stature species to grow more rapidly to the upper canopy, but this is at the cost of their safety margins.

6.4.4 Tropical vs. temperate forests

At low stem diameters (<30 cm), *Dicorynia*, *Goupia* and *Vouacapoua* had safety factors ranging from 1.0 to 1.8 (Table 6.3). Are these safety factors similar to, or different from, safety factors of temperate forest trees? King (1981, 1986, see also King & Loucks 1978) calculated safety factors for two temperate tree species: the light-demanding *Populus tremuloides* and the shade-tolerant *Acer saccharum*. He used, however, another constant c_1 (see equation (1)), depending on the crown mass/trunk mass ratio. For sake of comparison, the safety factors of his trees were calculated by substituting the diameter - height relationships of his trees (after King 1986) into the equation 7 and then by calculating the safety factor after equation 8, using the value 0.792 for constant c_1. The range of safety factors of our study species tends to be lower compared to those of *Populus* and *Acer* (Table 6.3). King also found a range of low values for *Acer* trees with one terminal leader, but these trees were selected by their apical dominance (one leader) and thus give values biased towards low safety margins (King 1986). Thus, all other factors being equal, the juveniles of tropical rain forest trees may have lower safety margins than juveniles of temperate forest trees. Their lower safety factors are mainly due to their more slender habit (see also Kohyama & Hotta 1990), and not to their wood properties (see E/ρ, Tables 6.3 & 6.4).

Table 6.3. Safety factors of tropical and temperate tree species. For calculation, see text.

	Diameter range (cm)	safety factor range (m/m)	E/ρ (10^3 m)	Selection criteria
<u>Tropical</u>				
Dicorynia	1-30	1.0-1.3	1949	at random, in natural forest
Goupia	1-30	1.0-1.6	1857	at random, in natural forest
Vouacapoua	1-30	1.3-1.8	1793	at random, in natural forest
<u>Temperate</u>				
Populus	3-22	1.5-2.7	2050	individuals in dense stands
Acer	1-10	2.0-2.9	1871	planar crowns, natural forest
	1-10	1.3-2.0	1871	one leader, natural forest
	> 18	1.9-2.6	1871	individuals in dense stands

-Elastic modulus (E) was 822.10^6 kg/m^2 for *Populus tremuloides* and $1265\ .10^6$ kg/m^2 for *Acer saccharum*, and wood density (ρ) was 401 kg/m^3 for *Populus* and 676 kg/m^3 for *Acer* (from Niklas 1994a). For values of tropical species, see Table 6.1.

Kohyama and Hotta (1990) also found a more slender habit for small saplings of tropical rain forest tree species as compared with saplings of temperate species. Given the small size of these saplings, it is not likely that the more slender habit of tropical trees resulted from the early death of the more slender temperate seedlings and saplings. Instead, it may be hypothesised that the more slender habit of tropical rain forest trees resulted by natural selection, and that tropical trees invest more in height and less in thickness than temperate trees. This growth habit may be related to the fact that tropical rain forest trees produce denser (and stiffer), and thus more expensive, wood (Tables 6.1, 6.3 & 6.4).

Table 6.4. Wood properties for 51 canopy tree species of the tropical rain forest in French Guiana (CIRAD-CTFT 1989), and for 53 canopy tree species of temperate forest in North-America (Niklas 1994a).

Wood properties		Tropical species			Temperate species			Difference *
		mean		sd	mean		sd	P-value
Elastic modulus E	(10^6 kg/m^2)	1507	±	420	1050	±	226	0.0000
wood density ρ	(kg/m^3)	773	±	196	542	±	133	0.0000
E/ρ ratio	(10^3 m)	1950	±	20	1980	±	37	ns

- Species with an adult stature below 20 m (see original data set, Niklas 1994a) were omitted from the analysis.
-* Differences between tropical and temperate species were tested using Mann-Whitney U test. ns means not significant; $P > 0.05$

In line of the elastic-stability model, these wood properties did not account for the difference in safety factors between tropical and temperate trees, because the ratio of the elastic modulus and wood density was the same for either group of species (Tables 6.3 & 6.4). However, trees with denser and stiffer wood may reduce their risk on mechanical failure (e.g. Putz *et al.* 1983). Thus, tropical rain forest trees may produce a more slender habit than temperate trees, but not be more risk-prone to mechanical damage as would be predicted by the elastic-stability model. Indeed, tropical rain forest trees may snap as frequently as tree species of temperate forests (67% snapped in a temperate forest in North America (Runkle 1982), and 70% snapped in a tropical rain forest in Panama (Putz *et al.* 1983), and approximately 60 % in a forest in French Guiana (Van der Meer & Bongers 1996)). However, the percentage of snapped trees does not only depend on the above ground mechanical design of trees, but also on the anchoring strength of their roots and on external environmental factors, e.g. wind rates and snow loads.

Thomas (1996a) found lower growth rates and higher wood densities in the species of lower stature in a Malaysian rain forest. He argued that low light levels in the understorey may predispose these smaller stature species to low growth rates and (correlated) high wood densities. In turn, he hypothesised that the high wood density would allow these species to have high rates of height extension relative to diameter increase. Given that light levels are further reduced in tropical rain forest than in temperate forests (Terborgh 1985, Canham *et al.* 1990, see also Chapter 4), these differences between understorey and overstorey species parallel these differences between the tropical rain forest trees and temperate trees.

An alternative 'adaptive' explanation for the differences in the mechanical designs between tropical and temperate trees is found in the climatic differences between the studied tropical and temperate forests. In the North American forests, heavy storms and snow-loads may cause very high levels of mechanical stress on trees (King 1986, 1991b), while these factors do not occur in French Guiana. Thus, tropical trees were exposed to lower levels of external stress than temperate trees, assuming that storms and snow cause more stress than epiphyte or liana loads. The higher safety margins of North American tree species may have evolved in response to these higher external stress. Given these arguments, it is hypothesised that, also for tropical rain forests, safety factors are higher in heavy storm or hurricane prone forests than in forests where heavy storms or hurricanes do not occur.

Interestingly, part of the large variation in size and allometry between individuals may be related to the environment, e.g. light availability (Chapter 4). Taking the model as a starting point, the intra- and interspecific variation in size and allometry (and the underlying process of allocation) may be related to the environmental conditions of individuals and species, respectively. The suggested relationships between ontogenetic changes in tree size and allometry and other species traits (e.g. shade tolerance, adult stature, light habitat) should be tested for their validity on larger numbers of tree species. Such species comparisons may help us to understand the ecology and evolution of species and their growth characteristics in their natural habitat.

7

TREES AND LIGHT: SYNTHESIS

7.1 Introduction

Tropical rain forest trees spend their life in a heterogeneous light environment. During their life history, they may change their growth in relation to different levels of light availability. Some of their physiological processes (e.g. photosynthesis, carbon allocation, and meristem activity) change with light availability, and tune their development and morphology to the ambient light levels. The focus of this thesis is on the development and morphology of trees of canopy species in relation to the light availability in tropical rain forest. The underlying physiological processes are not included. The possible consequences for survival, growth, and reproduction are not assessed directly, but are discussed on a speculative basis.

Many, but not all, aspects of tree development and morphology were investigated. The development and morphology of roots were neglected (but see Chapter 2). Roots have to be excavated to monitor their growth. For taller trees, the excavation of roots is a hard job. Moreover, trees may not follow their natural course of development after excavation. The roles of roots as soil resource suppliers and tree anchors are not further discussed here. With respect to the development and morphology above ground, the losses of plant components were not included. Over the 2-3 years of field work, the losses were too small and variable to relate them to variation in light availability. Apart from these limitations, tree development was investigated at different organisation levels (leaves, metamers, extension units, sympodial units, and whole crown (Table 1.1, Chapter 1) over a period of 2-3 years. Morphological characters referred to tree size, tree weight, tree allometry, leaf display, and mechanical design, as well as to the weight, size, and number of different components. Using large samples of trees of different size, the changes in development and morphology with ontogeny were assessed, and related to light levels in the forest. This approach provided many answers to the first main question: 'How are tree development and morphology affected by light availability in tropical rain forest?'. The second main question, 'What are the ecological consequences of different traits of development and morphology for trees in tropical rain forest', could only be addressed tentatively.

The remaining part of this chapter starts with a discussion on the spatial variation in light availability in tropical rain forest (7.2). The responses in development and morphology to this variation in light availability are reviewed for the studied species, and compared with such responses in other tree species, both in tropical and temperate forests (7.3). Rates of development are used to asses changes in age with increasing tree height. The influence of ambient light levels on development rates and tree ages is evaluated (7.4). Until this point, the chapter focuses on the growth responses as shown by empirical studies. These studies are usually biased with respect to the range of light levels they consider. Therefore, response types to the whole range of light availability are also considered from a theoretical perspective (7.5). In addition, the changes in morphology with ontogeny are discussed with respect to their consequences for mechanical tree design (7.6). Furthermore, the implications of the whole study for forest management systems are evaluated (7.7). Finally, the major general conclusions of this thesis are presented (7.8).

7.2. Spatial heterogeneity in light

Tropical rain forests are characterised by a highly variable light environment, both in the horizontal and vertical direction (e.g. Yoda 1974). Early studies focused on the relative contribution of sunflecks, but lacked absolute measures of light intensity (Evans 1939, 1956, Whitmore & Wong 1959). In later studies, it was shown that light levels varied between 1 to 50 % of the light level in the open sky (e.g. Chazdon & Fetcher 1984, Van der Meer 1995), and that light levels increased with the size of openings in the canopy. Hubbell & Foster (1986) and Van der Meer *et al.* (1994) showed that gaps occurred more frequently with increasing height in the forest. Also, light levels were found to increase from the forest floor to the upper canopy (Yoda 1974, Koop & Sterck 1994). In a transect of Malaysian rain forest, Yoda (1974) found slowly increasing light levels up to 47 m, and a sharp shift to higher light levels above 47 m. For a transect of forest in French Guiana, Koop & Sterck (1994) found slowly increasing light levels up to 30 m, and a sharp shift to higher light levels above 30 m. Clearly, the transects did not include canopy gaps, through which sunlight may penetrate to lower levels in the forest. The transects indicate, however, that trees may be exposed to a wide range of light levels before they reach the upper canopy layer of the forest.

Trees of a particular species dwell in a light environment that may differ from the general light environment in the forest. These trees may establish, grow, and survive at a particular range of light levels. This is most clearly shown by the rather artificial dichotomy between light demanding species (also referred to as pioneers or early successionals) and shade-tolerant species (climax species, late successional, e.g. Schulz 1960, Whitmore & Swaine 1989, Clark & Clark 1992, Alvarez-Buylla & Martinez-Ramos 1992). Because light demanding species are either unable to establish (Swaine & Whitmore 1988) or survive (Lieberman *et al.* 1990, Alvarez-Buylla & Martinez-Ramos 1992) at lower light levels, they usually occur at higher light levels. In contrast, shade tolerant species establish and survive at both low and high light levels, and thus occur within a wider range of light levels.

Few studies report on the light environments that are encountered by trees of the same species (and the same population). For the studied tree species *Dicorynia* and *Vouacapoua*, which are both known as shade tolerants (e.g. Schulz 1960), canopy openness (expressed as a percentage of the open sky, used as an estimate of light availability) varied between 0.8% and 11% in trees less than 4 m tall, between 4.8% and 30% in trees 4-20 m tall, and between 12% and 80% in trees taller than 26 m in the Nouragues forest (Chapters 4 & 5). These estimates of canopy openness were based on hemispherical photographs (e.g. see Whitmore *et al.* 1993). On the basis of the crown position index values (a visual estimate of canopy openness), the largest increase in canopy openness occurred between 20 and 35 m. Using the same index, a similar pattern was found for *Pourouma bicolor* (Bongers & Sterck in press). *Cecropia obtusa*, known as an early successional species, was more frequently exposed to higher light levels (Bongers & Sterck in press). In each of these species, the taller trees were more frequently exposed to higher light levels than the smaller ones, but (within given margins) trees of the same height also occurred at different light levels. The same trend was found for tree species in a Costa Rican rain forest (Clark & Clark 1992, Lieberman *et al.* 1995), and this is probably the case for the majority of tree species in forests.

Light levels may also widely vary within individuals. Leaves on one single plant are exposed to different light levels, because they face in different directions and angles (Oberbauer *et al.* 1988, Chazdon *et al.* 1988). Also, the lower leaves in the crown may be shaded by overtopping crown parts, and are exposed to lower light levels than leaves in the top of the crown (unpublished data). This variation in light within trees falls beyond the scope of this thesis.

7.3. Responses in development and morphology

As shown above, trees may encounter many different light environments, but the taller they grow, the more frequently they encounter higher light levels. At the same time, trees change their morphology and development as they become older and taller. This is shown, for example, by a change from pole sapling (one apical meristem) to a heavily branched individual (more apical meristems). In the literature, the relationships between tree development (and morphology) and light availability have been shown for seedlings (e.g. Augspurger 1984, Popma & Bongers 1988), and for small saplings (e.g. Shukla & Ramakrishnan 1986, King 1991a, 1994). For taller trees, individuals were compared between forest sites and 'urban' clearings (Fisher & Hibbs 1982, Borchert & Tomlinson 1984), but not between different light conditions in the forest. In the current study, trees of different size were investigated, and their development and morphology were related to light levels in the forest. In general, trees that still head for the canopy (shorter than 20 m) showed the same direction of response to light availability.

These trees shorter than 20 m produced more growth units (Table 1.1, metamers for *Dicorynia*, and units of extension for *Vouacapoua*) at higher light availability (Chapters 2, 3, & 4). Whereas the young and short pole saplings produced more growth units along their main axis (Chapter 2), older and taller individuals produced more growth units mainly by producing more apical meristems (by a more frequent release of axillary meristems, Chapter 4). In *Dicorynia*, these growth units consisted of one leaf by definition. In *Vouacapoua*, these growth units consisted of more leaves at higher light availability. Thus, both these species produced their leaves at faster rates at higher light levels. As their leaves did not change in size in response to light, both species increased their total leaf area and LAI at higher light levels. Similar responses were found in other tropical rain forest tree species (e.g. Shukla & Ramakrishnan 1986) and in temperate tree species, e.g. *Acer saccharum* (Steingraeber *et al.* 1979, Canham 1988). Under persisting high light levels, the increased total leaf area may enable these trees to fix more carbon for future growth and survival (Chapters 2 & 3). A high LAI at higher light availability, in combination with more columnar shaped crowns (Chapter 4), is consistent with the predictions of Horn (1971) and Borchert & Tomlinson (1984). They argued that trees with more columnar crowns and high LAI achieve net photosynthesis in their leaves at the lowest cost for leaf area support. In contrast, trees with more planar crowns and lower LAI may avoid self-shading of leaves under low light levels, but this is at the expense of higher costs for leaf area support. However, this measure of support costs for leaf display refers to the construction of the crown (costs of support over the whole tree life-history), and not to the production costs of the amount of supported leaf area (costs of support during latest period of tree life-history).

The influence of light availability on the costs of displaying leaf area is more directly assessed by the space between leaves. Trees of *Dicorynia* and *Vouacapoua* produced shorter growth units at lower light availability, and thus spaced their leaves at shorter distances (Chapters 2, 3 & 4). King (1991a) found the same pattern in 1-2 m tall saplings of his shade tolerant tree species. As leaf size did not change in relation to light, trees displayed their leaf area more economically (at lower carbon costs) at lower light availability. In this way, they increased light interception per carbon investment, lowered their whole plant compensation point, and may therefore be better able to survive the shade (e.g. Givnish 1988, King 1991a). Thus, whereas Horn's (1971) and Borchert & Tomlinson's (1984) arguments indicate higher support costs for leaf display in shaded trees, the shaded trees produce their leaf area at lower costs.

For shade tolerant temperate tree species, Canham (1988) calculated the costs of leaf display on the basis of the space between leaves. Trees of these species produced their leaves at similar (*Fagus grandiflora*) or at higher costs (*Acer saccharum*) with decreasing light availability. In tropical rain forests, light demanding species (King 1991a, 1994), including *Goupia glabra* (Chapter 2), produced their leaf area at similar costs at different light levels. Thus, like the light demanding species in tropical rain forest, the shade tolerant species in temperate forest did not show an ability to decrease their costs of producing leaf area at lower light availability. If light levels in tropical rain forest are indeed lower than in temperate forest (see Terborgh 1995, Canham *et al.* 1990, Chapter 4), the temperate shade tolerant trees may be exposed to higher light levels than the tropical shade tolerant trees. Thus, in contrast to individuals of shade tolerant species of tropical rain forest, the trees of shade tolerant species of temperate forest may not need not to reduce their costs of leaf display in order to survive in the shaded understorey.

Trees of *Dicorynia* and *Vouacapoua* produced more total branch length at higher light levels (Chapters 3 & 4). This was caused by the higher production rates of growth units, and by producing longer growth units. As such, 1 m tall pole saplings grew faster in height at higher light levels (Chapter 2). Taller trees produced more, and longer, growth units at their active apical meristems, and also grew faster in height with increasing light availability. Increasing height growth at higher light availability was found in trees of other shade tolerant species as well, both in tropical rain forest (King 1991a, 1994, Clark & Clark 1992) and temperate forest (Canham 1988, Sipe & Bazzaz 1994). In general, trees of these species may reduce their height growth because of low light availability. Under these conditions, they cannot compete with their taller tree neighbours which intercept the majority of light above them, but they may survive by producing their leaf area slowly and efficiently (see above, and also King 1994). When light levels increase because one (or more) of the taller neighbours falls down, these trees start to increase their height growth, and may compete with their neighbours of similar or smaller size for new available light and space (see also Canham 1988). The more light demanding species have inherent high growth rates, irrespective of the light environment (e.g. King 1991a, 1994). These high growth rates enable them to compete efficiently with their neighbours for light and space at high light levels, but not to survive at lower light levels (e.g. King 1991a, 1994, Alvarez-Buylla & Martinez-Ramos 1992).

Individuals growing in large canopy gaps (high light) showed preferential growth of the leader (axis which supports the most upper apical meristem of the crown) over the other axes in the crown (Chapter 3). In contrast, individuals growing below a closed canopy (low light) did not show preferential growth of the leader. This trend was not found for individuals that grew in a range of light levels in the forest (Chapter 4). The response of dominant growth of the leader probably only occurred at high light levels in large canopy gaps, which only occur rarely in the forest (Chapter 4).

These growth responses to light refer to trees that still head for the canopy. The taller trees above the upper canopy did not always show the direction of response that would be expected on the basis of the high light levels they were exposed too. Compared with trees that still headed for the canopy, they further increased their total leaf area and total branch length by increasing their number of apical meristems. Also, they produced much larger and more planar shaped crowns, did not increase their LAI, and decreased their leader growth and the space between leaves. The shift to a wider crown was found for other tree species as well (Bongers *et al.* 1988b, King 1996), and is probably caused by increasing light (and space) availability, and not by increasing tree height. This shift may constrain further increases in the LAI. Lower leader growth and the production of leaves at short distances indicate that these trees changed from investments in vertical expansion to the replacement of leaves (and the production of flowers).

7.4 Rates of development and tree age

Leader growth is correlated with height growth, and was used to estimate the amount of time trees spend on growing through successive height classes. Given the minimum and median time trees spend in these height classes, 20 m tall trees were estimated to be 68 years (*Vouacapoua*) or 84 years old (*Dicorynia*) (minimum age), or between 235 years (*Vouacapoua*) and 288 years old (*Dicorynia*) (median age). Given that leader growth increases with light availability (Chapters 2, 3, 4, & 5), the minimum and median ages reflect hypothetical ages for trees that mature in relatively high and low light environments, respectively. The fast growers in the higher light environment have more chance on survival than slow growers, because they suffer less from both low light availability and falling debris (e.g. Clark & Clark 1991). In reality, the individuals that make it to the canopy are expected to encounter both the lower and higher light levels (Chapters 4 & 5). Thus, although trees of the same height may differ in age, these age differences may be smaller than is suggested from the estimates of minimum and median tree age. However, actual tree ages remain unknown.

The age estimates for trees of *Dicorynia* and *Vouacapoua* were compared with similar age estimates for trees of six canopy or emergent tree species in a Costa Rican rain forest (Clark & Clark 1992). Interestingly, trees of *Dicorynia* and *Vouacapoua* were older than the Costa Rican trees of the same size, because they grew slower than the Costa Rican trees. The slow growth may be due to lower soil fertility or lower annual rain fall in the Nouragues forest in French Guiana.

In general, tropical rain forest trees are hard to date. Their age cannot easily be measured due to the absence of annual growth rings (Bormann & Berlyn 1981, Baas & Vetter 1989). As a result, other methods have been applied to date tropical rain forest trees. For example, Lieberman & Lieberman (1985) and other researchers (Kornig & Balslev 1994, Clark & Clark 1992) used diameter increments in successive size classes, O'Brien *et al.* (1995) used diameter increments in successive size classes in combination with height-diameter relations, and Condit *et al.* (1995) used mortality rates of trees in two size classes. Methods based on wood properties have been applied as well (e.g. Jacoby 1989, Worbes & Junk 1989). The influence of light availability on the time tropical rain forest trees spend to grow from seedling to adult was not assessed directly in these studies.

7.5. Different response types to ranges of light availability

The studies discussed so far focus on responses in development and morphology to a particular range of light levels, for example two contrasting light levels (Chapters 2 & 3, e.g. Steingraeber *et al.* 1979, Augspurger 1984), more than two different light levels (e.g. Loach 1970, Popma & Bongers 1988, Cornelissen 1994), or a range of light availability (Chapters 4 & 5, e.g. Bonser & Aarssen 1994). The observed response in relation to light availability depends on the considered light range, as well as on the response type of the species. Three hypothetical responses types were discussed (Chapter 4). In the case of a linear response, different ranges of light availability do not affect the observed direction of response, but the larger the light range the more easily a response is demonstrated at a given level of variation. In the case of a curved response, different ranges do not affect the direction of response, but may affect the magnitude of an observed response. Some light ranges cause a large response, while other ranges cause only a minor response which is harder to demonstrate, at a given level of variation. In the case of a bell-shaped response, different light ranges may result in responses in the same direction, in responses in the opposite direction, or in no response at all. Thus, for each of these response types, the range of light availability may affect the observed response. In general, the response to the whole range of light levels can be assessed by including many different light levels in a controlled experiment (e.g. Sasaki & Mori 1981, Veenendaal *et al.* 1996). Larger individuals, however, are hard to grow under controlled conditions. Alternatively, their responses can be observed along the whole gradient of light levels in the forest. Trees at different positions along the whole light gradient were investigated in Chapters 4 and 5. They show large variation in their responses, probably because individuals were exposed to different, unknown, light conditions during their growth history. Trees at high levels of light availability in large canopy gaps were not included because these conditions were rare in the forest. Thus, in order to study the responses in larger trees to the whole range of light levels, large samples of trees should also be investigated (see Chapter 4), and trees under rarely occurring light levels should be included as well (see Chapter 3).

7.6. Ontogenetic changes in morphology and mechanical design

The previous discussion focused on aspects of tree development which result from the activity of the apical meristems, but not of the cambial meristems. Whereas the apical meristems accommodate the increase in tree stature, the cambial meristems accommodate thickness growth of stem and branches. In general terms, the apical meristems enable the tree to occupy new space, and higher light levels at increasing height in the forest. The cambial meristems produce the new vessels for water and nutrient transport from roots to (an increasing number of) leaves, and also provide additional mechanical strength (thickness) to carry the increasing tree weight and to resist the wind stress that increases with stature. The mechanical design expresses the balance between tree stature (in terms of tree weight or wind force) and (mechanical) tree strength. The changes in mechanical design with ontogeny are further discussed below.

McMahon (1973, 1975) and other researchers (e.g. King & Louks 1978, Niklas 1992, O'Brien *et al.* 1995, Mattheck 1991) have discussed models of mechanical tree design. The elastic-stability (or elastic-similarity) model was described by Greenhill in 1881, (for mathematical expression see Chapter 6) and was adapted and refined by McMahon (1973) and others (e.g. King & Loucks 1978, Holbrook & Putz 1989). This model emphasises the stress due to self-weight (or self-loading, e.g. Niklas 1992). The constant-stress model was introduced by Metzger (1893) and further explored by other researchers (e.g. Dean & Long 1986, Niklas 1992, Mattheck 1991). This model emphasises wind resistance. A third model is the geometric-similarity model. This model assumes that the proportions of trees are constant. The elastic-stability model and the constant-stress model were further explored in this thesis, but not the geometric-similarity model (see e.g. King & Loucks 1978, Niklas 1994b, O'Brien *et al.* 1995).

The changes in mechanical design with ontogeny are not usually consistent with any one of the presented models. In the literature, the slopes of log-transformed height-diameter relationships usually differed from the slopes predicted by the elastic-stability model, the constant-stress model, and the geometric-similarity model (e.g. Rich *et al.* 1986, Claussen & Maylock 1995, Niklas 1994b, but see O'Brien *et al.* 1995). These linear regressions through double-log transformed data do not account for the asymptotic nature of height-diameter relationships, and this may mask changes in mechanical design with ontogeny (see Thomas 1996a). For *Goupia*, *Dicorynia*, and *Vouacapoua*, asymptotic regressions were fitted using height-diameter data. These regressions were used to show ontogenetic changes in mechanical design, using the elastic-stability model.

On the basis of the elastic-stability model, the mechanical design was expressed by the safety factor. In theory, trees with a safety factor of 1 have a stem which is just thick enough to support their own weight, and trees with a safety factor of, for example, 2 have stems which are twice as thick at the same weight or stature. Trees with safety factors below 1 are not stable and will buckle or snap under their own weight. For the study species, trees decreased their margins of safety during early ontogeny, but increased their margins of safety later. The minimum safety margins were largest for *Vouacapoua* (1.5), intermediate for *Dicorynia* (1.3), and lowest for *Goupia* (1.0).

The safety margins of the tropical study species were lower than those of temperate tree species. This was due to the greater tendency towards slenderness of the tropical tree species (taller at a given diameter), and not due to different wood properties. For 1 m tall saplings, Kohyama & Hotta (1990) also found that tropical rain forest tree species were more slender than temperate forest tree species. Thus, the tropical trees may invest more in height and less in thickness than the temperate trees. This growth habit may be related to the denser and stiffer wood of the tropical trees, which reduce the risk of mechanical failure (e.g. Putz *et al.* 1983). Thus, although they have a more slender habit, tropical rain forest trees need not be more risk-prone than temperate trees.

Temperate trees may also have higher safety factors because they are exposed to storms or snow loads (King 1991b). The least slender trees have the highest chances of survival under such conditions, and are likely to dominate the forest. On an evolutionary time scale, such conditions may select for tree species which tend to be less slender than tropical rain forest tree species. It should be noted, however, that these adaptive arguments concerning the more slender habit of tropical rain forest trees are highly hypothetical.

The margins of safety against wind forces were calculated on the basis of the constant-stress model. Wind forces are assumed to increase with increasing tree height and crown size. The resistance of trees to wind force depended on the stem diameter. Safety margins against wind force did not differ significantly between the species studied, and increased with ontogeny in each of the species studied (Chapter 6). This increase with ontogeny was in line with the expectations, as wind rates are likely to increase with ontogeny. These margins were not compared with temperate tree species, as safety margins have rarely been assessed in this way (but see Dean & Long 1986 for conifers).

The safety margins differed between individuals of the same size. No significant response in safety margins to light availability could be shown for the study species, neither on the basis of the elastic-stability model nor on the basis of the constant-stress model (Bongers & Sterck in press). In contrast, under controlled conditions, shaded trees grow at lower safety margins than trees in half-shade (Holbrook & Putz 1989). In the latter study, seedlings were grown at these contrasting light levels, and they responded directly to the light levels they were exposed to. The trees studied for *Dicorynia* and *Vouacapoua*, however, have long life-histories under unknown light conditions, and may therefore not have shown these responses in mechanical design within the 2-3 years of the present study (data set of Chapter 4, see Bongers & Sterck in press). The same trees are currently being monitored in order to obtain long term data on their light environments and mechanical design. Long term data may show whether light availability is related to the mechanical design of trees living in tropical rain forest. Also, such data may show the influence of mechanical tree design, and its changes with ontogeny and light availability, on the survival chances of trees in the forest.

7.7. Implications for forest management

The species studied (*Dicorynia*, *Goupia*, and *Vouacapoua*) are well known timber species in French Guiana and surrounding countries (e.g. de Graaf 1986). Auto-ecological studies on commercial species are expected to be useful for the fine tuning and improvement of forest management systems (Gomez-Pompa & Burley 1991, Oldeman & van Dijk 1991). The use of the present study for forest management is discussed below.

Gomez-Pompa & Burley (1991) distinguished four types of forest management (or silvicultural) systems. These systems create different sized canopy gaps, and depend either on natural or artificial regeneration. In *natural regeneration systems*, only a few trees are selected at a time for removal. These systems allow natural regeneration to fill gaps and maintain standing volumes of all tree species. In *clearing systems*, some valuable commercial tree species are cut. Also, some unwanted individuals are killed on purpose. In this way, commercial trees are exposed to higher light levels in order to increase their rates of growth and timber production. The Celos system, developed for a tropical rain forest in Surinam (e.g. de Graaf 1986), is an example of such a system. In *replacement systems*, the forest is clear-cut and replaced by forest plantations, for example *Pinus* species in French Guiana. In *restoration systems*, the focus is on the restoration of forest in clear-cut areas where the regeneration of the natural vegetation is arrested by some dominant species, for example the grass-species *Imperata* in Asia.

Trees of the species studied grow faster in response to higher light levels (Chapters 2, 3, 4 & 5) in their natural habitat. For example, in large canopy gaps (canopy openness of approximately 15-30% relative to the open sky), *Dicorynia* and *Vouacapoua* trees produce a more than 10-fold increase in height growth (and thus increase their timber production) as compared with trees in the understorey (canopy openness approximately 1-5%, Chapters 3 & 5). Given that large canopy gaps are created by natural regeneration systems and clearing systems, such systems may provoke faster rates of growth and timber production in *Dicorynia* and *Vouacapoua* trees. In contrast to these two systems, the replacement- and the restoration systems start with open sky light levels. Growth rates at open sky light levels were not investigated in this thesis.

Trees of the species studied also change their morphology in relation to light availability. For example, trees shorter than 20 m were shown to increase their crown length/width ratio with increasing light availability (Chapter 4), probably because their leaders grow faster than lateral axes (Chapter 3). Where this response occurred in the range of 1 to 30 % of light levels in the open sky, trees taller than 26 m were often exposed to higher light levels and their crown length/width ratio decreased (Chapter 4). Smaller individuals of the same species in replacement systems (monoculture plantations) also had a lower crown length/width ratio than trees of the same size in the forest (unpublished data). From this it may be inferred that the decrease in the crown length/width ratio is a response to open sky light levels, and not the result of the increasing tree height. If the response to open sky light levels resulted from arrested leader growth, it might result in lower stem extension and would be disadvantageous for timber production.

Thus, these results show that manipulations of light availability in forest may increase the timber production in trees of the studied tree species. Manipulations may be based on shading in replacement- and restoration systems, and on liberation thinning in clearing- and natural regeneration systems. In general, the influence of manipulations that create light levels beyond the natural range of light levels in the forest remains unknown. Knowledge of the growth responses to the whole range of light levels (0-100%) may show the light levels at which tree growth, in terms of timber production, is maximised. More importantly, the growth responses have to be assessed for trees of different size because growth responses may change with ontogeny. If the growth responses are known for a given species, levels of light availability may be manipulated so as to create the light conditions that provoke the desired growth response.

Interestingly, morphological traits have been used to indicate the growth potential of trees (Oldeman 1990). In this thesis, the influence of tree development on morphological traits was assessed, but not the influence of morphological traits (in interaction with the light environment) on future growth. This latter issue is part of the follow-up of the present study (data set Chapter 4), and may serve as a starting point for defining the meaning of morphological traits for the growth potential of trees at different light levels. In the forest management systems, this information may be used to characterise tree individuals of commercial species, and to tune manipulations applied to these individual trees in order to create the light conditions that provoke the desired growth response. As for the growth response, the growth potential of trees on the basis of morphological traits should be related to the whole range of light levels. In general, the fundamental research on tree growth in a natural habitat, extended by research on tree growth at the higher light levels outside the natural habitat, may provide valuable insights for the improvement of forest management systems.

7.8 General conclusions

The two canopy tree species *Dicorynia* and *Vouacapoua* change their development and morphology with ontogeny in tropical rain forest. Tree height and light availability affected tree development and morphology at all organisation levels (leaves, growth units, sympodial units, and whole crown). Trees that still head for the canopy (shorter than 20 m) produced more and larger plant components (except leaves) with increasing light availability, and thus increased their total leaf area, leaf area index (LAI), height growth, crown expansion, and the space between leaves. Trees that had their crown exposed above the upper canopy (26-37 m tall) may produce more plant components, but they produced smaller leaves and growth units. These tall and fully exposed trees further increased their total leaf area and crown expansion, but did not further increase their LAI, and reduced their height growth and the space between leaves, compared with the smaller trees that were still in the race for the canopy.

These aspects of above-ground tree development and morphology are the result of growth at the apical meristems. Likewise, the cambial meristems accommodate the thickness growth of stem and branches, and thus provide the tree with the mechanical strength to carry its own increasing weight and withstand wind stress. Using a theoretical model, the safety margins for the support of the trees' own weight decrease during early ontogeny, and increase later on. The minimum safety margins are close to the theoretical minimum. This means that trees are just thick enough to carry their own stature and weight. On the basis of another theoretical model, the margins of safety against wind stress increased with ontogeny. In this way, trees may resist higher wind rates.

The tropical rain forest tree species studied were compared with other tree species, both in tropical and temperate forests. There were both interspecific similarities and dissimilarities in the responses to light availability. The similarities often referred to the higher growth rates at increasing light availability. Dissimilarities usually referred to other traits than growth rates. In some cases, they occurred between species that may be found in different light habitats, and may reflect growth adaptations to these habitats (e.g. tropical rain forest versus temperate forest). In other cases, they may simply result from differences in the light range that was investigated (e.g. forest versus clearing, or a range of forest light levels), and they reflect only different parts of the same growth response to light availability. In general, these comparisons between tree species are often hampered by the lack of comparable data on the light environment.

The consequences of tree development and morphology, and their relation to light availability, for the ecological and evolutionary success of trees in tropical rain forest were evaluated. These considerations were however highly speculative, because of lack of data on three major issues. Firstly, the physiological processes (photosynthesis, carbon allocation, meristem activity, costs of growth) underlying tree development were not assessed. These processes determine the balance between carbon intake and carbon use for the maintenance and growth of the tree. These processes, and their consequences for tree development and morphology, are currently being studied for *Dicorynia*, *Vouacapoua*, and *Goupia* (for the latter species see Chapters 2 & 7). Secondly, the 2-3 years of field work were too short to demonstrate the ecological success of trees on the basis of fitness criteria, namely survival, growth, and reproduction. In the long run, the ongoing monitoring research on large samples of trees (see Chapter 4) may provide the data to relate light availability, development and morphology to these fitness criteria. Thirdly, trees were investigated for two canopy tree species, but not for the hundreds of tree species that co-exist with them in the same forest, nor for the thousands of tree species that live in other forest-ecosystems. The way in which these tree species differ in their growth patterns in relation to ambient light levels in their natural habitat remains largely unexplored.

SUMMARY

Tropical rain forest trees spend their life in a heterogeneous light environment. During their life history, they may change their growth in relation to different levels of light availability. Some of their physiological processes (e.g. photosynthesis, carbon allocation, and meristem activity) change with light availability, and tune their development and morphology to the ambient light levels. The underlying physiological processes are not investigated in the present study. The focus is on the development and morphology of trees of canopy species in relation to the light availability in tropical rain forest. The possible consequences for survival, growth, and reproduction of trees are not assessed directly, but are discussed on a speculative basis.

The relationships between the light environment, tree development, and morphology are investigated for trees of different size, ranging from small saplings to trees of adult stage. Trees of increasing size are compared in order to explore the changes in tree development and morphology, and their relation to the light environment, with ontogeny. Ontogeny is referred to as the overall growth and development pattern during tree life, both for individual trees and (in more general) for a given tree species.

The field work for this thesis was carried out in French Guiana. This country in the north-east of South America has an area of 83.000 km^2 and is covered by evergreen tropical rain forest. The field work was conducted at two biological stations. 'The Piste St. Elie' station is located 30 km from the coast, south of the town of Sinnamary, and the biological station 'Les Nouragues' is located 100 km from the coast, south of Cayenne. Two canopy tree species were selected for this study: *Dicorynia guianensis* Amshoff. (Caesalpiniaceae) and *Vouacapoua americana* Aubl. (Caesalpiniaceae). Both are common species in the forests of French Guiana, and are considered late successionals or shade-tolerant species (Schulz 1960). In some chapters, these species are compared with an early successional (light demanding) species, *Goupia glabra* Aubl. (Celastraceae). Trees of these three species are harvested for their timber in French Guiana and its surrounding countries.

The trees that were shorter than 20 m had not yet reached the open upper canopy. These trees usually occur at relatively low light levels. Although these trees may differ in height (from 0 to 20 m), they usually show the same type of growth response to ambient light levels. They produced more growth units and more leaves at higher light availability. They thus increased their total leaf area and leaf area index (LAI, a measure for the number of leaf layers in the crown) as a response to higher light levels. Under persisting high light levels, the increase in total leaf area may enable these trees to fix more carbohydrates (i.e. carbon) for successful growth and survival in the future. Trees with a high LAI at higher light availability, in combination with more columnar shaped crowns, achieve net photosynthesis (more carbon intake than consumption by leaves) at the least possible cost for leaf area support. In contrast, trees with more planar crowns and lower LAI at lower light availability may avoid self-shading of leaves, but risk higher costs for leaf area support.

Trees also produced shorter growth units at lower light availability, and thus spaced their leaves at shorter distances than trees at higher light availability. In more closely spaced leaves, the investments for the support of one leaf are lower. As leaf size did not change in relation to light availability, trees displayed their leaf area more economically (at lower carbon costs) at lower light availability. In this way, they increased light interception per unit of fixed carbon, and they may thus be better able to survive the shade.

Dicorynia and *Vouacapoua* trees also grew faster in height with increasing light availability. In general, trees may reduce their height growth because low light levels simply limit growth. At low light levels, trees are shaded by taller neighbouring trees which intercept the majority of light above

them, but they may survive for some time by producing their leaf area slowly and efficiently. When light levels increase because one (or more) of the taller neighbours falls down, trees start to increase their height growth, and may compete with their neighbours for newly available light and space. For both species studied, it was shown that height growth further increased at very high light levels in large gaps through preferential growth of the leader (axis which supports the uppermost apical meristem of the crown) over the other axes in the crown. At lower light levels, individuals did not show preferential growth of the leader. Thus, height growth increased not only because the higher light levels are less growth limiting, but also because of preferential growth of the leader.

These growth responses to light refer to trees (up to 20 m tall) that were still heading for the canopy. The taller trees (heights of sampled trees range between 26 and 37 m) at higher light availability in the upper canopy had a larger total leaf area and total branch length than the trees shorter than 20 m. These taller trees also produced larger and more planar shaped crowns, did not further increase their LAI, and decreased their leader growth and the space between leaves, as compared with the smaller individuals. The shift to a wider crown is probably caused by increasing light (and space) availability, and may constrain a further increase in the LAI (the leaves occurred over a much larger horizontal area). The lower leader growth and the production of leaves at shorter distances indicate that these taller trees changed from investments in vertical expansion to investments in the replacement of leaves (and flowers).

The increasing stature with ontogeny has to be balanced by mechanical strength (thickness). This strength is needed to carry the increasing tree weight and to resist wind stress. The mechanical design expresses the balance between overall tree stature (in terms of weight or wind force experienced by the tree) and tree (mechanical) strength. The changes in mechanical design with ontogeny were investigated for *Goupia*, *Dicorynia*, and *Vouacapoua* using two models. (1) The elastic-stability model emphasises the mechanical strength against its own weight. Using this model, it was shown that trees of the study species decreased their 'safety margins' (strength) early in ontogeny, but increased their margins of safety later. Trees had their lowest margins at a stem diameter of 15 to 25 cm. These margins were close to the theoretical minimum, i.e. trees would buckle under their own weight if they were slightly more slenderly built (taller at a given diameter). In comparison with some temperate tree species, the trees of the present study appeared to have lower safety margins because they were more slender. Slenderness (height/diameter ratio), however, is only one of the factors determining the strength of a tree. The denser and stiffer wood of tropical trees may increase the mechanical strength of tropical trees in comparison with temperate trees. Another explanation for the lower safety margins of tropical trees is that they are exposed to lower external stress forms than temperate trees. Temperate trees experience heavy storms and snow loads during their life, whereas the trees of the present study do not experience such forms of stress. (2) The constant-stress model emphasises the mechanical strength over wind stress on the tree. For the species of study, it was shown that the safety margins against wind stress increased with ontogeny. This was in line with the expectations, because wind stress is likely to increase with increasing tree stature. Finally, the influence of light availability on mechanical tree design could not be investigated. The trees studied had long life-histories under unknown light conditions, and therefore did not show a significant response within the 2-3 years of investigation.

The ecological knowledge on commercial tree species presented in this work is thought to be useful for the fine tuning and improvement of forest management systems. In these systems, canopy gaps of different size are created, and they may affect the growth of trees. The results of this thesis indicate that manipulations of light availability (either by killing dominant trees thus inducing light level increase, or by shading) in forests may increase the timber production in trees. Besides this, the follow-up to this study may provide morphological traits that can be used to indicate the growth potential of trees in relation to the light environment. It is suggested that there is a need for knowledge on the growth response of trees (both in terms of timber production, morphology and development) to the whole range of light availability. Manipulations of the light environment may then be tuned to individual trees of commercial species in order to approach the light conditions that provoke the desired growth response. In general, fundamental research on tree growth in a natural habitat, extended by research on tree growth at higher light levels outside the natural habitat, may provide valuable insights for the improvement of forest management systems.

BOMEN EN LICHT

De morfologie en ontwikkeling van bomen in relatie tot de lichtbeschikbaarheid in een tropisch regenbos in Frans Guyana.

F.J. Sterck
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Samenvatting

Bomen van tropische regenbossen leven in een heterogene lichtomgeving. Zij passen hun groei aan de beschikbaarheid (intensiteit) van licht aan. Fysiologische processen zoals de fotosynthese en de aktiviteit van meristemen staan aan de basis van deze groeiaanpassingen en sturen de veranderingen in de ontwikkeling en morfologie. In dit proefschrift staan de invloeden van de beschikbaarheid van licht op de ontwikkeling en morfologie van bomen centraal. Relaties tussen licht, boomontwikkeling en -morfologie zijn onderzocht voor bomen vanaf het zaailing-stadium tot en met het volwassen (kronendak-) stadium. Door bomen van toenemende grootte met elkaar te vergelijken werd inzicht verkregen in de wijze waarop bomen gedurende hun levensloop hun ontwikkeling en morfologie aan licht aanpassen. Over de consequenties hiervan voor de overleving, groei en reproduktie van bomen in tropisch regenbos wordt gespeculeerd.

Het veldwerk voor deze studie is verricht in Frans Guyana. Dit land is gelegen in het noordoosten van Zuid-Amerika en nog grotendeels bedekt met tropisch laagland regenbos. Voor het veldwerk waren twee biologische onderzoeksstations in gebruik; het onderzoeksstation 'Piste de St. Elie', 30 km ten zuiden van Sinnamary, en het onderzoeksstation 'Les Nouragues', 100 km ten zuiden van de hoofdstad Cayenne. Twee boomsoorten van het kronendak werden geselecteerd voor deze studie, te weten *Dicorynia guianensis* Amshoff (Caesalpiniaceae) en *Vouacapoua americana* (Aubl.) (Caesalpiniaceae). Beide soorten komen veel voor in de bossen van Frans Guyana. Zij staan bekend als soorten die overleven onder schaduwrijke omstandigheden. In enkele hoofdstukken worden deze twee soorten vergeleken met *Goupia glabra* Aubl. (Celastraceae). Dit is eveneens een algemene soort in Frans Guyana, maar deze soort staat bekend als een soort die niet overleeft onder schaduwrijke omstandigheden. De drie soorten worden vanwege de handelswaarde van hun hout beschouwd als commercieel.

Uit het onderzoek blijkt dat bomen vanaf het zaailing-stadium tot en met het 20 m- (hoge) stadium het open kronendak meestal nog niet bereikt hebben. Deze bomen kunnen onder verschillende lichtintensiteiten staan. Ondanks hun grote onderlinge verschillen in hoogte passen deze bomen hun groei op vergelijkbare wijze aan het heersende lichtniveau aan. Onder lichtrijke omstandigheden produceren zij meer groei-eenheden (scheuten, internodiën) en meer bladeren dan onder schaduwrijke omstandigheden. Aldus produceren zij een groter oppervlak aan blad en hebben zij een hogere 'leaf area index' (LAI, een maat voor het aantal bladlagen in een boomkroon). Onder een blijvend hoog lichtniveau kunnen zij met een groter bladoppervlak meer energie vastleggen en aanwenden voor hun groei en overleving in de toekomst. Tevens verkleinen zij door een hogere LAI hun blad support kosten terwijl hun bladeren netto blijven fotosynthetiseren. Onder een blijvend laag lichtniveau kunnen bomen door een lagere LAI hun netto fotosynthese vergroten doordat bladeren elkaar minder overschaduwen. Deze bomen hebben daardoor echter hogere blad support kosten.

Bomen onder schaduwrijke omstandigheden produceren kortere groei-eenheden en produceren daardoor hun bladeren op kortere afstand van elkaar dan bomen onder lichtrijke omstandigheden. Omdat bladeren niet verschillen in grootte onder verschillende lichtomstandigheden, betekent dit dat bomen onder schaduwrijke omstandigheden hun bladoppervlak goedkoper produceren dan bomen onder lichtrijke omstandigheden. Op deze wijze zijn zwaar overschaduwde bomen in staat tot het onderscheppen van een grotere hoeveelheid licht onder de gegeven omstandigheden, hetgeen hun overlevingskansen kan vergroten.

Bomen van beide soorten groeien langzamer in hoogte onder lagere lichtniveaus. Dit is gedeeltelijk te verklaren door groei-beperkende omstandigheden. Bomen onder lagere lichtniveaus worden overschaduwd door hogere buurbomen. Waarschijnlijk kunnen zij deze schaduwrijke omgeving overleven door langzamer te groeien en bladeren in kortere groei-eenheden (en tegen lagere kosten) te maken. Als een of meerdere hogere buurbomen omvallen neemt de hoogtegroei van de (voorheen) overschaduwde bomen toe waardoor ze beter in staat zijn te concurreren om licht en ruimte. Voor beide soorten is aangetoond dat bomen onder zeer lichte en open omstandigheden hun topscheut sterker ontwikkelen dan andere scheuten in de kroon. Een dergelijke versterkte ontwikkeling van de topscheut treedt niet op onder schaduwrijke omstandigheden. Bomen onder zeer lichtrijke omstandigheden groeien dus niet alleen sneller in de hoogte omdat er meer licht beschikbaar is, maar ook omdat hun topscheut relatief snel groeit.

Tot zover zijn de groeireakties van bomen kleiner dan 20 m nader belicht. Grotere bomen (bomen geselecteerd vanaf 26 tot en met 37 m) in meer open en lichtere regionen boven in het kronendak hebben een groter totaal bladoppervlak en produceren meer taklengte dan bomen onder de 20 m. Daarnaast produceren deze grotere bomen een grotere en meer afgeplatte kroon, hebben zij eenzelfde LAI, ontwikkelt hun topscheut langzamer en produceren zij hun bladeren op kortere afstand van elkaar dan bomen onder de 20 m. De meer afgeplatte kroon is waarschijnlijk het gevolg van een sterke toename in de beschikbaarheid van licht (en ruimte). Op haar beurt beperkt de grotere en meer afgeplatte kroonvorm een verdere toename in LAI. De verminderde ontwikkeling van de topscheut en het produceren van bladeren op kortere afstand van elkaar duidt erop dat deze hoge bomen minder investeren in hun vertikale expansie dan bomen onder de 20 m.

Gedurende de levensloop van een boom neemt zijn grootte toe. De toename in boomgrootte is in balans met de mechanische sterkte van de boom. Een boom heeft mechanische sterkte nodig om zijn eigen gewicht te kunnen dragen en om windkrachten te weerstaan. Het mechanisch ontwerp van een boom drukt deze balans tussen grootte en sterkte uit. Veranderingen in die balans gedurende de levensloop van bomen werden nader onderzocht voor *Dicorynia*, *Vouacapoua*, en ook *Goupia*. Hierbij werd gebruik gemaakt van twee theoretische modellen. (1) In het 'elastische stabiliteit' model wordt de sterkte om het eigen gewicht te dragen beschreven als een functie van de hoogtedikte verhouding en houteigenschappen. Met behulp van dit model blijken de sterktemarges af nemen in een vroeg deel van de levensloop van een boom, maar nemen deze sterktemarges later weer toe. De laagste marges hebben bomen als zij een stamdikte van 15-25 cm bereiken. Deze marges liggen dicht bij het theoretisch minimum, hetgeen wil zeggen dat bomen zouden omvallen als ze nog iets slanker gebouwd zouden zijn (hoger bij gegeven diameter). In vergelijking met enkele gematigde boomsoorten hebben de soorten van deze studie lagere sterktemarges omdat ze slanker gebouwd zijn. De slankheid van een boom (hoogtedikte verhouding) is echter maar één van de factoren die de mechanische sterkte beïnvloedt. Het hout van tropische bomen heeft een grotere dichtheid en stijfheid dan dat van gematigde bomen. Deze eigenschappen kunnen ertoe bij dragen dat zij een grotere mechanische sterkte bereiken dan gematigde soorten (maar dat wordt niet uitgedrukt in het elastische stabiliteit model). Bovendien is het waarschijnlijk dat tropische bomen minder bloot staan aan omgevingsstress zoals zeer hoge windsnelheden en zware sneeuwlagen.

(2) In het 'constante stress' model wordt de weerstand tegen windstress benadrukt en beschreven als een verhouding tussen de stamdikte en de boomgrootte (hoogte en kroonomvang). Voor de drie bestudeerde soorten blijken deze sterktemarges toe te nemen gedurende de levensloop. Dit is in de lijn der verwachting aangezien windsnelheden toenemen met de grootte van een boom. Aanpassingen in het mechanisch ontwerp van een boom aan licht zijn niet aangetoond.

De ecologische kennis die dit onderzoek oplevert zou gebruikt kunnen worden in bosmanagement systemen. Bij deze systemen worden open gaten in het bos gemaakt waardoor de groei van bomen wordt beïnvloed. De resultaten van dit proefschrift geven aan dat manipulaties van de lichtbeschikbaarheid in het bos (door bomen te doden, of door het overschaduwen van bomen) een bijdrage kunnen leveren aan de houtproduktie. Bovendien kan het vervolg van deze studie gebruikt worden om morfologische karakteristieken te definiëren waardoor de potentiële groeimogelijkheden van een boom in relatie tot zijn lichtomgeving voorspeld kunnen worden. De studie van groeiaanpassingen van bomen (in termen van houtproduktie, morfologie, ontwikkeling) in relatie tot de hele range van lichtbeschikbaarheid wordt aanbevolen. Op grond hiervan kunnen manipulaties van het lichtklimaat worden afgestemd op individuele bomen van commerciële soorten op dusdanige wijze dat deze bomen de gewenste groei vertonen in de toekomst. In het algemeen kan fundamenteel ecologisch onderzoek naar boomgroei in relatie tot het lichtklimaat, zowel binnen als buiten het bos, veel waardevolle inzichten opleveren waardoor bosmanagement systemen verbeterd kunnen worden.

ARBRES ET LUMIERE

Développement et morphologie de l'arbre en fonction de l'intensité lumineuse dans une forêt tropicale humide de Guyane française

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1997

Résumé

Les arbres des forêts tropicales humides vivent dans un milieu lumineux hétérogène et adaptent leur croissance à (l'intensité de) la lumière environnante. Ce sont les processus physiologiques, tels que la photosynthèse et l'activité du méristème, qui sont à l'origine de ces adaptations de croissance et qui régissent les changements dans le développement et la morphologie. Cette thèse étudie les influences de l'intensité lumineuse sur le développement et sur la morphologie des arbres. Les relations entre la lumière, le développement et la morphologie de l'arbre ont été examinées depuis le stade de plantule jusqu'au stade adulte (canopée) inclus. La comparaison d'arbres de plus en plus grands a permis d'analyser la façon dont les arbres, au cours de leur vie, adaptent leur développement et leur morphologie à la lumière. Les conséquences de ce phénomène pour la survie, la croissance et la reproduction des arbres en forêt tropicale humide sont également examinées.

L'étude sur le terrain a été réalisée en Guyane française, pays situé au nord-est de l'Amérique du Sud et en grande partie encore recouvert de forêt tropicale humide de plaine. Deux stations d'études biologiques ont servies à cette étude: le site de recherches de la 'Piste de St. Elie', à 30 km au sud de Sinnamary, et celui des 'Nouragues', à 100 km au sud de Cayenne, la préfecture. Deux espèces d'arbres de la canopée ont été sélectionnées pour cette étude, à savoir le *Dicorynia guianensis* Amshoff (Césalpiniacée) et le *Vouacapoua americana* (Aubl.) (Césalpiniacée). Ces deux essences sont largement représentées dans les forêts guyanaises et sont connues comme étant des espèces pouvant survivre en milieu ombragé. Dans certains chapitres, ces deux essences sont comparées au *Goupia glabra* Aubl. (Célastracée). Cette dernière est également très présente en Guyane française, mais ne constitue pas une espèce pouvant survivre en milieu ombragé. Ces trois essences ont une importance commerciale en raison de la valeur marchande de leur bois.

L'étude a montré que les arbres, depuis le stade de plantule jusqu'à 20 m de haut, n'ont le plus souvent pas encore atteint la partie supérieure de la canopée. Ces arbres peuvent pousser sous différentes intensités lumineuses. En dépit de leurs grandes différences de hauteur, ils s'adaptent néanmoins de façon similaire à l'intensité lumineuse ambiante. Ils produisent plus d'unités de croissance, d'entre-noeuds et de feuilles en milieu lumineux qu'en milieu ombragé. Ils disposent donc également d'une plus grande surface foliaire et d'un 'index foliaire' (LAI, leaf area index, mesure indiquant le nombre de couches de feuilles dans la couronne) plus élevé. En milieu à forte intensité lumineuse permanente, ces arbres peuvent, avec leur surface foliaire plus importante, fixer et transformer une plus grande quantité d'énergie pour leur croissance et leur survie. En outre, grâce à un LAI plus élevé, ils réduisent leur coût de support par feuille tout en gardant un bilan photosynthétique positif. En milieu à faible intensité lumineuse permanente, les arbres peuvent, grâce à un LAI moins élevé, augmenter leur bilan photosynthétique puisque les feuilles se font moins d'ombre entre elles. Toutefois, ces arbres ont pour cette raison un 'coût de support' par feuille plus élevé.

Les arbres en milieu ombragé produisent des unités de croissance et des entre-noeuds plus courts et leurs feuilles sont donc plus rapprochées les unes des autres que sur les arbres en milieu lumineux.

Etant donné que la taille des feuilles ne diffère pas selon l'intensité lumineuse, cela signifie que les arbres en milieu ombragé produisent leur surface foliaire à un coût moins élevé que les arbres poussant en milieu lumineux. Ainsi, les arbres en milieu fortement ombragé sont capables d'intercepter une plus grande quantité de lumière dans le milieu donné, ce qui augmente leurs chances de survie.

Les deux espèces étudiées grandissent moins vite en milieu à plus faible intensité lumineuse. Ceci peut s'expliquer en partie par la présence de conditions limitant la croissance. En effet, les arbres en milieu à faible intensité lumineuse poussent dans l'ombre des arbres avoisinants plus grands. Ils réussissent vraisemblablement à survivre à ce milieu ombragé grâce à une croissance lente et à une production de feuilles en plus petites unités de croissance (et à moindre coût). Lorsque l'un ou plusieurs des arbres avoisinants vient à tomber, les arbres qui se trouvaient en milieu (auparavant) ombragé grandissent, ce qui leur permet ainsi d'occuper une meilleure place dans la course à la lumière et à l'espace. Pour les deux espèces, il a été prouvé que les spécimens situés en milieu très lumineux et ouvert développent davantage leurs leaders (pousses au sommet de la couronne) plutôt que les autres pousses. Un tel développement accentué des leaders ne s'observe pas en milieu ombragé. Les arbres en milieu très lumineux grandissent donc plus rapidement, non seulement grâce à la plus forte intensité lumineuse, mais aussi parce que leurs leaders poussent relativement vite.

Jusqu'ici, seuls les arbres inférieurs à 20 m ont été étudiés. Les arbres dépassant cette hauteur (à partir de 26 m et jusqu'à 37 m) en zones plus ouvertes et plus lumineuses dans la partie supérieure de la canopée possèdent une surface foliaire plus importante et produisent une plus grande longueur de branches par rapport aux arbres inférieurs à 20 mètres. En outre, ces grands arbres ont une couronne plus grande et plus aplatie, ont le même LAI, développent leurs leaders plus lentement et leurs feuilles sont plus rapprochées les unes des autres que sur les arbres inférieurs à 20 mètres. La couronne plus aplatie résulte certainement du fait de l'augmentation de l'intensité lumineuse (et de l'espace disponible). A son tour, la forme plus aplatie et plus large de la couronne limite une augmentation du LAI. Le développement réduit des leaders et la production de feuilles rapprochées les unes des autres indiquent que ces arbres investissent moins dans leur expansion verticale que les arbres inférieurs à 20 mètres.

Au cours de sa vie, un arbre voit sa taille augmenter. Cette augmentation de taille est déterminée selon un rapport d'équilibre avec la résistance mécanique. Un arbre a besoin de résistance mécanique pour pouvoir supporter son propre poids et lutter contre les forces éoliennes. Le processus mécanique d'un arbre exprime cet équilibre entre la taille et la résistance. Les modifications de cet équilibre au cours de la vie des arbres ont été étudiées de façon plus approfondie pour le *Dicorynia*, le *Vouacapoua* et le *Goupia*. Deux modèles théoriques ont été utilisés à cet effet. (1) Dans le modèle `stabilité élastique', la capacité à supporter le propre poids est décrite comme une fonction du rapport hauteur/grosseur et des propriétés du bois. Ce modèle a permis de mettre en évidence que la marge de résistance diminuait au début de la vie de l'arbre, avant d'augmenter à nouveau plus tard. Les marges les plus faibles sont constatées lorsque le tronc atteint un diamètre de 15-25 cm. Ces marges ne sont guère éloignées du minimum théorique, ce qui signifie que ces arbres pourraient se renverser s'ils étaient plus élancés (c'est-à-dire plus haut pour un diamètre donné). En comparaison avec certaines essences des régions tempérées, les espèces étudiées possèdent des marges de résistance plus faibles à cause de leur forme plus élancée. Cependant, la sveltesse d'un arbre (rapport hauteur/épaisseur) n'est qu'un des facteurs influant sur la résistance mécanique. Le bois des espèces tropicales est plus dense et plus rigide que celui des espèces en régions tempérées. Ces propriétés peuvent contribuer à l'obtention d'une plus grande résistance mécanique par rapport aux espèces en régions tempérées (mais ceci n'est pas exprimé dans le modèle `stabilité élastique'). De plus, il est probable que les essences tropicales sont moins exposées au stress environnant comme de violents vents ou d'épaisses couches de neige.

(2) Le modèle de `stress constant' met l'accent sur la résistance aux forces éoliennes, qui est présentée comme le rapport entre l'épaisseur du tronc et la taille de l'arbre (hauteur et ampleur de la couronne). Pour les trois espèces étudiées, les marges de résistance s'avèrent augmenter au cours de la vie de l'arbre. Ce résultat correspond aux attentes étant donné que les vitesses éoliennes augmentent proportionnellement à la taille de l'arbre. Il n'a pas a été démontré que des adaptations à la lumière se produisent dans le processus mécanique de l'arbre.

Les connaissances écologiques que nous apporte cette étude pourraient servir dans les systèmes de sylviculture. Dans ces systèmes, des trouées sont réalisées dans la forêt pour influencer la croissance des arbres. Les résultats de cette thèse indiquent que des manipulations sur l'intensité lumineuse de la forêt (par abattage d'arbres ou création d'un milieu ombragé) peuvent agir sur la production de bois. En outre, le prolongement de cette étude peut être utilisé pour définir des caractéristiques morphologiques permettant de prévoir les possibilités de croissance d'un arbre en relation avec son milieu lumineux. Il est recommandé d'étudier les adaptations de croissance des arbres (en termes de production de bois, de morphologie et de croissance) en relation avec l'ensemble des différentes intensités lumineuses. A partir de là, il est possible de manipuler le climat lumineux en l'adaptant individuellement à des espèces commerciales, de façon à ce que ces arbres présentent la croissance voulue dans le futur. En règle générale, la recherche écologique fondamentale sur la croissance des arbres en fonction du climat lumineux peut, aussi bien en forêt qu'ailleurs, fournir de précieuses informations pour l'amélioration des systèmes de sylviculture.

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CURRICULUM VITAE

Frank Sterck werd geboren op 8 maart 1964 te Nijmegen. Hij behaalde zijn diploma VWO-B in 1982, en begon datzelfde jaar een studie biologie aan de Landbouw Universiteit te Wageningen. In 1989 studeerde hij af met als afstudeervakken tropische -bosecologie, vegetatiekunde, plantentaxonomie en filosofie. In 1991 startte hij zijn promotie studie aan de vakgroep Bosbouw van de landbouwuniversitei te Wageningen. Hiervoor verrichtte hij tussen 1991 en 1995 vele maanden veldwerk in het tropisch regenbos van Frans Guyana. Sinds juli 1996 is hij wederom in dienst van de vakgroep Bosbouw. In he kader van een internationaal samenwerkingsproject bestudeert hij momenteel de concurrentie tussen kronendak- en ondergroei bomen in een regenbos op Borneo.