GROWTH OF TROPICAL RAIN FOREST TREES AS DEPENDENT ON PHOSPHORUS SUPPLY

Tree saplings differing in regeneration strategy and their adaptations to a low phosphorus environment in Guyana

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Growth of tropical rain forest trees as dependent on phosphorus supply

Tree saplings differing in regeneration strategy and their adaptations to a low phosphorus environment in Guyana

Groei van bomen uit het tropisch regenwoud in relatie tot fosfor voorziening

Zaailingen met een verschillende regeneratiestrategie en hun aanpassingen aan een lage beschikbaarheid van fosfor in Guyana

(met een samenvatting in het Nederlands)

Proefschrift

Ter verkrijging van de graad van doctor
aan de Universiteit Utrecht,
op gezag van de Rector Magnificus,
Prof. Dr. J. A. van Ginkel,
ingevolge het besluit van het College van Decanen
in het openbaar te verdedigen
op donderdag 12 januari 1995
des morgens te 10.30 uur

door

Dorinne Raaimakers

geboren op 26 mei 1963 te Best

Promotor: Prof. Dr. J. T. Lambers
verbonden aan de Faculteit Biologie van de Universiteit Utrecht

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TROPENBOS SERIES

The Tropenbos series presents the results of studies and research activities related to the conservation and wise utilization of forest lands in the humid tropics. The series continues and integrates the former Tropenbos Scientific and Technical Series. The studies published in this series have been carried out within the international Tropenbos programme. Occasionally, this series may present the results of other studies which contribute to the objectives of the Tropenbos programme.

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The investigations reported in this thesis were carried out for the Tropenbos Programme Guyana, 12E Garnettstreet, Campbelville, Georgetown, Guyana and the Department of Plant Ecology and Evolutionary Biology, Utrecht University, P.O. Box 800.84, 3508 TB Utrecht, The Netherlands.

Given so much time,
the 'impossible' becomes possible,
the possible probable,
and the probable virtually certain.

(George Wald, 1954).

CONTENTS

List of tree species

Botanical and vernacular names of the 16 species used in this thesis. Names and authorities are according to Mennega et al. (1988), except for *Chlorocardium rodiei* and *Tapirira obtusa*, which have been renamed recently.

Botanical name	Vernacular name
Anacardiaceae	
Tapirira obtusa (Benth.) Mitchell	Duka
Bombacaceae	
Catostemma fragans Benth.	Baromalli
Caesalpiniaceae	
Chamaecrista adiantifolia (Benth.) Irwin & Barneby	Imirimiaballi
Chamaecrista apoucouita (Aublet) Irwin & Barneby	Apokuita
Dicymbe altsonii Sandw.	Clump Wallaba
Eperua falcata Aublet	Soft Wallaba
Eperua grandiflora (Aublet) Benth.	Ituri Wallaba
Mora excelsa Benth.	Mora
Mora gonggrijpii (Kleinhoonte) Sandw.	Morabukea
Peltogyne venosa (Vahl) Benth.	Purpleheart
Celastraceae	
Goupia glabra Aublet	Kabukalli
Lauraceae	
Chlorocardium rodiei (R.H. Schomb.) Rohwer, Richter and Van der Werff	Greenheart
Lecythidaceae	
Eschweilera sagotiana Miers	Black Kakaralli
Lecythis corrugata Poit.	Wina Kakaralli
Meliaceae	
Carapa guianensis Aublet	Crabwood
Moraceae	
Cecropia obtusa Trecul	Congo Pump

List of abbreviations

Abbreviations used in this thesis and the units in which they are expressed, listed in alphabetical order. In Chapter 6 mmol P or N is used instead of mg P or N.

Abbreviation	Meaning	Units
A_{sat}	Light saturated rate of photosynthesis	μmol CO_2 (m leaf)$^{-2}$ s^{-1}
EM	ectomycorrhiza	
N concentration	Nitrogen concentration	mg N (g tissue)$^{-1}$
N content	Nitrogen content	mg N (m tissue)$^{-2}$
P/N ratio	Phosphorus:nitrogen ratio	
P concentration	Phosphorus concentration	mg P (g tissue)$^{-1}$
P content	Phosphorus content	mg P (m tissue)$^{-2}$
RGR	Relative growth rate	mg plant (g plant)$^{-1}$ day^{-1}
RLR	Root length ratio	m root (g plant)$^{-1}$
RR	Recovery rate of fertilizer	% fertilizer (plant)$^{-1}$
RWR	Root weight ratio	g root (g plant)$^{-1}$
SAR_l	Specific absorption rate	μg P (m root)$^{-1}$ day^{-1}
SAR_w	Specific absorption rate	μg P (g root)$^{-1}$ day^{-1}
SLM	Specific leaf mass	g leaf (m leaf)$^{-2}$
SRL	Specific root length	m root (g roots)$^{-1}$
VAM	Vesicular-arbuscular mycorrhiza	

Chapter 1

General Introduction

1.1 Tropical rain forests

Evergreen tropical rain forests are found in the humid tropics and are regarded as the epitome of biological complexity and variety (Connell and Lowmann, 1989) with their very high diversity of animal and plant life forms and species (Richards, 1952, Whitmore, 1984). In contrast to this richness in species, the substrates of neotropical forests are often nutrient-poor, as a result of weathering and excessive rainfall over long periods (Lathwell and Grove, 1986). Thus these soils are mostly unsuitable for land use other than low intensity forestry or nature conservation (Jordan, 1985).

Despite the constraints imposed by the infertility of the soils, tropical rain forests are being converted to other uses at a fast rate. The exact rate at which deforestation occurs is disputed, but it is generally agreed that much of the world's primary tropical rain forest will have disappeared by the end of this century. Deforestation in the tropics has become a global problem.

Effective planning is limited by gaps in our understanding of the factors which sustain growth in tropical forest regions. Too often it is assumed that techniques developed for temperate ecosystems are equally suitable for the wet tropics (Jordan, 1985). However, nutritional demands of plants growing under natural low-fertility conditions are quite different from crop plants in fertile environments (Chapin, 1980). To contribute to the wise use and conservation of tropical rain forests, the Dutch government established the "Tropenbos" foundation in 1988. The objectives were (1) to generate knowledge and develop methodologies in order to conserve and sustainably manage rain forests and (2) to involve and strengthen local institutions in their capacity of managing tropical rain forests.

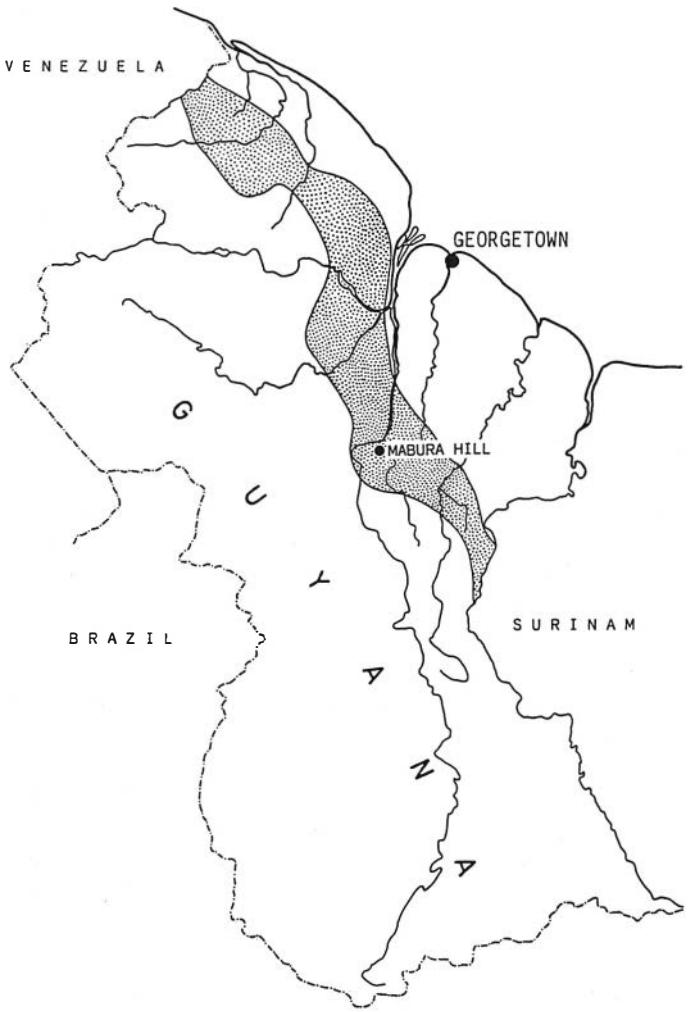

Figure 1.1. Map of Guyana: the main timber area (shaded) and the research area Mabura Hill (from Ter Steege, 1993b, with permission).

1.2 Tropenbos-Guyana Programme

About 2/3 of Guyana's land area is covered by forest. In general nutrient losses from the different pathways involved in the cycling of nutrients among ecosystem compartments are low in these forests (Herrera et al., 1984). When the system is disturbed, the nutrient-conserving mechanisms cease to function, nutri-

ent losses greatly increase and the recovery of the system can be severely impaired (Herrera et al., 1984). Nutrient cycling affects the trees' physiology, population biology and community ecology.

Pressure from local people on the forest is relatively low compared to that in other countries, since the population is small (<1,000,000 people on 21.5 million hectares) and most people live in the coastal zone. Approximately 5 million hectares have been allocated to logging companies, in a zone parallel to the coast (Fig. 1.1) and presently 1.5 million hectares are logged selectively (Van der Hout, 1992). Greenheart (*Chlorocardium rodiei*) is Guyana's most renowned timber resource and has traditionally constituted 70% of the country's timber export (Ter Steege, 1993c). For many years, greenheart has been extracted from the natural forest via selective felling on a local scale, but now the demand for timber is increasing and the Guyanese government considers an increase in timber harvest to be of great economic importance. Therefore, as logging increases, there is a need for information not only on the impact of logging, but also on the regeneration potential of tree species.

In 1989 the Tropenbos programme has been established on a 250,000 ha timber concession in the Mabura Hill region in Central Guyana, 250 km south of the capital Georgetown (5°11'17"N and 58°43'36"W) located in the main forestry belt (Fig. 1.1). The concession is presently managed by Demerara Timbers Limited (DTL). A comprehensive research programme was set up to investigate effects of logging on water balance, nutrient cycling and population dynamics. Tree growth was studied in relation to environmental constraints, which included light, water, nutrients and herbivores. Inventories of soil types, vegetation and valuable timber species and their characteristics were made and studies on logging intensity and biodiversity have also recently started. This thesis contributes to the multidisciplinary research programme and concentrates on tree growth and productivity in relation to nutrient availability.

1.3 Climate and vegetation

The largest area of continuous, moist forest in South America is that of Amazonia and the Guianas (Guyana, Surinam and French Guiana), which are similar in floristic composition and structure (Prance, 1989). Guyana is situated on the north-eastern part of South America and has a land area of approximately 21.5 million hectares. Seasonal change in Guyana is related to north-south movements of the Inter Tropical Convergence Zone, which influences annual rainfall distribution (Jetten, 1994) and phenology of the tree species (Ter Steege and Persaud, 1991). A long wet season occurs from May to August and a short wet season from December to February; resulting in an annual rainfall of approximately

2700 mm for the Mabura Hill area (Jetten, 1994). Both temperature (annual mean of 25° C) and relative humidity (rarely below 60% during the day, even in the dry season) are high and strongly related to the radiation level (Khan et al., 1980, Jetten, 1994).

Forest types and species distribution in the interior are closely correlated to soil types (Fanshawe, 1952, Ter Steege et al., 1993). As a rule, dry evergreen forests are found on the white sand soils, and mixed forests on the more loamy (brown) sands (Ter Steege, 1993b). In Guyana, the forest on white sands is called Wallaba forest, after the dominant species *Eperua falcata* and *Eperua grandiflora*. Other names for this forest type in the Amazonian region include *Amazonian caatinga* (Rio Negro), *campinarana* (Central Amazonia), *charravascal* (Roraima) and *varillal* (Peru) (Prance, 1989). There is a limited number of species and a tendency towards dominance (Richards, 1952, Fanshawe, 1952, Prance, 1989). In the mixed forests on brown sands, various species may be locally dominant (Ter Steege et al., 1993) and Fanshawe (1952) even suggested a subdivision of these forests in associations. One of these brown-sand dominants is greenheart (*Chlorocardium rodiei*). Greenheart accounts for 45% of all harvested timber, whereas it constitutes only 0.5-1.5% of the total standing timber in the country (Tropenbos, 1991). Selective logging of greenheart currently leads to extensive damage. On average, two trees each of half the basal area are damaged for each tree felled. This applies to species other than greenheart as well (Hammond, pers. com.).

1.4 Soils

As a result of excessive rainfall in combination with the geological stability of tropical landscapes over long periods, highly weathered soils are common in tropical South America, Africa and parts of Asia (Lathwell and Grove, 1986, Burghouts, 1993). In the Guianas, particularly in Surinam and Guyana, there is a large area of these soils, stretching as an east-west belt south of the coastal plain and occupying approximately 2 million hectares (Ahmad, 1989). Most of the geological formations in Guyana date from the Pre-Cambrian. On top of this formation thick sand layers were deposited known as the Berbice Formation in the late Pliocene to early Pleistocene; commonly referred to as the White Sand Plateau. The soils of the White Sand Plateau (FAO-Unesco soil map of the world terminology / Guyanese classification) consist of white sand soils (Albic Arenosols/Tiwiwid Sand) and brown sandy to loamy soils (Ferralic Arenosols / Tabela Sand and Haplic Ferralsols / Kassarama Loamy Sand and Ebini Sandy Loam). Where the White Sand Plateau is thin, streams have cut through the sandy and loamy layers into the Pre-Cambrian Plateau where more clayey soils have been formed. White sands consist of more than 95% quartz and organic matter con-

Table 1.1. Soil characteristics of white and brown sands. Range found in soil survey for Central Guyana for pH(H_2O), pH(KCl), organic matter content and percentage of quartz, Fe and Al-oxides, at 0-15 and 15-80 cm depth, "-" indicates missing values (after Van Kekem et al., 1995).

		white		brown	
	Unit	0-15	15-80	0-15	15-80
pH(H_2O)		3.8-4.4	4.6-5.9	3.8-4.7	4.1-5.0
pH(KCl)		2.4-3.4	3.5-4.8	2.6-4.3	4.0-4.7
Organic matter	%	0.4-7.2	0.1-0.2	0.4-5.9	0.1-1.0
SiO_2	%	>95	>95	90-98	88-92
Fe_2O_3	%			0.3-2.1	0.9-2.8
Al_2O_3	%			1.0-3.8	4.0-6.5

tent is low (Table 1.1). Al- and Fe-oxides make up to 6.5 and 2.8%, respectively, of the elemental composition of brown sands. Acidity, especially in the upper soil layers, is high on both white and brown sand soils. In addition to these soil types, extensive areas with very gravelly or shallow soils on hills and lateritic plateaus, with gravelly and stony soils over massive laterite, are also found in the region.

1.5 A wealth of adaptations on a nutrient-poor substrate

On acid soils, plant growth may be limited by a variety of specific chemical factors and interactions. It is not necessarily the low pH per se (i.e. the high H^+ concentration) that limits growth, but rather deficiency and/or toxicity of elements induced by the low pH (Fig. 1.2). The availability of the macronutrient P in the soil solution is relatively low at a low pH and the macronutrient N may easily leach from sandy soils, especially from the white sands (Vitousek and Sanford, 1986). Given the importance of P and N for plant growth, the question arises as to whether phosphorus and/or nitrogen are limiting growth in the Mabura Hill region. To investigate this, fertilizer experiments were carried out under natural conditions (with P and N, Chapter 2) and controlled conditions (with P only, Chapter 3). In addition to fertilizer experiments, tissue P and N status were analyzed for tree species growing on white and brown sands (Chapter 2). It transpired that P is more limiting for plant growth than N, and consequently the research was directed more towards P than to N.

Jordan and Herrera (1981) have demonstrated the pivotal role of nutrient-conserving mechanisms in oligotrophic systems. The major nutrient reserves of the system are locked up in biomass and soil organic matter. Nutrient input and output of the system are small in comparison to nutrient fluxes within the

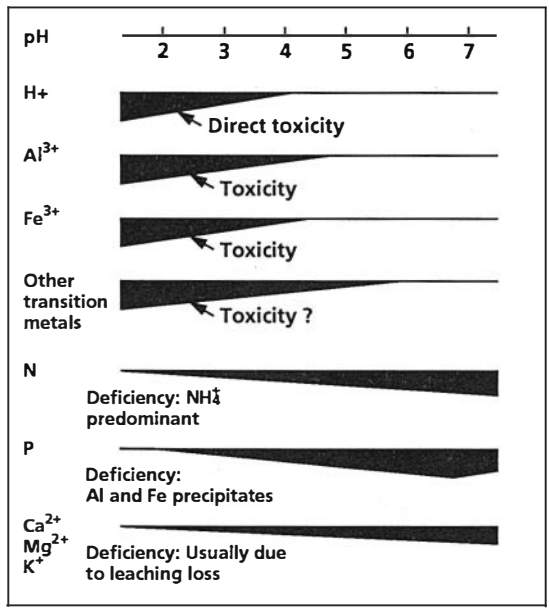

Figure 1.2. The relationship of soil chemical characteristics to soil pH. Increasing height of the shaded band indicates increasing soil solution concentration and/or availability to plants (after Etherington, 1982).

system. When P supply is a major determinant of plant growth, survival may either depend on an efficient uptake or use of P. Both strategies have been examined in this thesis.

The inflow of phosphorus into the tree can be regulated by varying the relative size of the absorbing root system or the capacity of its uptake mechanisms (Clarkson, 1985). A high specific root length and degree of mycorrhizal infection facilitate the acquisition of ions which diffuse slowly in the soil, such as phosphate (Chapter 4). A low inflow of P has consequences for the processes of growth, allocation of biomass and P (Chapters 4 and 5) and photosynthesis (Chapter 6). Trees may reallocate phosphorus before abscission of the leaves, and consequently reduce losses to the environment, (Chapter 7).

1.6 Regeneration of the forest

Tropical rain forest species are generally grouped according to their gap dependence (Bongers and Popma, 1988). Based on differences in seed germina-

Table1.2. Character syndrome of pioneer tree species in tropical rain forest (from Swaine and Whitmore, 1988).

1	Seeds only germinate in canopy gaps open to the sky and which receive full sunlight
2	Plants cannot survive in shade - young plants never found under a closed forest canopy
3	Seeds small and produced copiously and more-or-less continuously
4	Seeds produced from early in life
5	Seeds dispersed by animals or wind
6	Dormant seeds usually abundant in forest soil
7	Seedling carbon-fixation rate high; light compensation point high
8	Height growth rapid
9	Growth indeterminate with no resting buds
10	Branching relatively sparse
11	Leaves short-lived
12	Rooting superficial
13	Wood usually pale, low density, not siliceous
14	Leaves susceptible to herbivory; sometimes with little chemical defence
15	Wide ecological range
16	Often short-lived

tion and seedling establishment, tropical rain forest tree species have been classified as pioneer and climax species (Swaine & Whitmore, 1988). All pioneers require full sunlight for seedling establishment and growth.

The syndrome of characters of most pioneer species, in addition to the vital ones used to define them, is listed in Table 1.2. Collectively, these characteristics provide a selective advantage for success in open areas (Swaine and Whitmore, 1988). Seedlings and saplings of pioneers are found in openings in the forest: tree-fall gaps, roadsides and felled areas. In these gaps, the availability of resources, including light, water and nutrients differs from that in the surrounding forest (Denslow, 1987). Nutrients may be released more rapidly from decaying dead material (Anderson and Swift, 1983, Vitousek and Denslow, 1986), but data on higher nutrient levels in gaps are not consistent. Still, the nutrient-availability per seedling will be higher in a gap compared to that in the undisturbed forest, since there is less or no competition for nutrients of mature trees.

In the process of recolonization of a gap, pioneer species are replaced by climax species. Climax trees are those whose seedlings can establish and perform in forest shade, and which usually do not possess the characteristics listed in Table 1.2. Their saplings are commonly found below a canopy, but they also occur in open environments. Many important timber species in Guyana belong to this group of climax species. Generally, their seedlings have to cope with an even lower availability of P than seedlings in a gap, since they have to compete with mature trees. In pioneer and climax species, different adaptive traits might have evolved to cope with the low availability of P, according to their habitat. By stud-

ying these two extremes of the forest species continuum, we can gain insight into adaptations to P stress and their relation with recolonization of gaps. For the studied adaptations to a low P-availability, described in Chapters 4 to 7, a comparison was made between pioneer and climax species. These studies have resulted in an overall view of the strategy of pioneer and climax species in a tropical rain forest ecosystem with a low P-availability (Chapter 8).

Chapter 2

N and P as possible limiting factors for tree growth on acid sandy soils in tropical rain forest in Guyana

with Franka den Ouden, Marno van der Marel and René Boot

Summary

On the acid white and brown sands of Guyana, availability of the macronutrients nitrogen (N) and phosphorus (P) might be expected to be limiting for growth of tropical rain forest trees. The macronutrients P and N were supplied, separately and in combination, to saplings of the non-legume *Chlorocardium rodiei* and the legume *Dicymbe altsonii* growing naturally in the forest. In addition, for 15 species, leaves, stem and roots of saplings and leaves of mature trees were analyzed for their N and P concentration. Since the functioning of the symbiotic association with *Rhizobium* enhances both a plant's acquisition of N and demand for P, a comparison was made between legumes and non-legumes, growing on white or brown sands.

Relative growth rates of the controls were very low, 0.4 and 0.9 mg g^{-1} day^{-1}, for *C. rodiei* and *D. altsonii* saplings, respectively. The addition of N fertilizer (in the form of urea) did not increase the growth of *D. altsonii*, whilst all treated *C. rodiei* saplings died. When P fertilizer (as superphosphate) was added, the relative growth rate doubled for the legume *D. altsonii*. Despite its original low P concentration, *C. rodiei* did not show a growth response to P-fertilization, but instead stored extra P in its root and stem.

Leaves of mature trees and saplings of the 15 species growing on either soil type had a very low P concentration (0.52-0.86 mg P g^{-1}(DW)) and P/N ratio (0.03-0.05); these values are among the lowest reported for tropical trees. N concentrations of the leaves (14.4-18.3 mg N g^{-1} (DW)) were not particularly low. P concentration of stems and roots of saplings appeared to correlate with seed size. Saplings of species with large seeds (0.1 - 60 g) had high P concentrations in their stem and roots, in contrast to small seeded species (< 0.1 g), whereas their N concentrations were similar. This supports the hypothesis that due to the P-reserves in the seed large seeded species have an advantage over small seeded species during seedling establishment in a P-poor environment.

All the studied legumes belonged to the subfamily of the Caesalpinioideae. Leaf P concentration and P/N ratio of mature legumes were higher than those of non-legumes. The number of leguminous saplings with root nodules was small, 11%, so that their abundance in the study area is unlikely to be due to an advantage by rhizobial dinitrogen fixation. The abundance of species from the Caesalpinioideae (which are predominantly ectomycorrhizal) and their poor nodulation, together with the results of the fertilizer experiment, the low P/N ratio and P concentration of leaves of saplings and mature trees and the high number of species with large seeds, point to P, rather than N as a major growth-limiting nutrient in the study area.

2.1 Introduction

In the forestry belt of Guyana, South America, acid soils, locally referred to as white and brown sands, are very common. They are characterized by their high quartz content, low pH, low organic matter content and susceptibility to leaching of nutrients by high rainfall (Khan et al., 1980). The availability of P is particularly low due to phosphate-fixing Al and Fe oxides in the brown sands (Van Kekem et al., 1995) and a low total P content of white sands (8 $\mu g\ g^{-1}$, Chapter 3).

The abundance of legumes might point to N being a major factor limiting tree growth in the study area, as symbiotic dinitrogen fixation is advantageous for trees when the availability of soil nitrogen is low. The percentage of leguminous trees is very high, up to 60%, in forests growing on these soils (Ter Steege et al., 1993). However, symbiotic dinitrogen fixation is only possible when the P supply is relatively high, because acquiring nitrogen in a symbiotic association with *Rhizobium* requires more P than when other nitrogen sources are used (Robson et al., 1981). P plays an important role in initiation, growth and functioning of nodules and a deficiency of P lowers the efficiency of the *Rhizobium* symbiosis (Israël, 1987). Given the susceptibility of the acid sands of central Guyana for leaching of nutrients, the low availability of P, the abundance of legumes and the importance of N and P for plant growth, the question arises whether either N or P are limiting plant growth.

Plants from nutrient-poor sites generally have lower concentrations of limiting nutrients in their tissue than those from nutrient-rich sites (Chapin, 1980) and nutrient concentrations in individual leaf tissues are a good indicator of the nutrient availability of the soil (Vitousek and Sanford, 1986). Because P and N are functionally related in the plant, the P/N ratio of leaf tissue can be used to determine whether N or P is a principal growth-limiting factor (Penning de Vries et al., 1980). The P/N ratio of plants grown under natural conditions varies between 0.04, indicating P-deficiency, and 0.15, indicating N-deficiency. Data on concentrations of P and N in leaves can thus be an indication of nutrient limitations in different species growing on different soils. P/N ratios and possible nutrient limitations may change with age. Young plants are more susceptible to P shortage than adults until they have developed an extensive root system to increase the acquisition of immobile P (Lathwell and Grove, 1986). Therefore, we addressed the following questions for saplings and adult tree species:

(i) Are P and/or N limiting for growth of trees on acid sandy soils in Guyana?

(ii) Do species differ on white and brown sands in leaf P and N concentration and leaf P/N ratio?

(iii) Do legumes and non-legumes differ in their leaf P and N concentration and leaf P/N ratio?

In addition to chemical tissue analyses, a fertilizer experiment under field conditions was conducted with saplings of *Chlorocardium rodiei* (non-legume), the most important timber species of Guyana, and *Dicymbe altsonii*, a leguminous dominant species to test the hypothesis that both N and P restrict growth of saplings on sandy soils. If the applied nutrient is limiting, the dry matter accumulation should increase in response to its uptake. Because most legumes have the possibility to exploit an extra N source, but one which demands more P, we expected less response to N fertilizer for the legume *D. altsonii* than for *C. rodiei*. Instead growth of the legume *D. altsonii*, might be limited more by P.

2.2 Methods

2.2.1 Study site

The present study was carried out at the Tropenbos research site in the Mabura region in central Guyana (5°18'N 58°42'W). The soils fall within two broad groups of acid soils, locally referred to as "white sands" (Albic Arenosols) and "brown sands" (Ferralic Arenosol and Haplic Ferralsols, Van Kekem et al., 1995). Acidity, especially in the upper soil layers is high on both soil types (Table 1.1). Most of the variation between soil types is attributed to water-holding capacity, availability of P and drainage (Ter Steege et al., 1993). White sands contain less water at field capacity (Simpson, 1989), have a higher availability of P (Chapter 3) and better drainage (Fanshawe, 1952) than brown sands. Mabura has a wet tropical climate with two wet and two dry seasons, but even in the dry season the average rainfall exceeds 100 mm per month (Khan et al., 1980); the annual precipitation averages 2700 mm (Jetten, 1994). Air temperatures are high and relatively constant with an annual mean of about 25 °C and a diurnal fluctuation of about 8-10 °C (Khan et al., 1980).

2.2.2 Fertilizer experiment

The fertilizer experiment was carried out with tree saplings growing naturally in the Mabura Hill Forest Reserve. For both, *Dicymbe altsonii* and *Chlorocardium rodiei*, one experimental plot was established on a skid trail on white sand (Arenosols, Van Kekem et al., 1995). The pH(H_2O) of the soil was 4.1 - 5.4 on the *D. altsonii* plot (Gleyic Arenosol), and 3.7 - 4.5 on the *C. rodiei* plot (Albic Arenosol). A hemispherical photograph was made of the sky in a horizontal plane to calculate openness of the canopy (Ter Steege, 1993a) and used as

a measure of the total daily irradiance (Chazdon and Field, 1987). For the site of *D. altsonii* and *C. rodiei* openness was 6 and 12%, respectively. At the start of the experiment, mean total dry weights of saplings were 20.5 g and 12.0 g, for *D. altsonii* and *C. rodiei*, respectively.

Once every four months, 72 individual plants received 2.5 g N, 1 g P, 2.5 g N plus 1 g P, or no fertilizer (control) in a randomized design. N and P were added as urea and superphosphate, respectively, in slow-release fertilizer grains, carefully placed around the stem of a sapling. The minimum distance between two saplings was 1 m. Plants were harvested 18 months after the start of the treatments. Leaves, stems and roots were dried separately at 70 °C for 48 hours and then weighed. For chemical analyses, 18 replicates of one treatment were pooled to 3 bulk samples.

2.2.3 Tissue collection of species

We sampled four leguminous and four non-leguminous tree species on white sand and three leguminous and four non-leguminous tree species on brown sand (Table 2.1). Of the legumes, all Caesalpinioideae, *Eperua grandiflora* (Aubl.) Benth., *Eperua falcata* Aubl., *Dicymbe altsonii* Sandw. and *Chamaecrista adiantifolia* (Benth.) Irwin & Barneby occur with greater frequency on white sand, and *Mora gonggrijpii* (Kleinh.) Sandw., *Peltogyne venosa* (Vahl) Benth. and *Mora excelsa* Benth. more frequently on brown sand (Ter Steege et al., 1993). *Lecythis corrugata* Poit. (Lecythidaceae), *Catostemma fragans* Benth. (Bombacaceae), *Cecropia obtusa* Trécul (Moraceae) and *Tapirira obtusa* (Benth.) Mitchell (comb.nov.ined.; formerly named *T. marchandii* Engl.; Anacardiaceae) were chosen as non-legumes with a high frequency on white sand. *Eschweilera sagotiana* Miers (Lecythidaceae), *Chlorocardium rodiei* (R.H. Schomb.) Rohwer, Richter and Van der Werff (Lauraceae), *Carapa guianensis* Aubl. (Meliacae) and *Goupia glabra* Aubl. (Celastraceae), are non-legumes, which occur more frequently on brown sand.

Saplings were found in a wide range of light climates, and where possible 3 sites per species were sampled. Of each species, 9 saplings, up to 1 m tall (1.5 to 13.0 g), were carefully excavated in the forest. Saplings were divided into leaf, stem and root, and root nodules were counted. Accompanying a timber harvesting-team, we collected leaf tissue of mature trees. Per species, 9 leaf samples were taken of the crown of one tree. Plant tissue was dried at 70 °C for 48 hours and then weighed.

Table 2.1: Mean P and N concentration (mg.g^{-1}DW) of leaves stem and roots of saplings and leaves of mature trees of 15 species (n=9) and their seed weights (g DW, * data from D. Hammond, unpublished).

Species	Phosphorus (mg g^{-1})				Nitrogen (mg g^{-1})				Seed*
	saplings			mature	saplings			mature	weight
	leaf	stem	root	leaf	leaf	stem	root	leaf	(g DW)
Legumes (white)									
Chamaecrista adiantifolia	1.15	2.56	1.52	0.89	24.5	12.7	11.7	17.8	0.235
Dicymbe altsonii	0.53	1.50	0.61	0.65	14.9	6.5	6.0	17.3	4.67
Eperua falcata	0.74	1.36	1.29	0.62	16.2	3.5	4.3	13.6	5.74
Eperua grandiflora	1.03	2.04	1.29	0.68	17.1	9.3	10.1	15.3	10.58
Legumes (brown)									
Peltogyne venosa	0.52	0.31	0.24	0.77	11.2	6.0	6.0	15.8	0.26
Mora gonggrijpii	0.66	0.88	1.81	0.58	17.1	6.1	7.4	16.0	60
Mora excelsa	0.52	1.63	1.26	0.72	16.5	11.5	10.8	17.8	61.65
Non-legumes (white)									
Cecropia obtusa	0.75	0.65	0.35	0.78	19.3	14.3	10.0	22.6	$6x10^{-5}$
Tapirira obtusa	0.56	0.43	0.35	0.51	14.1	5.7	6.7	18.4	0.13
Lecythis corrugata	0.60	0.65	1.02	0.44	17.8	8.3	7.0	19.0	0.95
Catostemma fragans	0.59	0.70	0.69	0.57	12.2	4.3	6.0	13.3	24.60
Non-legumes (brown)									
Goupia glabra	0.86	0.37	0.26	0.64	19.2	6.1	6.4	17.6	$9x10^{-4}$
Eschweilera sagotiana	0.65	0.99	1.55	0.46	12.4	6.4	6.8	17.0	1.11
Carapa guianensis	0.67	0.64	0.28	0.53	10.9	3.2	3.8	15.5	16.71
Chlorocardium rodiei	0.55	1.51	1.00	0.46	15.0	6.7	9.5	17.7	45.75

2.2.4 Chemical analyses

Tissue was dried at 70 °C and total nitrogen and phosphorus were analyzed with a modified micro-Kjeldahl digestion method, using concentrated sulphuric acid and a catalyst mixture of Se, $CuSO_4$ and Na_2SO_4 in a ratio of 1:1:62 (Bradstreet, 1965). Phosphorus and nitrogen were analyzed colorimetrically, using the ammonium molybdate method (Houba et al., 1989) and the indophenol method (Cataldo et al., 1975), respectively.

2.2.5 *Calculations and statistics*

Relative growth rate (RGR) was calculated as:

$$RGR = \frac{(\ln W_1 - \ln W_0)}{(t_1 - t_0)} \times 1000 \quad [\text{mg g}^{-1}\text{ day}^{-1}]$$

where W_0 and W_1 are total plant dry weight at time t_0 and t_1, respectively. The recovery rate (RR) of a nutrient was calculated as:

$$RR = \frac{(NC_{fert} - NC_{control})}{NA} \times 100 \quad [\%]$$

where NC_{fert} and $NC_{control}$ are the mean content of a nutrient in the total plant of the plus fertilizer treatment and control, respectively and NA is the total amount of a nutrient added to the plant as slow-release fertilizer.

Data were analyzed using the procedure GLM of the SAS statistical package, which uses the method of least squares to fit general linear models (SAS, 1988). A significant effect was followed by Tukey's Studentized Range Test.

Table 2.2. Mean dry weight (g, n=18), P and N concentration (mg.g^{-1}DW, n=3) for leaves stem and roots, relative growth rates (RGR, mg.g^{-1}DW.day^{-1})and recovery rates of N (RRN, %) and P (RRP, %) for *Dicymbe altsonii* saplings grown as control, with N (+N), with P (+P) or with N plus P (+N+P). For any row of data, values with different letters are statistically different at the 95% probability level.

		control	+ N	+ P	+ N + P
DW	leaves	8.1 b	9.4 b	16.7 a	9.9 b
	stem	16.6 b	17.2 b	31.2 a	20.2 b
	root	9.6 b	9.1 b	15.4 a	11.6 ab
	total	34.3 b	35.7 b	63.3 a	41.7 b
[P]	leaves	0.42	0.41	0.52	0.66
	stem	0.21 b	0.21 b	0.35 a	0.33 a
	root	0.19	0.19	0.35	0.28
[N]	leaves	11.7 b	15.0 a	13.4 ab	14.9 a
	stem	5.8	7.4	7.4	7.9
	root	5.9	8.7	6.7	8.2
RGR		0.90	0.97	1.98	1.25
RRN		-	1.0	-	1.5
RRP		-	-	0.40	0.19

2.3 Results

Leaf N concentration of N-fertilized *D. altsonii* saplings was 30 % higher than that of control plants, but stem and roots N concentration and leaf, stem and root dry weights were not different from plants without fertilizer (Table 2.2). Stem P concentration of P-fertilized *D. altsonii* saplings was 65 % higher than that of control plants and the total plant dry weight had almost doubled (Table 2.2). When both P and N were added, saplings had a 30 % higher leaf N concentration and a 57 % higher stem P concentration, but total dry weights were not significantly higher than those of the controls.

The addition of N had a lethal effect on saplings of the non-legume *C. rodiei*. All plants of the N and N+P treatment died, while the surrounding plants had a healthy appearance. The addition of P tripled the P concentration in stem and root, but total plant dry weight was not higher, and leaf dry weight even lower than that of the control plants (Table 2.3). Recovery rates of both nutrients were very low for both species in all treatments (Tables 2.2 and 2.3). The relative growth rates were very low. Calculated over a period of 18 months, the RGR of *D. altsonii* varied from 0.9 - 2.0 $mg.g^{-1}DW.day^{-1}$, and for *C. rodiei* from -0.04 - 0.4 $mg.g^{-1}DW.day^{-1}$. None of the excavated *D. altsonii* saplings had root nodules.

The P/N ratio of leaves of the saplings was not significantly different from that of mature trees. The P/N ratio of leaves of both mature trees and sap-

Table 2.3. Mean dry weight (g, n=18), P and N concentration ($mg.g^{-1}DW$, n=3) for leaves stem and roots, relative growth rates (RGR, $mg.g^{-1}DW.day^{-1}$)and recovery rates of P (RRP, %) for *Chlorocardium rodiei* saplings grown as control or with P (+P). For any row of data, values with differing letters are statistically different at the 95% probability level.

		control		+ P	
DW	leaves	3.8	a	2.8	b
	stem	7.6		6.4	
	root	3.8		2.7	
	total	15.2		11.8	
[P]	leaves	0.49		0.56	
	stem	0.37	b	1.16	a
	root	0.32	b	0.95	a
[N]	leaves	16.8		12.9	
	stem	8.2		7.9	
	root	11.4		9.9	
RGR		0.40		-0.04	
RRP		-		0.14	

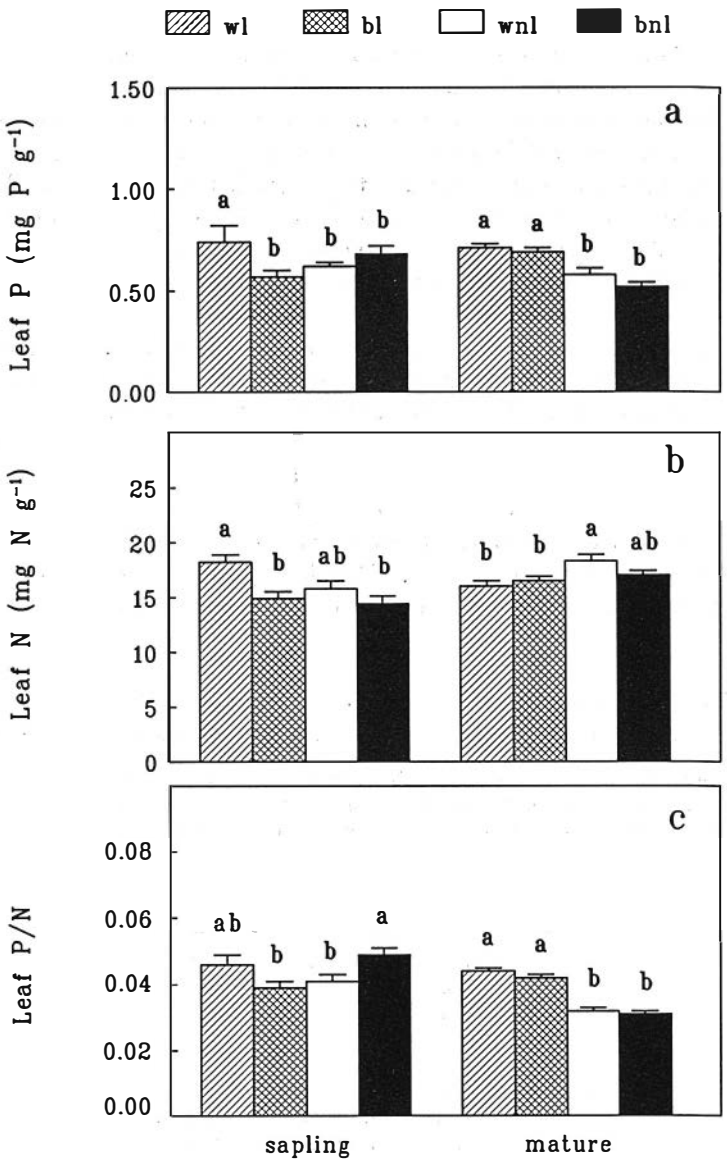

Fig. 2.1. P and N concentration of tropical rain forest trees a. Leaf P concentration (mg P g^{-1}DW), b. Leaf N concentration (mg N g^{-1}DW) and c. Leaf P/N ratio (g P/g N). Saplings and mature trees for legumes growing on white (wl) or brown (bl) sand, and non-legumes growing on white (wnl) or brown (bnl) sand. Mean values (n>27); bars indicate se. Letters indicate differences between groups of species at the 95% probability level.

lings was low, 0.031 - 0.049 (Fig. 2.1c), due to a very low P-concentration, 0.52 - 0.86 mg per g leaf DW (Fig. 2.1a, Table 2.1), rather than a high N-concentration, 14.4 - 18.3 mg per g leaf DW (Fig. 2.1b, Table 2.1). Leaves of the mature legumes had a higher P/N ratio than those of non-legumes (Fig. 2.1c), due to their higher leaf P concentration (Fig. 2.1a), and lower N concentration (Fig. 2.1b). There were no significant differences in nutrient concentrations and P/N ratio between leaves of mature trees collected on white and brown sands.

Highest leaf P and N concentrations were found in the leguminous saplings on white sand (Figs 2.1a and 2.1b); the P/N ratio was highest for non-legume saplings growing on brown sand (Fig. 2.1c). Of the legume saplings *M. excelsa* and *E.falcata* had many root nodules but nodulation of the other species was poor or absent (Table 2.4). P concentration of stems and roots of saplings appeared to relate to seed size (Table 2.1 and Fig. 2.2a); the species were classified into four seed size classes. Saplings from different seed size classes, did not differ in their leaf P concentration, but the plants of the smallest seed size class had a substantially lower P concentration in their roots and stem than those of larger size classes did (Fig. 2.2a). Contrary to P concentration, the N concentration was higher in leaf tissue than in stem or root tissue (Fig. 2.2b). There were only minor differences in N concentration between saplings of the four seed size classes (Fig. 2.2b).

2.4 Discussion

2.4.1 N and P fertilizer

The aim of the fertilizer experiment was to investigate whether the growth of saplings on white sand is restricted by the availability of P and/or N. Both *C. rodiei* and *D. altsonii* saplings increased P-uptake in response to P-fertilizer. As expected, growth of the legume *D. altsonii* was more limited by P (Table 2.2) than that of *C. rodiei*, but this difference was not caused by the P-requirement of nodules, since no nodules were found on its roots. Despite its original low P concentration, *C. rodiei* did not show an enhanced growth in response to P fertilizer (Table 2.3). There was a slight difference in pH of both plots; other factors of the acid soil complex, such as the low pH, might be (co)limiting as well on white sands. Aluminium is unlikely to be toxic on white sands, because of its fairly low concentration (1 mg kg^{-1}, Table 3.1).

N, added as urea with or without P, did not significantly increase growth of *D. altsonii* (Table 2.2), and was even lethal for *C. rodiei* saplings. It is most un-

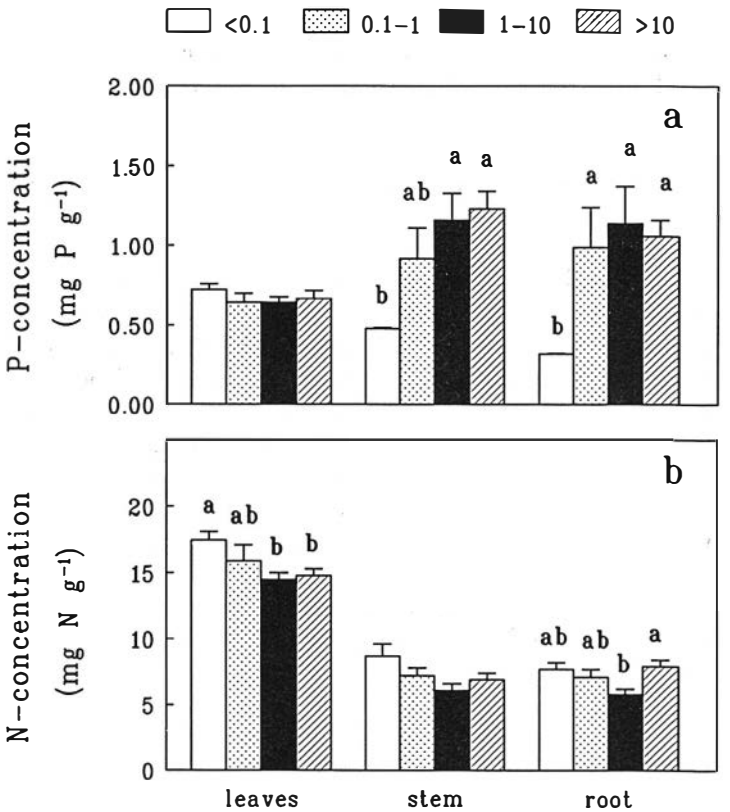

Fig. 2.2. P and N concentration of tropical rain forest saplings differing in seed size: a. P concentration (mg P g^{-1}) and b. N concentration (mg N g^{-1}) of leaves stem and roots of saplings originating from seeds smaller than 0.1 g DW, 0.1-1.0 g DW, 1-10 g DW or larger than 10 g DW; bars indicate se. Letters indicate differences between groups of species at the 95% probability level.

likely that this effect was due to the fertilizer rate, since only 10 g of N per 18 months was added as slow-release fertilizer. We suggest that the lethal effect was indirect, being a result of the form in which the N was applied. Nitrification of the NH_4^+ resulting from urea can have an acidifying effect (Adams, 1984), which may increase leaching of cations, i.e. K, Ca and Mg (Olsthoorn et al., 1991, Luxmoore et al., 1993). However, in acid soils nitrification is usually very slow and NH_4^+ is the predominant source of nitrogen (Marschner, 1986). Plants growing on these soils tolerate high levels of NH_4^+, but the uptake of ammonium would further decrease rhizosphere pH and could also induce Ca or Mg deficiency (Marschner, 1986). A decrease in the rhizosphere pH or a nutrient imbal-

Table 2.4. Number of nodulated (+no) and non-nodulated (-no) saplings found at n sites in this study and in the study of Norris (1969). Species not sampled by Norris are indicated with '-'.

Species	This study			Norris		
	n	+no	-no	n	+no	-no
White sand						
Eperua grandiflora	3	0	9	3	0	11
Eperua falcata	3	9	0	3	0	5
Dicymbe altsonii	3	0	9	-	-	-
Chamaecrista adiantifolia	1	4	150	-	-	-
Brown sand						
Mora gonggrijpii	3	0	9	2	0	11
Peltogyne venosa	3	0	9	3	0	9
Mora excelsa	1	8	1	1	0	5

ance might have been caused by the uptake of N, but does not explain the differences in response to N fertilizer between *C. rodiei* and *D. altsonii* saplings. We conclude that the use of urea fertilizer to promote growth of tree saplings is not to be recommended in this area, since it can cause death of saplings and N is unlikely to be the principal growth limiting factor.

Recovery rates for N and P are very low, 1.0-1.5 and 0.14-0.40%, respectively (Tables 2.2 and 2.3). Many studies have reported high N losses from urea (30-60% for pearl millet) in sandy soils from West Africa (Hafner et al., 1992). Luxmoore et al. (1993) reported recovery rates for N by *Platanus occidentalis* of 0.6-1.5% on highly weathered soils in Tennessee. The very low proportion of fertilizer taken up suggests that P and N may be leached, assimilated by microorganisms and/or incorporated into the soil organic matter. The low relative growth rates of 0-2 mg g^{-1} (DW) day^{-1} also indicate that the demands of the saplings for N and P were very low.

2.4.2 Soil type

Although white sands differ from brown sands in their nutrient content (Khan et al., 1980), mature tree species on these sands do not differ in their leaf P and N concentration and in their P/N ratio (Fig. 2.1). Leaf tissue P and N concentration are within the range found by Stark (1970) for plants from Brazil and Surinam and similar to values found by Vitousek and Sanford (1986) for infertile ultisols/oxisols, on average 0.06 mg P g^{-1} and 17.1 mg N g^{-1}. The latter concluded that these soils were extraordinarily low in phosphorus, and not in nitrogen. For white and brown sands, moderate leaf N concentrations and low P/N ratios (Figs 2.1b and 2.1c) also do not point to N as a principal growth-limiting nutri-

ent. Leaf P concentration (Fig. 2.1a; Vitousek and Sanford, 1986) and P/N ratio (Fig 2.1c; Lathwell and Grove, 1986) are among the lowest reported for tropical tree species. Like other Amazonian soil types, both white and brown sands in Guyana are likely to be more impoverished in P than in N.

2.4.3 Seed size

Atkinson (1973) concluded that seed size is important in determining the stage at which plants become dependent on external supplies of phosphorus. P concentration of the saplings was related to seed size (Fig. 2.2a); P concentration of stems and roots of species with small seeds (< 0.1 g) was less than half of those of species with larger seeds. In evergreen species, roots and stems are important storage organs (Chapin, 1980). P-fertilized trees in the fertilizer experiment also translocated extra P to stem and roots (Tables 2.2 and 2.3). We conclude that the species with large seeds store P in roots and stems. We have two possible explanations for the higher P concentration in root and stem of species with large seeds compared to species with very small seeds:

(i) The high P concentration might have originated from P-reserves in the large cotyledons. We do not have data on P concentrations of seeds of all the 15 species. Species like *Cecropia obtusa* and *Goupia glabra* have seeds too small to contain substantial P-reserves (Table 2.1). In a comparison of 16 Guyanese tree species, Boot (unpublished) found that cotyledons of 13 species with large seeds, including *Chamaecrista adiantifolia*, *Peltogyne venosa*, *Eperua falcata* and *Dicymbe altsonii*, had a P concentration higher than 1 mg P g^{-1}DW.

(ii) The high P concentration might be the result of carbon losses. Saplings of some species with very large seeds, like *Mora gonggrijpii* and *Chlorocardium rodiei*, had a total dry weight which was only one third of the seed dry weight, while total P content of saplings was similar to that of the seeds (Raaimakers, unpublished). The respiration of carbon, coupled with the conversion from seed to seedling, may have increased the P-concentration (Boot, 1994). The cause of the high P concentration in roots and stems of saplings originating from large seeds was not investigated here, but large seeds seem likely to confer an advantage for plants which have to establish in a P poor environment.

2.4.4 Legumes

Not all legumes do form root nodules (Högberg, 1986). Most leguminous saplings excavated by Norris (1969) and by us did not have nodules (Table 2.4), confirming earlier reports on trees in this area. Whitton (1962) also found that only 25% of the one-year old leguminous saplings in the Amatuk region in Guyana were nodulated. Nodulation failure in soils of pH 5.0 or less is common (Aarons and Graham, 1991). Low pH is usually associated with low P availability

and Al excess (Marschner, 1991); these factors reduce nodulation and limit *Rhizobium* survival (Israël, 1987).

The mature legume trees in the study area had a higher leaf P concentration and P/N ratio than non-leguminous trees (Figs 2.1a and 2.1c). However, if these trees were not nodulated, this suggests that legumes have an inherently higher P requirement than non-legumes. This might explain the difference in response to P fertilizer between the leguminous and non-leguminous saplings (Tables 2.2 and 2.3). But how could they achieve a higher leaf P concentration than non-legumes in a low P environment?

All the legumes in this study belong to the subfamily of the Caesalpinioideae (Mennega et al., 1988). Gartlan et al. (1986) found a strong correlation of species of the Caesalpinioideae with soils low in available phosphorus (5 mg kg^{-1}) in Cameroun. Tree species of this subfamily rarely nodulate and are predominantly ectomycorrhizal (Högberg, 1986), which is an advantage in a P-poor environment. Ectomycorrhizal associations are able to secure nutrients in both organic and inorganic form before they are available to VA-mycorrhizal associations (Herrera et al., 1978, Connell and Lowman, 1989), and can even reduce the activities of saprophytic fungi (Newbery et al., 1988). Connell and Lowman (1989) hypothesized that these characteristics, together with a greater host specificity, give EM host trees a competitive advantage, which enable them to achieve and maintain dominance over VAM host trees. Tree species with EM attain dominance on the most infertile soils in humid areas of tropical Africa (Högberg, 1986). For the genera *Eperua* and *Mora*, associations with ectomycorrhiza (EM) have been reported (Connell and Lowman, 1989). *Eperua falcata*, *Eperua grandiflora* and *Mora gonggrijpii* belong to the seven most abundant species in our study area (Ter Steege et al., 1993). In the inventory of a part of the study area made by Ter Steege et al. (1993), only 8 % of the leguminous individuals were from families other than the Caesalpinioideae. The abundance of this subfamily in the P-poor study environment is likely to be connected with their ability to form ectomycorrhizal associations, rather than their ability to fix dinitrogen via rhizobial infection.

Acknowledgements

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Chapter 3

P-availability in acid sandy soils; a case study carried out in Guyana

with René Boot, Harry Olde Venterink, Kristel Perreijn and Hans Lambers

Summary

The highly weathered acid white and brown sands, which support dense tropical rain forests in Guyana, South America, have a low nutrient status. The pH of these soils is low, and brown sands contain phosphate-fixing Al and Fe oxides. To study P-availability for regenerating tree seedlings on these soils, two pioneer tree species with a relatively high P-requirement (*Cecropia obtusa* Trécul and *Goupia glabra* Aubl.) and two climax species with a lower P-requirement (*Chamaecrista adiantifolia* (Benth.) Irwin & Barneby and *Chamaecrista apoucouita* (Aubl.) Irwin & Barneby) were grown on white or brown sand, with or without a supply of KH_2PO_4, with or without leaf litter.

Despite the higher total P-concentration of brown sand (55 mg kg^{-1}) compared to that of white sand (8 mg kg^{-1}), seedlings extracted more P from white sand, indicating a higher availability of P on white sand. This was most likely associated with lower Fe, Al and organic matter content of white sands. Adding KH_2PO_4 to white sand increased both the total amount of P taken up by seedlings and the P-concentration in tissues. However, it did not result in a greater dry weight of the tree seedlings, suggesting that factors other than P-availability limit growth of seedlings on white sand, particularly the low pH. Despite their low P-concentration, the addition of 50 mg P per seedling resulted in no increase of the P-concentration or growth by seedlings of climax species, on brown sand. The pioneer species, responded to P-addition with increased P-concentrations and growth, demonstrating that on brown sand their growth is limited by P.

The addition of leaf litter improved seedling growth on both sands. On brown sand P-uptake of seedlings was increased when seedlings were grown with litter. P-uptake of seedlings did not significantly increase when seedlings were grown on white sand with litter, their P-concentrations decreased and their dry weights increased. Possible beneficial effects of litter on seedling growth other than an increase in P-availability, include an increase in mycorrhizal hyphae, an increase in availability of micronutrients and a decrease of Al^{n+} toxicity, f.e. by the formation of non-toxic organo-Al complexes.

Despite the low P-availability of white and brown sands, addition of P will not always result in enhanced seedling growth, since other factors of the acid soil complex, i.e. Al toxicity or low pH, are likely more limiting for growth.

3.1 Introduction

In Guyana, South America, between 60 and 70 percent of the acid sandy soils are covered by dense rain forests. For many years, timber has been extracted from these natural forest on a small and local scale, but now the demand for timber is increasing and the Guyanese government considers the stimulation of timber harvesting to be of great importance. Therefore, as logging increases, there is a need for information not only on the impact of logging, but also on the regeneration potential of tree species.

Problems associated with tree generation may be influenced by soil characteristics. In the Guianas, Brazil and Venezuela there are large areas of acid sandy soils derived from parent rocks such as sandstone, granite and granitic gneiss (Ahmad, 1989). These materials are almost always severely impoverished by weathering as well as by leaching and eluviation. Guyana's severely bleached sandy deposits, locally referred to as white sands, consist of more than 95 percent quartz. Brown sands, also acid and susceptible to leaching, have a higher clay content and a higher water-holding capacity than white sands (Khan et al., 1980, Van Kekem et al., 1995).

On acid mineral soils, such as those occur in Guyana, plant growth may be limited by a variety of specific chemical factors and interactions between them including: low pH, Al and Mn toxicity, deficiencies of P, Mo, Mg, Ca and K and water deficiency (Marschner, 1991). The relative importance of these constraints depends on plant species, soil type and horizon, parent material, soil structure and aeration and climatic conditions. The low leaf P-concentrations (0.6 mg/g, Chapter 2) of trees and seedlings growing on white and brown sands in Guyana suggest that phosphorus may be a key nutrient in controlling the growth of regenerating seedlings. The purpose of this study was to evaluate the effect of P addition on growth and P-uptake of tree species of successional and mature forests.

Based on differences in seed germination and seedling establishment, tropical rain forest tree species have been classified as pioneer and climax species (Swaine and Whitmore, 1988). Pioneer species regenerate in large gaps and generally have a higher potential growth rate than climax species, whose seedlings can establish and persist in forest shade (Swaine and Whitmore, 1988). P uptake of seedlings not only depends on the amount of available P in the soil, but also on plant P requirement and uptake characteristics (Föhse et al., 1988). Pioneer species would be expected to have a higher P-requirement than climax species, because of their higher potential growth rates (Lambers and Poorter, 1992). Two pioneer and two climax species were chosen to test whether the addition of inor-

ganic phosphate fertilizer (KH_2PO_4) improves P-availability of white and brown sands and growth of tree seedlings.

Research has underlined the importance of the readily mineralizable pool of organic P in the phosphate fertility of soils (Haynes, 1982). The annual input of P in precipitation is small ranging from 0.5-1 kg/ha (Brouwer, pers. com.). The rates of release through mineral weathering are less well known, but appear to be of similar magnitude (Binkley, 1986). Therefore, decaying leaf litter and roots are an important source of P for growth in undisturbed forests. We evaluated the role that leaf litter, the main source of P to soil, might play in controlling seedling growth by growing two pioneer and two climax species with and without the addition of leaf litter on white and brown sands.

3.2 Methods

Seedlings were collected from two pioneer species: *Cecropia obtusa* Trécul, Moraceae (25 mg seedling dry weight) and *Goupia glabra* Aubl., Celastraceae (10-15 mg seedling dry weight), and two climax species, with small seeds, *Chamaecrista adiantifolia* (Benth.) Irwin & Barneby, Leguminosae (170 mg seedling dry weight) and *Chamaecrista apoucouita* (Aubl.) Irwin & Barneby, leguminosae (170 mg seedling dry weight). *C. obtusa* and *C. adiantifolia* usually grow on white sand, and *G. glabra* and *C. apoucouita* on brown sand. The seedlings were grown in 5 l plastic bags, in a replicated randomized block design, in a nursery with shade cloth (50% of full sunlight). The nursery was located in the Mabura area in central Guyana (5°18'N 58°42'W).

Per pot, 0.5 l of a solution containing 50 mg P was poured on the soil (equals about 7 mg P per kg soil), two weeks before the seedlings were planted. To prevent nutrient limitation other than P, all bags received 60 ml of a nutrient solution once a week containing 0.88 mg $Ca(NO_3)_2 . 4H_2O$, 0.50 mg KNO_3, 0.41 mg $MgSO_4 . H_2O$, 2µg $MnSO_4 . 7H_2O$, 1.5µg $ZnSO_4 . 7H_2O$, 0.2µg $CuSO_4 . 5H_2O$, 7.7 µg H_3BO_3, 0.4 µg $Na_2MoO_4 . H_2O$ and 1.8 µg Fe-EDTA. Seedlings were watered when necessary.

White sand (Albic Arenosol) and brown sand (Haplic Ferralsol; Van Kekem et al., 1995) was collected below 1 m depth and sieved to homogenize the soil. Seedlings were grown in white sand or brown sand, with or without the addition of 50 mg P per pot as KH_2PO_4 or with or without leaf litter on top (ratio litter(v):sand(v) = 1:1). In order to mimic the field situation leaf litter was collected in forest on brown sand for the brown sand plus litter treatment, and leaf litter in forest on white sand for the white sand plus litter treatment. Leaf litter was

Table 3.1. Sand and litter characteristics. Mean values (SE in brackets) for n replicates of pH, P, and Al concentration, organic matter content and bulk density. Differences between soils at P=0.05 are indicated with lower case letters.

	Unit	n	Sand		Litter	
			White	Brown	White	Brown
pH-$CaCl_2$(0.01 M)		3	3.7 c (0.1)	4.4 b (0.0)	4.6 a (0.0)	3.9 c (0.0)
P-total	mg/kg	4	8 c (1)	55 b (0)	60°b (3)	162°a (1)
Al concentration	mg/kg	3	1.0 c (0.05)	4.4 a (0.4)	0.1 c (0.05)	2.2 b (0.7)
Organic matter	%	5	0.3 d (0.0)	2.0 c (0.0)	9.4°b (0.0)	14.6°a (0.2)
Particle density	kg/l	4	2.2 a (0.1)	2.0 a (0.0)	1.5°b (0.0)	1.4°b (0.0)

° Values measured for litter mixed with soil.

collected from under *Dicymbe altsonii* Sandw., a species growing on both soil types (Table 3.1). The study began in January 12 and of each treatment six pots, containing one plant, were harvested at the beginning of June.

Leaves, stems and roots from the harvested seedlings were dried at 70 °C for at least 24 hours and then weighed. Dried plant and soil material were stored for return to the Netherlands for chemical analysis. P-fractions in the soil were too low to be determined, so only total P was analyzed. Soil samples were prepared for P-analysis by a digestion with Fleischmann's acid (Houba et al., 1986). Dried plant material was digested using a modified micro-Kjeldahl digestion (concentrated sulphuric acid and a catalyst mixture of Se, $CuSO_4$ and Na_2SO_4 in a ratio of 1:1:62, Bradstreet, 1965). Both soil and plant P, were analyzed colorimetrically, using the ammonium molybdate method (Houba et al., 1989). The pH of the soil and litter was measured potentiometrically in the supernatant of a 50 ml 0.01 M $CaCl_2$ solution, shaken for 2 hours with 20 or 5 g of air-dry soil or litter, respectively. Al content of the supernatant was determined by atomic absorption spectrophotometry. To determine organic matter content, soil and litter samples were ashed in a combustion oven at 550 °C for ten hours.

A small experiment was carried out to test whether white and brown sands differ in the amount of fertilizer needed to increase P-availability in the sands. Solutions (7.5 ml) with varying concentrations of P as KH_2PO_4 were added to 40 g of white or brown sand, to supply 15, 150, 750 or 1500 mg P per kg

Table 3.2. Water-extractable P (mg kg^{-1}), one week after KH_2PO_4 was supplied to white and brown sand. Samples were divided into two depth intervals as shown.

P-supply (mg kg^{-1})	15	150	750	1500
White sand				
0-20 cm depth	10.40	> 12.5	> 12.5	> 12.5
20-50 cm depth	6.23	> 12.5	> 12.5	> 12.5
Brown sand				
0-20 cm depth	0.03	1.00	> 12.5	> 12.5
20-50 cm depth	0.00	0.10	> 12.5	> 12.5

sand. Sand was stored in closed polypropylene tubes for one at 30 °C, after which water-extractable P was analyzed.

Data were analyzed with the SAS statistical package (SAS, 1988). Soil parameters were tested with a one way ANOVA. To compare differences in plant parameters between treatments a two way ANOVA and between treatments within species a one way ANOVA was used per soil type, because of the different origin of the leaf litter. If differences were found to be significant, treatments were compared to the control treatment using a Dunnett's two-tailed t test. Because of the large variation in total P per seedling of *C. obtusa* on brown sand plus P, a ranking was carried out for this parameter on brown sand before the ANOVA was carried out. Differences in ranking were tested with a Student-Newman-Keuls test.

3.3 Results

Whilst particle densities were similar for both soil types, all parameters associated with soil P-availability (i.e. pH, total P, and Al concentrations and % organic matter) were higher for brown sand (Table 3.1). At lower rates of P-application (<150 mg per kg), more P was extracted with water from white sand than from brown sand (Table 3.2). Seedlings grown on white sand took up more P ($p<0.0001$, Figs 3.1b and 3.2b) and had higher P-concentrations than those on brown sand ($p<0.0001$, Figs 3.1e and 3.2e). Final yield per seedling did not differ significantly (Figs 3.1h and 3.2h) partly because pioneer species on brown sand control showed poor growth (Fig. 3.2h). This poor growth was probably due to sand splash with heavy rain, since their relatively large leaves were positioned close to the soil surface (Fig. 3.2h). Climax species had their leaves positioned higher on the stem, and so were not affected by sand splash.

When KH_2PO_4 was added to seedlings growing on white sand, there was an overall effect on P uptake (Figs 3.1a and 3.1b) and all species had a signifi-

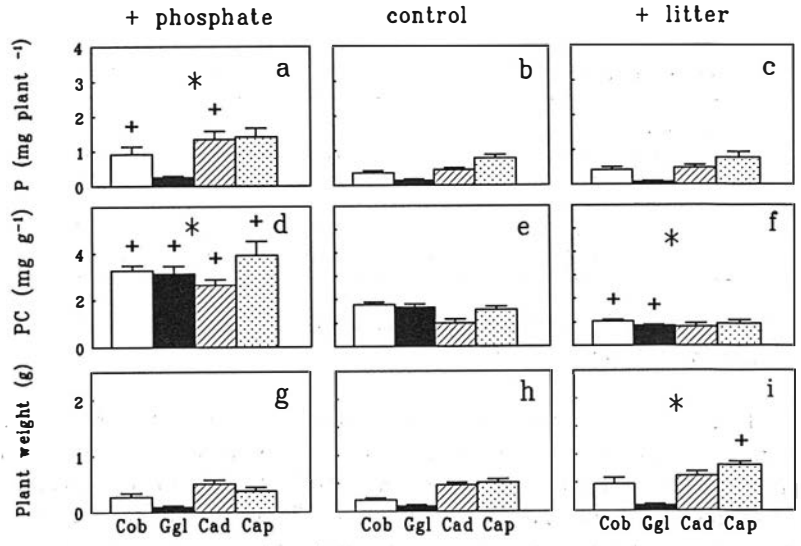

Figure 3.1. Plant parameters of plus phosphate, control and plus litter treatment on white sand. Mean (+SE, n=6) total amount of P taken up by seedlings (P, a, b and c), P-concentration in the seedlings (PC, d, e and f) and plant dry weight per seedling at final harvest (g, h and i). Significant differences between controls and either plus phosphate or plus litter treatment are indicated with a *, for the four species together, and with a + for the individual pioneer species, *C. obtusa* (Cob) and *G. glabra* (Ggl), and climax species, *C. adiantifolia* (Cad) and *C. apoucouita* (Cap).

cantly higher P-concentration (Figs 3.1d and 3.1e), but dry weights were not different from the controls (Figs 3.1g and 3.1h), indicating that P was not limiting growth. On brown sand, pioneer and climax species responded differently to P addition. The addition of 50 mg P per pot was not sufficient to increase P uptake for *C. adiantifolia*, and for both climax species, *C. adiantifolia* and *C. apoucouita*, P-concentration and dry weights were not significantly higher than those of the control plants (Figs 3.2d, 3.2e, 3.2g and 3.2h). However, for the pioneer species, *C. obtusa* and *G. glabra*, P-concentration and growth were enhanced (Figs 3.2d, 3.2e, 3.2g and 3.2h), indicating that P was limiting growth of these species when grown on brown sand.

The substrate P-concentration of the litter plus sand treatment was higher than that of the control, and litter collected on brown sand contained more P, 162 mg kg^{-1}, than litter collected on white sand, 60 mg kg^{-1} (Table 3.1). Brown sand contained more Al than litter collected on brown sand (Table 3.1). Although Al can accumulate in and on roots to extremely high levels, Al enrichment in above-ground plant parts is usually low, even at high external Al levels (Keltjens and Van Loenen, 1989), which explains the low Al content of leaf litter

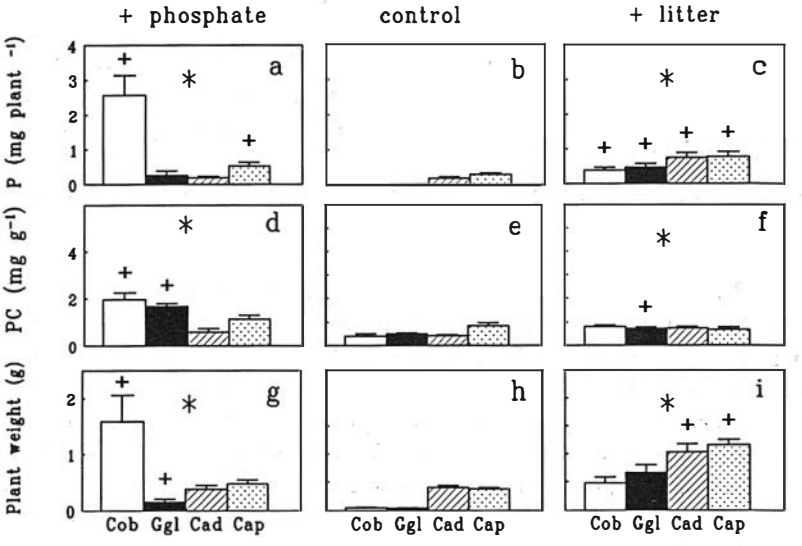

Figure 3.2. Plant parameters of plus phosphate, control and plus litter treatment on brown sand. Mean (+SE, n=6) total amount of P taken up by seedlings (P, a, b and c), P-concentration in the seedlings (PC, d, e and f) and plant dry weight per seedling at final harvest (g, h and i). Significant differences between controls and either plus phosphate or plus litter treatment are indicated with a *, for the four species together, and with a + for the individual pioneer species, *C. obtusa* (Cob) and *G. glabra* (Ggl), and climax species, *C. adiantifolia* (Cad) and *C. apoucouita* (Cap).

compared to sand (Table 3.1). On brown sand, all species contained significantly more P per seedling when grown with litter (Figs 3.2b and 3.2c) and there was only an treatment effect for *Goupia glabra* on P-concentration (Figs 3.2e and 3.2f). There was an overall effect on plant dry weight, but only the two climax species were significantly larger than the control plants (Figs 3.2h and 3.2i). The overall litter effect on seedlings grown on white sand was a significant decrease in P-concentration and increase in dry weight (Figs 3.1h and 3.1i). These results indicate that on white sand a component of leaf litter, other then its P content stimulated growth.

3.4 Discussion

P-availability does not only depend on absolute quantities of P in the soil, but also on the degree of binding at the soil particles. Although the total P concentration of the soil was higher for brown sand (Table 3.1), P availability was higher in white sand (Table 3.2, Figs 3.1b and 3.2b). The lower availability of P in brown sand is likely to be due to binding of P by Fe- or Al- oxides and/or

organic matter. Fe-oxides and Al-oxides can make up to 2.8 and 6.5%, respectively, of the elemental composition of brown sands (Van Kekem et al., 1995). Hydrated Al and Fe oxides adsorb phosphate, especially at pH values slightly below 4 (Haynes, 1982). At low soil pH, soil organic matter may bind extra H^+, thus providing a positive charge and adsorbing anions such as phosphate (Binkley, 1986). The higher clay content of brown sand (Khan et al., 1980) can also increase adsorption of anions by electric attraction to the positively charged clay particles (Binkley, 1986).

Plant species differ in their capacity to extract P from soil and P requirement. When 50 mg P had been added to the pots containing brown sand, the slow-growing climax species *C. adiantifolia* and *C. apoucouita*, did not respond in growth to P addition on brown sand (Figs 3.2g and 3.2h), whereas the pioneer species *C. obtusa* and *G. glabra* had both higher P-concentrations, and dry matter production (Figs 3.2d, 3.2e, 3.2g and 3.2h). Probably, without P-fertilization, low P availability limits the growth of pioneer species on brown sand. The lack of response to added P for the climax species suggests that 50 mg P was not enough to increase P availability (*C. adiantifolia* Figs 3.2a and 3.2b, Table 3.2, see also Chapter 4) or some other factor was even more limiting, on brown sand.

Since P-fertilization increased P uptake, but not total dry weight of seedlings on white sand (Figs 3.1a, 3.1b, 3.1g and 3.1h), P is not a growth limiting factor for the seedlings on white sand. Low phosphorus concentrations in leaf tissue of trees growing on white sands (Chapter 2) may simply be an indicator of an acid soil infertility complex (Haynes, 1982), explaining why application of P-fertilizer did not necessarily alleviate growth limitation. Toxic concentrations of H^+ or mineral elements like Al, and/or low availability of other mineral nutrients may also be factors contributing to growth limitation (Marschner, 1991). The fairly low Al concentrations (1.0 mg kg^{-1}) on white sand are not likely to be toxic (Table 3.1; Tan and Keltjens, 1990), but a pH of 3.7 (Table 3.1) might be limiting growth on this soil type. For example, at a pH value of about 3.5 - 3.8, H^+ toxicity symptoms occurred in *Bromus benekii* (Anderson et al., 1993). An extreme low pH is known to have a damaging effect on cell membranes and reduces the cation uptake by competition of H^+ for ion absorption sites. Moreover, the rhizosphere pH may differ from the bulk soil pH by more than two units, depending on plant species, nutritional status of the plants, the form of nitrogen, and pH buffering capacity of the soil (Marschner, 1991). Since NH_4^+ is likely to be the main source of nitrogen at this pH, we envisage that the rhizosphere pH may even have been lower than soil pH. Further investigation is needed to establish whether the low soil pH (3.7) is the principal growth limiting factor for the seedlings on white sand.

Seedling growth was stimulated by litter addition (Figs 3.1h, 3.1i, 3.2h and 3.2i). For pioneers on brown sand, this may be due to a higher availability of (organic) P in litter compared to that in sand, since P concentration of litter was higher than that of sand (Table 3.1) and P-uptake increased when plants were grown with litter (Figs 3.2b and 3.2c). A lower concentration of toxic Al^{n+} forms in leaf litter compared to brown sand (Table 3.1) may also have enhanced growth compared to the controls and consequently increased P-requirement of the seedlings grown on brown sand plus litter. Al toxicity is a common phenomenon on acid soils (Haynes, 1982). High concentrations of Al^{n+} may inhibit root growth by inhibiting both cell division and/or cell elongation (Marschner, 1991).

On white sand, Al concentrations were low (Table 3.1) and P-uptake did not increase with the addition of litter to soil (Figs 3.1b and 3.1c), although litter had a beneficial effect on growth (Figs 3.1h and 3.1i). Growing the plants on a substrate of 50% litter and 50% sand may have increased the pH compared to the control treatment, since white sand litter had a higher pH than white sand (Table 3.1). Furthermore, the addition of leaf litter might enhance growth via:

(i) Increased mycorrhizal infection levels, promoted by the higher levels of organic matter in the soil (Soedarjo and Habte, 1993, Table 3.1). Mycorrhizae, in turn, can increase the uptake of scarcely mobile nutrients (Bolan, 1991). On brown sand, mycorrhizae might also relieve Al toxicity symptoms for seedlings. This has been reported for ectomycorrhiza, which accumulate Al in their sheath (Egerton-Warburton et al., 1993).

(ii) An increased availability of one of the immobile micronutrients. Macronutrients, except P, were added weekly in sufficient amounts, and are not likely to have been limiting for growth on white sand in this experiment. Since micronutrients were added at the usual low concentrations, it is difficult to predict whether they were sufficiently available for growth. Other physical differences between litter and sand, such as aeration or water-holding capacity, may also have led to an (indirect) increase in growth.

3.5 Conclusions

On the brown sands in Guyana, P was limiting for rain forest pioneer species, which have a high P-requirement. For the climax species *C. apoucouita*, with an inherently lower P-requirement, P was not limiting on brown sands. Since the addition of 50 mg P did not increase P-uptake for *C. adiantifolia* seedlings, the P fertilizer was probably not available for this species. Brown sands have a lower P availability than white sands likely due to a higher content of Fe- and Al-oxides and/ or organic matter. On white sands, none of the species was

growth-limited by P. The results of the present work indicate that other components typical of an acid soil complex might be more limiting for growth, particularly the low pH on white sand and high concentrations of Al^{n+} on brown sands.

The present results point to an important role of leaf litter in seedling growth; litter improved growth compared to that of the controls. There is still a need for further clarification of the effect of litter on growth, and the possible role of Al^{n+} or mycorrhizae. Specifically, the interaction between litter and low pH and/or Al toxicity seems to be very essential.

Acknowledgements

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Chapter 4

P acquisition and P utilization by tropical rain forest tree species differing in regeneration strategy

with René Boot, Arian Brouwer, Harry Olde Venterink, Kristel Perreijn and Hans Lambers

Summary

The highly weathered white and brown sands in Guyana, South America, are low in pH and nutrients, especially in phosphorus. Species from such an environment have a suite of attributes to cope with low P-availability. P-uptake and growth of seedlings were studied in three tree species differing in regeneration strategy. *Cecropia obtusa* Trécul, a ruderal species, *Goupia glabra* Aubl., a large-gap species, and a small-gap species *Chamaecrista adiantifolia* (Benth.) Irwin & Barneby were grown with or without added KH_2PO_4 on white and brown sand.

The habitats of establishment of *C. obtusa* and *G. glabra* largely overlap, i.e. larger gaps, and their growth as well as their P-uptake characteristics were very similar in this study. They had high Specific Absorption Rates of P per unit root weight (SAR_w, 4-240 $\mu g\ g^{-1}\ day^{-1}$) associated with high Relative Growth Rates (RGR, 5-40 $mg\ g^{-1}\ day^{-1}$) in contrast to *C. adiantifolia*, the small-gap species, which had a low SAR_w (0-20 $\mu g\ g^{-1}\ day^{-1}$) and low RGR (6-10 $mg\ g^{-1}\ day^{-1}$). *C. adiantifolia* had a lower P demand, i.e. a lower RGR and P concentration, than the other two species. This might contribute to the success with which this species establishes in lower light forest habitats.

All species had VA-mycorrhizae, whilst *G. glabra* also had ectomycorrhizal associations. Neither mycorrhizal infection rates nor Root Weight Ratio (RWR, root dry weight per plant dry weight) fully accounted for the observed interspecific differences in SAR_w. *C. obtusa* and *G. glabra* had a 5-10 times greater Specific Root Length (SRL, m root g^{-1} root dry weight) than that of the small-gap species *C. adiantifolia*, which accounted for the differences in SAR_w. These relatively high SRLs of *C. obtusa* and *G. glabra* are supposed to favour the competitive ability of these species in large gaps.

4.1 Introduction

Acid sandy soils are common throughout the tropics (Binkley, 1986). In Guyana, South America, severely bleached sandy deposits, locally referred to as white and brown sands, consist of over 95 and 88% of quartz, respectively and have a very light texture (Khan et al., 1980, Van Kekem et al., 1995). Between

60 and 70 % of these sandy soils are covered by forests (Ahmad, 1989). On such acid soils, which are susceptible to leaching of nutrients, the low nutrient levels, high Al levels or a low pH might restrict tree growth (Chapter 3). On white and brown sands, P is scarcely available for tree growth (Chapter 3) and trees growing on these substrates have extremely low leaf P concentrations, around 0.6 mg g^{-1} (Chapter 2).

Species, evolved in habitats with a low availability of P, have a suite of attributes either to cope with low P-availability and/or enhance P-uptake. Morphological as well as physiological root traits influence P-uptake from soil. When grown at a low P-availability, plants allocate a higher proportion of their biomass to the roots and thus explore a greater volume of the soil. This is particularly relevant for acquisition of phosphate, which diffuses only slowly in soil (Brewster et al., 1975). The exploratory geometry of the root system is increased most by investment in root length or root surface area, rather than root weight. Junk and Barber (1974) found a close positive relationship between P-uptake per plant and root length. Similarly, root hairs and/or external mycorrhizal hyphae, which extend into the soil far beyond the shells of P-depleted soil that surround the roots, contribute to the acquisition of P (Clarkson, 1985). It is well established that roots exude a range of organic compounds, including polysaccharides, organic acids and phosphatases, which enhance P-availability (Clarkson, 1986). The effectiveness of physiological and morphological adaptations of the roots in acquiring phosphate is reflected in the Specific Absorption Rate (SAR), defined as the rate of phosphorus uptake per unit root weight or length (Barrow, 1977).

In addition to enhanced P-uptake, species may also increase their efficiency of P utilization (Clarkson, 1985). Efficiency of P utilization is often defined as the reciprocal of P concentration in the entire plant (Gerlof, 1976), i.e. a low P concentration in the tissue is interpreted as an efficient use of P. Plants grown in a P-deficient soil tend to have a lower P concentration than those grown at higher P levels (Chapin and Bieleski, 1982). However, a low P concentration in the tissue can only be an indicator of an efficient use of P, if that tissue is able to function effectively with such a low amount of P. To gain insight into the P-utilization of plants, the P concentration should be studied in relation to growth. Growth is both a result and the driving force of nutrient inflow into the plants. This inflow is determined by the relative size of the absorbing system and the specific uptake capacity (Clarkson, 1985).

Growth, P-demand and P-uptake characteristics differ among species. Based on differences in seed germination, seedling establishment and growth, tropical rain forest tree species have been classified as ruderals, large-gap specialists and small-gap specialists (Denslow, 1987). Tropical ruderal tree species are

Table 4.1. Characteristics and habitat constraints for ruderal species (RS), large-gap species (LGS) and small-gap species (SGS); after Denslow (1987).

	RS	LGS	SGS
Physiological traits			
relative growth rate	high	high	low
photosynthesis rate	high	high	low
respiration rate	high	low	low
Habitat constraints			
germination	gap	gap	understorey/ small clearing
growth	secondary forest	primary & secondary forest	primary forest
seed production	large gap	gap	some canopy opening

characterized by traits classically ascribed to pioneer species (Bazzaz and Pickett, 1980). This group is most successful in the recolonization of large gaps (Table 4.1).

Like ruderals, large-gap species require the high light intensity of large gaps for their germination and seedling establishment and their early growth is rapid. They are able to tolerate lower light levels than ruderal species do (Denslow, 1987), which might be accompanied by a somewhat lower growth rate, and therefore lower P-demand than that of ruderal species. Small-gap species germinate in the understorey or in small clearings. These species grow slowly, even in favourable light conditions (Denslow, 1987, Table 4.1) and therefore might have a lower P-demand than the other two species (Chapin, 1980).

These three classes of tree species coexist on the white and brown sands with a low P-availability. Do these species, differing in regeneration strategy, differ in their suite of traits allowing them to cope with low P-availability? In order to study the factors associated with successful growth in P-deficient soils, we examined root morphology, mycorrhizal infection rate, P-uptake, growth and P tissue concentration of a ruderal, a large-gap and a small-gap species on two soil types low in P-availability, white and brown sand. To test whether these characteristics change with an increase in P-supply, seedlings were grown with or without added KH_2PO_4.

4.2 Methods

4.2.1 Species

Cecropia obtusa Trécul (Moraceae) is a typical pioneer tree of medium stature, 8-29 m tall (Swaine and Whitmore, 1988). It grows in large gaps, adjacent to roads and at other disturbed sites on white sand. *Goupia glabra* Aubl. (Celastraceae) grows up to a large forest tree and can attain a height of 30 m or more, and predominantly occurs on brown sands. *Chamaecrista adiantifolia* (Benth.) Irwin & Barneby (Caesalpinioideae) is also a large tree and predominantly occurs on white sand (Ter Steege et al., 1993). We collected seedlings from *C. obtusa* (on a gap), *G. glabra* (adjacent to a trail) and *C. adiantifolia* (in the understorey of the forest) of 25, 10-15 and 170 mg seedling dry weight, respectively.

4.2.2 Experimental design and chemical analyses

The seedlings were grown in 5 L plastic bags, in a replicated randomized block design, in a nursery with shade cloth (50% of full sunlight). The nursery was located in the Mabura Hill region in central Guyana (5°18'N 58°42'W). Seedlings were grown in white sand (Albic Arenosol) or brown sand (Haplic Ferralsol) (Van Kekem et al., 1995), with or without the addition of KH_2PO_4 (see Chapter 3 for chemical characteristics of soils). Per pot, 50 mg P was added two weeks before the seedlings were planted. To prevent nutrient limitation other than that by P, all bags received 60 ml nutrient solution once a week with 0.88 mg $Ca(NO_3)_2 . 4H_2O$, 0.50 mg KNO_3, 0.41 mg $MgSO_4 . H_2O$, 2µg $MnSO_4 . 7H_2O$, 1.5µg $ZnSO_4 . 7H_2O$, 0.2µg $CuSO_4 . 5H_2O$, 7.7 µg H_3BO_3, 0.4 µg $Na_2MoO_4 . H_2O$ and 1.8 µg Fe-EDTA. Seedlings were watered when necessary. The study began in January 1992 and of each treatment six pots containing one plant were harvested at the end of February and about 100 days later.

Leaves, stems and roots were dried at 70 °C for at least 24 hours and then weighed. Dried plant material was digested using a modified micro-Kjeldahl digestion (concentrated sulphuric acid and a catalyst mixture of Se, $CuSO_4$ and Na_2SO_4 in a ratio of 1:1:62; Bradstreet, 1965). P was analyzed colorimetrically, using the ammonium molybdate method (Houba et al., 1989).

4.2.3 Mycorrhizal infection rate

To study mycorrhizal infection rates of plants grown without additional P, the experiment was repeated with white and brown sand collected at 0-30 cm depth from November, 1992 till April, 1993. Those seedlings collected in the

forest, but not used for the pot experiment, were used to estimate initial VAM infection rates. Seedlings grown in plastic bags were harvested in January and April. After harvesting, 3 of the 6 replicates were used for the determination of VAM infection percentage. Plant roots were washed with tap water and cut into pieces of about 1 cm. Roots were bleached in 10% KOH at 90 °C for 60 minutes, followed by 15 minutes in 10% H_2O_2 and 3 minutes in 2% HCl. Roots were stained with 0.05% aniline blue at 90 °C for 10 minutes and then examined with a binocular microscope (64X magnification). To estimate the percentage of total roots infected by mycorrhiza, 30 estimates were made. Soil was sieved to determine the presence of viable VAM spores. Viable spore content in both white and brown sand was high, 40 - 100 spores per 250 ml of soil.

4.2.4 Calculations and statistics

The Root Length Ratio (RLR, root length per unit plant dry weight ($m\ g^{-1}$)) and Specific Root Length (SRL, root length per unit root dry weight ($m\ g^{-1}$)) were calculated. Root length was determined with the line-intersect method (Tennant, 1975). The uptake of P by the roots is expressed as the Specific Absorption Rate (SAR_w, $\mu g\ P\ g^{-1}day^{-1}$ or SAR_l, $\mu g\ P\ m^{-1}day^{-1}$) defined as the increase in the P content of the plant per unit time and either root dry weight (SAR_w or root length (SAR_l):

$$SAR = \frac{(\ln P_1 - \ln P_0)}{(t_1 - t_0)} \times \frac{P_1}{R_1}$$

where R_t is the dry weight (g) or length (m) of the roots and P_t is the total amount of P (μg) in a plant at time t. Relative Growth Rate (RGR, $mg\ g^{-1}day^{-1}$) was calculated as:

$$RGR = \frac{\ln W_1 - \ln W_0}{t_1 - t_0} \times 1000$$

where W_t is total plant dry weight of the plant (g) at time = t.

Data were analyzed with the SAS statistical package (SAS, 1988). To compare differences between species a two way ANOVA and within species a one way ANOVA was used. If differences were found to be significant, the species or treatment rank order was determined using Tukey's Studentized Range Test. A comparison of regression lines was made with an analysis of covariance (Sokal and Rohlf, 1981).

4.3 Results

4.3.1 Morphology and mycorrhyzal infection of roots

In all the treatments, the ruderal species, *C. obtusa*, and the large-gap species, *G. glabra*, produced more root length per unit root dry weight (SRL) than the small-gap species, *C. adiantifolia* (Fig. 4.1a). The latter also had the lowest root weight ratio (RWR, Fig. 4.1b). Because of its lower SRL and lower RWR, *C. adiantifolia* also had the lowest root length ratio (RLR, data not shown). Only when grown on brown sand minus P, *G. glabra* had a higher SRL and higher RWR, and consequently a higher RLR than *C. obtusa* (Figs 4.1a and 4.1b). In the present work no detailed measurements were made on root hairs, but visual inspection of roots showed that *C. obtusa* and *G. glabra* had many and very long root hairs in contrast to *C. adiantifolia*.

Growth of the seedlings in the 'mycorrhiza' experiment was less than in the first experiment, possibly because substrates appeared to have a very low pH (pH($CaCl_2$) of white sand was 2.9) or high Al content (16.8 mg kg^{-1} in brown sand soil solution). Despite this difference in growth, the data on mycorrhizal infection rates are presented in this paper, because such data on tropical rain forest trees are scarce. All species had VA-mycorrhizae (Table 4.2). Although *G. glabra* also had ectomycorrhizae, its total mycorrhizal infection rate is virtually the same as the VA-mycorrhizal infection rate, because the ectomycorrhizal infection rate was not very pronounced.

In the forest, *C. adiantifolia* had the highest infection rate (90%) of all species, but this decreased in the pot experiment to only 31-36% at the last harvest for unknown reasons (Table 4.2). *C. obtusa* and *G. glabra* had higher infection rates, 54-83%, than the small-gap species, 31-61 (Table 4.2). A high density of arbuscules and vesicles was found within the same cortical area. *C. adiantifolia* had less arbuscules and vesicles, but coiled hyphae were abundant.

Table 4.2. VAM infection percentage of plants (±se) growing in their natural forest habitat (F), brown sand treatment (B) or white sand treatment (W) 11 weeks (B1, W1) and 20 weeks (B2, W2) after planting. Significant differences between species are indicated with different letters.

Species	F	B1	B2	W1	W2
C. obtusa	74 ab 9	63 a 4	81 a 3	74 a 7	83 a 2
G. glabra	65 b 7	76 b 3	54 b 1	65 a 6	79 a 79
C. adiantifolia	90 a 4	40 c 1	31 c 2	61 c 5	36 b 9

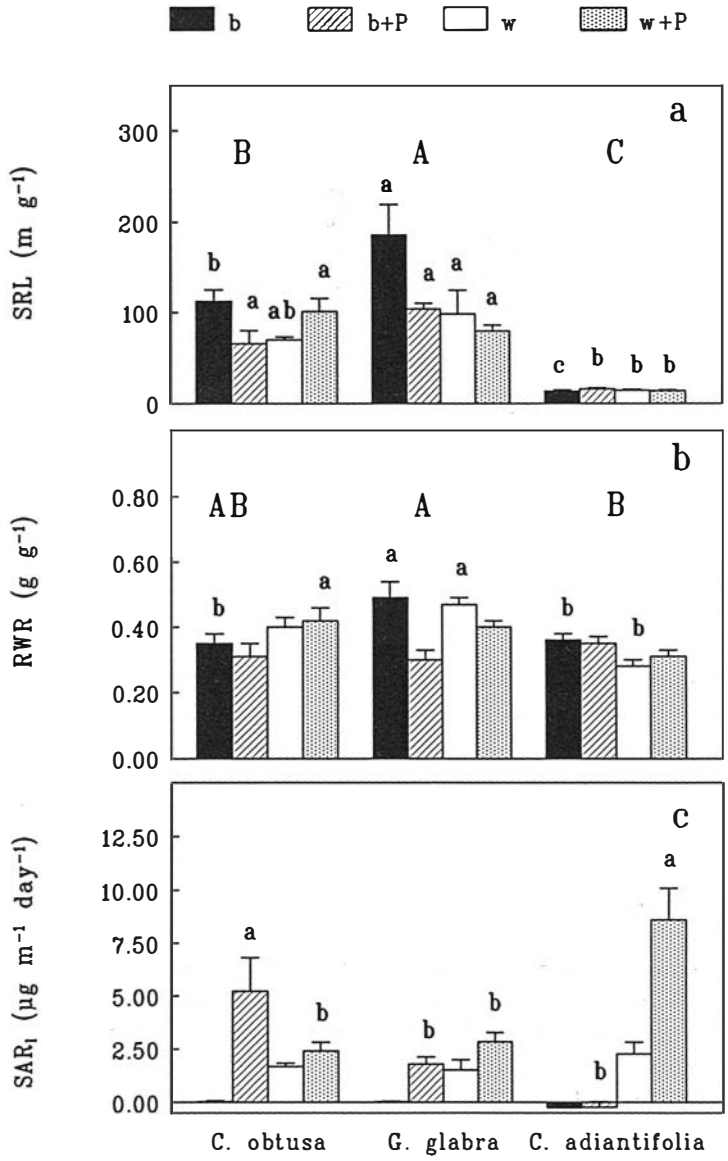

Figure 4.1. Mean (± SE, n=6) Specific Root Length (SRL m g^{-1};a), Root Weight Ratio (RWR g g^{-1}; b), Root Length Ratio (RLR m g^{-1}; c) and Specific Absorption Rate (SAR_I µg(P) m^{-1} day^{-1}; d) for *C. obtusa*, *G. glabra* and *C. adiantifolia* at the final harvest. Species were grown on brown sand (b), brown sand with P (b+P), white sand (w) or white sand with P (w+P). Significant differences ($P<0.05$) between species averaged over treatments are indicated with capital letters, differences between species per treatment are indicated with lower case letters.

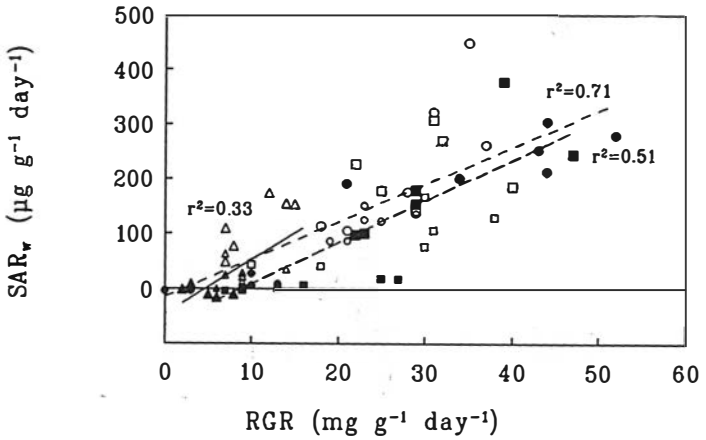

Figure 4.2. Specific Absorption Rate (SAR_w µg (P) g^{-1} day^{-1} versus Relative Growth Rate (RGR mg g^{-1} day^{-1}) for *C. obtusa* (○), *G. glabra* (□) and *C. adiantifolia* (△) growing on brown sand (small closed symbols), brown sand with P (large closed symbols), white sand (small open symbols) or white sand with P (large open symbols).

4.3.2 P-uptake of roots

Averaged over the four treatments, the species did not differ in P-uptake expressed per unit root length (SAR_l; Fig. 4.1c). In general, the SAR_l increased with increasing availability of P in the soil. The high SAR_l of *C. obtusa* grown on brown sand plus P fertilizer strongly contrasts with the SAR_l of *C. adiantifolia*, which was close to nil, while *G. glabra* showed an intermediate response (Fig. 4.1c). This suggests that *C. obtusa* has a physiological mechanism allowing P-uptake from a substrate which binds P rather strongly, which is less pronounced in *G. glabra* and lacking in *C. adiantifolia*.

When expressed per unit root weight, P-uptake was less for the slow-growing *C. adiantifolia*, than for the faster-growing *C. obtusa* and *G. glabra*, which reflects the difference in SRL between the species. However, all species showed a similar positive relationship between SAR and RGR; slopes were not significantly different (Fig. 4.2).

4.3.3 Growth and P concentration

The RGR of the small-gap species, *C. adiantifolia*, was very low; 6 to 10 mg g^{-1} day^{-1}. Both *C. obtusa* and *G. glabra* reached much higher RGRs; up to 40 mg g^{-1} day^{-1}, except in the brown-sand treatment minus P, where the RGR was 4 and 16 mg g^{-1} day^{-1}, for *C. obtusa* and *G. glabra*, respectively (Fig. 4.3a). Sand

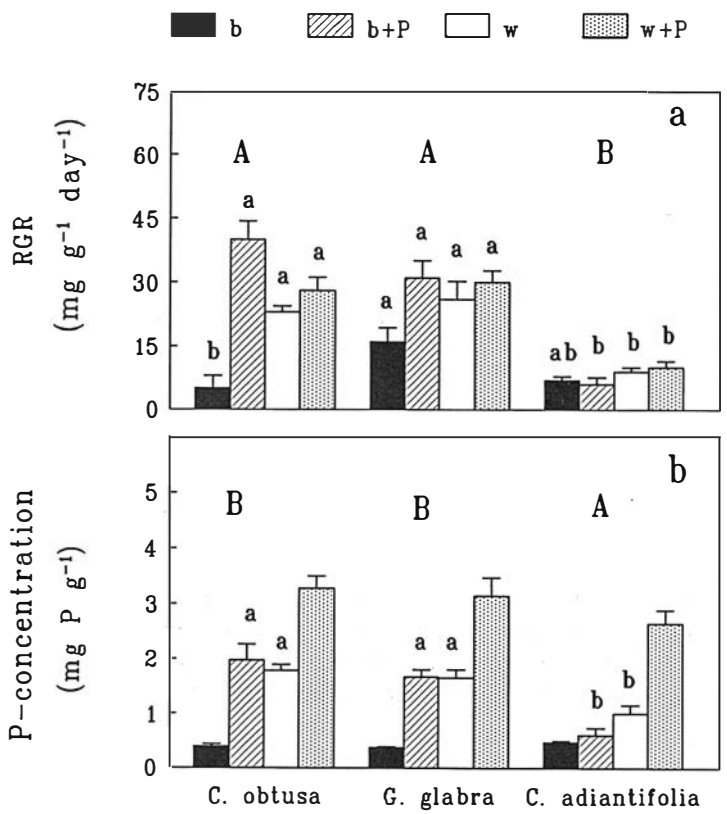

Figure 4.3. Mean (± SE, n=6) Relative Growth Rate (RGR mg g^{-1} day^{-1}; a) and P concentration (mg (P) g^{-1}(DW); b) for *C. obtusa*, *G. glabra* and *C. adiantifolia* at the final harvest. Species were grown on brown sand (b), brown sand with P (b+P), white sand (w) or white sand with P (w+P). Significant differences ($P<0.05$) between species averaged over treatments are indicated with capital letters, differences between species per treatment are indicated with lower case letters.

splash, caused by rain, most strongly affected *C. obtusa* and *G. glabra* seedlings growing on brown sand minus P. Their relatively large leaves, positioned close to the soil surface, made them more vulnerable to sand splash than the other species. This sand splash might partly explain the low RGR of *C. obtusa* and *G. glabra* on brown sand minus P. Leaves of seedlings grown with P soon reached a height where they were less affected by sand splash.

Averaged over the four treatments, *C. adiantifolia* had a slightly lower P-concentration than the other two species. However, the range of P concentrations

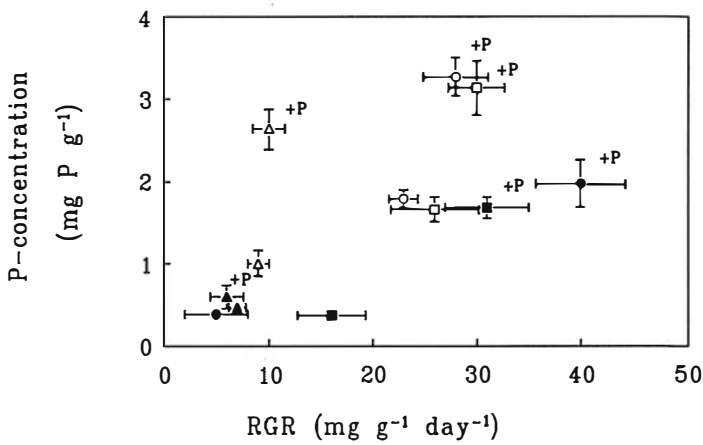

Figure 4.4. Mean (± SE, n=6) P concentration (mg(P) g^{-1}(DW)) versus Relative Growth Rate (RGR mg g^{-1} day^{-1}) for *C. obtusa* (○), *G. glabra* (□) and *C. adiantifolia* (▽) growing on brown sand (closed symbols), brown sand with P (closed symbols +P), white sand (open symbols) or white sand with P (open symbols +P).

was similar for the three species (Fig. 4.3b). When the availability of P was relatively high (white sand plus P treatment), P concentration was relatively high, and vice versa (brown sand minus P treatment). A low P concentration coincided with a low RGR, but the highest P concentrations did not coincide with the highest RGR's (Fig. 4.4).

4.4 Discussion

4.4.1 Differences in P-uptake

Species have adapted to infertile soils by an enhanced capacity to extract nutrients from soil through fine roots (Junk and Barber, 1974) and/or mycorrhizal associations (Bolan, 1991). The higher RLR of *C. obtusa* and *G. glabra* compared to that of the small-gap species *C. adiantifolia* was mainly due to a higher SRL (Fig. 4.1a), the RWR's of the three species were rather similar across all treatments (Fig. 4.1b). A high SRL usually correlates with a small mean root diameter and vice versa (Fitter, 1985). It depends on differences in % dry matter in root fresh weight between the species, whether the SRL can be taken as a measure of the root diameter. Since the % root dry matter only varied by a factor of 2, we conclude that the 5 to 10 times higher SRL of *C. obtusa* and *G. glabra* was mainly due to a larger investment of root biomass in fine roots (Fig. 4.1a).

All three tree species have the ability to form VAM associations (Table 4.2). The genus *Cecropia* was already mentioned by St John et al. (1983) in a list of mycorrhizal plants. For *G. glabra* no information about its mycorrhizal associations was found in the literature. This species has both types of mycorrhizae, EM and VAM. *C. adiantifolia*, belonging to the Caesalpinioideae, was expected to be an ectomycorrhizal species (Högberg, 1990), but no ectomycorrhizal associations were found in this experiment. Assuming that mycorrhizal infection rates in the two experiments were similar, the higher mycorrhizal infection rates of *C. obtusa* and *G. glabra* (Table 4.2) did not result in a higher uptake of P per unit root length on brown and white sand compared to *C. adiantifolia* (Fig. 4.1c).

The P-uptake per unit root length was similar for the three species grown on white sand (Fig. 4.1c.). Contrary to the other species, *C. adiantifolia* did not have a higher SAR_l and P concentration when P-fertilizer was added to brown sand. We have two hypotheses for the low SAR_l of *C. adiantifolia* in this treatment:

(i) *C. adiantifolia* possibly lacks a physiological mechanism, allowing P-uptake from a substrate which binds P rather strongly, e.g. exudation of chelating compounds. Such a mechanism might be less pronounced in *G. glabra* and would explain the high SAR_l of *C. obtusa* in the brown sand plus P treatment. Alternatively,

(ii) A major growth-limiting factor, e.g. aluminium toxicity (Chapter 3) might play a more important role for growth of *C. adiantifolia* on brown sand and thus have resulted in a SAR_l close to nil.

The P uptake per unit root weight is the product of the SAR_l and the SRL. Since, except for the brown sand plus P treatment, the SAR_l was similar for the three species, interspecific variation in P uptake per unit root weight, SAR_w, was mainly due to differences in SRL (Table 4.3).

4.4.2 Differences in growth and P utilization

In their early growth phase seedlings of the ruderal *C. obtusa* and large gap species *G. glabra* resemble each other in P-uptake characteristics, growth and P-concentration (Table 4.3). *C. obtusa* and *G. glabra* had a higher SAR_w, accumulated a greater amount of P and had a higher RGR than the small gap species *C. adiantifolia.* (Fig. 4.2). It is unlikely that *C. obtusa* and *G. glabra* grew faster than *C. adiantifolia* because of their higher SAR_w. Rather, the higher SAR_w may be a result of their higher potential growth rate (Lambers and Poorter, 1992). The rate of P-uptake is, at least partly, determined by demand, which results in a strong negative feedback when growth rate is low (Clarkson, 1985).

Table 4.3. Plant characteristics for ruderal species (RS), large-gap species (LGS) and small-gap species (SGS).

	RS/LGS	SGS
SRL	high	low
RWR	=	=
VAM infection	high	intermediate
SAR_l	=	=
SAR_w	high	low
RGR	high	low
P concentration	intermediate	low

While a low concentration of phosphorus in the tissues may be considered indicative for efficient use of P, it will only be so if that tissue is able to function effectively with that low amount of P. P concentrations of the roots were very low for those treatments which yielded a very low and sometimes negative SAR_l; 0.20, 0.37, 0.45 and 0.53 mg(P) g^{-1} (DW) for *G. glabra*, *C. adiantifolia* and *C. obtusa* on brown sand minus P and *C. adiantifolia* on brown sand plus P, respectively. Mulligan and Sands (1988) reported also very low SAR_l-values for 3 *Eucalyptus* species with low root P concentrations. Low P concentrations in roots are likely to be associated with low levels of phospholipids and increase leakage of metabolites from the root cells (Ratnayake et al., 1978). These plants may have been close to critically low phosphorus concentrations (Fig. 4.4). Thus P concentration has to be viewed in relation to growth and survival; a low P concentration might point to poor functioning.

All species had the ability to take up phosphorus in excess of immediate growth requirements (Fig. 4.4). The high P concentrations on the white sand plus P treatment are most likely due to luxury uptake, and result in a low efficiency of P utilization (Figs 4.3b and 4.4). Meanwhile the characteristic to take up P in excess of immediate requirements may be ecologically important for long-term survival of species in a P-poor environment, since in their natural habitat nutrients become available largely during pulses of mineral release of organic matter (Chapin and Bieleski, 1982).

4.4.3 Ecological consequences

Chapin et al. (1986) suggested that there would be a strong selection for a high phosphate uptake rate in plants adapted to relatively fertile soils, but not in plants adapted to infertile soils. The seedlings of *C. adiantifolia*, growing naturally in the forest understorey, had a low SRL, SAR_w, RGR and P concentration (Table 4.3), and did not adjust their SRL in response to P-availability (Fig. 4.1a).

In the understorey, light might be more limiting for seedling growth than P availability. A root system with a high SRL might have a high turnover rate (Boot, 1990); it might well take more P for production of new roots than returns under these circumstances (Lambers and Poorter, 1992). Next to a higher longevity, roots with a low SRL may also have an advantage over roots with a high SRL in terms of a higher resistance to mechanical and herbivore damage and a better anchoring (Boot, 1990). Slowly growing species, which absorb nutrients slowly, are less likely to exhaust available soil nutrients (Chapin, 1980). Tree seedlings with a low RGR and P concentration can survive a relatively long period of time, pending the chance to become a mature tree, i.e. the occurrence of a small gap.

When disturbance creates a gap, seedlings from infertile soils may experience (at least temporarily) an increased nutrient availability. The larger the gap, the lower the competition for P from surrounding mature trees, which in turn will lead to a relatively higher availability of P per seedling. The species mainly adapted to regenerating in larger gaps, *C. obtusa* and *G. glabra*, had a root morphology which allows exploitation of the soil for P. In a large gap, it is important to have a high SAR_w and low investment of biomass in roots, since only fast shoot growth can ensure survival and reproduction in this environment. With the age of a gap competition for light and P will increase. *C. obtusa* and *G. glabra* were able to increase their uptake capacity at low P-availability (brown sand minus P treatment, Fig. 4.1a). This adaptation to a decreasing availability of P and the relatively high SRLs of *C. obtusa* and *G. glabra* favour the competitive ability of these species in a dynamic environment like a large gap. The difference in response of the small-gap species and larger gap species to phosphorus availability is likely to contribute to the success with which these species establish in different forest habitats.

Acknowledgements

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Chapter 5

Response to phosphorus supply of tropical tree seedlings: a comparison between a pioneer species (*Tapirira obtusa* (Benth.) Mitchell) and a climax species (*Lecythis corrugata* Poit.)

with Hans Lambers

Summary

The highly weathered acid sandy soils in Guyana, South America, are very low in nutrients, especially in phosphorus. Earlier experiments demonstrated that P was growth-limiting for some tree seedlings on these soils, but other species, with a very low P concentration, failed to increase their growth in response to a higher P-availability. To investigate this, we measured growth and distribution of biomass and P of a pioneer tree species: *Tapirira obtusa* (Benth.) Mitchell, and of a climax tree species: *Lecythis corrugata* Poit., at 10 levels of P-supply under controlled conditions in a glasshouse. At intervals of 3 weeks, dry weights of plant parts and their phosphorus concentrations were measured.

The pioneer and the climax species took up similar amounts of P, when grown at high P-supply. The pioneer tree *T. obtusa* maintained a low P concentration (0.25 mg g^{-1}), independent of P-supply and used the P taken up to increase growth. At high P-supply it had a low investment of biomass in roots and reached a relative growth rate (RGR) of 40 mg g^{-1} day^{-1}. The climax tree species, *L. corrugata* maintained a low RGR of 10 mg g^{-1} day^{-1} and constant distribution of biomass at all P-supply rates and stored the extra P in a structure between the stem and root derived from the former hypocotyl, which persisted for over 7 months after germination.

The differences in growth and distribution of biomass and P in response to P-supply of the two species are likely to contribute to the establishment of their seedlings in the field. If *L. corrugata* is capable of retranslocating P from the hypocotyl, this storage of P has ecological advantages for long-term survival, which may be more important than growth, under low light conditions and enables it to maintain P-reserves until a gap occurs. In a newly created gap, P availability per seedling increases, and pioneers, with their higher P uptake and growth potential, can benefit from these relatively higher levels of P availability. This is an important advantage in high-light gap environments where the tallest tree seedling is generally the most competitive one.

5.1 Introduction

Acid sandy soils are common throughout the tropics. In Brazil, Venezuela and the Guianas, there are large areas of acid sandy soils derived from parent

rocks such as sandstone, granite and granitic gneiss (Ahmad, 1989). These soils are severely impoverished. In Guyana bleached sandy deposits, locally referred to as white sands, consist of over 95 percent of quartz (Van Kekem et al., 1995). Most of these soils are covered with tropical rain forests. Extremely low leaf P-concentrations of the trees (0.6 mg g^{-1}DW) indicate that P-availability might limit growth of regenerating tree seedlings (Chapter 2). However, the results of a field fertilizer experiment carried out with two climax tree species in these forests indicate that different species have very different responses to P-fertilizer. *Dicymbe altsonii* seedlings increased their relative growth rate (RGR) from 1 to 2 mg g^{-1} day^{-1} after addition of P-fertilizer, but *Chlorocardium rodiei* seedlings remained at a low RGR of 0.4 mg g^{-1} day^{-1} (Chapter 2). The P content in the leaves also remained low with the extra P being stored in stem and roots. Plant communities occupying the most infertile sites are not always the most responsive to nutrient addition (Chapin et al., 1986). The questions now arise: How do different tree species from these P-poor sands respond to P-fertilizer addition and how large is their capacity to increase growth in response to P-fertilizer.

Based on differences in seed germination and seedling establishment, tropical rain forest tree species have been classified as climax species and pioneers (Swaine and Whitmore, 1988). Climax tree species have the ability to regenerate in the shaded understorey of a closed canopy forest. Most timber species in Guyana belong to this group. P-availability per seedling under the closed canopy will be relatively low compared to gaps, due to competition with mature trees. Pioneers require high levels of sunlight for seedling establishment and growth. Consequently, their seedlings and saplings are restricted to openings in the forest: tree-fall gaps, roadsides and logged-over areas. Pioneers have a higher maximum RGR than climax species (Bazzaz and Picket, 1980) and are therefore expected to respond more strongly to P-fertilizer than climax species. With an increase in P-availability less biomass is needed to explore the soil for P and the relative growth rate is expected to increase (Lambers and Poorter, 1992). One pioneer, *Tapirira obtusa* (Benth.) Mitchell, and one climax species, *Lecythis corrugata* Poit., were chosen to study the response in growth and distribution of biomass and P to phosphorus fertilizer.

5.2 Methods

In March 1990, 400 seeds of both the pioneer *Tapirira obtusa* (Benth.) Mitchell and the climax species *Lecythis corrugata* Poit. were collected in the Mabura Hill region in central Guyana (5°18'N 58°42'W). Both species occur mainly on white sands (Albic Arenosols). The mean seed weights (mg DW/seed) were 131 mg for *T. obtusa* and 954 mg for *L. corrugata*. The seeds were transported to

Utrecht, the Netherlands (52°5'N 5°8'E) within a week and sown under glass in germination boxes, at 20° C. After germination, seedlings were transplanted to 10 L pots (16 cm 49) containing silver sand. In the case of *L. corrugata* the smallest and largest seedlings were not used. The water-extractable P concentration of this sand was 3.6 $\mu g\ g^{-1}$; total P concentration was 150 $\mu g\ g^{-1}$. The seedlings were grown with 0, 4, 8, 16, 32, 64, 128, 256, 1024 or 4096 mg P, added as KH_2PO_4 before the experiment started, in a randomized block design, in a glasshouse from March to October 1990, at 70% relative humidity, a temperature of 22 °C (night) to 28 °C (day) with a minimum temperature of 20° C and a light intensity up to 400 $\mu mol\ m^{-2}\ s^{-1}$.

To prevent nutrient limitation, other than by P, all plants received 250 ml of a nutrient solution once a week containing 57 mg $Ca(NO_3)_2 . 4H_2O$, 32 mg KNO_3, 27 mg $MgSO_4 . H_2O$, 0.1 mg $MnSO_4 . 7H_2O$, 0.1 mg $ZnSO_4 . 7H_2O$, 15 µg $CuSO_4 . 5H_2O$, 0.5 mg H_3BO_3, 24 µg $Na_2MoO_4 . H_2O$ and 6 mg Fe EDTA. At the first and final harvest, the pH of the soil was measured potentiometrically in 50 ml of demineralized water containing 20 g of air-dry soil, shaken for 2 hours. For both species and all treatments the pH remained 5.5, which indicates that the supplied nutrients were available for plant uptake. Seedlings were watered when necessary with demineralized water.

Sampling began about 87 and 101 days after sowing for *T. obtusa* and *L. corrugata*, respectively. They were harvested every three weeks, 6 and 7 times, respectively. One plant per species and phosphate level was sampled at each time, so that a regression-approach could be used to calculate the relative growth rate. The regression estimate of the value of any one sample is influenced by all the other samples, rather than only by replicates treated alike. Height of the stem was measured and leaves, stems and roots were dried separately at 70°C for 48 hours and then weighed. *L. corrugata* was divided into 4 parts: leaves, stems, roots and hypocotyl (Fig. 5.1). Dried plant material was digested using a modified micro-Kjeldahl digestion (concentrated sulphuric acid and a catalyst mixture of Se, $CuSO_4$ and Na_2SO_4 in a ratio of 1:1:62, Bradstreet, 1965). Total P was analyzed colorimetrically, using the ammonium molybdate method (Houba et al., 1989). Root length was estimated with the line-intersect method (Tennant, 1975).

For both species, relative growth rate (RGR, mg g^{-1} day^{-1}) was calculated for each phosphate level, from the slope of the linear regression of ln(total dry weight) versus time. The r^2 of the linear regressions varied from 0.77 to 0.98 for *L. corrugata*. *T. obtusa* seedlings grown at 0 and 8 mg P had a very low r^2, 0.23 and 0.33 respectively, but at other P-levels r^2 varied from 0.63 to 0.97. To present data for distribution of biomass and P at high and low P treatment, we combined the data of the three highest and three lowest P levels, respectively.

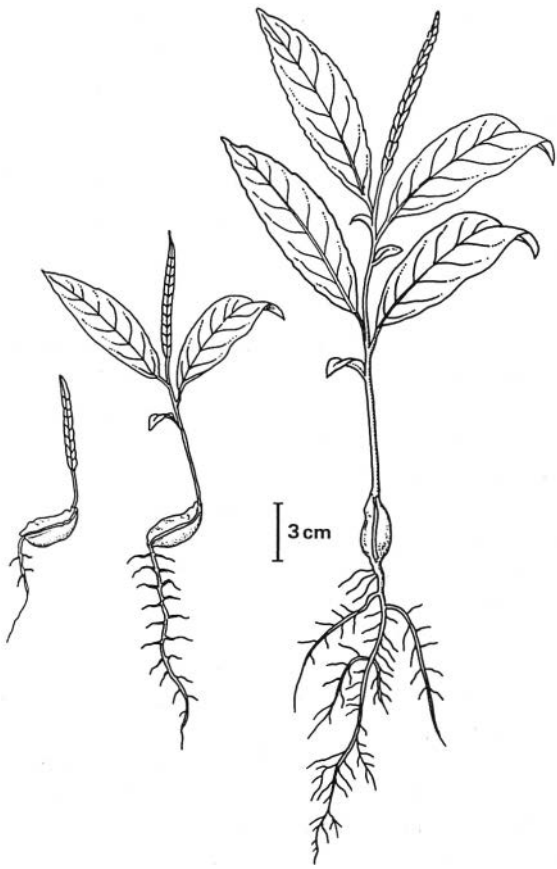

Figure 5.1. Development of a *L. corrugata* seedling 1 week (a) 2 weeks (b) and 5 weeks after germination (c), after Prance and Mori (1979). After 6 months the hypocotyl can still be distinguished from shoot and root.

The data were statistically analyzed using a one way ANOVA procedure for analysis of variance (SAS, 1988) to test differences between treatments within species.

5.3 Results

Seven weeks after sowing, 17% of the *T. obtusa* seeds had germinated; afterwards no more seeds germinated. By that time 62% of the *L. corrugata* seeds had germinated, and within two weeks another 21% germinated. During germi-

Table 5.1. Mean (± ste) Specific Root Length (SRL, m g^{-1}) of *T. obtusa* (192 days after germination) and *L. corrugata* (220 days after germination) grown at low and high P-supply. Differences between treatments within species were not significant).

Level of P-supply mg P $(plant)^{-1}$	*T. obtusa* SRL m g^{-1}	*L. corrugata* SRL m g^{-1}
0 - 8	370 ± 31	206 ± 33
128 - 4096	300 ± 43	255 ± 18

nation of the *L. corrugata* seedlings, the fruit wall (at least the endocarp) as well as the testa persisted around the hypocotyl. This part could still be distinguished from the other parts at the last sampling, 220 days after germination (Fig. 5.1).

Eighty seven days after sowing, seedlings of the pioneer *T. obtusa*, grown at vastly different levels of P-supply, did not differ in total dry weight or dry weight distribution (Fig. 5.2). Total plant P content at a high P level was fivefold that at low P supply (Fig. 5.3). About 100 days after this first harvest, total dry weight of the seedlings grown at high P was more than 15 times (Fig. 5.2) and total P amount more than 30 times (Fig. 5.3) that of seedlings grown at low P. Plants grown at low P invested 48% and 47%, respectively, of their biomass and P in roots, while the plants grown at high P invested 27% and 25%, respectively (Figs 5.2 and 5.3). Root length per gram root dry weight (specific root length, SRL) at high P was not significantly different from low P (Table 5.1). The RGR of *T. obtusa* increased from nil to 40 mg g^{-1} day^{-1} (Fig. 5.4a), with increasing P supply to the plants, but its P concentration did not increase (Fig. 5.4b). The cotyledons were shrivelled or shed at the final harvest.

Total dry weight and distribution of dry weight of the seedlings of the climax species *L. corrugata* was not different across the wide range of P levels at either sampling date (Fig. 5.2), and neither did the Specific Root Length (Table 5.1). Ninety four days after germination, the hypocotyl accounted for 50% of the total biomass; this proportion was reduced to about 18% at the final sampling. By then about half of the biomass was present in the leaves (Fig. 5.2). During the 126 days of the experiment, *L. corrugata* had a RGR of about 11 mg g^{-1} day^{-1} at all levels of P supply (Fig. 5.4a), whilst the P concentration in the biomass increased more than 2-fold with an increase in P supply (Fig. 5.4b). At low P supply there was a difference between the two species' ability to take up P, as shown by the total amounts of P per seedling during the course of the experiment (Fig. 5.3). *T. obtusa* seedlings did not take up P, 164 µg P at t=87 vs 141 µg P at t= 192, whereas *L. corrugata* seedlings increased their amount of total P: 2153 µg P at t=94 vs 3005 µg P at t=220 (Fig. 5.3).

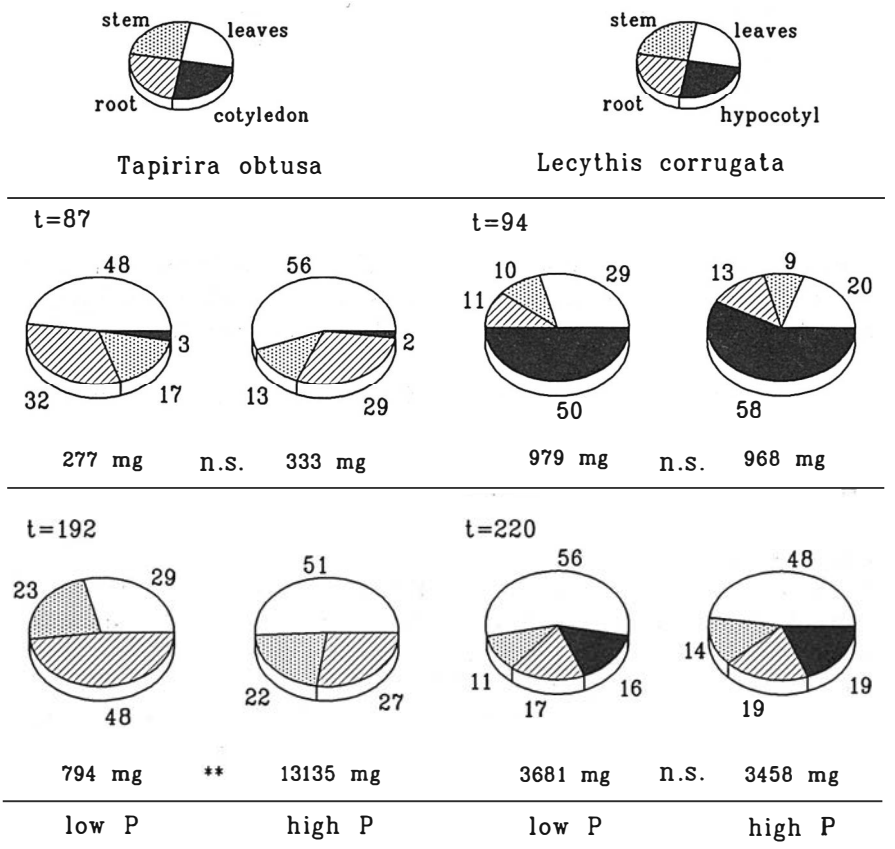

Figure 5.2. Total plant dry weight and biomass distribution of *T. obtusa* (87 and 192 days after sowing) and *L. corrugata* (94 and 220 days after sowing) grown at low P-supply (< 10 mg P per plant) and high P-supply (> 250 mg P per plant). Significant differences between low and high P-supply are indicated by ** ($P<0.01$) and n.s. is not significant.

5.4 Discussion

The pioneer, *T. obtusa*, and the climax tree species, *L.corrugata*, differed in growth and distribution of biomass and P in response to P-addition. Small seeded pioneers, like *T. obtusa* are adapted to an ecological niche which differs from that of the large-seeded climax species; rapid increase in height enhances their chance to fill a gap (Swaine and Whitmore, 1988). The pioneers display a set of traits (short leaf life-span, low specific leaf mass and high photosynthetic

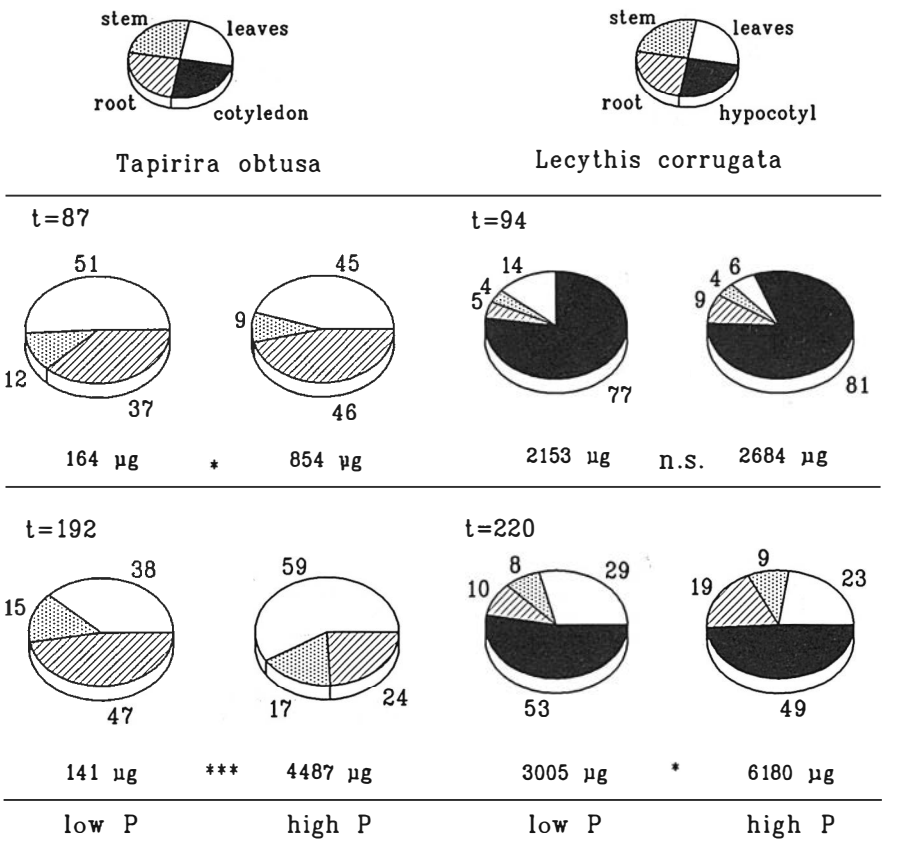

Figure 5.3. Total amount of P and P-distribution of *T. obtusa* (87 and 192 days after sowing) and *L. corrugata* (94 and 220 days after sowing) grown at low P-supply (< 10 mg P per plant) and high P-supply (> 250 mg P per plant). Significant differences between low and high P-supply are indicated by * ($P < 0.05$), *** ($P < 0.001$); n.s. is not significant.

capacity) conducive to resource acquisition and rapid growth in high light environments (Reich et al., 1994). Tree fall gaps may not necessarily have any increase in the soil P concentration compared to that in the undisturbed situation (Vitousek and Denslow, 1986), but the available P for seedlings can be expected to be higher due to decreased competition by mature trees. Hence, the increase in light is generally accompanied by increased availability of P per seedling. All the P taken up by *T. obtusa* was used to increase growth, up to 40 mg g^{-1} day^{-1}, whilst the plant P concentration remained low (0.4 mg g^{-1}). Due to the low P

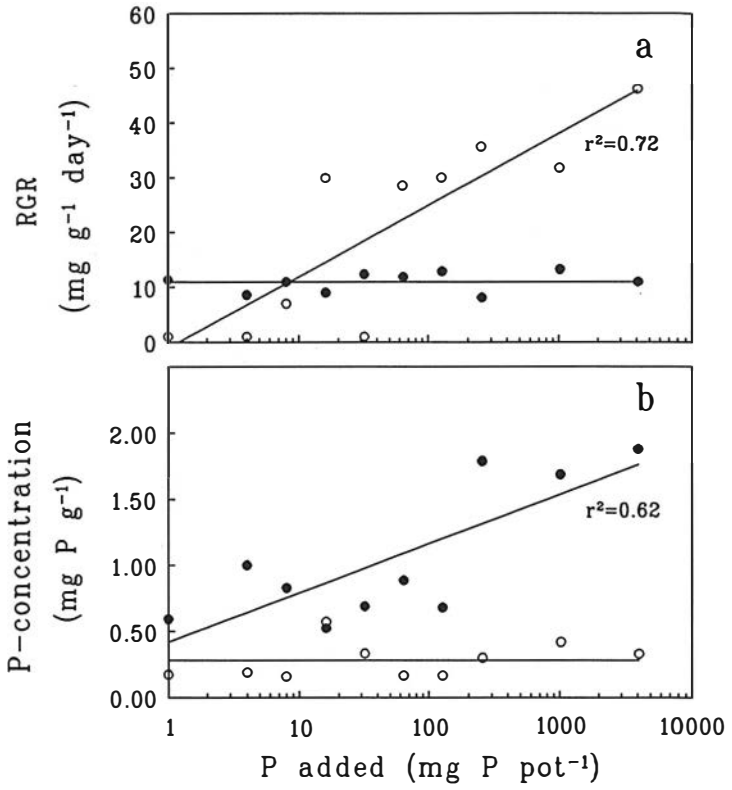

Figure 5.4. Relationship between Relative Growth Rate (RGR, mg g^{-1} day^{-1}, a) and P concentration (mg (P) g^{-1}(plant DW), b) and P added to the plants (mg), for *T. obtusa* (○), 192 days after germination, and *L. corrugata* (●), 220 days after germination. Regression equations: RGR slope for *T. obtusa* = -2.05 + 6.35 x log (mg P added) - 0.08 x (log (mg P added))^2, $p < 0.011$, P concentration slope for *L. corrugata* = 0.42 + 0.16 x log (mg P added), $p < 0.007$. The RGR of *L. corrugata* and P concentration of *T. obtusa* showed no significant relationship with the amount of P added per pot; the lines represent their means.

concentration (Fig. 5.4b), P demand, i.e. growth rate times P concentration in the plant, was not significantly higher for the pioneer than for the climax species *L. corrugata* in this experiment, despite the higher RGR (Fig. 5.4a). Swaine and Whitmore (1988) mention phenotypic plasticity as a characteristic typical of tropical pioneer species. Thus at low P-availability, *T. obtusa* had its highest % biomass invested in the roots (Fig. 5.2 see t=192) which would allow exploration of a somewhat greater volume of soil, but no significant increase in SRL (Table 5.1). This was associated with the retention of a larger proportion of the phosphorus in the roots and did not result in a larger P supply to the shoot (Fig. 5.3). This means that *T. obtusa* can only grow faster than the climax species *L.*

corrugata when the external P supply is relatively high (Fig. 5.4a), e.g. in gap environments.

Although grown with sufficient nutrients, *L. corrugata* had a very low RGR, 11 mg g^{-1} day^{-1}, and showed no change in SRL or distribution of biomass and P over the range of P supply ((Table 5.1 and Figs 5.2, 5.3 and 5.4a). Similar results have been reported for Western Australian tree seedlings from extremely infertile soils by Barrow (1977), who found that *Banksia grandis* did not respond to phosphate addition. He suggested that this lack of response was probably due to an inherently low RGR and large P reserves stored in the seeds of this species. The other 5 species in his study did respond to phosphate, but the time at which the response appeared was affected by seed reserves of phosphorus. Since *L. corrugata* seedlings had a low RGR and relatively large P reserves, they did not respond to phosphate addition with an increase in growth.

Germination in *L. corrugata* has some unusual features described by De Vogel (1979) as the "Barringtonia" type. The embryo is undifferentiated, and at germination the seedling penetrates the seed coat at opposite ends (Fig. 5.1, Prance and Mori, 1979). The hypocotyl is a massive, food-storing body completely filling the fruit wall and testa which persists till long after germination (De Vogel, 1979). The acquisition of P by *L. corrugata* seedlings exceeded the input of P into growth (Fig. 5.4b); P accumulated, mainly in the hypocotyl. This plant part did not increase in dry weight in time, but its total P content increased from 2174 to 2989 µg P for the high P treatments (Fig. 5.3). This suggests that the former hypocotyl is a storage organ; nutrient concentrations in storage organs generally increase more in response to fertilization than do concentrations in vegetative tissues. Phosphorus is usually stored as inorganic phosphate or polyphosphate, and to a lesser extent as ribonucleic acids and phospholipids, depending on the species (Chapin et al., 1990). If the stored P is available for subsequent retranslocation to other plant parts it may have two ecological advantages. Firstly large seed reserves of P are likely to give an advantage in establishing on P-deficient soils; P reserves make the tree seedling independent from external P sources. Thus, to achieve a height and RGR greater than those of *L. corrugata* seedlings with their high P seed reserves, *T. obtusa* seedlings needed external P (Fig. 5.4a). Secondly, P reserves in the seed are likely to be an advantage in recovering from catastrophic events (Chapin et al., 1990). The hypocotyl of *L. corrugata* becomes a woody plant part between root and stem, so that the stored P is protected from herbivory and other damage. Thus the lack of increased growth in *L. corrugata* seedlings in response to P addition is attributed to a combination of a low potential Relative Growth Rate and large reserves of P stored in the former hypocotyl.

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Chapter 6

Photosynthetic rates in relation to leaf phosphorus content in pioneer vs climax tropical rain forest trees

with René Boot, Paul Dijkstra, Sander Pot and Thijs Pons

Summary

In Guyana dense rain forest occurs on intensely weathered acid soils, low in soil phosphorus. To investigate whether low P availability limits photosynthesis of trees growing on these soils more than N does, leaf P and N content, and their relationship with the photosynthetic capacity (A_{sat}, μmol $CO_2.m^{-2}.s^{-1}$) were studied for 9 pioneer and climax tree species in a range of light climates. Light environment was described using hemispherical photographs.

For both pioneer and climax species, leaf P content (r^2 = 0.71 and 0.23, respectively) is a more important determinant of A_{sat} than leaf N content (r^2 = 0.54 and 0.12, respectively). Pioneer species have a higher leaf P and N content than climax species. At similar P or N content, pioneers have a higher A_{sat} than climax species. The studied saplings had a relatively high A_{sat}, considering their low P concentration (15-30 μmol P g^{-1}).

All species studied had a constant leaf P and N concentration and photosynthetic capacity across light climates, because Specific Leaf Mass (g m^{-2}) increased similarly with light availability. This acclimation to a change in light environment makes a possible limitation of A_{sat} by P or N independent of light environment.

6.1 Introduction

The light-saturated rate of photosynthesis (A_{sat}) represents the leaf's capacity to assimilate CO_2, at ambient CO_2-concentrations. It reflects the maximum possible benefits from a given investment in photosynthetic machinery tuned to the constraints of the environment (Field & Mooney, 1986). Whereas A_{sat} in relation to light environment and leaf N content has been studied intensively (Pons, 1977, Field and Mooney, 1986, Chazdon and Field, 1987, Walters and Field, 1987, Evans, 1989 and Reich et al., 1994), there is very little information on the relationship between light-saturated rate of photosynthesis and the leaf's P content for plants growing in their natural environment. In white pine seedlings, grown in forest soils, no relationship was found between A_{sat} and foliar

N whereas A_{sat} and foliar P content showed a positive relationship (Reich and Schoettle, 1988). On P-limited Tierra Firme oxisols, A_{sat} is only weakly correlated with leaf N content in the 23 amazonian tree species measured by Reich et al. (1994). They suggested that this might be the result of P or Ca limitation. Oxisols, which also prevail in our study area, have a low availability of P, and not of N, resulting in very low foliar P concentrations (Vitousek and Sanford, 1986) and low P:N ratios (Chapter 2). The question now arises: Are photosynthetic rates of trees growing on these poor soils limited by phosphorus?

P is an essential macronutrient for photosynthesis, because it is required to produce and export triose-P which is the major photosynthetic product exported from the chloroplast (Stitt, 1990). The level of phosphate in the cytosol of leaf cells regulates photosynthesis and carbon partitioning between the chloroplasts and the cytosol (Rao and Terry, 1989). The CO_2 assimilation rate is very sensitive to P nutrition (Kirschbaum and Tompkins, 1990), with P deficiency limiting the rate of RuBP regeneration (Rao et al. 1986, Jacob and Lawlor, 1992).

Based on regeneration characteristics, rain forest tree species have been classified as pioneer or climax species (Swaine and Whitmore, 1988). Pioneer saplings regenerate in large gaps and generally have a high A_{sat} (Bazzaz and Pickett, 1980). In trees with a high A_{sat}, potential Photosynthetic N Use Efficiency (A_{sat} per unit N) is also high (Field and Mooney, 1986). Climax tree species, whose seedlings can establish and persist in forest shade, have a low CO_2-fixation rate and A_{sat} per unit N, compared to pioneer species (Thompson et al., 1992b and Reich et al., 1994). Analogous to the potential Photosynthetic N Use Efficiency, we can divide A_{sat} by the leaf P content (A_{sat} per unit P) to gain insight into the A_{sat}-P relationship of pioneer and climax tree species. Few data are available about A_{sat} in relation to leaf P content. Reich and Schoettle (1988) hypothesized that when the P:N ratio in leaves is low, both N and P will influence the photosynthetic capacity, because the relative efficiency of nitrogen use in photosynthesis is directly dependent on the availability of other major nutrients, in particular phosphorus. However, their data show a low correlation coefficient between A_{sat} and leaf P concentration.

The present study was carried out with pioneer and climax tree species in a tropical rain forest. Relatively little is known about photosynthesis and nutrient relations for tree species from tropical rain forests. We investigated the extent to which A_{sat} is determined by P and or N content in this forest environment where P is scarcely available. Because of its low availability, P, rather than N, was expected to determine A_{sat}. Saplings were measured at a range of light environments that covered their natural distribution, to test whether the A_{sat}-P or A_{sat}-N

relationships are light dependent. Pioneer and climax species were chosen in this study to investigate whether high-light adapted species differ from low light-adapted species in these relationships.

6.2 Study site and species

The present study was carried out near Mabura Hill in central Guyana (5°18'N 58°42'W). Soils commonly occurring in this region can be classified in two broad groups of oxisols, locally referred to as "white sands" and "brown sands" (Khan et al., 1980). White sands have lower nutrient contents and a better drainage than brown sands (Ter Steege et al., 1993). The study area has a tropical climate with two wet and two dry seasons, but even in the dry season average rainfall does not fall below 100 mm per month (Khan et al., 1980). Annual precipitation averages 2700 mm (Jetten et al., 1993). Air temperatures are about 25°C and relatively constant throughout the year (Khan et al., 1980).

Nine tropical rain forest tree species differing in regeneration strategy were studied. The pioneers *Tapirira obtusa* (Benth.) Mitchell (formerly named *T. marchandii* Engl.; Anacardiaceae), growing on white sands, and *Cecropia obtusa* Trécul (Moraceae) are widely distributed in Guyana (Mennega et al., 1988). *Goupia glabra* Aubl.(Celastraceae) is also widely distributed (Polak, 1992); it regenerates from seed in large clearings, and grows up to a large forest tree as opposed to the other two pioneers that are small trees. *Chlorocardium rodiei* (R.H. Schomb.) Rohwer, Richter and Van der Werff (Lauraceae), a climax tree, up to 45 m high, can be dominant in forests on sandy-loam brown sands and *Mora excelsa* Benth. (Leguminosae), a semi-deciduous tree, 50 m high, is locally abundant to dominant along rivers and creeks (Polak, 1992). *Peltogyne venosa* (Vahl) Benth. (Leguminosae) and *Eschweilera sagotiana* Miers (Lecythidaceae), a co-dominant of *C. rodiei*, are climax species growing on the brown sands. *Eperua falcata* Aubl. (Leguminosae), an evergreen, 35 m high, growing on the white sands, and *Dicymbe altsonii* Sandw. (Leguminosae), found on both types of soils, are also climax species.

6.3 Methods

The examined plants were growing naturally in undisturbed forest and in adjacent logged forest. In the forest selective logging had been carried out and saplings were found in a wide range of light environments. In March 1992, light-saturated rates of net photosynthesis were measured in situ on fully expanded young leaves of 15 saplings of the 9 species mentioned above.

CO_2 assimilation was measured in a Parkinson leaf chamber with a portable infrared gas analyzer (Analytical Development Company Hoddesdon, UK, model LCA2), which is an open system. Photosynthetic light response curves were made to determine light saturation points for sun and shade leaves. Supplemental lighting from a 35 W or 50 W halogen lamp, 500 or 1000 μmol $m^{-2}s^{-1}$, respectively, was used to increase photon flux density (PFD) to the saturation point. The increase in photosynthesis upon an increase in light intensity was monitored until a constant rate was reached (this took 5-15 minutes). The latter was used as a measure of A_{sat}. Air was supplied from plastic containers which were filled outside the forest in case of a high CO_2 concentration inside the forest. Air was not dried before entering the cuvette, resulting in a relative humidity of 70 % or more. Mean leaf temperature was 27° C (range 25 to 30°C), partial CO_2-pressures inside the leaf chamber were 35-40 Pa. Measurements in open habitats were carried out in overcast weather conditions only.

After measuring photosynthesis, the leaf was excised from the tree to determine leaf area, dry weight and P and N content. At the position of the leaf, a hemispherical photograph was made in a horizontal plane, using a camera with a fish-eye lens (Sigma 8 mm f3.5). Canopy openness was calculated from these photographs according to Ter Steege (1993a) and used as a measure of the total daily irradiance (Chazdon and Field, 1987). Canopy openness was defined as the percentage of unobscured sky, weighted for angle of incidence, corresponding to a horizontal plane at the leaf location (Ter Steege, 1993a).

Leaf tissue was dried at 70°C and total P and N content were analyzed with a modified micro-Kjeldahl digestion method, using concentrated sulphuric acid and a catalyst mixture of Se, $CuSO_4$ and Na_2SO_4 in a ratio of 1:1:62 (Bradstreet, 1965). P and N were analyzed colorimetrically, using the ammonium molybdate method (Houba et al., 1989) and the indophenol method (Cataldo et al., 1975), respectively.

Data were analyzed using the procedures GLM and REG of the SAS statistical package (SAS, 1988). A comparison of regression lines was made with an analysis of covariance (Sokal and Rohlf, 1981). When slopes were equal, adjusted means were compared to test differences between species.

6.4 Results

Leaf nutrient content of pioneer species varied from 0.5 to 3.2 (mmol P) m^{-2} and 37 to 196 (mmol N) m^{-2}, respectively (Fig. 6.1a and 6.1b). They were found over a range of 7 - 59 % canopy openness (Fig. 6.2a). The climax species

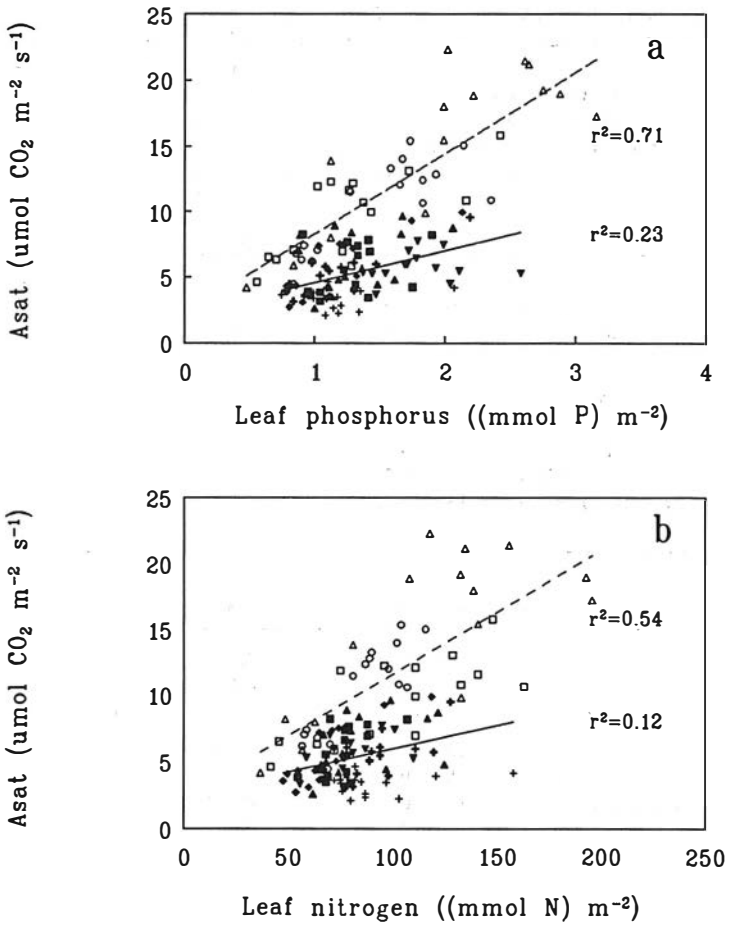

Figure 6.1: Light-saturated rate of photosynthesis (A_{sat}) in relation to nutrient content A. Leaf phosphorus per unit area (slopes = 2.15 + 6.14 x P and = 2.15 + 2.43 x P for pioneer and climax species respectively) and B. leaf nitrogen per unit area (slopes = 2.24 + 0.094 x N and = 2.49 + 0.035 x N for pioneer and climax species respectively) versus A_{sat} for 9 different species.
Pioneer species: *Cecropia obtusa* (Δ), *Tapirira obtusa* (O), *Goupia glabra* (□). Climax species: *Peltogyne venosa* (◆), *Dicymbe altsonii* (▲), *Mora excelsa* (▼), *Eperua falcata* (■), *Eschweilera sagotiana* (✣), *Chlorocardium rodiei* (+).

grew over a smaller range of canopy openness, 2 - 36 % (Fig. 6.2a), and showed less variation in P content, 0.8 to 2.6 (mmol P) m^{-2}, and N content, 46 to 158 (mmol N) m^{-2} (Fig. 6.1a and 6.1b). P and N were highly correlated within species, r^2 varied from 0.56 to 0.88 (data not shown).

Table 6.1: Linear regression statistics and analysis of covariance describing the relationship between A_{sat} (μmol CO_2 m^{-2} s^{-2}(dependent variable)) and phosphorus content ((mmol P) m^{-2}) and nitrogen content ((mmol N) m^{-2}) (independent variables); * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, n.s. = not significant, significant differences between species have been indicated with different letters in separate columns. Differences in slopes or adjusted means (when slopes were not different) for a group of species are indicated in the same column (see section methods).

	P content (mmol m^{-2})						
Sample	n	r^2		slope	y	y_{adj}	
Cecropia obtusa	15	0.71	***	6.14	3.17	12.05	a
Tapirira marchandii	16	0.66	***	5.74	1.97	10.00	abc
Goupia glabra	15	0.54	**	4.59	3.90	10.41	ab
Peltogyne venosa	15	0.72	***	5.15	-0.23	7.05	bc
Dicymbe altsonii	15	0.22	ns	-	-	-	
Mora excelsa	15	0.12	ns	-	-	-	
Eperua falcata	15	0.10	ns	-	-	-	
Eschweilera sagotiana	15	0.56	**	3.73	0.95	6.51	c
Chlorocardium rodiei	15	0.02	ns	-	-	-	
				n.s.		***	
	N content (mmol m^{-2})						
Sample	n	r^2		slope	y	y_{adj}	
Cecropia obtusa	15	0.56	**	0.092	4.19	12.47	a
Tapirira marchandii	16	0.72	***	0.151	-2.38	10.72	ab
Goupia glabra	15	0.53	**	0.063	3.26	8.53	abc
Peltogyne venosa	15	0.75	***	0.109	-1.89	7.30	bc
Dicymbe altsonii	15	0.19	ns	-	-	-	
Mora excelsa	15	0.31	*	0.047	1.92	6.43	c
Eperua falcata	15	0.30	*	0.086	-0.90	6.71	bc
Eschweilera sagotiana	15	0.47	**	0.063	-0.34	5.13	c
Chlorocardium rodiei	15	0.05	ns	-	-	-	
				n.s.		***	

Both pioneer and climax species, demonstrated a positive relationship of A_{sat} with leaf P and N content on an area basis (Fig. 6.1a and 6.1b), this was also the case on a weight basis (data not shown). Pioneer species had steeper slopes than climax species for both relationships ($p < 0.001$, Fig. 6.1a and 6.1b). For the individual climax species these relationships were less pronounced; *Mora excelsa* and *Eperua falcata*, showed no correlation between A_{sat} and phosphorus content and *Dicymbe altsonii* and *Chlorocardium rodiei* showed no correlation with either P or N content (Table 6.1). For the other species, there were no differences in slopes. The pioneer *Cecropia obtusa* had the highest adjusted mean, and the climax tree *Eschweilera sagotiana* the lowest (Table 6.1). On average the pioneers had a considerably higher A_{sat} per unit P (7.8 mmol CO_2 (mol P)$^{-1}$ s^{-1}) and A_{sat}

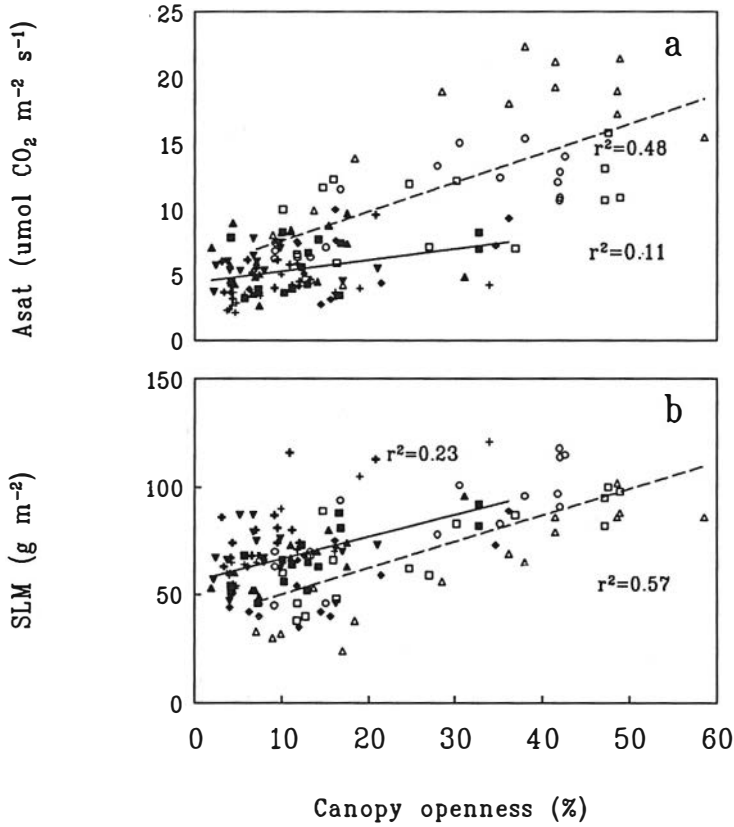

Figure 6.2: Leaf parameters in relation to canopy openness. A. light saturated rate of photosynthesis (A_{sat}, slopes = 5.34 + 0.22 x canopy openness and = 4.40 + 0.09 x canopy openness for pioneer and climax species respectively) and B. Specific Leaf Mass (SLM, slopes = 37 + 1.23 x canopy openness and = 56 + 1.03 x canopy openness for pioneer and climax species respectively) versus canopy openness (%) for 9 species. For species and symbols see legend Fig. 6.1.

per unit N (118 μmol CO_2 (mol N)$^{-1}$ s^{-1}) than the climax species 4.2 mmol CO_2 (mol P)$^{-1}$ s^{-1} and 66 μmol CO_2 (mol N)$^{-1}$ s^{-1}, respectively (Table 6.2).

As for P and N content, A_{sat} also showed a positive relationship with canopy openness (Fig. 6.2a). With an increase in canopy openness, A_{sat} of pioneers increased more than that of climax species, slopes = 0.22 and 0.09, respectively ($p < 0.01$, Fig. 6.2a). Within species, A_{sat} correlated with canopy openness for most species, except for the climax species *Dicymbe altsonii*, *Mora excelsa* and *Eperua falcata* (data not shown). This relationship of A_{sat} with canopy openness was only found on an area basis, because Specific Leaf Mass (SLM) increased

similarly with canopy openness (Fig. 6.2b). The SLM was higher in a more exposed environment as compared to the forest understorey, both for climax and pioneer species. Slopes were not significantly different for climax and pioneer species, but pioneers had lower adjusted means ($p < 0.001$). For the individual species, a similar significant relationship of SLM with canopy openness was found, except for *Mora excelsa* (data not shown). This acclimation to different light climates gave, besides a constant A_{sat}, also a constant amount of P and N per unit leaf weight, for species growing at different light climates. Consequently, the ratios of these parameters, A_{sat} per unit P and A_{sat} per unit N, were also constant across light climates. See for species' averages Table 6.2.

6.5 Discussion

6.5.1 The relation between A_{sat} and leaf P and N

A_{sat} increased with leaf P and N content and canopy openness (Figs. 6.1a, 6.1b and 6.2a). An increase of A_{sat} with canopy openness and leaf N content has been reported before by Field and Mooney (1986), Chazdon and Field (1987) and Ellsworth and Reich (1992). A positive relationship between photosynthesis and P has been found in laboratory studies (Kirschbaum and Tompkins, 1990) and in field experiments with conifers (Reich and Schoettle, 1988), but such a relationship was not found under natural conditions in tropical trees (Tuohy et al., 1991, Reich et al., 1994). The high leaf P contents of the Zimbabwean trees compared to those in our study, 13.3-17.0 and 0.5-3.2 mmol P m^{-2}, respectively (Tuohy et al., 1991, Fig. 6.1a), make it more likely that other factors than P limit photosynthesis in these trees. The study of Reich et al. (1994) was carried out on the Tierra Firme soils of Venezuela, which are comparable to the soils in our study area, also in terms of vegetation and P/N ratio of the leaves. However, their study comprised only climax tree species, and our study showed that the A_{sat}-P relation is less pronounced for climax species than for pioneers (Fig. 6.1a). Our results confirm the contention of Reich and Schoettle (1988), that P limitation may interact with N in controlling photosynthetic capacity.

Differences in A_{sat} of leaves exposed to different light levels may arise from variation in SLM (Reich et al., 1994), N (Walters and Field, 1987, Fig. 6.1b) or P content (Fig. 6.1a). The limitation of A_{sat} by P or N, on the contrary, is independent of light environment, A_{sat} per unit P and N is constant across different light environments (Table 6.2). Trees and shrubs generally have a low potential photosynthetic N use efficiency compared to herbs; Table 6.2 shows mean values of A_{sat} per unit N ranging from 39 to 133 μmol CO_2.(mol N)$^{-1}$.s-1, which is within the range found in the literature (Pons et al., 1994). In contrast to the

Table 6.2: Mean (±se) A_{sat}/N (mmol CO_2 (mol N)$^{-1}$ s^{-1}) and A_{sat}/P (mmol CO_2 (mol P)$^{-1}$ s^{-1}) for 9 species and groups of species. Significant differences between the group of pioneers and climax species are indicated with different capital letters, and between the 9 species with lower case letters.

	n	A_{sat}/N			A_{sat}/P		
		Mean	se		Mean	se	
All species	136	84	3		5.4	0.2	
Pioneer species	46	118	5	A	7.8	0.3	A
Cecropia obtusa	15	133	9	a	8.1	0.5	a
Tapirira marchandii	16	121	6	ab	7.2	0.3	a
Goupia glabra	15	100	7	bc	8.1	0.5	a
Climax species	90	66	2	B	4.2	0.2	B
Peltogyne venosa	15	80	5	cd	4.9	0.3	b
Dicymbe altsonii	15	74	6	d	4.7	0.4	bc
Mora excelsa	15	72	4	d	3.3	0.2	bc
Eperua falcata	15	74	6	d	4.5	0.4	bc
Eschweilera sagotiana	15	59	3	de	4.6	0.3	bc
Chlorocardium rodiei	15	39	3	e	3.1	0.3	c

A_{sat} per unit N, the A_{sat} per unit P for the tree species appears to be relatively high, compared to the few reported data of other studies. From these studies we calculated an A_{sat} per unit P for tropical trees of 0.2-4.1 (Tuohy et al., 1991, Thompson et al., 1992a and 1992b) and for *Pinus* trees of 0.5-2.5 mmol CO_2. (mol P)$^{-1}$.s^{-1} (Reich and Schoettle, 1988, De Lucia and Schlesinger, 1991). The other studies show trees with a similar A_{sat}, but a higher phosphorus content, and thus a lower A_{sat} per unit P. Only *Eucalyptus franeus* had values comparable to that of the Guyanese pioneers, 5.3-9.4 mmol CO_2.(mol P)$^{-1}$.s^{-1} (Kirschbaum and Tompkins, 1990).

6.5.2 Pioneer versus climax species

Climax species were found over a narrower and lower range of canopy openness than pioneers (Fig. 6.2), which is consistent with Swaine and Whitmore (1988) who defined climax species as those whose seeds can germinate and establish in forest shade. Ellsworth and Reich (1992) suggest that these saplings might be susceptible to photoinhibition, at high quantum flux densities. Pioneer species, which have a lower SLM (Fig. 6.2b) and shorter leaf life spans than climax species (Swaine & Whitmore, 1988), were not found at less than 7% openness of the canopy. Perhaps, the production costs of a leaf exceed photosynthetic benefits for pioneer species at low light intensities, in which the rate of CO_2 fixation may be limiting growth. Their leaves, with a low SLM and toughness, are also more vulnerable to herbivory and mechanical damage (Walters et al., 1993).

With changing light environment, pioneer and climax species show a similar response in SLM (Fig. 6.2b). There is hardly any evidence from other studies for differences in plasticity in SLM with respect to light environment between species with low growth rates, like climax species, and high growth rates, like pioneer species (Lambers and Poorter, 1992). Despite the same response in SLM with changing light environment, pioneers show a greater plasticity in leaf P and N content and consequently in A_{sat} on an area basis (Figures 6.1a, 6.1b and 6.2a).

A_{sat}, per unit leaf area or dry weight, of pioneer species was higher than that of climax species (Fig. 6.2a). Because of their steeper slopes, pioneers do also have a higher A_{sat} at similar P or N content (Fig. 6.1a and 6.1b). A low photosynthetic nitrogen use efficiency, as found for the climax species, may be a consequence of a large investment of N in cell walls, specialized cells or compounds that are not associated with photosynthesis. It might also reflect a suboptimal distribution of N between components of the photosynthetic apparatus, or a Rubisco enzyme with a low catalytic capacity (Lambers and Poorter, 1992, Pons et al., 1994). P is not directly involved in the photosynthetic machinery to the same quantitative extent as N. Rather, it is a component of photosynthetic metabolites. So far, the basis for a difference in A_{sat} per unit P between pioneer and climax species is unknown. As for N, the distribution of P over cell compartments and metabolites might differ and/or P limitation may interact with N in controlling photosynthetic capacity.

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Chapter 7

Phosphorus and nitrogen resorption by evergreen trees, differing in leaf turnover rate, on poor sandy soils

with Marion Cambridge

Summary

Resorption efficiency of P and N and their content in fresh and senescent leaves were compared for trees growing on sandy soils which are low in available nutrients, from a rain forest in South America and an open sclerophyll woodland in Australia. Two pioneer rain forest species with short-lived leaves, *Cecropia obtusa* Trécul and *Goupia glabra* Aubl., were compared to two climax species with long-lived leaves, *Chlorocardium rodiei* (R.H. Schomb.) Rohwer, Richter and Van der Werff and *Dicymbe altsonii* Sandw. In the woodland, *Eucalyptus gomphocephala* DC was chosen as a species with shorter-lived leaves and *Banksia menziesii* R. Br. as a species with long-lived leaves.

Within each site, there was no difference in P and N resorption between species, irrespective of leaf longevity. Resorption was high for P (51-82%) in all species, but N resorption of the South American rain forest species was much lower (0-33%) than that of the Australian woodland species (60-73%). *B. menziesii* was most efficient in P and N resorption, 82% and 73%, respectively. In view of the similarity in resorption efficiency, leaf age will be the most important factor determining differences in leaf nutrient losses between species. It is suggested that the high N resorption of the Australian woodland trees may be related to seasonal fluctuations in N availability in this environment, due to summer drought and periodic N losses during fires, respectively.

7.1 Introduction

Impoverished sands support dense rain forest in tropical Guyana, South America, and a species-rich open woodland in south-western Australia. Sands from both sites are critically low in essential nutrients, especially in extractable P, (Foulds 1993, Ahmad, 1989) and N (Khan et al., 1980, Stewart et al. 1993). Extremely nutrient-poor soils pose special problems to plants which they may solve by utilizing normally inaccessible sources of nutrients, efficient internal cycling and/or minimizing the loss of nutrients to the environment (Lamont, 1984). In low nutrient habitats, plants with characteristics which reduce nutrient losses are most competitive (Berendse et al., 1987). Nutrient losses can be decreased by: (1) a low turnover rate of leaves and roots; (2) the synthesis of low nutrient tissues

Table 7.1. Soil, climate and vegetation characteristics for the South American (SA) and West Australian site (WA). ([a]Data from Ahmad, 1989; [k]Khan et al., 1980; [f]Foulds, 1993 and [v]Van Kekem et al., 1995)

Characteristic	unit	SA	WA
Soil			
N content	$\mu g\ g^{-1}$	30-340[v]	17-44[f]
P content (available)	$\mu g\ g^{-1}$	4-6[a]	1-12[f]
K content	$\mu g\ g^{-1}$	100[a]	25-40[f]
Climate			
Average rainfall	mm $year^{-1}$	2700[k]	700[f]
Average temperature	°C	25[k]	15-30[f]
Vegetation			
Canopy	closed	very open	
Specific Leaf Area	$m^2\ kg^{-1}$	11-14	3-5
N concentration	$mg\ g^{-1}$	17.1	8.3
P concentration	$mg\ g^{-1}$	0.6	0.7
K concentration	mgg^{-1}	6.1	9.0

e.g.(woody) stems; (3) an efficient resorption of limiting nutrients from senescing tissues (Aerts, 1990).

Nutrient resorption is the process by which plants withdraw nutrients from senescing leaves, and other organs, making nutrients available for later investment in new structures (Pugnaire and Chapin, 1993). This increases the (re-)use of absorbed nutrients and reduces dependence on soil nutrient supply. The macronutrients P, N and K are generally resorbed in substantial proportions; other ions are removed in much smaller proportions, whereas calcium, due to its low mobility in the phloem and immobilization in cell walls, is not removed at all (Jonasson, 1989). Escudero et al. (1992) have shown that variation in leaf longevity between species contributes more to differences in nutrient losses between species than resorption does. However, on nutrient poor soils, a species with a high leaf turnover rate may compensate the resulting high losses by increased nutrient resorption, in order to compete with a co-occurring species with a low leaf turnover rate.

To test this hypothesis P and N resorption were compared for tree species with relatively short-lived and long-lived leaves. In Guyana, South America, these comprised the classic categories of pioneer species which regenerate in gaps, and climax species, which gradually exclude the pioneer species during succession. Pioneer trees, like *Cecropia obtusa* and *Goupia glabra*, have a high leaf turnover rate (Bongers and Popma, 1988, Boot, 1994) in comparison with climax species which have a higher investment in woody tissue (Swaine and Whitmore,

1988). Of the climax species *Dicymbe altsonii* almost 60% of the leaves persisted for more than 2 years on the branches in a field experiment (Raaimakers and Boot, unpublished data). In the Australian sclerophyll woodland, with frequent fire and subsequent recovery of many of the individuals in the vegetation, categories such as "pioneer" and "climax" cannot be so readily applied, but there are clear differences in leaf turnover rates between species. *B. menziesii* may hold its leaves for 3 years or more, whereas *Eucalyptus* leaves have shorter life spans; 1 to 2 years (Rogers and Westman, 1981). The sites in South America and Australia differ in many aspects, particularly in climate and vegetation but share extremely depauperate sandy soils. We tested whether P and N resorption differed between the species with contrasting leaf longevity at the two nutrient poor sites with widely different growth conditions.

7.2 Methods

7.2.1 Study sites and species

The study sites were located in South America and Australia. The South American site, near Mabura Hill in central Guyana (5°18'N 58°42'W), has infertile soils which are classified as Arenosols and Ferralsols (Van Kekem et al., 1995). These soils (mainly quartz-rich sand), locally referred to as "white sands" and "brown sands" (Khan et al., 1980), were deposited in the late Pliocene to early Pleistocene (Jetten, 1994). Both sands are low in nutrients (Table 7.1; Ahmad, 1989) and support dense rain forest up to 45 m in height (Ter Steege et al., 1993, Van Kekem et al., 1995). The climate is tropical with two wet and two dry seasons. Annual precipitation averages 2700 mm (Jetten et al., 1993) and even in the dry season average rainfall does not fall below 100 mm per month (Khan et al., 1980) Air temperatures are about 25°C and relatively constant throughout the year (Khan et al., 1980).

The Australian site, Bold Park Reserve in Perth, West Australia (33° S, 115° E) comprised an open sclerophyll woodland (Table 7.1) dominated by Tuart (*Eucalyptus gomphocephala*) up to 10 m in height and several species of smaller *Banksia* trees and undergrown with a dense species-rich understorey, including nitrogen-fixing species. Tuart trees tend to be specific to areas with deep sands above a limestone layer or pinnacles, leached from the overlying sands. The infertile sandy soils are derived from the Spearwood dune system of Pleistocene age, 2-3 km inland from the present coastline (McArthur and Bettenay, 1960). The deep sandy soils are mostly acidic and may have iron-coated grains, heavily leached and depleted in macro- and micro-plant nutrients. The climate is defined as Mediterranean with an average rainfall of 700 mm, most of which falls during

the cool moist winters from April-October. Summers are warm and dry with almost no precipitation for 3-4 months.

In the tropical rain forest, saplings up to 7 m tall were sampled from gaps. The pioneer *Cecropia obtusa* Trécul (Moraceae) is widely distributed on white sands in Guyana and matures to form a small tree up to 20 m (Mennega et al., 1988). The second pioneer species *Goupia glabra* Aubl. (Celastraceae) is also widely distributed (Polak, 1992), regenerating from seed in large clearings to form a large forest tree on brown sands. *Chlorocardium rodiei* (R.H. Schomb.) Rohwer, Richter and Van der Werff (Lauraceae), is a climax tree, up to 45 m high, and can be dominant in forests on sandy-loam brown sands. *Dicymbe altsonii* Sandw. (Leguminosae), also a climax tree can be dominant on white sands (Ter Steege et al., 1993).

At the Australian site, *Eucalyptus gomphocephala* DC (Myrtaceae) up to 10 m in height, and *Banksia menziesii* R. Br. (Proteaceae) up to 5 m, were sampled from open woodland, using where possible adjacent trees of each species. No data are available for growth rates of *E. gomphocephala* but the eucalypts are considered as fast-growing trees. *B. menziesii* has a low relative growth rate (Barrow, 1977).

7.2.2 Leaf sampling and analysis

Leaves from 7 saplings of each South American species were collected during February 1993 and from 5 trees of each Australian species in October 1993. Per tree four sets of fresh leaves were taken differing in leaf age. With the exception of *Banksia menziesii*, leaf age could not be determined but the relative age, class 1 - 4, was derived from the growth habit of each species. Class 1 comprises the youngest fresh leaves and class 4 the oldest. Leaves from *B. menziesii* could be aged into year classes on the basis of markings on the woody stems, as a result of the highly seasonal growth pattern over a limited period during late spring and summer (Nov.-Dec.). Leaves of *E. gomphocephala* could not be divided into 4 age classes, so only fully expanded young leaves (class 1) and more mature but still green leaves were collected (class 2) from two different branches. Senescent leaves of all species were collected where possible by picking dead leaves which had not abscised by gently shaking the branches. *G. glabra* saplings did not develop "visible" senescent leaves, as green leaves blackened and fell within one day, so nets were used to collect fallen leaves daily.

Leaf area and dry weight of leaves were measured. Leaf tissue was dried at 70°C for 48 h and total N and P content were analyzed with a modified micro-Kjeldahl digestion method, using concentrated sulphuric acid and a catalyst mix-

ture of Se, $CuSO_4$ and Na_2SO_4 in a ratio of 1:1:62 (Bradstreet, 1965). P and N were analyzed colorimetrically, using the ammonium molybdate method (Houba et al., 1989) and the indophenol method (Cataldo et al., 1975), respectively.

Pool size of resorbed P and N was calculated per unit of leaf area, because mass-based data are misleading when significant amounts of leaf mass are lost during senescence (Pugnaire and Chapin, 1993). If differences in nutrient content between fresh and dead leaves were significant, the percentage of nutrient resorption was calculated per sapling, by expressing the nutrient pool of the senescent leaves as a percentage of the largest nutrient pool found in green leaves.

7.2.3 Statistical analysis

In testing for differences in P and N content between species, dead leaves were excluded from calculations. The data were statistically analyzed using the General Linear Models procedure for analysis of variance (SAS, 1988) to test differences in nutrient content and resorption between species, leaf age classes and sites. If differences were found to be significant, the species rank order was determined using Tukey's Studentized Range Test.

7.3 Results

Leaf tissue, collected from the Australian site had a higher P content, on an area basis, than tissue from the South American site ($p<0.0001$). The Australian *E. gomphocephala*, with short-lived leaves, had the highest P content of all the species (230 mg m^{-2}), whereas *B. menziesii* (100 mg m^{-2}) had only slightly higher values than most South American rain forest species (Fig. 7.1a). Of the rain forest trees, the pioneer *C. obtusa* had the highest P tissue content, 800 mg m^{-2}, *D. altsonii*, *C. rodiei* and *G. glabra* had the lowest content, 40-50 mg P m^{-2}. Both Australian species had similar N contents (mean of 2200 mg m^{-2}), with the N values slightly higher ($p < 0.0001$) than those of the South American species (Fig. 7.1b). Of the tropical pioneers, *C. obtusa* had a higher N content, but *G. glabra* had values similar to those for climax species (Fig. 7.1b).

Nutrient (N and P) content of living leaves were similar for all age classes (1-4, Fig. 7.1a and 7.1b). P content in dead leaves was significantly lower than in fresh leaves, for most species (Fig. 7.1a). The difference in N content between fresh and dead leaves was significant for both Australian species, but not for the South American species with the exception of *D. altsonii* (Fig. 7.1b). So, for *C. obtusa*, *G. glabra* and *C. rodiei* there was no N resorption (Table 7.2). Within each site, there were no differences in P and N resorption, irrespective of whether

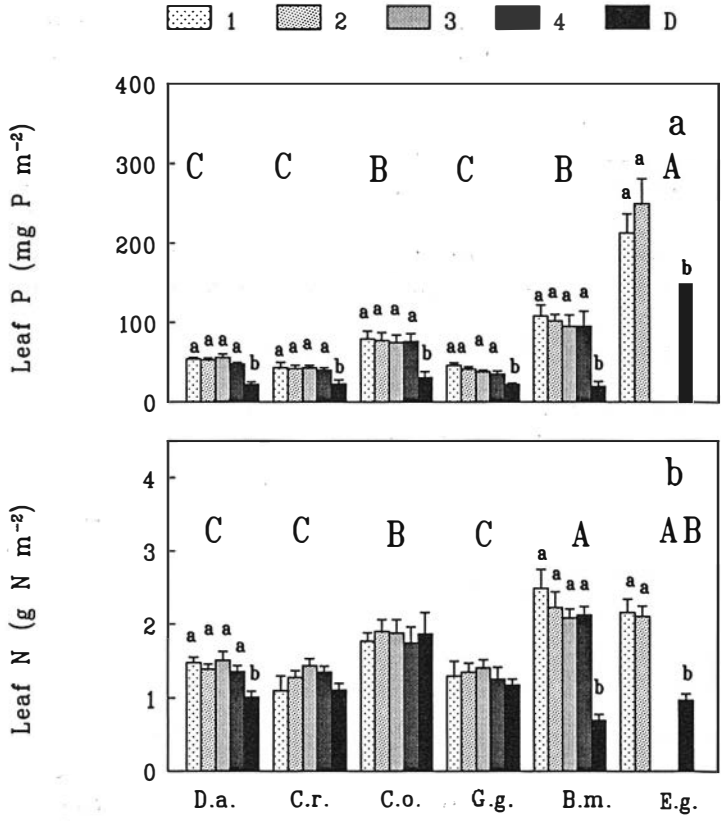

Fig. 7.1 :Mean leaf (± se) P (a) and N (b) content (mg m^{-2}) for 4 South American species (n=7): *G. glabra* (G.g.), *C. obtusa* (C.o.) , *D. altsonii* (D.a.) and *C. rodiei* (C.r) and 2 Australian species (n=5): *B. menziesii* (B.m.) and *E. gomphocephala* (E.g.) of 5 successive leaf age classes (1 young - 4 adult and dead (D)). Differences in nutrient content of fresh leaves between species are indicated with capital letters, differences within species with lower case letters, no letters indicates that no significant differences were found between leaf age classes within a species.

they had short and long-lived leaves. All species were efficient in the resorption of P (51-82%) and differences between sites in P resorption were very small (Table 7.2.). However, the Australian species showed a much enhanced resorption of N (61-73%), in comparison to the South American species (up to 33%, Table 7.2). Of all the species examined, *Banksia menziesii* was most efficient in the resorption of P and N; 82% and 73%, respectively (Table 7.2).

Table 7.2. Mean percentage (± se) of P and N resorption for 6 species (*n = 7 for the South American species, °n = 5 for the Australian species). Significant differences between species are indicated with different capital letters.

Species	P resorption		N resorption	
	%	se	%	se
G. glabra *	53.0	4.4 b	0.0	- c
C. obtusa *	63.3	5.9 ab	0.0	- c
D. altsonii *	59.6	7.1 ab	33.3	6.3 b
C. rodiei *	50.8	8.0 b	0.0	- c
B. menziesii °	82.4	3.5 a	73.0	1.7 a
E. gomphocephala °	55.3	6.1 ab	60.6	5.1 a

7.4 Discussion

There were no significant differences in N and P content between living leaves of different ages but significant reductions in N and P content were found when leaves senesced (Fig. 7.1a-1b). Drastic reductions in leaf nutrient concentrations are often found just prior to shedding (Staaf, 1982). The proportion of nutrients resorbed during senescence depends largely on their mobility within the plant, which is in turn determined by their functions and the structure of the molecules they comprise. Contrary to K, which leaches before and during senescence (Staaf, 1982), the reduction of P and N can largely be attributed to resorption (Chapin and Kedrowski, 1983).

Resorption of P is generally high as phosphorus compounds are fairly mobile, with nucleic acids forming the largest mobile organic P pool (Chapin and Kedrowski, 1983). Approximately 66% of the P was resorbed by Amazon rain forest trees (Medina, 1984). Rain forest and woodland species resorbed 51-63% and 55-82%, respectively, of their P before leaf fall (Table 7.2). A substantial portion of leaf P, 29-76% is usually resorbed by mediterranean woody species prior to abscission (Escudero et al., 1992) but only rarely does a species exceed 80% resorption of P, as found here for *B. menziesii*. For most South American rain forest trees there were no differences in N content between fresh and dead leaves. The exception was *D. altsonii* with an N resorption of 33%, a value considerably lower than 43-53% reported for trees from the Amazon (Medina, 1984) and the 55-60 % reported by Reich et al. (1992) as an average for most species. In contrast, the Australian woodland species proved to be highly efficient in the resorption of N (61%-73%).

Despite selecting species with contrasting leaf turnover rates, we found no difference in the resorption of P and N within a site (Table 7.2). The success of a species is not only determined by the amount of nutrients resorbed, but also

by those lost. Evolutionary trade-offs mean that plants cannot combine genotypically determined features which maximize both leaf longevity and nutrient uptake (Aerts and de Caluwe, 1989). Species can allocate resources towards a high photosynthetic assimilation rate for a brief time, or provide resistant physical structures that result in a lower rate of carbon assimilation over a longer time (Reich et al., 1991). Since species with short lived leaves lose more nutrients, they will have a higher nutrient demand per unit time than species with long-lived leaves. The tropical pioneers do indeed have high specific absorption rates (SAR) for P, when expressed on a weight basis (Chapter 4). Eucalypts are also reported to have a high SAR compared to *Banksia grandis* (Barrow, 1977). This implies that species with a high leaf turnover rate will have a higher net biomass increase in early succession (Aerts and van der Peijl, 1993). Since resources usually decrease with time if not chronically disturbed by fire like in the Australian woodlands, species with a short-lived leaves will be replaced by species with long-lived leaves later in succession (Reich et al., 1992).

Due to similar resorption rates, trees with long-lived leaves were more efficient in reducing nutrient losses to the environment than trees with short-lived leaves. For example if leaves of *Banksia* were on average 3 years old, then only 20% of its leaf P would have been lost after a period of 3 years, in contrast with *Eucalyptus* which will lose more nutrients in a shorter time. Comparison with other published results shows similar patterns. The evergreen shrubs *Erica tetralix* and *Calluna vulgaris* also restrict nutrient losses mainly by reducing litter production and apparently not by a high nutrient resorption from senescing plant parts (Aerts, 1990). Numerous authors have reported that the abundance of evergreens increases as soil nutrient availability declines (Escudero et al., 1992); an increase in leaf longevity seems to be the best adaptation to decrease nutrient losses to the environment.

There are two hypotheses about what determines the difference in N resorption between the sites. The first is that N resorption does not seem to be related to N status of a leaf, but more to the form of N compounds present (Pugnaire and Chapin, 1993). Plants with a low N resorption usually have most leaf N structurally bound and less accessible to hydrolysis (Lajtha, 1987) and in plants containing phenolic compounds, protein may be precipitated before protein hydrolysis can occur (Aerts and de Caluwe, 1989). Leaf and shrub tissue collected from nutrient poor Mediterranean soils resorbed 65% of N before leaf abscission, while their soluble N content was relatively high (Pugnaire and Chapin, 1993). Some of this soluble N was thought to represent specific 'stress' proteins of the sort commonly produced in response to pathogens, drought or salt stresses. In the open Australian woodlands drought and fire might be considered to frequently cause stress. But a possible existence of stress proteins in these trees, ac-

cessible to hydrolysis, can only partly explain the difference in N-resorption found between the sites.

The second hypothesis is that nutrient resorption is related to nutrient availability at a site. Although results in literature are not consistent about this point (see Pugnaire and Chapin, 1993), it is argued that a high nutrient resorption is a phenotypic response to low-nutrient environments. Heavily leached sands, extremely depauperate in macronutrients are common to both sites in South America and in Australia. In the Australian woodland, nutrient availability is highly transient on the sandy soils, partly due to the seasonal drying out of the soil profile, especially in the upper layers where specialized roots or microbial symbioses enhancing nutrient uptake are concentrated. Fires consume green foliage and the surface litter, leading to deposition of ash rich in all elements except N, which is mostly lost in the form of ammonia or nitrogen oxides (Pate and Dell, 1984). With the prevalence of fire and the loss of most N from the system, reserves of N must build up again after each fire, from free living N_2-fixing organisms in the soil or in symbiotic associations with plants. In such a system with periodic slow accumulation and sudden loss of N, and consequently a low soil N content (Table 7.1), a high resorption of N is advantageous. This contrasts with the situation in the rain forest, where N losses will be relatively small, and N_2-fixing processes and N retrieval from the thin litter layer via mycorrhiza can proceed undisturbed, resulting in a higher N availability (Table 7.1). Our data support the hypothesis that nutrient resorption is related to nutrient availability of a site.

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Chapter 8

Discussion and summary

8.1 P- and N-availability of the sandy soils

On acid soils, plant growth may be limited by a variety of specific chemical factors and interactions between these. It is not necessarily the low pH per se (i.e. the high H^+ concentration) that limits growth, but rather deficiency and/ or toxicity of minerals. In the forestry belt of Guyana, acid sandy soils, locally referred to as white and brown sands, are very common. They are susceptible to leaching of N, and the availability of P (Chapter 3) is very low. Forests growing on these soils are often dominated by leguminous tree species, which might suggest a low availability of N (Chapter 2). The question, whether the macronutrients N or P limit tree growth on the acid sandy soils of central Guyana, was addressed in Chapter 2.

Various results suggest that N is not limiting for the regeneration of trees. N concentrations of soil (30 - 340 $\mu g\ g^{-1}$) and of leaves of saplings and mature trees (10.9 - 24.5 $mg\ g^{-1}$) were not particularly low compared to values reported for other tropical forest tree species (Chapters 2 and 7). Furthermore, slow release urea fertilizer ($CO(NH_2)_2$) did not increase the growth of *Dicymbe altsonii* saplings and all N-treated *Chlorocardium rodiei* saplings died (Chapter 2). For *Chlorocardium rodiei*, as well as for *Cecropia obtusa* and *Goupia glabra*, no resorption of N from senescing leaves was found; N-resorption for *Dicymbe altsonii* was as little as 33% (Chapter 7). Whereas values reported for Amazonian trees were much higher, varying from 43 to 60% (Medina, 1984, Reich et al., 1992). Assuming that the Guyanese species have the capacity to resorb N, then these percentages, together with the results of the fertilizer experiment, and soil and leaf N concentrations, indicate that N is not the principal factor limiting growth.

P seemed a more likely candidate for growth limitation of regenerating trees. Most leguminous tree species in the Mabura Hill region belong to the subfamily of the Ceasalpinioideae, and most of their seedlings did not have nodules (Chapter 2). Species of this subfamily rarely nodulate and are instead predominantly ectomycorrhizal (Högberg, 1986). This is advantageous for plants when P-availability of the soil is very low (Chapter 2). Thus, the abundance of leguminous tree species in the study area does not necessarily point to N, but more likely to P as a growth limiting nutrient. The low amounts of P taken up by tree seedlings from white and brown sands (less than 8 $\mu g\ g^{-1}$) and low P concentration and P/N ratio of the leaves of saplings and mature trees (0.4 - 1.1 mg g^{-1} and 0.03 - 0.05, respectively) point to a very low availability of P for growth (Chapters 2 and 3). Naturally growing *Dicymbe altsonii* saplings fertilized with superphosphate ($Ca(H_2PO_4)_2.H_2O$) doubled their relative growth rates (Chapter 2) and also pioneer species, grown on brown sand, increased their growth after P-addition (Chapter 3). The P resorption from senescing leaves (51-63%) for Guyanese trees is high compared to N resorption (Chapter 7) and in agreement with the data of Medina (1984) on P resorption of approximately 66% for Amazonian trees. We conclude that in the Mabura Hill region, as on Amazonian ultisols and oxisols (Vitousek & Sanford, 1986), the availability of P is very low, to the extent that it may well limit tree growth.

However, the availability of P is not always the principal growth-limiting factor, since climax species grown on brown sand and climax and pioneer species grown on white sand, did not increase growth in response to P-fertilizer (Chapter 3). Also, naturally growing *Chlorocardium rodiei* saplings did not respond in growth when superphosphate was added (Chapter 2). *Chlorocardium rodiei* saplings might not be capable to increase growth in response to P-addition. Some species, e.g. *Lecythis corrugata* (Chapter 5) and *Banksia grandis* (Barrow, 1977), do not (immediately) respond to phosphate addition. This may be associated with large seed reserves and an inherently low relative growth rate (Barrow, 1977). *Lecythis corrugata* stored P, taken up from the soil, in the former hypocotyl without increasing its low relative growth rate (Chapter 5). The climax species, *Chamaecrista adiantifolia* and *Chamaecrista apoucouita*, did increase their growth when grown with leaf litter (Chapter 3), indicating that a factor other than P was limiting growth. The soils in the Mabura Hill region are extremely acid (Table 1.1). P-deficiency is merely one of the symptoms of the acid soil complex (Marschner, 1991). It often co-occurs with Al toxicity, which might be a factor limiting growth on brown sand, and low pH, which might limit the growth on white sand (Table 1.1, Chapter 3). Thus, despite the low P-availability of white and brown sands, other factors of the acid soil complex might be more limiting for growth of regenerating tree species.

8.2 Pioneer vs climax species in a P-poor environment

Species have adapted to P-poor soils by an enhanced capacity to extract P from soil and/or more efficient use of P (Chapin, 1980, Aerts, 1990). The species studied here, had the capacity to form ecto- and/or endomycorrhizal associations, to resorb 51-63% of their leaf P before abscission of the leaves and to take up P in excess of immediate growth requirements when P-availability (temporarily) increased (Chapters 4, 5 and 7). In line with the low P-availability of the environment, P-demand of these species is low due to a low tissue P concentration and a low relative growth rate (Chapters 2, 4 and 5).

However, within a forest environment with a low P-availability tree species will experience differences in P-availability. When a gap occurs, an increase in light availability is generally accompanied by an increase in P availability per individual (Chapters 1 and 4). The occurrence of gaps within forests has led to the evolution of different adaptive traits for different tree species.

Based on differences in seed germination and seedling establishment, tropical rain forest species have been classified as pioneer and climax species (Swaine and Whitmore, 1988, Chapter 1). All pioneers require full sunlight for seedling establishment and growth, climax tree species can establish and perform in the shade. There is no sharp boundary between pioneer and climax species, and the pioneer *Cecropia obtusa*, used in most comparisons (Chapters 3 to 7), is one of the two extremes in this tree species continuum. It has a high potential relative growth rate and photosynthetic capacity (Chapters 4 and 6) together with the characteristic of low construction costs by producing large leaves supported by sparse branch frameworks, soft tissue and wood with a low density (Bazzaz and Pickett, 1980). To avoid making statements about pioneers in general which in fact only pertain to one exceptional species like *Cecropia obtusa*, growth as well as P-uptake characteristics of *Cecropia obtusa* were compared with the widely branched and long-lived pioneer *Goupia glabra*, which can attain a height of 30 m or more (Chapter 4). The results for these two different pioneers were very similar (Chapter 4) and in the other chapters, the group of pioneer species was not subdivided.

Evolutionary trade-offs mean that plants cannot combine genotypically determined features which maximize both leaf longevity and nutrient uptake (Aerts and de Caluwe, 1989). Pioneer species do not invest in durability but rather in quick use of available resources, effective competition with neighbours, and rapid reproduction (Bazzaz and Pickett, 1980). Their saplings are found at sites with a higher availability of light compared to sites with saplings of climax species (Chapter 6). Recent gaps, with a higher availability of light and P per individual

compared to the undisturbed forest, are most effectively exploited by pioneers. Such species, like *Cecropia obtusa* and *Goupia glabra*, often have very small seeds and hence do not supply P to their seedlings from these seeds (Chapter 2). The P necessary for rapid growth is provided by a finely branched root system (Chapter 4). The high specific absorption rate for P depends upon a high photosynthetic activity since carbon is needed for growth, functioning and maintenance of the roots. The photosynthetic capacity of their leaves, which provide the carbon and energy for their rapid growth, was strongly correlated to leaf P concentration, more than to leaf N concentration (Chapter 6). Pioneer species with a high photosynthetic capacity have a low specific leaf mass (Chapter 6) and consequently short leaf life spans (Bongers and Popma, 1988, Boot, 1994). Their P losses from the leaves to the environment are high compared to those of climax species, despite a high P resorption (Chapter 7). Like leaves, roots are subject to a continuous turnover (Aerts, 1990) and a high specific root length correlates with a high turnover rate which will also result in more losses, including P. If P absorption and C assimilation are not maintained at a high rate, growth rates cannot be supported by recently acquired P and C and must go at the expense of reserves (Chapter 4). Moreover, species like *Cecropia* maintain a high turnover rate irrespective of light environment (Bongers and Popma, 1988). Seedlings with a relatively high turnover rate of leaf and root tissue will not succeed in maintaining a positive C and P balance when carbon and phosphate availability are low, i.e. in the forest understorey.

The forest understorey is most successfully occupied by seedlings of climax species. They pass C and P reserves to their seedlings via large seeds (Chapter 2) and so keep the whole-plant carbon and P balance positive under very low light conditions, pending the occurrence of a (small) gap (Boot, 1994). Their seedlings maximize P acquisition primarily by maintaining a long-lived root biomass with a low Specific Root Length (Chapter 4); a higher specific absorption rate would provide little advantage as long as light is limiting. The low relative growth rate and the capacity to resorb large quantities of P before leaf abscission reduce leaf P losses to the environment (Chapters 4 and 7). These seedlings accumulate P in stem and roots (Chapter 2) or the former hypocotyl (*Lecythis corrugata*, Chapter 5). This enables the climax seedlings to maintain nutrient reserves until a (small) gap occurs. Then they have an advantage over pioneer species which still have to germinate and depend on external P and C sources for their growth. It will depend on the gap size, i.e. the availability of light and P whether a pioneer seedling will outcompete a seedling of a climax species (Chapter 5).

The strategies of tropical pioneer and climax tree species resemble those reported for fast- and slow-growing species by Poorter et al. (1990). However, in

contrast to fast- and slow-growing herbaceous species, pioneer and climax tree species do differ in their rate of photosynthesis expressed per unit leaf area, also when compared at similar light (and P) availability (Chapter 6). This difference might be related to life form or growth conditions; Poorter et al. (1990) grew their herbaceous seedlings at optimum nutrient supply and a PPFD of 350 μmol m^{-2} s^{-1}.

8.3 Recommendations for further research

This thesis points to the following themes and problems for further work:

1. P is likely to be only one of the growth limiting factors on the acid white and brown sands. Other factors of the acid soil complex, e.g. low pH and Al toxicity, might also have limited growth in the experiments described here (Chapters 2 and 3). The acid soil complex and the interactions of its various factors need further investigation.
2. Leaf litter stimulated the growth of seedlings (Chapter 3). Possible effects of litter on ameliorating soil moisture conditions, mycorrhizal infection rates, nutrient deficiencies or pH and toxicities of Al or other elements, need further investigation. A first attempt was made to investigate the possible influence of litter on mycorrhizal associations and plant growth (Brouwer and Van der Woude, 1994). Unfortunately, this experiment failed, possibly because white sand had a low pH-$CaCl_2$ (2.9) and brown sand a high exchangeable Al content (17 μg g^{-1}).

8.4 Implications for management

The very low P-availability (Chapters 2 and 3) makes the ecosystem vulnerable to disturbance.

1. Extraction of P in biomass should be minimized where possible. Trees killed in refinements should be left to decompose in the forest. Conversion of natural forest to plantations or agricultural land should be discouraged (Ter Steege, 1993c).

Leaf litter stimulates the growth of seedlings (Chapter 3).

2. Disturbance of the litter layer should be as little as possible, to ensure the best regeneration. Skidding distances should be reduced by better planning and the use of winching. The result would be less soil damage, less damage to saplings and less removal of litter (Ter Steege, 1993c).

Greenheart (*Chlorocardium rodiei*), the most important timber species of Guyana, had a very low photosynthetic capacity (Chapter 6) and very low relative growth rate, which could not be increased by the addition of N and/or P fertilizer (Chapter 2).

3. The rate of recruitment and growth of greenheart is too low for large scale exploitation (Ter Steege, 1993c).

At present, Greenheart is considered to be over-harvested (GNRA, 1989), and other timber species need to be considered. The category of long-lived pioneers (e.g. large-gap species such as *Goupia glabra*, Chapter 4) offers good candidates (Denslow, 1987). They have a high rate of substitution, due to their high growth rate, in combination with their tolerance to a wide range of light climates and large adult sizes.

Nutrients leach more easily in a gap as compared to undisturbed forest. In the process of regeneration of a gap, pioneers play an important role in capturing nutrients. They have a larger investment of biomass in fine roots and due to their inherently higher growth rates they will take up more P (Chapter 4) and other nutrients than climax species.

4. Pioneer trees should not be regarded as "weeds" of no economical value; establishment of pioneers in large gaps may decrease leaching losses and facilitate regeneration.

Although P-availability is low, some climax species might not be capable to increase their growth rate (immediately) in response to P-fertilizer; because they store the extra P taken up (Chapter 5). This storage, in combination with a low inherent growth rate, means that a response to P fertilizer, if there is an effect at all, might take several years. Our fertilizer experiment over a period of two years (Chapter 2), was too short to reach a final conclusion about a positive effect of P on growth.

5. A response to P fertilizer of desirable timber species, if there is an effect at all, might take several years.

The previous (see 4) also implies that pioneers, with a large investment in fine roots, will possibly benefit more from fertilizer addition than most timber species.

N is unlikely to limit growth and applied in the form of urea, it caused death of *Chlorocardium rodiei* saplings (Chapter 2).

6. The use of urea fertilizer to promote growth of tree saplings is not to be recommended in the Mabura region.

Samenvatting

Tropenbos-Guyana programma

Het grootste aaneengesloten gebied van tropisch regenwoud bevindt zich in Zuid Amerika: in Amazonia en de Guianas (Guyana, Suriname en Frans Guiana). In Guyana strekt zich ten zuiden van de kustvlakte, over een gebied van ongeveer 2 miljoen hectare, een dik pakket zand uit. Dit pakket is grotendeels begroeid met tropisch regenwoud. De bevolkingsdruk op dit gebied is laag want het is nauwelijks bewoond en slecht ontsloten. De (selectieve) houtkap geschiedde voornamelijk voor de eigen markt.

Een verhoging van de houtexport is van groot economisch belang voor Guyana en de vraag naar tropisch hardhout is stijgende. De druk op het bos is de laatste jaren dus toegenomen. Om de economische en ecologische functies die het regenwoud vervult veilig te stellen, zijn aanbevelingen voor beheer dringend gewenst. Helaas is onze kennis over effecten van houtkap op het regenwoud en (her)groei van tropische bomen beperkt.

In 1989 werd een uitgebreid onderzoeksprogramma opgestart door de Stichting Tropenbos in samenwerking met de Universiteit Utrecht en een aantal Guyanese onderzoeksinstituten. De Mabura Hill regio, zo'n 250 km ten zuiden van de hoofdstad Georgetown, is de lokatie waar dit onderzoek is uitgevoerd. Het gebied is door de regering van Guyana voor enkele tientallen jaren in concessie gegeven aan een houtkapmaatschappij, Demerara Timbers Limited (DTL).

Dit proefschrift behandelt slechts één van de vele studies die in dit kader zijn uitgevoerd. Het beschrijft het onderzoek naar de (her)groei van bomen in relatie tot de beschikbaarheid van voedingsstoffen.

De arme zandgronden van midden Guyana

Het tropisch regenwoud kent een grote verscheidenheid aan levensvormen en soorten. Deze rijkdom aan plant- en diersoorten leeft op een zandpakket dat bijzonder arm is aan voedingsstoffen. De bodemtypes van dit pakket worden plaatselijk wit zand en bruin zand genoemd. Beide zanden zijn erg zuur, vooral in de bovengrond. Het bruine zand bevat veel ijzer en aluminium. Ijzer en aluminium hebben de eigenschap voedingsstoffen, zoals fosfor, aan zich te binden, zodat deze niet of nauwelijks kunnen worden opgenomen door plantenwortels. Het witte zand bestaat voornamelijk uit kwarts (zie voorkant proefschrift). Voedingsstoffen, zoals stikstof, spoelen hier gemakkelijk uit. Eén van de kernvragen van dit onderzoek is de vraag of geringe hoeveelheden fosfor en/of stikstof in de bodem beperkend zijn voor de (her)groei van bomen in de Mabura Hill regio.

Pionier- en climaxsoorten

Het is erg moeilijk uitspraken te doen die algemeen gelden voor alle boomsoorten, indien men een willekeurige boomsoort kiest voor het onderzoek. Als we alle boomsoorten op een rijtje zetten op grond van verschillen in kieming en vestiging van hun zaailingen, dan vinden we aan de ene kant pioniersoorten en aan de andere kant climaxsoorten. Enkele soorten van deze twee groepen boomsoorten zijn in deze studie nader onderzocht.

Zaailingen van pioniersoorten vindt men doorgaans op open plekken in het bos: daar waar een boom omgevallen of gekapt is en langs de weg. Ze hebben veel licht nodig om zich te kunnen vestigen. Congo Pump (*Cecropia obtusa*) is een typisch voorbeeld van zo'n pioniersoort (zie voorkant proefschrift). Deze soort heeft een relatief hoge potentiële groeisnelheid en hoge fotosynthesecapaciteit (Hoofdstukken 4 en 6). Relatief veel biomassa wordt in bladeren geïnvesteerd en relatief weinig in ondersteunend weefsel. De grote bladeren worden door slechts een paar takken van zacht hout gedragen.

In de loop van de tijd groeit een open plek dicht en worden de pioniersoorten vervangen door climaxsoorten. Zaailingen van climaxsoorten kunnen meer schaduw verdragen en worden tevens in de ondergroei van het bos gevonden. De meeste economisch interessante houtsoorten behoren tot de climaxsoorten. Een voorbeeld hiervan is Greenheart (*Chlorocardium rodiei*), Guyana's belangrijkste houtsoort. Deze soort heeft een relatief lage groeisnelheid en lage fotosynthesecapaciteit (Hoofdstukken 4 en 6), hetgeen gepaard gaat met een goede houtkwaliteit.

Door vertegenwoordigers van deze twee groepen boomsoorten (pionier- en climaxsoorten) met elkaar te vergelijken en hun verschillende eigenschappen te bestuderen, kunnen we een beter inzicht krijgen in hergroei van bomen na kappen.

Beschikbaarheid van stikstof voor groei

Tijdens het onderzoek werd snel duidelijk dat de beschikbaarheid van stikstof waarschijnlijk niet beperkend is voor de plantengroei. Hier zijn een 4-tal aanwijzingen voor gevonden. De stikstofconcentraties in wit en bruin zand (30-340 μg g^{-1}) en in boombladeren (10.9-24.5 mg g^{-1}) waren niet uitzonderlijk laag vergeleken met die van andere tropische bossen (Hoofdstukken 2 en 7). De bomen gingen daarbij ook niet zuinig met stikstof om (Hoofdstuk 7). Drie van de vier onderzochte soorten bleken stikstof niet uit afstervende bladeren terug te trekken voor hergebruik. Eén soort trok slechts 33% van de stikstof terug. De toediening van stikstof in de vorm van de meststof ureum kon bovendien de groei van Clump Wallaba (*Dicymbe altsonii*) niet stimuleren. Alle Greenheart zaailingen gingen dood na de toediening van ureum (Hoofdstuk 2). Deze laatste bevinding maakt duidelijk dat het gebruik van ureum om de groei van gewenste zaailingen te bevorderen, nadrukkelijk moet worden afgeraden in deze regio.

Beschikbaarheid van fosfor voor groei

In verhouding tot stikstof is het fosfor gehalte in de bladeren laag. Een plant heeft doorgaans 10 maal zoveel stikstof nodig dan fosfor om goed te kunnen functioneren (stikstof:fosfor als 10:1). De concentratie fosfor in de Guyanese bomen was uitzonderlijk laag (0.4-1.1 mg g^{-1}, Hoofdstuk 2). De verhouding stikstof:fosfor was 25:1.

In het witte zand zijn heel lage concentraties fosfor (8 μg g^{-1}) aangetroffen. Het bruine zand bevat hogere concentraties fosfor dan het witte zand, maar ook hogere concentraties ijzer en aluminium (Hoofdstuk 3). Deze binden fosfor, zodat op het bruine zand uiteindelijk minder fosfor beschikbaar is voor de groei van planten, dan op het witte zand.

Met superfosfaat bemeste Clump Wallaba zaailingen verdubbelden hun relatieve groeisnelheid. Ook pioniersoorten verhoogden hun groeisnelheid op bruin zand na de toediening van fosfor. Niet alle soorten verhoogden echter hun groei na het toedienen van fosfor. Sommige boomsoorten zijn waarschijnlijk niet in staat hun groei te verhogen, maar slaan na bemesting de fosfor simpelweg op

(Hoofdstuk 5). Een positief effect van fosfor op de groei van gewenste boomsoorten kan enige jaren vergen.

We kunnen concluderen dat in de regio van Mabura Hill de beschikbaarheid van fosfor erg laag is; zo laag dat het mogelijk de groei van bomen beperkt. De lage beschikbaarheid van fosfor, en mogelijk andere voedingsstoffen, maakt dit oecosysteem gevoelig voor verstoringen. Er mogen slechts weinig voedingsstoffen, zoals b.v. aanwezig in hout, aan het regenwoud onttrokken worden.

Andere groeibeperkende factoren

Een lage beschikbaarheid van fosfor op wit en bruin zand is niet de enige factor die de groei van bomen in het gebied kan beperken (Hoofdstukken 3 en 4). Een gebrek aan fosfor is vaak slechts één van de kenmerken van zure bodems. Er zijn nog andere factoren die ook de groei van regenererende bomen kunnen beperken, zoals: de zuurgraad van de bodem, de aanwezigheid van te veel metalen (b.v. ijzer of aluminium) en/of de afwezigheid van voldoende voedingsstoffen (b.v. calcium)

Door het toevoegen van wat strooisel (het bovenste laagje bosbodem met half verteerde bladresten) werd de groei van zaailingen gestimuleerd (Hoofdstuk 3). Hoe dit precies wordt bewerkstelligd weten we nog niet, en dient verder onderzocht te worden. Dit betekent echter wel dat de strooisellaag in het bos een belangrijke functie vervult en niet onnodig verstoord moet worden bij het kappen van bomen in het bos.

Pionier- en climaxsoorten in een fosforarme omgeving

In de loop van de tijd hebben zowel pionier- als climaxsoorten zich aangepast aan het groeien op een zure bodem met weinig fosfor. Hun wortels leven samen met een schimmel die een fijnvertakt stelsel van schimmeldraden heeft (mycorrhiza). In ruil voor de bouwstof koolstof neemt de schimmel fosfor uit de bodem op voor de plant (Hoofdstuk 4). De bestudeerde boomsoorten hebben, vergeleken met die op rijkere bodems, een lage behoefte aan fosfor door een lage groeisnelheid, lage concentraties fosfor in het weefsel en een efficint hergebruik van fosfor (Hoofdstukken 2,4,5 en 7).

In het bos is niet overal de beschikbaarheid van fosfor gelijk. Op plaatsen waar een boom is omgevallen doet zo'n boom niet meer mee in de competitie om fosfor en is er per zaailing relatief meer fosfor beschikbaar. De omgevallen boom

heeft tevens een venster in het kronendak achtergelaten, waardoor het lichtklimaat op de bosbodem veranderd is. Vestiging in een omgeving met relatief meer licht en voedingsstoffen vereist een andere set van eigenschappen dan die nodig is voor vestiging in de ondergroei van het bos.

Pioniersoorten hebben zich gespecialiseerd in het kiemen en vestigen in een open omgeving. Ze hebben erg kleine zaden, zonder reserves (Hoofdstuk 2). De fosfor die nodig is voor snelle groei, wordt opgenomen door middel van een heel fijn vertakt wortelstelsel. Dit wortelstelsel kan alleen bestaan bij de gratie van een hoge fotosynthesesnelheid van de bovengrondse delen. De fotosynthesesnelheid van pioniersoorten bleek sterk gerelateerd te zijn aan de fosforconcentratie in de bladeren (Hoofdstuk 6).

De bladeren met een hoge fotosynthetische activiteit blijken geen lang leven te hebben. Ondanks de hoge percentages fosfor die hergebruikt worden, verliezen ze toch veel fosfor en koolstof aan de omgeving door de korte levensduur van de bladeren (Hoofdstuk 7). Door een relatief hoge groeisnelheid van bovengrondse en ondergrondse delen, kan nieuwe koolstof vastgelegd en fosfor opgenomen worden, zodat de verliezen worden gecompenseerd. Deze strategie werkt dus alleen in een omgeving waar genoeg licht en fosfor aanwezig is om de machinerie draaiende te houden.

In de ondergroei van het bos, waar minder licht beschikbaar is, vinden we voornamelijk zaailingen van climaxsoorten. De zaailingen moeten er met volwassen bomen concurreren om fosfor. Ze zijn gekiemd uit grote zaden die veel koolstof en fosfor reserves bevatten (Hoofdstuk 2). Hun wortelstelsel is veel minder fijn vertakt en vraagt ook minder koolstof voor groei en onderhoud van de bovengrondse delen. Ze groeien langzamer en beperken het verlies van fosfor en koolstof door te investeren in weefsel met een lange levensduur. Als er een keer meer fosfor beschikbaar is, dan slaan ze dat op in wortel of stengel (Hoofdstukken 2 en 5). Ze wachten in de ondergroei op het omvallen van een boom. Ze hebben zo een goede uitgangspositie ten opzichte van pioniersoorten, die eerst nog moeten kiemen als er een open plek ontstaat. Het zal onder andere van de grootte van de open plek afhangen, met andere woorden de beschikbaarheid van licht en fosfor, of een zaailing van een climaxsoort die van een pioniersoort weg kan concurreren.

Er is nog geen plant gevonden die een zuinig gebruik van koolstof en fosfor kan combineren met een hoge opname van koolstof en fosfor. Pioniersoorten maken snel gebruik van beschikbare bronnen, maar gaan er niet zuinig mee om. Climaxsoorten investeren in duurzaamheid en kunnen daardoor de groeisnelheid slechts beperkt verhogen onder optimale groeiomstandigheden.

Na het ontstaan van een open plek in het bos, op natuurlijke wijze of door menselijk toedoen, zullen er eerst voornamelijk pioniersoorten gaan groeien. De houtkwaliteit van pioniersoorten is economisch gezien weinig interessant en men zou ze kunnen wieden om economisch interessantere climaxsoorten meer kans te geven. Maar het is niet juist pioniersoorten als onkruid, zonder economische waarde te beschouwen. Pioniersoorten beschermen de bodem tegen het uitspoelen van de schaarse voedingsstoffen door tropische regenbuien. Ze kunnen voedingsstoffen sneller vastleggen dan climaxsoorten. Ze hebben een fijner vertakt wortelstelsel en, mede door hun relatief hogere groeisnelheid, leggen ze meer voedingsstoffen vast dan climaxsoorten (Hoofdstukken 4 en 5). Door de korte levensduur van de bladeren wordt er spoedig een strooisellaag gevormd, waar de climaxsoorten dan weer gebruik van kunnen maken. Pioniersoorten hebben dus een belangrijke functie in het oecosysteem.

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Boomfysiologie met oecologie in tropische saus (hoofdgerecht)

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Curriculum vitae

Dorinne Raaimakers werd op zondag 26 mei 1963 geboren te Best. In 1981 behaalde zij haar Atheneum B diploma aan het Mgr. Zwijssen College te Veghel en startte in september van hetzelfde jaar met de biologie studie aan de Universiteit Utrecht. Het kandidaatsprogramma werd in april 1985 voltooid.

Zij bewerkte de bijvakken Landschapsoecologie, Onkruidkunde (Wageningen) en Transportfysiologie in de doctoraalfase. Als onderdeel van dit studieprogramma verrichtte zij 4 maanden landbouwkundig onderzoek in Egypte. Hierna nam zij voor een jaar zitting in het dagelijks bestuur van de fakulteit Biologie. Vervolgens begon zij aan haar hoofdvak Oecofysiologie (in combinatie met Theoretische Produktie Ecologie, Wageningen). In augustus 1989 slaagde zij voor het doktoraal examen. Naast haar studie heeft zij van 1983 tot 1992 als vrijwilligster bij de Wetenschapswinkel Biologie projecten begeleid op gebied van milieu en onderwijs.

Van februari 1990 tot februari 1994 heeft zij, als assistent-in-opleiding bij de vakgroep Botanische Oecologie en Evolutiebiologie, onderzoek verricht in samenwerking met de Stichting Tropenbos en een aantal Guyanese instituten. In deze periode werd het onderzoek verricht waarvan het grootste deel van de resultaten in dit proefschrift is vastgelegd. Een deel van het onderzoek is verricht in Guyana, waar zij in totaal ruim een half jaar verbleef. Sinds februari 1994 is zij werkzaam als gastmedewerkster bij de vakgroep Botanische Oecologie en Evolutiebiologie.