Patterns in tropical rain forest in Guyana

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Patterns in tropical rain forest in Guyana

Patronen in tropisch regenbos in Guyana

(met een samenvatting in het Nederlands)

PROEFSCHRIFT

ter verkrijging van de graad van doctor

aan de Rijksuniversiteit te Utrecht

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Hans ter Steege

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Promotor: Prof.Dr.M.J.A. Werger
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Universiteit Utrecht

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

Foreword

In 1987 the Utrecht University and the University of Guyana initiated a collaborative project, the Forest Project Mabura Hill. From November 1987 till November 1989 I worked as coordinating scientist for this project. During this first period of my stay a research project was initiated at Mabura Hill and I was also teaching at UG. Several people have been of great help to me in this first, sometimes difficult period. I especially want to thank Dr. Tej Singh for his enormous support and friendship, without it we might have left before the end. Unfortunately Tej left soon for a better future in the US, a lot had preceded, a great number would still follow. I also want to thank the students at UG, who participated in the courses with great enthusiasm, the people at Ballast Nedam for their great logistical support and all at Demerara Woods Ltd.

In 1989 the Government of The Netherlands and the Government of Guyana signed a memorandum of understanding, initiating the TROPENBOS Programme in Guyana. Until October 1992 I worked for this project as project leader. During this period I learned a lot about administration and management but often had dreams of a 'normal' PhD time with all time devoted to research. It is no secret that it sometimes led to hard confrontations. After all I have found enough time to finish the work required for this thesis, but obviously not without the help of a great number of people. I will make a try to thank all in the hope not to forget anyone. First of all thanks to Dr. George Wallcott and Dr. Indarjit (Charlie) Ramdass for their continuous support to the TROPENBOS Programme and thanks to all members of the National Committee, who devoted some of their precious time to supervise and collaborate in the project. Thanks also to the management of Demerara Timbers Ltd. and Boskalis for the continuation of logistical support to our programme, to Caroline Alink and Mr. D.E. (Harry) Hariprasad for logistical and managerial support, Mrs. Joan Watson for housekeeping of our guesthouse and occasional babysitting and Mrs. Sybil Stewart for her excellent cooking.

Thanks to Carla Bokdam and José Dobbelsteen who participated in the initial phase of the research and were often left unattended for longer periods in the, at that time very isolated, field station. Thanks to Miranda Boland and Ivo Verburg, who stayed in no less primitive circumstances in their 'Pipo Wagon' even further away. All four showed a lot of courage, necessary to compete with the harsh life in the wet forest. Thanks to Claude Persaud for his help with the location of valuable information in far away files and the aid in the gathering and processing of phenology data. Thanks to all my colleagues and students at Mabura, René Boot for relieving me of many organizational duties, the many interesting discussions and editing of several manuscripts, Leo Brouwer for many weatherdata, Victor Jetten for weather and soil data and the many turbo programming tips, both for data sharing their geographical viewpoint of the forest. Of course all, René, Carmen, Leo, Jet, Victor, Roderick, David, Alisson, Dorinne, John, Peter, Marissa, Marcel, Caroline, thanks for the many discussions, practical help, swimming trips and often rum filled nights. Thanks also to Koos Biesmeijer, Renske Ek and Herold Prins, who devoted substantial time of their stay in Guyana to the experiments. I should also mention the extensive work of the core of our field staff, Dennis, Collin, Oswald, who had to deal with the most arduous jobs and working hours, Mr. (Mac) McKenzie, Mr. Carlton Holder

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All colleagues at the Herbarium and the Department of Plant Ecology and the TROPENBOS head office have contributed in some way, especially I like to thank Gerrit Cornelissen and Rob Bakker for their continuous filling and sending of crates to Guyana, Hans Cornelissen, Erik Veneklaas for reading many manuscripts, Erik Veneklaas and Feike Schieving for the many stimulating discussions on theoretical backgrounds. Erik Veneklaas, Riki van den Boogaard, Rene Kwant, Rob Kreulen and Anita van Leeuwen were of great assistance with last minute nitrogen and $\delta^{13}C$ determinations. The final lay out of the thesis was done by Marjolein Kortbeek-Smithuis. Hendrik Rijpkema made figure 1 of chapter 1.

A few 'Whities' have contributed in a more than average manner, Ben ter Welle, as location coordinator, but certainly also as a friend, even if we have dealt often seriously with each other in many discussions and Marinus Werger for scientific support and extensive comments on all manuscripts.

Very special thanks are due to my friend Leonnard Wong Kam, who has helped in many ways to make our programme a success, as a true Jack of all trades and master of all his support has been of great significance. Very special thanks also to Sandra Mohabeer, who's housekeeping and, more importantly, cooking kept the spirits high.

Last and in this case certainly not least most thanks to my parents for their continuous support during my study, and to Petra and Arua who had to share husband and daddy with science, day and night.

Contents

Introduction

Tropical rain forest

Tropical rain forests are found in hot, perhumid areas between 23°N and 23°S. Average yearly temperatures are usually above 25°C, while average minimum temperatures are over 20°C. Average yearly rainfall is usually over 1800 mm and no month has an average rainfall less than 60 mm (Jacobs 1981). Tropical rain forest is a term that may cover a wide array of forest types. Richards (1952) gives a definition after Schimper '*Evergreen, hygrophilous in character, at least 30 m high, but usually higher, rich in thick-stemmed lianes and in woody as well as herbaceous epiphytes*'. In comparison to temperate forests, it is indeed the lack of herbs and the dominance of the woody component of the forest that is most striking of these forests. Often more than 50 percent of the species are woody (Jacobs 1981). It is also the woody component that makes these tropical rain forests interesting for their current most common commercial use, timber extraction. The rate of loss of tropical forests is high, often discussed (e.g. Luning 1987, Werger 1992), and needs no further elaboration here.

Guyana and Tropenbos

Logging in Guyana is practised in an area parallel to the coast (Figure 1). Several species are logged, but there is strong emphasis towards one species, Greenheart (*Chlorocardium rodiei* (Schomb.) Rowher, Richter & v.d. Werff). Greenheart may account for 45% of all harvested timber, whereas it constitutes only 0.5-1.5% of the total standing timber in the country (Tropenbos 1991). As the size of the human population is small in relation to the size of the country (approximately 800,000 people on 215,000 km^2) and most of the people live in the coastal area the pressure on the forest is low. Luning (1987) estimates the annual deforestation rate in 1985 to be negligible. A condition, worldwide only rivalled by the neighbouring countries, Surinam and French Guiana. In this respect Guyana, economically one of the poorest countries in South America, can be considered one of the richest. However, this should only be reason for moderate optimism as a concise plan for conservation of the forests is still lacking (e.g. Lindeman & Mori 1989), while the National Forest Policy and National Forestry Action Plan suffer from constrained implementation (Tropenbos 1991). In 1989 the Guyanese Govern-

ment and the Dutch Government signed a Memorandum of Understanding concerning the execution of a research project in the interior of Guyana. Aims of the Tropenbos programme in Guyana are to formulate management systems based on a thorough understanding of the forest ecosystem. Projects to be carried out and actually being carried out range from description of valuable timber species, wood technology and wood anatomy, soil and vegetation inventories, water and nutrient cycles and the effects of logging thereupon, tree species population structure, dynamics and reproduction of important tree species, growth in relation to environmental constraints, logging intensities studies and the effects of logging on bio-diversity. The studies presented in this thesis are also part of that comprehensive research programme. They deal with the occurrence patterns in the forest of Guyana and their relation to spatial and temporal processes.

Forest patterns

Tropical rain forests are not homogeneous. Soil nutrient status and hydrology play an important role in the determination of forest stand composition (e.g. Beard 1946, Richards 1952, Austin et al. 1972, Gartlan et al. 1986, Ashton 1989, Basnet 1992, Johnston 1992). The high species diversity and thus low density of many species makes the analysis of those patterns often difficult, however (e.g. Baillie et al. 1987). Species richness in rain forests is affected by soil fertility (a.o. Ashton 1989), soil water status (a.o. Richards 1952) and gap dynamics (e.g. Hartshorn 1978, 1980, Bongers & Popma 1988 and many references therein). While the effect of soil nutrient status and hydrology are mostly stable in time and vary mainly in a spatial manner, gap formation is found on all soil types but is stochastic in nature, affecting different forest parts at different times. The latter can thus be considered a temporal factor. Gap formation promotes species diversity within one forest type, since gap species mostly are different from climax species. However, if light is the most important factor for establishment of gap species and if similar species are found in gaps in different forest types (e.g. Brokaw & Scheiner 1989), gap formation may lower the dissimilarities between forest types. This would further complicate the analysis of patterns in forest types. The role of the gaps in the maintenance of species diversity becomes very clear if we realize that as much as 50 % of the forest species may need gaps to complete their life-cycle (Hartshorn 1980).

Single dominance

Not all tropical forests are rich in species. Dominance of a few or even a single species is commonly found in all three major tropical rain forest blocks around the world (Richards 1952, Connell & Lowman 1989, Hart et al. 1989, several chapters in Lieth & Werger 1989) and areas dominated by one species can be very extensive (see Hart et al. 1989). Such forests occur often adjacent to mixed forests (Hart et al. 1989) on exactly similar soils, while gap dynamics, recruitment of canopy species and seedling mortality are also comparable. Hart et al. (1989) hypothesised that in the absence of major disturb-

ing events any tropical rain forest area would finally be dominated by one or a few species. Major disturbing events could be extensive storm damage (Whitmore 1989, Turton 1992, Brokaw & Walker 1992, Walker et al. 1992), landslides (Garwood et al. 1979), increased river perturbance (Salo et al. 1986, Räsänen et al. 1987), drought (Davis & Richards 1933, Ashton 1989) and subsequent fire (Hart et al. 1989, Ashton 1989). Storm damage may play a role, even in those areas outside the main hurricane belt and has been reported from south east Asia (Jacobs 1981), Africa (Hart et al. 1989) and South America (Schulz 1960, Jonkers 1987). Extensive forest fires may happen, especially during severe droughts. Such droughts are not uncommon (see below) and large fires are thought to have occurred in major areas of South America (Schulz 1960, Sanford et al. 1985, Saldarriaga & West 1986, Horn & Sanford 1992) and recently occurred in Borneo (Leighton & Wirawan 1986, see also Lieth & Werger 1989).

Connel et al. (1989) offered an additional explanation for the single dominance in tropical forests. In their explanation the possession of ecto-mycorrhiza is of crucial importance. The exact mechanism is not yet fully understood, but species known to become dominant (or co-dominant) are often ecto-mycorrhizal: Dipterocarpaceae in south-east-Asia (Richards 1952, Hart et al. 1989, Connel & Lowman 1989), Legumes (Ceasalpinioideae) in Africa and South-America (Richards 1952, Hart et al. 1989, Gartlan et al. 1986, Newberry et al. 1988) and Myrtaceae in south-east-Brazil (Mori et al. 1983).

The (ir-)regular climate and the forest

Rainfall patterns are fairly predictable on an average basis in the tropics and are, especially in coastal areas, closely tied to the Intertropical Convergence Zone (ICZ) (Molion 1987, Paegle 1987). This causes a general bi-modality in rainfall patterns, as found in many tropical coastal regions. Phenology of many species is closely tied to these weather patterns, as has often been documented (Medway 1972, Daubenmire 1972, Frankie et al. 1974, Sabatier & Puig 1982, Sabatier 1985). It is still not completely clear in most cases what would be the causal factor in triggering flowering and fruiting in tropical species. Triggers mentioned are rainfall (Daubenmire 1972, Frankie et al. 1975), rehydration (Borchert 1983), temperature changes (Walter 1968 cited in Frankie et al., Ashton et al. 1988) and photoperiod (Stubblebine et al. 1988). In the wet tropics water is mostly not limiting growth of mature individuals and flushing and flowering may be tied to the dry season, when sunshine hours are at maximum, and productivity can be highest (v. Schaik & Terborgh manuscript). Fruitfall in the tropics is often tied to the rainy season (Sabatier & Puig 1982) and even if seeds drop far before the rainy season they may remain dormant until the rainy season (Garwood 1982, Sabatier 1985). Timing of germination in respect to the rainy season seems beneficial. Rain provides the moisture necessary for establishment and growth of seedlings. Seedlings are likely to be more vulnerable to drought as they can only explore the upper part of the soil and lack a storage of water. Furthermore, locally, seedlings may benefit from the peak in gap formation in the rainy season, caused by heavy rainfall and wind squalls (Brokaw 1985, Martinez-Ramos et al. 1988). Irregular droughts may lead to periodical, localized mortality among seedlings

and canopy trees (Davis & Richards 1933, Ashton 1989) and may thus have a strong effect on the composition of forest stands. On soils with poor water retaining characteristics such mortality may be enhanced. Irregular excessively rainy periods can cause flooding in otherwise well drained terrain and may have a similar effect (Mori & Becker 1991). Heavy mortality caused by irregular droughts has been documented from south east Asia (Ashton 1989) and South America, Davis & Richards 1933). These irregular droughts are to a great extent related to another macro-climatological phenomenon, the El-Niño-Southern-Oscillation (Cane 1983, Rasmusson & Wallace 1983, Kousky et al. 1984). Droughts occurring in south-east-Asia and north-east-Brazil and west Africa have all been tied to this phenomenon (Kousky et al. 1984). The mast flowering and fruiting of the Dipterocarpaceae in south-east-Asia may be triggered by a slight drop in night temperature also linked to this phenomenon (Ashton et al. 1988).

Guyana

Guyana is situated on the northeastern part of South America, between 56°20' and 61°23' west and 1°10' and 8°35' north (Figure 1). The climate is tropical with high average daily temperatures (25.9°C) and high rainfall, between 4400 to 1200 mm per year. Rainfall in the central part of the country, is on average between 2400 and 3200 mm per year. The climate is influenced by the movement of the Intertropical Convergence Zone, giving rise to two distinct wet seasons: a long one from May to mid-August and a short one from November to January. Occasionally either the short wet season or short dry season may be completely lacking. Phenology in the Guyana rain forest has been recorded since the late 1800's but the data were never processed nor presented.

Four main landscape types are distinguished in Guyana: the Pre-Cambrian Plateau, the Pakaraima Mountains, the White Sands Area and the Coastal Plain. The White Sand Area, in which the study area, Mabura Hill, is located, extends from the coast to about 200 km southwards. It is gently undulating but at some part penetrated by laterite covered ridges from the Pre-Cambrian Plateau. The White Sands Area has a typical drainage pattern of many small creeks. Despite their small size they form wide valleys, because of the coarseness of the sand. Where the White Sands Formation is thin, as is the case in the study area, the streams have cut through the white sandy layers into the Brown Loamy Sands and Sandy Loams below. The latter soils are associated with the Pre-Cambrian Plateau.

Forest covers some 80% of Guyana and can be broadly classified as swamp forest in the coastal belt and rain forest, seasonal forest and dry forest in the interior (Fanshawe 1952). Recently it has been argued, that due to the seasonal aspect of the climate, all forests in Guyana should be referred to as seasonal evergreen forests (Lindeman & Mori 1989). Forest types in the near interior appear neatly correlated to soil types (e.g. Richards 1952, Fanshawe 1952). The correlation is so strong that soil maps are often slightly modified vegetation maps, made from aerial photograph interpretations. This, however, may lead to erroneous circular argumentation. Generalizing, dry evergreen forests are found on the White Sand Soils, ranging from excessively drained soils with forest domi-

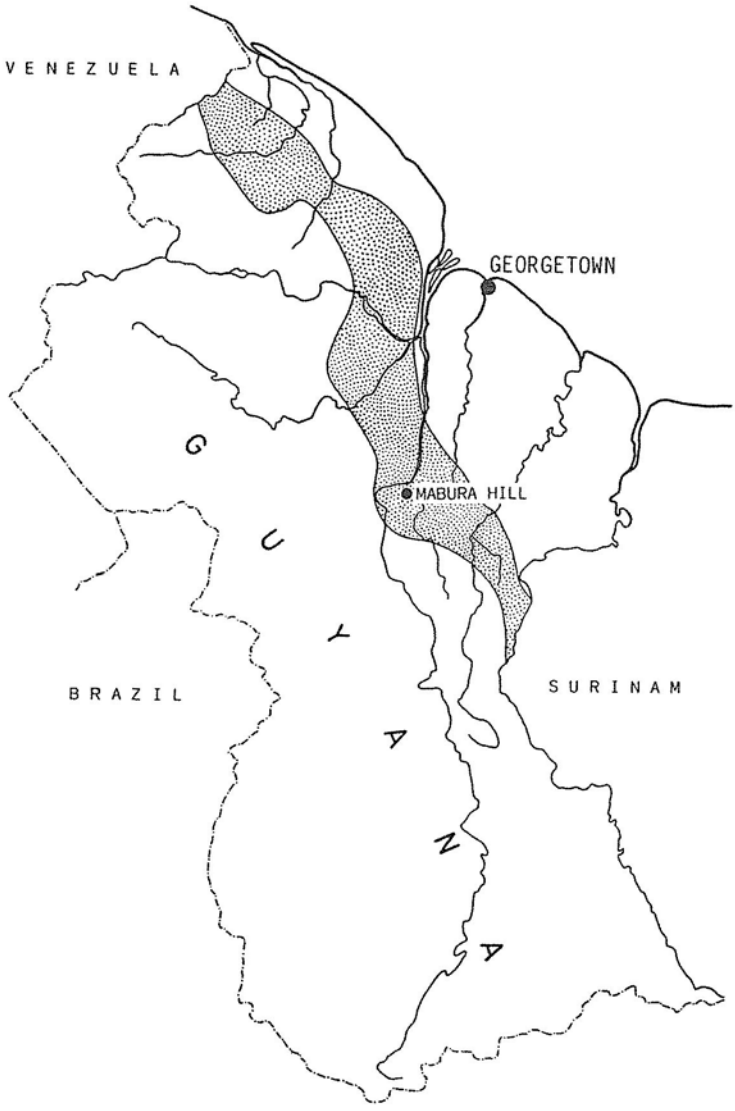

Figure 1. Map of Guyana. The main timber is shaded.

nated by *Dimorphandra conjugata* or by *Eperua* spp. to poorly drained with often peat formation (pegasse). In the latter forest palms such as *Mauritia flexuosa* and *Jessenia bataua* are often dominant. On the more loamy (brown) sands mixed forests are found. Still in a great number of cases one or a few species appear dominant in these mixed forest. A great many associations have been described (Fanshawe 1952). Along rivers forests dominated by *Mora excelsa, Carapa guianensis* or *Eperua rubiginosa* are often found.

Aim of this study

The general concept of the relation between patterns in vegetation and patterns in soil types and soil hydrology is becoming clearer with the increase of descriptive work carried out in the tropics. Substantial knowledge has been gathered on the floristics of the Guianas (e.g. Davis & Richards 1933 and 1934, Fanshawe 1952, see Lindeman and Mori 1989 for a review). Data on ecology, phenology and forestry have recently been compiled for Guyana (ter Steege 1990). However, very little experimental work has been carried out to test many of the hypotheses generated by those studies. Factors controlling the occurrence of canopy species in tropical rain forest of Guyana are still insufficiently known. These factors may include temporal as well as spatial elements. The aim of this thesis is to increase our knowledge both on the temporal as well as on the spatial element. Experimental work is carried out with a few species to test the link between environment and tree seedlings. It may be clear from the above that the results should be useful for forest management.

The experimental studies reported in this thesis make use of seedlings. There are two reasons for this choice. The first one is very obvious, seedlings are easier to manipulate than mature trees. Secondly, most mortality, up to 80%, takes place in the first year of a seedling's life. After saplings have reached 10 cm diameter mortality remains fairly constant throughout the rest of their lifespan (Swaine et al. 1987). Arguably the seedling stage is thus the most vulnerable stage in a tree's life, where most of the selection takes place.

Outline of this thesis

Chapter 2 discusses the regular temporal element, fluctuations in rain fall and sunshine are related to the production of flowers and fruits. An appendix lists the flowering and fruiting periods for almost 200 Guyanese timber species and may be helpful if seeds are needed for experiments and nursery practices.

The relation in the spatial pattern of forests and soil type and soil hydrology is discussed in chapter 3.

Chapter 4 deals with the plasticity of *Chlorocardium rodiei* (Greenheart) in relation to (artificial) gaps. Seed germination, mortality and morphology are studied in field experiments of short and longer duration.

In chapter 5 the plasticity of *Mora gonggrijpii* to different light climate and soil types is investigated. *Mora gonggrijpii* occurs on similar soils as does *Chlorocardium rodiei*, they often grow next to each other but exhibit very different strategies in relation to gaps. This chapter is also the first of three in which the occurrence of *Mora excelsa* and *Mora gonggrijpii* is investigated along a soil water gradient. Chapter 6 further deals with the flooding tolerance and chapter 7 with drought tolerance of these two *Mora* species. In these chapters the significance of irregularly occurring temporal elements is also discussed.

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The phenology of guyanese timber species: A compilation of a century of observations

Hans ter Steege & Claude A. Persaud

Abstract

Flowering and fruiting of timber trees have been recorded in Guyana for over a century. Although the data are dispersed over a large number of non-consecutive years, from 1887 until 1989, they give a very good estimate of the probability of a species being in flower or fruit in a certain month. Flowering seems correlated with peak sunshine, while fruiting is related to maximum rainfall.

keywords: Guyana, phenology

Introduction

Phenology is the regular yearly pattern of visible events in a natural system. Phenomena that may be regular are: flowering, fruiting, leaf-fall and -flush and growth. Several authors have written on the phenology of tropical rain forests (e.g. Medway 1972, Daubenmire 1972, Frankie et al. 1974, Sabatier & Puig 1982, Sabatier 1985).

It is still not completely clear what is the causal factor in flowering and fruiting in tropical trees. Triggers are mentioned, such as rainfall (Daubenmire 1972, Frankie et al. 1974), rehydration (Borchert 1983), temperature changes (Walter 1968, cited in Frankie et al. 1974) and photoperiod (Stubblebine et al. 1978). Recently v. Schaik (1986) and v. Schaik and Terborgh (manuscr.) hypothesized that in arid areas rainfall will be a limiting factor in production (flushing and subsequent flowering) and thus a driving factor behind phenology (see e.g. Werger et al. 1991). However since water is often not limiting in the humid tropics, insolation would be the limiting factor for production there. Thus insolation patterns could trigger leaf fall and flowering patterns. Since insolation has a bimodal annual pattern between the tropics, a bimodality in phenology can be expected.

Fruit fall usually takes place after the fruits/seeds have matured. This can be shortly after flowering up till almost a year afterwards (e.g. *Chlorocardium rodiei*). Although fruits/seeds can drop far before the rainy season, they may remain dormant until the rainy period, sometimes also up to a year. This dormancy can be innate, as seeds of some species will not even germinate earlier under favorable conditions (Garwood 1982, Sabatier

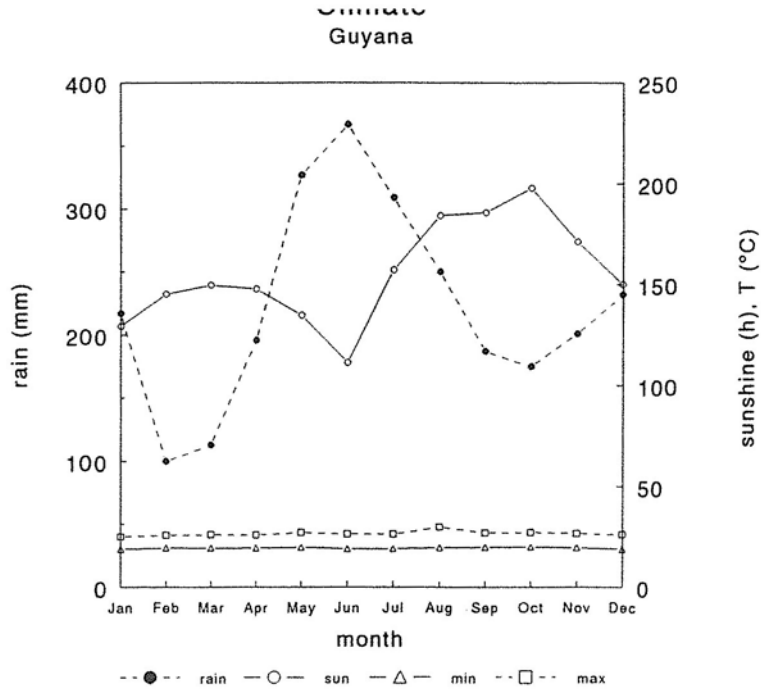

Figure 1. Average number of sunshine hours per day per month, total amount (mm) rainfall per month and mean temperatures for the forestry belt of Guyana. See text for sources.

1985). Timing of germination in respect to the rainy season seems beneficial. Rain provides the moisture necessary for establishment and growth. Furthermore, seedlings may benefit from the peak in gap formation in the rainy season, caused by heavy rainfall and wind squalls (Brokaw 1985, Martinez-Ramos et al. 1988).

Mast flowering/fruiting is a well known feature of Dipterocarpaceae in South-East Asia (v. Schaik 1986, and many references therein). Masting is also reported for some years in French Guiana (Sabatier 1985).

Studies on phenology in the Guianas have been carried out by Sabatier & Puig (1982), Sabatier (1985), Mori & Prance (1987) in French Guiana and v. Roosmalen (unpublished data) in Surinam. In this paper we present phenological data for Guyanese timber species in relation to climatic data. The total data set for many species covers a timespan of over a century. With the best eleven years of observations we evaluate the possible existence of mast fruiting in a few common families.

Methods

The observations in the "Autecology of Guyanese trees" (14 unpublished volumes) are the main source of information for this compilation. Systematic recording of phenology of forest trees in Guyana started in the 1930's and were maintained on a regular basis un-

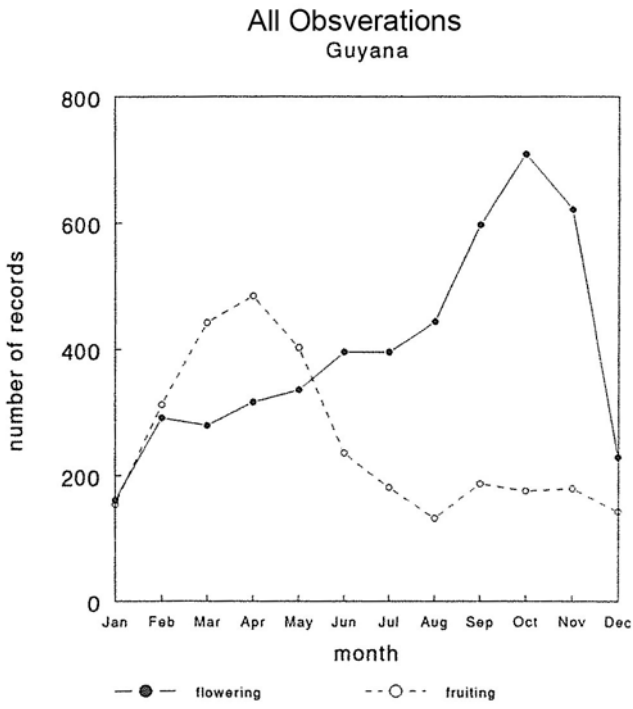

Figure 2. All observations of flowering and fruiting per month for the forestry belt in Guyana, as recorded from 1887 to 1989.

til the early 1950's, under the supervision of T.A.W. Davis, B.R. Wood & D.B. Fanshawe, assisted by J. Boyan, R. Boyan & C.A. Persaud. Earlier (from 1887) and later records were on an irregular basis. Observations were made during long routine field trips, with a bias towards the low rainfall periods however. In addition 960 trees of important timber species were numbered and observed monthly on their phenology in the 'His/Her Majesty's Penal Settlement' Forest Reserve (HMPS), the last mainly in the 40's and 50's.

The data in the "Autecology of Guyanese trees" were extracted and flowering and fruiting were scored per month. In addition information from available herbarium sheets was included (in the case of *Mora* spp., *Eperua* spp., and *Chlorocardium rodiei*). Using 86 species with a 'smooth phenology pattern' and sufficient observations a cluster analysis (CSS, StatSoft, Tulsa, Oklahoma) was performed (Squared Euclidean Distances, Ward's Averaging), in order to find patterns in phenology. The monthly data were transformed to percentages. For these species correlations were calculated between flowering and fruiting on one hand, and rainfall, average maximum and minimum temperature, and hours of sunshine on the other hand. The correlations were calculated with the climatic parameter of the same month of observation, the month before, two months before, up to 11 months before. In the same way correlations were calculated between flowering and fruiting.

'Evenness of Flowering' (EF) was calculated with the Coefficient of Variation in flow-

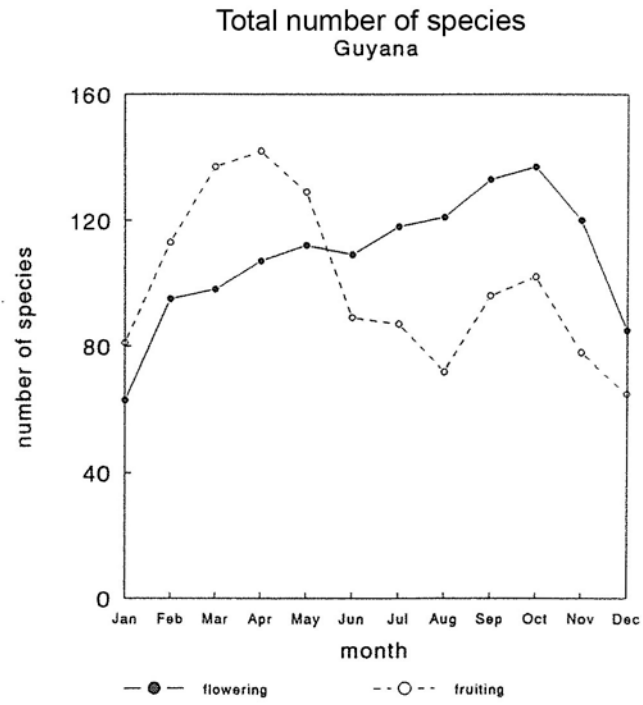

Figure 3. Total number of species in flower or fruit per month, for the forestry belt in Guyana, as recorded from 1887 to 1989.

ering over the 12 months. EF can range from 346 if all flowering is found in one month to 0 if flowering is evenly spread.

Uni-modality versus bi-modality was calculated with circular statistics (see Zar 1984). Unimodal species will have a high z-value with a normal performed Ralleigh-test, bimodal species will have a low z-value, but a high one if all angles are doubled, and thus the two opposite peaks are added. Z_{single}/Z_{double} was used as an 'Index of Modality' (IM). A unimodal species will have an IM << 1, a bi-modal species an IM >> 1. 'Non-modal' species have an IM of 1 and a low EF.

Climatic data were obtained from the Department of Hydrology and Meteorology in Georgetown. Rainfall data are for Bartica (06°24'N, 58°39'W, 1958 - 1975), temperatures for Ebini (05°34'N, 57°47'W) and Georgetown (06°48'N, 58°08'W, both stations 1973, 1974). Sunshine hours were taken from Persaud (1982), for five stations in or at the border of the forestry belt; Timehri (06°31'N, 58°16'W, 1966-1970), Mazaruni Prison (06°24'N, 58°39'W, 1961-1975), Tiboku (05°48'N, 59°36'W, 1971-1975), Kaieteur (05°11'N, 59°29'W, 1971-1975), Ebini (05°34'N, 57°47'W, 1969-1975). A summary of the climatological data is given in Figure 1.

Phenology data of some families of the best eleven years of observations (Mazaruni station 1943-1953) are compared with rainfall and sunshine data for the corresponding period. Unfortunately no data on sunshine are available for the forestry belt for that time. For that analysis data from the Georgetown Botanical Garden are used. Sunshine for

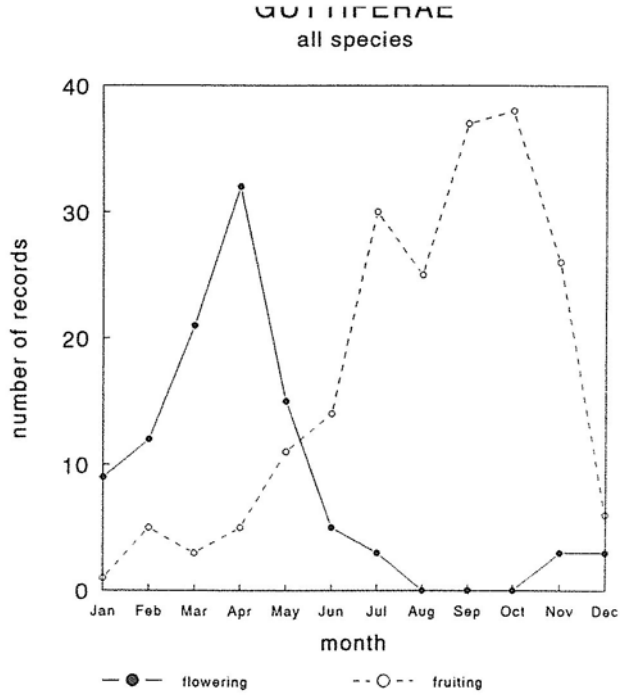

Figure 4. The total number of records for flowering and fruiting in all species of the Guttiferae in the forestry belt of Guyana. The small peak of flowering in July is caused by a somewhat different flowering pattern in *Symphonia globulifera*.

Mazaruni Station (06°24'N, 58°39'W) and Georgetown (06°48'N, 58°08'W) are correlated (1961-1965, r=.79), and maxima and minima do not differ in time in the year.

Data from cited references, from the Flora of Surinam and from V. Roosmalen (unpubl.) for Chrysobalanaceae, Lecythidaceae, and Sapotaceae were compared separately with the data of the same families in Guyana.

Results

All observations for single species are given in Appendix 1. Full names and authorities are according to Mennega et al. (1988).

The climatic data are summarized in Figure 1. Rain and hours of sunshine are clearly bimodal in Guyana. The weather in Guyana is dry when the ICZ (Inter-tropical Convergence Zone) is either north of the country (July-October), or to the south (January-March). The long dry season of August to December is less dry than the short one in February and March. The long dry season, although 'rainier' is also the one with highest average sunshine hours.

The overall flowering and fruiting pattern for the 190 species considered is given in Figure 2 and 3. Peak flowering is in September-November, when some 74% of all spe-

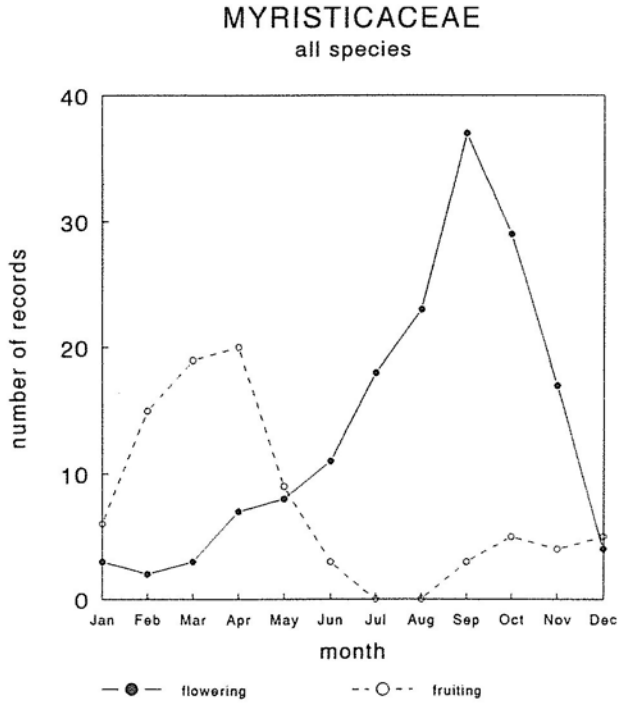

Figure 5. The total number of records for flowering and fruiting in all species of the Myristicaceae in the forestry belt of Guyana.

cies have been found in flower. In the month with the lowest number of species still 34% of all species have been found flowering. The overall flowering pattern closely resembles the sunshine pattern in Figure 1; flowering peaks one month later. Fruiting in Guyana has a stronger bimodality than flowering. Fruiting takes place within the dry seasons, shortly before the rainy seasons. Again some 74% of all species have been found in fruit in the top fruiting season. In the second peak season 50% of the species have been found in fruit.

With CSS 17 clusters of species were found. In most groups flowering has the highest correlation with sunshine in the months around the flowering peak. Two clusters of species differ in their flowering behavior as related to sunshine. These species (e.g. *Anacardium giganteum*) flower 3 to 4 months and (e.g. *Schefflera* spp.) 4 to 6 months after peak sunshine.

Seed fall patterns are closely linked to rain fall, and this seems to be a major factor in the grouping by CSS. Fruiting is mostly short before the main rainy season. Some groups however fruit before or in the short rainy season (e.g. *Chamaecrista adiantifolia* and *Senna multijuga*). This contributes to the bimodality of fruiting found in Figure 2 and 3.

Evenness and Index of Modality are not a factor of importance in the clustering. Still IM was a good measure to distinguish between uni- and bi-modality in most cases. For clustering the modality is less important than the position in time of the highest peak.

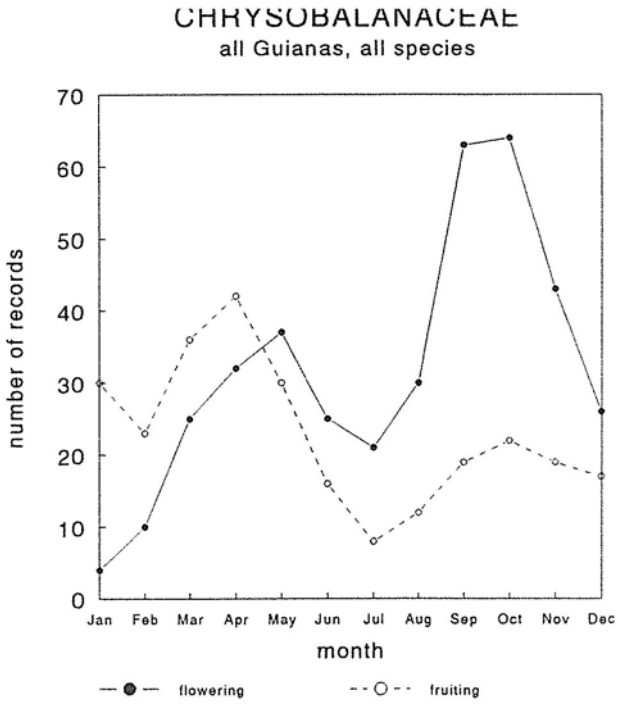

Figure 6. The total number of records for flowering and fruiting in all species of the Chrysobalanaceae for Guyana, Surinam and French Guiana summarized.

Figures 4 to 8 give examples of phenological patterns of some common taxa. Guttiferae mainly flower in or just after the dry sunny period; only *Symphonia globulifera* flowers before the rest of the family causing a spike on the flowering graph. Fruiting of Guttiferae is roughly 1 month before the rainy season. Myristicaceae follow basically the same pattern as Guttiferae, but start fruiting a little earlier. The patterns of Chrysobalanaceae, Lecythidaceae, and Sapotaceae are consistent throughout the Guianas. Usually species start to flower slightly earlier in French Guiana. In Figures 6, 7, and 8 summarize the data for the three countries. Chrysobalanaceae may start to flower in either one of the dry seasons in the year. Flowering does not occur twice per year, but on a yearly and/or one and a half yearly basis. Still flowering starts more often in the sunnier period in September. Fruiting takes place one to two months before the rainy season. Lecythidaceae mainly flower in the sunniest dry season of the year. Only rarely flowering will start during the short, less sunny dry season in March-April. Sapotaceae mainly flower in the more sunny September-October months. Fruiting starts in February and lasts until June.

Ten species of Lecythidaceae were found flowering in Mazaruni Station, between 1943 and 1953. In most years at least three to four species flowered (see Figure 9). This 'regular' flowering is usually found in dry periods, but sometimes in wet. Exceptionally good flowering periods, such as the end of 1943, 1945, 1946, 1948, mid 1950, and end 1953 had five or more species in flower. These peaks are all in long dry, sunny periods at

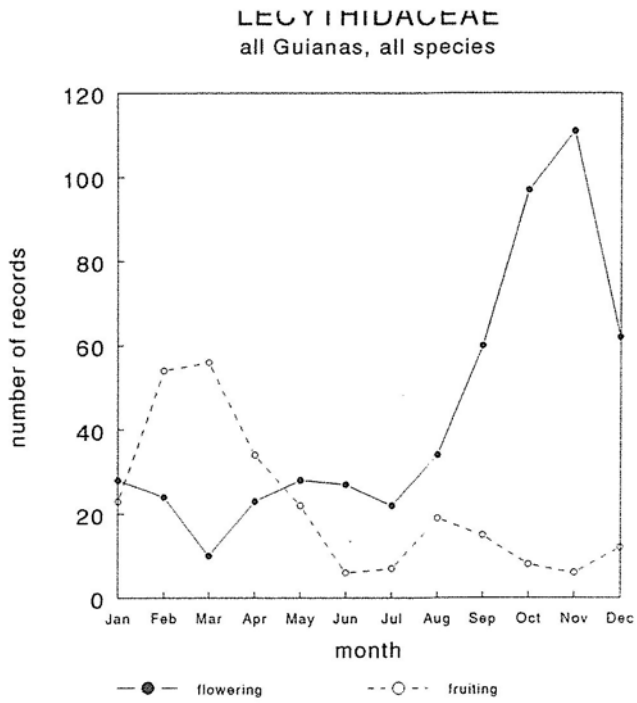

Figure 7. The total number of records for flowering and fruiting in all species of the Lecythidaceae for Guyana, Surinam, and French Guiana summarized.

the end of the year, except in 1950. Although the data are not exhaustive it seems that the dry season of end 1949 was not dry and/or sunny and/or long enough to promote flowering in many species. The shorter dry, less sunny period in mid 1950 offered the next opportunity to flower. After 1950 the next dry period long enough to set many species into flower was end 1953. Apart from regular flowering species, such as *Eschweilera decolorans* and *E. sagotiana*, the species composition of flowering peaks of five and more species is not always the same.

For Chrysobalanaceae good years were mid 1945, mid July 1946 and end 1948. There are less observations of flowering for Chrysobalanaceae than expected from their abundance in the forest. The same may be said of Sapotaceae.

Discussion

Flowering and fruiting are clearly seasonal in the forest of Guyana. The peak of flowering in September to November agrees well with the peak of flowering in the forest of French Guiana (Sabatier 1985). Flowering in French Guiana seems to start a little in advance of flowering in Guyana. This difference is related to the movement of the ICZ (Inter-tropical Convergence Zone), which leaves French Guiana a little earlier than it does Guyana, on its way to the North. Most species tend to flower around the period when

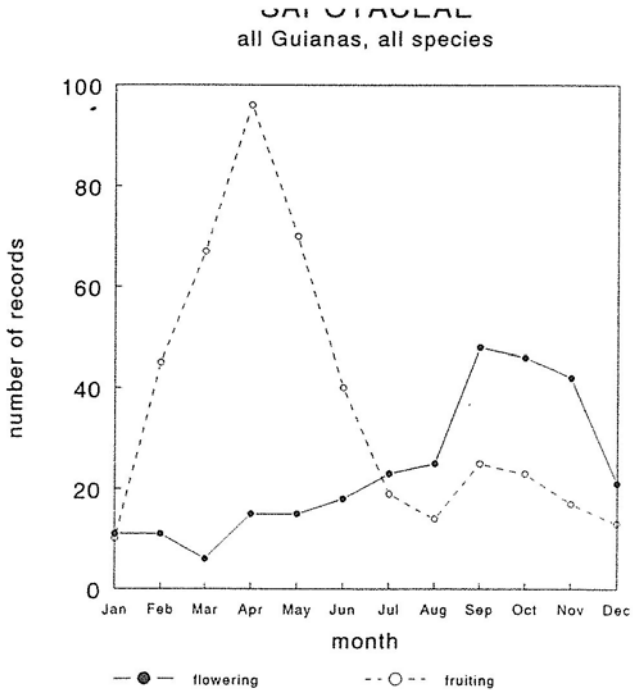

Figure 8. The total number of records for flowering and fruiting in all species of the Sapotaceae for Guyana, Surinam and French Guiana summarized.

the amount of sunshine hours is at peak. This agrees well with the findings of v. Schaik and Terborgh (manuscr.). If sunshine is limiting production, flowering around the peak sunshine is beneficial. Since many species start to flower before this peak, it is unlikely however that sunshine alone is the trigger for flowering. More likely the decrease in rain may act as an additional signal that the sunny period is arriving. In *Tabebuia* spp. it is indeed shown that flower buds are produced after leaf flush. Anthesis takes place after leaf fall in the next dry period (Borchert 1983). The leaf fall results in a relative re-hydration of the inflorescences. In other *Tabebuia* spp. the inflorescences need the first rain to re-hydrate properly.

Fruiting in Guyana is more bimodal than in French Guiana, as is rainfall. Fruiting is strongly related to rainfall. Most fruiting occurs just before maximum precipitation. Moving east to the French Guiana the importance of the dry season in February and March decreases (Mori & Prance 1987), leaving only one clear rainfall peak. The bimodality of fruiting in Guyana is caused by the fact that 1) some species (many Chrysobalanaceae) may flower in either sunny period, but more often in the September-November period, fruiting will be at the end of the next dry season, 2) some species (e.g. *Senna multijuga*) flower just before the peak sunshine and fruit just after it, in November-December. Bimodality in fruiting is very prominent in Trinidad (Snow 1965). In respect of bimodality Guyana is as intermediate as its geographical position.

Since collecting trips were not completely evenly spread over the year, some emphasis

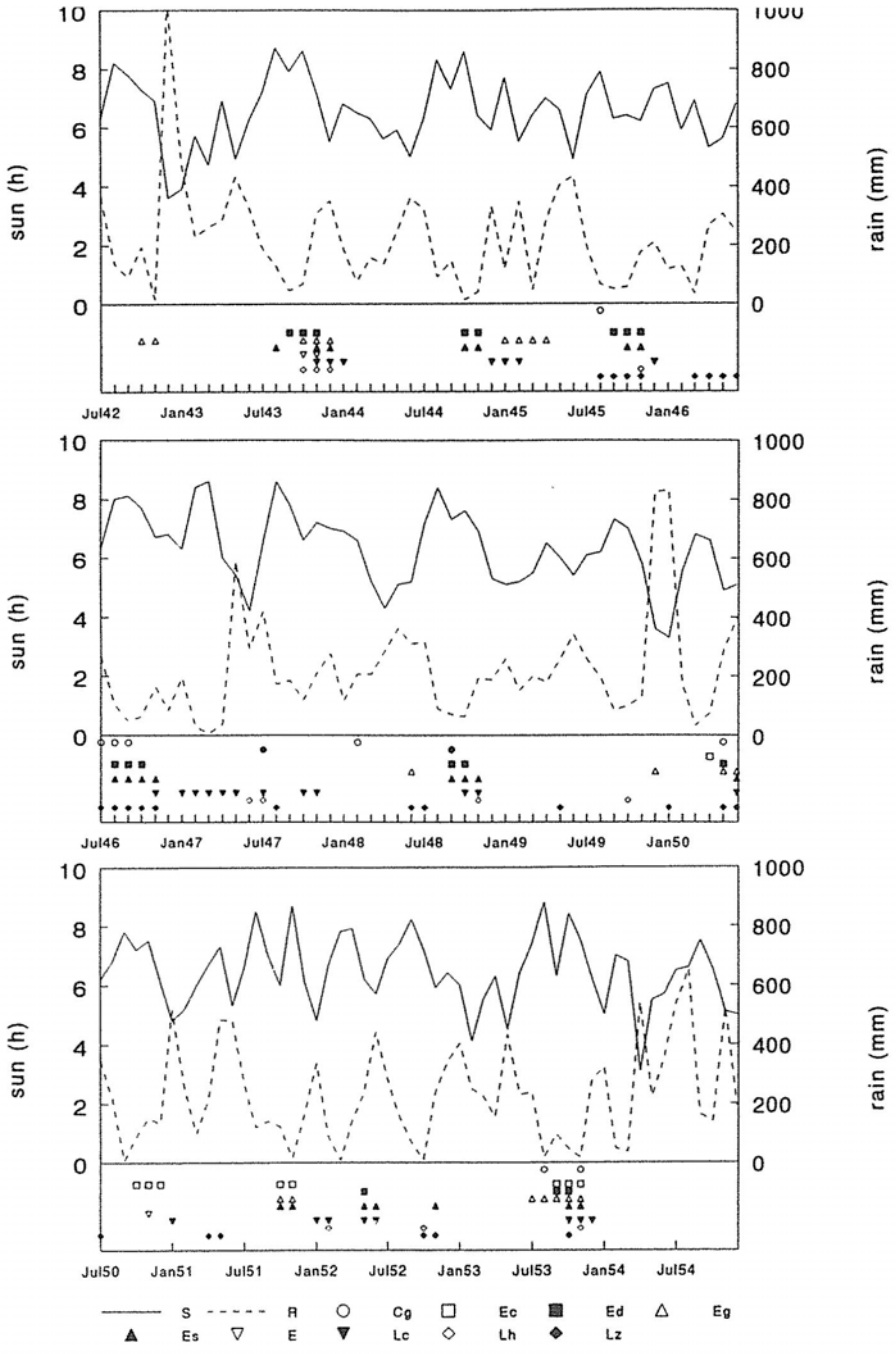

Figure 9. Total rainfall (mm), hours of sunshine/day (Georgetown, 06°24'N, 58°39'W), and flowering of ten species of Lecythidaceae (Mazaruni station, 06°48'N, 58°08'W) per month for the period July 1942 until June 1954.

may have been put on events in the dry seasons (flowering). This may be the cause for the lower overall number of fruiting records (wet season). Also the December - January period (Christmas holiday) may be under-collected. Visibility too is a major factor in recording. In Lecythidaceae flowers are conspicuously colored and readily noted, fruits are brown and far less noted. In Sapotaceae the flowers are small and whitish to greenish-white, but the fruits are big, colorful, and tasty. Here fruits are observed far more often than flowers. In the Surinam data (herbaria) this discrepancy is almost non-existent. Generally speaking flowers will be observed more easily than fruits. Still the maximum number of species per month is equal for both flowering and fruiting.

Mast fruiting, as found in the Dipterocarpaceae in South East Asia, does not seem to occur in Guyana. The existence of mast fruiting in the Guianas was mentioned by Sabatier (1985) for the Lecythidaceae. In March 1982 eight species of Lecythidaceae produced seeds at the same time (Sabatier 1985) and 16 species flowered in Saül, French Guiana in 1982 (Mori & Prance 1987). The data from Mazaruni station do not support the existence of mast fruiting in this family. Rather it seems that all species are triggered by the same climatological factor. Our data are partly from Mazaruni station (the trees) and partly from Georgetown (climate for those years). Therefore, they cannot give clear cut climatological triggers for the observed irregular flowering. Since all species flower in the dry season the trigger could either be drought or sunshine. Many canopy species of Lecythidaceae become bare before flowering; the subsequent flowering is observed just before or after leaf flush (Mori & Prance 1987). This type of flowering resembles the one found in *Tabebuia* and may well have the same physiological basis (see Borchert 1983). In Dipterocarpaceae flowering depends on the amount of sunshine in the months before flowering plus the internal energy status of the tree (v. Schaik 1986). The longer the interval between flowering, the lower the threshold for flowering becomes. In Dipterocarpaceae this threshold seems to be equal for all species - all species will flower at the same irregular intervals, between 1 and 7 years. In Lecythidaceae all individuals of a species are likely to have the same 'energy threshold' for flowering so that all individuals flower at the same time. Since not al species seem to react similarly, this does not hold on the family level. Flowering of most species may be described as irregular, but will almost always fall within a dry period. Mori & Prance (1987) also noted that in *Bertholletia excelsa* Humboldt and Bonpland a year of great seed production will usually be followed by a year of reduced flowering activity. Species such as *Lecythis corrugata* and *Eschweilera decolorans* flower almost every year. Within the Chrysobalanaceae nor within the Sapotaceae mast-like activities occur. Almost every year a few species of these families flower.

Although most species seem to flower around the time with maximum insolation, this is not always the case. In Chrysobalanaceae flowering occurs for almost 30% around the small insolation peak. In Lecythidaceae this is only about 15%, while in Guttiferae and Myristicaceae there is only one clear flowering peak. Although we may suggest that energy thresholds for flowering at the family level are different, our data are not of the kind to proof it. Neither can we give the exact clue for flowering, which again may be different for different taxa. In this respect it can also be noted that competition for pollinators may play a role in segregating flowering times of related species (Mori & Prance 1987), the same holds true for fruiting (Snow 1965). In order to produce good evidence for the

relation between flowering, fruiting and climatic events, good recording of all components should be exercised in the same areas, and for a very long time. In this respect South East Asia seems to have had the advantage. Recently a more extensive solar measuring network was set up in Guyana (Persaud 1982). However phenology measurements have come to an almost halt. It is hoped that the Guyana Forestry Commission will in due time restart with these measurements.

Acknowledgments

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Appendix 1. The complete data set for all 190 species found in the 'Autecology of Guyanese Trees'. Scored are the observations of flowering and fruiting of a species per month. E.g. an 8 for *Anacardium giganteum* for flowering under January means that in the said period flowering has been observed 8 times (in 8 different! years) in January. The data cover a time span from 1887 to 1989. Names and authorities are according to Mennega et al. (1988), exept for *Chlorocardium rodiei*, which has been renamed recently.

	month	J	F	M	A	M	J	J	A	S	O	N	D
Anacardiaceae													
Anacardium giganteum W. Hanc. ex Engl.													
	flowering	8	8	1	0	1	4	4	3	0	0	0	4
	fruiting	0	3	5	5	0	0	1	1	2	1	0	0
Loxopterygium sagotii Hook.f.													
	flowering	2	4	0	3	1	2	2	0	3	3	1	1
	fruiting	1	1	2	1	4	3	1	2	0	1	0	3
Spondias mombin L.													
	flowering	0	3	3	3	3	1	0	0	3	3	5	0
	fruiting	0	1	3	4	3	2	5	4	3	2	2	0
Tapirira guianensis Aubl.													
	flowering	1	0	1	14	14	12	8	2	11	19	14	6
	fruiting	1	7	8	2	0	0	1	0	5	3	1	1
Tapirira marchandii Engl.													
	flowering	1	0	0	8	8	2	1	1	6	13	13	1
	fruiting	0	3	8	3	2	2	0	2	5	3	2	0
Annonaceae													
Xylopia nitida Dunal													
	flowering	0	1	2	2	2	2	1	0	1	1	0	0
	fruiting	1	4	3	2	1	0	1	0	0	0	0	0
Xylopia pulcherima Sandw.													
	flowering	0	0	0	0	0	2	3	2	1	3	2	0
	fruiting	0	1	1	1	0	0	0	0	1	0	0	0
Apocynaceae													
Aspidosperma album (Vahl) Benth.													
	flowering	0	0	0	0	0	0	1	2	0	1	0	0
	fruiting	1	1	2	1	2	1	1	0	0	0	0	0
Aspidosperma exselsum Benth.													
	flowering	1	2	1	0	0	9	3	0	1	1	0	0
	fruiting	1	4	3	5	2	0	0	0	0	0	1	0
Himatanthus bracteatus (A.DC.) Woodson													
	flowering	3	9	4	2	6	7	10	8	10	12	13	11
	fruiting	0	1	2	0	1	1	0	1	0	0	1	2

Appendix 1. Continued.

	month	J	F	M	A	M	J	J	A	S	O	N	D
Macoubea guianensis Aubl.													
	flowering	0	0	0	0	1	0	0	1	2	3	0	0
	fruiting	0	0	2	1	3	0	0	1	2	1	1	1
Parahancornia fasciculata (Poir.) Benoist													
	flowering	1	0	0	0	0	1	0	2	2	3	2	0
	fruiting	1	3	8	8	6	3	1	1	0	0	1	1
Araliaceae													
Schefflera decaphylla (Seemann) Harms													
	flowering	0	2	2	0	0	0	0	0	0	0	0	0
	fruiting	0	1	1	2	11	2	0	0	0	0	0	0
Schefflera morototoni (Aubl.) Maguire, Steyerm. & Frodin													
	flowering	1	7	9	4	0	0	0	1	2	3	0	0
	fruiting	0	0	1	1	10	8	3	2	1	3	2	1
Bignoniaceae													
Jacaranda copaia (Aubl.) D. Don													
	flowering	0	2	5	6	7	4	2	7	9	18	17	9
	fruiting	0	0	7	4	2	0	1	0	1	1	0	0
Tabebuia capitata (Bureau & Schumann) Sandw.													
	flowering	0	0	2	4	1	0	0	1	1	4	3	0
	fruiting	0	0	0	0	0	0	0	0	0	0	0	0
Tabebuia insignis (Miq.) Sandw. var. *monophylla* Sandw.													
	flowering	1	10	4	5	1	1	4	4	3	1	2	0
	fruiting	1	1	3	3	0	0	0	0	0	0	0	0
Tabebuia serratifolia (Vahl) Nicholson													
	flowering	0	1	3	4	1	0	0	0	1	2	3	1
	fruiting	0	0	0	0	1	0	0	0	0	0	0	0
Bombacaceae													
Bombax flaviflorum Pulle													
	flowering	0	0	0	0	0	0	0	0	0	2	1	0
	fruiting	0	2	4	2	0	0	1	0	0	0	1	0
Bombax surinamense Uittien													
	flowering	0	0	0	0	0	0	0	0	2	4	2	0
	fruiting	0	0	0	0	0	0	0	0	1	1	0	2
Catostemma altsonii Sandw.													
	flowering	0	0	2	0	0	0	0	1	3	1	1	0
	fruiting	1	0	1	3	3	1	1	1	1	1	0	1

Appendix 1. Continued.

	month	J	F	M	A	M	J	J	A	S	O	N	D
Catostemma commune Sandw.													
	flowering	0	3	9	7	4	0	0	0	0	0	0	0
	fruiting	4	6	5	0	0	0	2	0	2	7	11	7
Catostemma fragrans Benth.													
	flowering	2	1	0	1	0	0	1	1	1	0	0	1
	fruiting	1	2	0	1	1	1	2	3	1	1	1	1
Ceiba pentandra (L.) Gaertner													
	flowering	1	1	2	1	0	0	0	1	0	0	1	0
	fruiting	0	0	0	2	3	3	3	1	1	1	0	0
Pachira aquatica Aubl.													
	flowering	1	2	0	1	1	3	4	2	1	1	7	6
	fruiting	0	1	1	2	2	1	2	5	4	4	2	1
Boraginaceae													
Cordia exalta Lam. var. *melanoneura* I.M.Johnston													
	flowering	1	1	2	3	4	2	4	12	15	12	2	1
	fruiting	5	9	3	2	0	0	1	1	0	0	0	2
Burseraceae													
Protium decandrum (Aubl.) Marshall													
	flowering	1	0	1	1	0	2	2	1	1	1	1	1
	fruiting	1	4	6	3	0	0	2	1	3	2	3	2
Protium heptaphyllum (Aubl.) March.													
	flowering	0	0	0	0	0	0	0	0	0	0	3	1
	fruiting	0	0	0	0	0	0	0	1	2	2	0	0
Protium hostmannii (Miq.) Engl.													
	flowering	2	0	0	0	0	0	0	0	0	1	2	3
	fruiting	1	2	3	3	2	0	1	2	2	1	0	0
Tetragastris panamensis (Engl.) Kuntze													
	flowering	0	0	0	0	0	0	0	0	0	1	0	0
	fruiting	0	1	2	4	4	2	2	2	2	1	0	0
Caesalpiniaceae													
Campsiandra comosa Beth. var. *comosa*													
	flowering	0	0	0	0	1	0	1	6	11	8	0	0
	fruiting	0	3	2	5	5	2	0	0	0	0	0	1
Cassia cowanii Irwin & Barneby var. *guianensis* (Sandw.) Irwin & Barneby													
	flowering	1	3	7	6	2	0	1	1	6	10	2	0
	fruiting	0	0	0	1	2	0	0	0	0	1	0	1

Appendix 1. Continued.

month	J	F	M	A	M	J	J	A	S	O	N	D
Chamaecrista adiantifolia (Benth.) Irwin & Barneby var. *pteridophylla* (Sandw.) Irwin & Barneby												
flowering	0	0	0	7	6	4	1	0	5	12	15	2
fruiting	0	0	1	0	0	0	0	1	2	1	0	0
Dimorphandra conjugata (Splitg.) Sandw.												
flowering	0	0	0	0	6	5	0	0	0	0	1	0
fruiting	0	0	0	0	0	0	0	0	2	2	1	0
Eperua falcata Aubl.												
flowering	2	0	3	9	6	6	4	10	19	21	20	8
fruiting	2	6	5	7	5	2	2	3	3	3	3	1
Eperua grandiflora (Aubl.) Benth. ssp. *guianensis* Cowan												
flowering	2	1	3	5	4	5	3	5	13	14	12	8
fruiting	2	4	2	2	1	1	1	0	0	0	1	0
Eperua jenmanii Oliver												
flowering	2	1	1	8	10	8	5	6	22	23	20	14
fruiting	1	2	5	8	4	2	1	0	0	0	0	0
Eperua schomburgkiana Benth.												
flowering	0	0	0	1	1	1	3	9	10	4	0	0
fruiting	0	1	3	3	4	1	1	0	0	1	1	1
Hymenaea courbaril L.												
flowering	0	0	0	1	5	7	2	1	0	1	0	0
fruiting	0	0	3	2	1	0	1	1	3	1	1	2
Hymenaea oblongifolia Huber var. *davisii* (Sandw.) Lee & Langenheim												
flowering	0	1	3	0	3	4	0	0	2	2	1	1
fruiting	0	0	3	7	8	4	0	1	1	0	0	0
Macrolobium bifolium (Aubl.) Persoon												
flowering	1	1	2	4	5	3	5	11	16	20	13	4
fruiting	0	2	3	4	2	0	0	0	0	0	0	0
Mora excelsa Benth.												
flowering	5	12	10	2	0	0	2	3	1	0	0	0
fruiting	0	0	0	0	1	5	7	0	1	3	4	0
Mora gonggrijpii (Kleinhoonte) Sandw.												
flowering	2	6	3	1	0	0	2	2	0	0	0	0
fruiting	1	1	0	0	1	4	2	0	1	6	7	1
Peltogyne paniculata Benth. ssp. *pubescens* (Benth.) M.F. Silva												
flowering	0	0	0	0	0	4	2	2	3	9	12	5
fruiting	0	0	0	4	4	0	0	0	0	0	0	1

Appendix 1. Continued.

	month	J	F	M	A	M	J	J	A	S	O	N	D
Peltogyne venosa (Vahl) Benth. ssp. *densiflora* (Spruce ex Benth.) M.F. Silva													
	flowering	0	1	3	2	2	2	1	1	2	1	1	0
	fruiting	0	0	0	0	1	1	0	0	1	0	0	0
Sclerolobium guianense Benth.													
	flowering	0	0	0	0	0	0	0	1	1	4	4	0
	fruiting	1	0	3	3	0	0	1	1	0	0	0	0
Senna multijuga (Rich) Irwin & Barneby													
	flowering	0	0	0	1	4	9	20	25	18	14	0	0
	fruiting	0	0	0	0	0	0	0	0	3	10	14	3
Caryocaraceae													
Anthodiscus trifoliatus G. Meyer													
	flowering	1	1	0	0	0	1	3	1	1	0	0	1
	fruiting	0	3	2	0	0	0	1	1	0	1	2	3
Caryocar microcarpum Ducke													
	flowering	7	6	2	0	0	0	0	1	2	3	2	2
	fruiting	0	0	0	3	5	2	1	0	0	0	0	0
Caryocar nuciferum L.													
	flowering	4	3	1	1	1	3	5	3	5	13	18	13
	fruiting	0	0	1	4	12	12	7	1	0	0	0	0
Celastraceae													
Goupia glabra Aubl.													
	flowering	0	1	0	0	3	2	0	3	10	9	20	2
	fruiting	4	3	0	0	0	0	1	0	1	2	4	9
Chrysobalanaceae													
Couepia guianensis Aubl.													
	flowering	0	0	0	1	2	2	1	2	1	0	0	0
	fruiting	0	0	1	0	0	1	1	2	1	1	0	2
Licania alba (Bernoulli) Cuatrec.													
	flowering	1	3	7	8	5	4	2	6	15	17	11	4
	fruiting	3	4	9	13	12	4	3	2	5	4	1	1
Licania buxifolia Sandw.													
	flowering	0	0	0	0	0	0	0	0	5	5	1	0
	fruiting	1	2	3	4	5	5	1	1	2	1	0	0
Licania cuprea Sandw.													
	flowering	0	0	1	2	1	0	0	0	0	1	2	2
	fruiting	0	1	2	3	2	0	0	0	2	1	1	0

Appendix 1. Continued.

month	J	F	M	A	M	J	J	A	S	O	N	D
Licania densiflora Kleinhoonte												
flowering	0	0	3	3	11	9	1	2	3	5	8	4
fruiting	0	0	0	0	0	0	0	1	1	0	0	1
Licania heteromorpha Benth. var. *perplexans* Sandw.												
flowering	0	3	5	7	5	0	3	0	2	1	0	1
fruiting	4	1	2	1	1	0	0	0	0	5	5	5
Licania laxiflora Fritsch												
flowering	2	0	1	2	1	3	2	0	2	2	3	0
fruiting	0	0	1	3	3	0	0	0	1	4	4	0
Licania majuscula Sagot												
flowering	0	1	1	0	0	0	0	1	4	3	1	1
fruiting	3	3	0	2	2	0	0	0	0	0	0	0
Licania micrantha Miq.												
flowering	1	0	2	2	0	1	0	0	0	0	2	4
fruiting	0	0	2	2	0	0	0	0	0	1	1	0
Parinari campestris Aubl.												
flowering	0	1	2	0	6	4	0	6	14	6	3	0
fruiting	1	1	3	3	0	1	1	1	0	0	0	0
Parinari excelsa Sabine												
flowering	0	1	2	3	1	0	1	1	0	1	1	2
fruiting	1	2	3	3	3	3	1	1	1	1	0	0
Parinari parvifolia Sandw.												
flowering	0	0	0	1	1	0	0	3	3	4	3	0
fruiting	1	2	2	1	1	1	1	1	2	0	0	0
Parinari rodolphi Huber ?(see Mennega et al. 1988)												
flowering	0	0	0	1	0	0	0	0	1	4	4	1
fruiting	1	1	1	1	1	0	0	1	0	0	0	1
Combretaceae												
Buchenavia fanshawei Maguire ex Exell.												
flowering	0	0	0	0	0	0	0	0	0	0	0	1
fruiting	1	1	2	4	3	3	1	1	2	2	2	2
Terminalia amazonica (J. Gmelin) Exell												
flowering	1	4	3	6	3	3	0	1	0	1	0	0
fruiting	1	3	2	6	8	6	2	0	1	0	0	0
Terminalia dichotoma G. Meyer												
flowering	1	5	2	1	0	3	6	4	3	2	0	0
fruiting	1	2	2	2	1	1	2	0	1	1	0	0

Appendix 1. Continued.

	month	J	F	M	A	M	J	J	A	S	O	N	D
Elaeocarpaceae													
Sloanea grandiflora Smith													
	flowering	0	0	0	0	2	2	3	5	9	6	1	1
	fruiting	0	2	7	7	4	1	1	0	0	0	0	0
Sloanea guianensis (Aubl.) Benth.													
	flowering	0	0	0	0	0	0	0	0	2	0	0	1
	fruiting	0	2	2	3	0	0	0	0	0	1	0	0
Euphorbiaceae													
Amanoa guianensis Aubl.													
	flowering	0	2	3	3	0	0	0	2	1	1	0	0
	fruiting	1	3	5	3	0	0	1	1	0	0	1	0
Chaetocarpus schomburgkianus (Kuntze) Pax & K. Hoffm.													
	flowering	0	2	0	1	2	1	0	0	1	6	10	5
	fruiting	5	9	6	1	3	0	0	1	1	1	1	5
Hevea ssp.													
	flowering	0	2	1	1	1	1	1	1	3	6	3	0
	fruiting	1	0	2	4	4	2	0	0	1	1	0	0
Hyeronima alchorneoides Allemao													
	flowering	1	0	0	0	3	5	9	3	2	3	6	3
	fruiting	1	2	2	0	0	1	1	0	0	1	1	0
Mabea piriri Aubl.													
	flowering	0	0	0	3	4	2	0	0	1	5	7	2
	fruiting	1	2	2	0	0	2	2	1	0	1	0	1
Maprounea guianensis Aubl.													
	flowering	0	0	0	1	2	1	1	1	1	2	3	0
	fruiting	1	4	3	1	1	0	0	0	2	1	2	1
Pera ferruginea (Schott) Muell. Arg.													
	flowering	0	0	0	0	3	3	2	1	1	2	1	1
	fruiting	0	0	0	0	0	1	1	0	0	0	0	0
Flacourtiaceae													
Laetia procera (Poeppig) Endl.													
	flowering	0	1	0	1	2	5	1	1	3	5	4	0
	fruiting	3	10	7	2	0	0	0	0	0	3	4	3
Guttiferae													
Calophyllum lucidum Benth.													
	flowering	0	0	0	0	0	0	1	0	1	3	2	0
	fruiting	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 1. Continued.

	month	J	F	M	A	M	J	J	A	S	O	N	D
Moronobea coccinea Aubl.													
	flowering	0	1	0	1	3	1	2	2	5	16	12	2
	fruiting	1	1	3	10	5	5	2	0	0	0	1	0
Platonia insignis C. Martius													
	flowering	0	0	0	0	0	0	0	0	1	1	0	0
	fruiting	1	1	1	6	4	0	0	0	0	0	0	0
Symphonia globulifera L.f.													
	flowering	1	3	3	3	6	7	17	15	13	11	8	1
	fruiting	1	2	7	5	1	0	1	0	0	0	0	0
Tovomita obovata Engl.													
	flowering	0	1	0	1	2	3	4	4	6	4	1	1
	fruiting	3	4	5	7	0	0	0	0	0	0	0	1
Hernandiaceae													
Hernandia guianensis Aubl.													
	flowering	0	0	1	0	0	0	3	3	1	0	0	0
	fruiting	0	0	1	3	2	0	0	0	1	1	1	0
Humiriaceae													
Humiria balsamifera (Aubl.) St. Hill.													
	flowering	0	0	0	1	5	5	1	0	1	2	0	0
	fruiting	1	1	2	1	0	0	0	0	3	2	1	1
Humiriastrum obovatum (Benth.) Cuatrec.													
	flowering	1	0	0	1	0	0	0	0	0	1	2	0
	fruiting	0	0	2	4	2	2	0	0	0	0	1	0
Saccoglottis guianensis Benth.													
	flowering	0	1	1	0	2	2	3	0	0	1	1	1
	fruiting	0	1	0	1	2	2	0	0	3	4	4	1
Icacinaceae													
Emmotum fagifolium Desv.													
	flowering	0	0	0	2	3	2	0	1	2	7	9	5
	fruiting	0	5	7	4	4	2	1	2	2	1	1	0
Lauraceae													
Aniba hypoglauca Sandw.													
	flowering	0	1	0	0	1	3	2	2	0	0	0	0
	fruiting	1	0	1	0	0	0	0	0	0	1	0	0
Chlorocardium rodiei (Schomb.) Rohwer, Richter & vd Werff													
	flowering	2	1	4	3	5	3	1	1	1	1	2	0
	fruiting	2	3	8	6	4	2	0	0	0	0	0	0

Appendix 1. Continued.

month	J	F	M	A	M	J	J	A	S	O	N	D
Licaria canella (Meissner) Kosterm.												
flowering	0	0	0	1	1	0	0	1	0	0	0	0
fruiting	4	2	0	2	0	0	1	1	1	1	2	1
Nectandra cuspidata Nees												
flowering	0	0	0	1	1	3	11	18	10	1	0	0
fruiting	3	4	3	0	2	0	0	0	0	1	1	1
Nectandra rubra (Mez) Allen												
flowering	0	0	0	0	0	0	0	0	0	1	0	0
fruiting	0	1	2	0	0	0	0	0	0	1	0	0
Ocotea canaliculata (Rich.) Mez												
flowering	0	1	1	0	4	6	2	1	0	0	1	1
fruiting	1	3	0	2	1	1	0	1	0	1	1	0
Ocotea oblonga (Meissner) Mez												
flowering	0	2	1	0	5	10	3	2	0	0	0	0
fruiting	0	0	0	0	1	0	0	0	0	0	0	0
Ocotea tomentella Sandw.												
flowering	8	9	4	0	0	0	1	0	0	1	0	0
fruiting	1	1	1	1	1	1	0	0	0	0	0	1
Ocotea wachenheimii Benoist												
flowering	0	1	1	1	1	5	5	0	0	0	0	0
fruiting	0	0	0	1	3	2	0	0	0	0	0	0
Lecythidaceae												
Couratari guianensis Aubl.												
flowering	0	1	1	0	1	0	3	8	7	0	1	0
fruiting	1	2	3	3	1	0	0	0	0	1	1	2
Couratari multiflora (Smith) Eyma												
flowering	0	0	0	0	0	0	2	2	2	0	0	0
fruiting	0	0	0	0	0	0	0	0	1	0	0	0
Eschweilera coriacea (DC.) C. Martius ex O. Berg												
flowering	0	0	0	3	2	0	0	0	1	8	10	3
fruiting	1	6	6	2	0	0	0	1	2	0	0	0
Eschweilera decolorans Sandw.												
flowering	0	0	0	5	6	3	1	3	14	20	16	8
fruiting	1	7	7	2	1	1	1	2	2	1	1	0
Eschweilera grata Sandw.												
flowering	1	1	1	1	1	3	3	2	3	9	10	6
fruiting	0	4	6	2	1	0	0	0	0	0	0	0

Appendix 1. Continued.

month	J	F	M	A	M	J	J	A	S	O	N	D
Eschweilera sagotiana Miers												
flowering	0	0	0	5	6	3	0	2	6	16	19	8
fruiting	1	7	8	2	1	0	2	4	3	1	0	0
Eschweilera subglandulosa (Steudel) Miers												
flowering	0	0	1	0	0	0	1	1	1	2	0	0
fruiting	0	0	1	0	0	0	0	0	0	0	0	0
Eschweilera wachenheimii (Benoist) Sandw.												
flowering	0	0	0	0	0	0	0	2	2	3	2	0
fruiting	0	2	2	1	1	0	0	0	0	0	0	1
Lecythis corrugata Poit.												
flowering	10	11	2	1	4	6	4	1	2	5	14	12
fruiting	0	3	4	3	3	1	1	3	3	0	0	0
Lecythis holcogyne (Sandw.) S. Mori												
flowering	0	3	2	1	0	3	1	3	3	6	7	2
fruiting	1	0	2	3	4	0	1	3	2	1	0	0
Lecythis zabucajo Aubl.												
flowering	2	3	2	4	5	5	5	8	7	7	8	2
fruiting	0	1	3	3	1	1	0	0	1	0	0	0
Linaceae												
Hebepetalum humiriifolium (Planchon) Benth. ex Jackson												
flowering	0	0	0	0	0	0	0	0	1	3	2	1
fruiting	0	1	0	1	0	0	0	0	0	1	0	0
Lissocarpaceae												
Lissocarpa guianensis Gleason												
flowering	0	0	0	1	0	0	1	1	5	7	10	3
fruiting	1	2	0	1	3	2	2	0	0	0	0	0
Malpighiaceae												
Byrsonima aerugo Sagot var. *occidentalis* Niedenzu												
flowering	0	1	3	4	2	4	5	1	4	4	2	0
fruiting	6	8	4	0	2	5	7	4	4	1	3	7
Byrsonima stipulacea Adr. Juss.												
flowering	0	3	3	3	4	14	20	23	12	1	0	0
fruiting	12	3	2	0	0	1	0	0	2	3	17	20
Melastomataceae												
Miconia guianensis (Aubl.) Cogn												
flowering	1	1	3	6	5	9	18	24	17	9	0	0
fruiting	1	0	0	0	0	0	0	0	0	0	5	5

Appendix 1. Continued.

month	J	F	M	A	M	J	J	A	S	O	N	D
Mouriria huberi Cogn.												
flowering	0	0	0	1	1	2	1	0	0	0	3	3
fruiting	0	3	3	3	2	0	3	3	2	2	1	1
Meliaceae												
Carapa guianensis Aubl.												
flowering	6	5	3	0	0	0	0	0	1	3	9	6
fruiting	0	1	2	4	4	3	3	0	1	1	1	0
Cedrela odorata L.												
flowering	0	0	0	0	0	0	0	2	1	1	1	0
fruiting	1	1	1	0	0	0	0	0	0	0	0	0
Guarea guidonia (L.) Sleumer												
flowering	0	2	1	1	1	4	2	1	0	0	0	0
fruiting	0	0	0	2	1	0	1	1	1	1	0	1
Mimosaceae												
Inga alba (Sw.) Willd.												
flowering	0	0	0	2	5	4	0	4	6	3	1	1
fruiting	4	3	3	0	0	0	0	1	2	3	4	4
Inga laterifolia Miq.												
flowering	3	2	0	0	0	0	1	1	0	0	3	8
fruiting	1	5	9	7	2	0	0	0	0	0	0	0
Inga pezezifera Benth.												
flowering	0	0	0	0	0	1	4	4	1	0	1	0
fruiting	0	1	3	3	1	0	0	0	0	0	0	0
Inga splendens Willd.												
flowering	0	2	3	2	2	2	2	0	0	0	0	0
fruiting	1	1	2	2	3	0	0	0	0	2	0	0
Newtonia suaveolens (Miq.) Brenan												
flowering	0	0	1	1	1	0	0	1	3	3	0	0
fruiting	0	0	3	2	1	2	0	0	0	1	0	0
Parkia ulei (Harms) Kuhlm. var. *surinamensis* Kleinhoonte												
flowering	0	0	0	2	2	2	2	3	2	5	5	1
fruiting	1	5	2	0	2	2	1	2	3	2	0	0
Pentaclethra macroloba (Willd.) Kuntze												
flowering	0	0	0	1	2	9	10	7	10	12	6	0
fruiting	0	2	6	4	4	1	0	0	0	0	0	1
Pithecellobium jupunba (Willd.) Urban												
flowering	4	7	9	6	4	8	10	8	5	5	6	4
fruiting	2	4	2	3	3	2	1	1	1	3	1	2

Appendix 1. Continued.

	month	J	F	M	A	M	J	J	A	S	O	N	D
Pithecellobium pedicellare (DC.) Benth.													
	flowering	0	1	0	0	1	0	0	0	2	2	0	0
	fruiting	1	0	3	2	0	0	0	1	2	0	1	0
Moraceae													
Bagassa guianensis Aubl.													
	flowering	0	1	0	0	0	0	2	3	2	0	1	0
	fruiting	1	3	6	8	6	5	5	1	0	0	0	1
Trymatococcus paraensis Ducke													
	flowering	1	0	0	0	0	0	0	0	0	0	1	2
	fruiting	2	2	0	1	2	3	6	3	4	2	1	1
Myristicaceae													
Iryanthera lancifolia Ducke													
	flowering	1	0	1	0	1	0	0	2	1	1	1	0
	fruiting	1	2	4	11	7	1	0	0	1	3	1	0
Virola sebifera Aubl.													
	flowering	0	0	1	1	0	0	4	5	4	2	0	0
	fruiting	2	1	1	0	0	0	0	0	1	0	1	1
Virola surinamensis (Rolander) Warb													
	flowering	1	2	1	5	7	10	10	4	16	21	17	4
	fruiting	0	1	5	6	2	2	0	0	0	0	1	1
Myrtaceae													
Eugenia arawakorum Sandw.													
	flowering	0	0	1	2	1	0	0	0	0	1	2	0
	fruiting	0	0	0	0	0	2	1	0	0	0	0	0
Eugenia patrisii Vahl													
	flowering	0	0	0	0	0	0	1	0	1	2	0	0
	fruiting	2	0	2	3	4	4	1	1	2	2	2	1
Nyctaginaceae													
Neea cauliflora Heimerl.													
	flowering	0	0	0	2	1	1	1	0	1	1	1	1
	fruiting	0	2	1	0	0	0	1	0	0	0	0	0
Ochnaceae													
Cespedezia amazonica Huber													
	flowering	1	0	0	1	2	2	3	0	1	2	2	1
	fruiting	0	0	0	0	0	0	0	1	1	0	0	0

Appendix 1. Continued.

	month	J	F	M	A	M	J	J	A	S	O	N	D
Olacaceae													
Chaunochiton kappleri (Sagot ex Engl.) Ducke													
	flowering	0	0	0	1	1	0	1	8	7	1	0	0
	fruiting	0	0	0	0	1	0	0	0	2	1	3	2
Palmae													
Astrocaryum aculeatum G. Meyer													
	flowering	0	0	0	0	0	0	0	0	0	0	0	0
	fruiting	4	8	10	9	7	11	12	8	4	4	2	2
Papilionaceae													
Acosmium nitens (Vogel) Yakovlev													
	flowering	0	1	5	4	2	1	1	1	1	0	0	0
	fruiting	0	0	1	1	0	0	1	0	0	0	0	0
Acosmium preaclara (Sandw.) Yakovlev													
	flowering	0	0	1	1	1	0	1	0	0	0	0	0
	fruiting	0	0	0	0	1	0	0	0	3	4	2	0
Aldina insignis (Benth.) Endl.													
	flowering	0	1	2	4	0	0	1	5	7	5	0	0
	fruiting	0	0	0	0	1	0	0	0	1	1	1	0
Alexa imperatricis (Schomb.) Britton													
	flowering	1	3	2	1	0	0	2	1	1	0	1	1
	fruiting	0	0	1	3	4	0	0	0	0	0	0	0
Alexa leiopetala Sandw.													
	flowering	9	6	1	0	2	5	4	4	1	0	5	9
	fruiting	0	0	4	8	5	0	0	0	0	0	0	0
Andira inermis (Wright) Kunth													
	flowering	0	3	1	3	1	3	0	0	0	1	1	0
	fruiting	0	1	1	1	4	1	1	0	1	0	0	0
Clathtropis brachypetala (Tul.) Kleinhoonte													
	flowering	2	4	8	6	5	6	9	11	14	12	6	2
	fruiting	0	1	1	2	4	2	4	2	2	1	0	0
Diplotropis purpurea (Rich.) Amshoff													
	flowering	7	8	3	0	0	0	0	0	0	0	0	0
	fruiting	0	0	0	8	4	0	0	0	0	1	0	0
Dipterix odorata (Aubl.) Willd.													
	flowering	0	1	0	0	1	2	5	0	0	1	4	0
	fruiting	4	6	5	2	1	1	2	0	1	1	0	1

Appendix 1. Continued.

	month	J	F	M	A	M	J	J	A	S	O	N	D
Hymenolobium sp. nov.													
	flowering	1	3	4	0	0	0	1	2	0	0	2	0
	fruiting	0	0	0	3	3	0	0	0	2	2	0	0
Ormosia coarctata B.D. Jackson													
	flowering	0	0	1	2	0	0	1	1	0	0	0	1
	fruiting	1	2	1	1	0	0	0	2	1	2	2	0
Ormosia coccinea (Aubl.) B.D. Jackson													
	flowering	0	2	1	0	0	1	0	0	1	2	4	1
	fruiting	0	0	2	1	1	2	0	0	1	1	1	0
Ormosia coutinhoi Ducke													
	flowering	0	3	4	0	0	1	2	3	2	1	0	0
	fruiting	2	3	2	1	2	2	1	1	1	1	0	0
Pterocarpus officinalis Jacq.													
	flowering	0	12	17	11	3	1	1	1	0	3	1	1
	fruiting	0	0	0	3	3	2	1	0	0	0	0	0
Swartzia benthamii Miq. var. *benthamii*													
	flowering	0	0	2	1	0	2	0	0	1	4	2	0
	fruiting	1	0	1	0	0	0	0	0	0	2	0	0
Swartzia leiocalycina Benth.													
	flowering	5	4	0	0	1	4	4	0	0	0	0	2
	fruiting	0	0	4	6	4	0	0	0	2	3	1	0
Swartzia oblanceolata Sandw.													
	flowering	0	6	4	0	0	2	4	1	1	1	1	0
	fruiting	0	0	0	2	2	3	1	0	1	2	1	0
Swartzia schomburgkii Benth. var. *schomburgkii*													
	flowering	0	0	1	1	1	0	5	9	11	9	2	0
	fruiting	7	4	1	0	0	0	1	0	0	0	1	1
Swartzia sprucei Benth. var. *tesselata* Cowan													
	flowering	2	0	0	1	0	1	0	0	0	6	7	4
	fruiting	0	0	0	2	0	0	0	0	0	1	0	1
Vatairea guianensis Aubl.													
	flowering	4	4	1	1	0	3	4	2	0	0	0	1
	fruiting	0	0	1	1	0	0	4	5	4	2	0	0
Proteaceae													
Panopsis sessilifolia (Rich.) Sandw.													
	flowering	0	0	0	0	2	5	1	1	3	3	5	0
	fruiting	0	0	0	2	1	0	0	0	0	0	0	0

Appendix 1. Continued.

month	J	F	M	A	M	J	J	A	S	O	N	D
Rubiaceae												
Duroia eriopila L.f. var. *eriopila*												
flowering	1	0	1	0	0	0	1	0	4	7	2	1
fruiting	0	0	0	3	5	3	1	1	0	1	0	0
Genipa americana L.												
flowering	0	0	0	0	0	0	0	0	2	1	1	0
fruiting	0	0	0	1	3	2	1	1	0	1	1	0
Guetarda acreana Krause												
flowering	0	0	0	0	1	2	2	0	0	0	0	0
fruiting	0	0	0	0	0	0	0	2	4	0	0	0
Rutaceae												
Hortia regia Sandw.												
flowering	0	0	1	0	0	0	2	0	1	0	4	3
fruiting	0	0	1	5	3	1	0	0	0	0	1	0
Sapindaceae												
Matayba opaca Radlk.												
flowering	2	2	1	0	1	2	0	0	0	0	0	1
fruiting	0	0	2	2	1	0	1	1	2	2	0	0
Talisia furfuracea Sandw.												
flowering	0	1	1	0	0	0	1	2	1	2	0	0
fruiting	0	0	0	0	1	0	0	0	0	0	0	0
Talisia squarosa Radlk.												
flowering	0	1	0	1	1	2	0	3	7	6	1	2
fruiting	1	1	0	1	1	0	0	0	0	0	3	2
Sapotaceae												
Chrysophyllum argenteum Jacq. ssp. *auratum* (Miq.) Penn.												
flowering	0	0	0	0	1	2	4	5	7	5	0	0
fruiting	0	1	2	1	0	0	0	0	0	0	0	0
Chrysophyllum pomiferum (Eyma) Penn. (Limonaballi)												
flowering	0	1	1	1	1	0	0	1	2	6	3	2
fruiting	0	2	3	7	11	8	1	0	0	0	0	0
Chrysophyllum pomiferum (Eyma) Penn. (Paripiballi)												
flowering	2	0	2	0	0	0	1	2	3	1	0	0
fruiting	0	5	6	3	2	2	0	1	2	5	3	0
Ecclinusa sanguinolenta (Pierre) Engl.												
flowering	0	0	0	0	0	1	1	2	1	0	0	0
fruiting	0	0	4	5	1	1	0	0	0	0	0	0

Appendix 1. Continued.

month	J	F	M	A	M	J	J	A	S	O	N	D
Manilkara bidentata (A. DC.) Chev. ssp. *bidentata*												
flowering	0	2	1	0	4	7	4	3	1	1	0	0
fruiting	0	2	5	3	0	0	0	0	0	2	1	0
Oxythece ambelaniifoilia (Sandw.) Cronq.												
flowering	0	0	0	0	0	0	1	0	1	4	2	0
fruiting	0	1	6	8	9	1	0	0	2	3	2	0
Pouteria cladantha Sandw.												
flowering	0	0	0	0	0	0	0	0	0	0	1	0
fruiting	0	1	2	3	2	1	0	0	0	0	0	0
Pouteria dura Eyma												
flowering	0	0	0	0	0	0	0	1	4	2	1	0
fruiting	0	0	2	2	1	1	0	0	1	1	1	0
Pouteri egregia Sandw.												
flowering	0	1	0	0	0	0	0	1	2	2	5	1
fruiting	0	0	0	4	3	7	6	5	2	0	0	0
Pouteria guianensis Eyma												
flowering	1	0	0	4	3	3	0	0	1	5	8	6
fruiting	0	0	5	11	2	0	1	2	1	0	0	0
Pouteria jenmanii (Pittier) Sandw.												
flowering	0	0	0	0	0	0	0	1	2	2	1	0
fruiting	0	1	3	10	7	3	0	0	2	1	1	0
Pouteria melinonii (Engl.) Baehni												
flowering	2	3	0	0	2	4	1	0	0	0	1	1
fruiting	0	4	7	12	9	1	0	0	0	1	3	3
Pouteria minutiflora (Britton) Sandw.												
flowering	0	0	0	0	2	1	1	1	0	0	1	1
fruiting	0	0	2	7	7	5	2	1	1	3	0	0
Pouteria reticulata (Engl.) Eyma												
flowering	0	1	2	1	0	0	1	0	0	0	0	1
fruiting	0	0	0	0	0	1	1	0	3	2	0	0
Pouteria speciosa (Ducke) Baehni												
flowering	0	0	1	1	3	3	0	1	5	2	0	0
fruiting	0	3	2	2	1	0	0	1	2	0	0	2
Pouteria venosa (C. Martius) Baehni												
flowering	1	2	0	1	0	2	0	0	0	6	5	0
fruiting	2	1	1	6	7	4	2	2	0	0	0	1

Appendix 1. Continued.

	month	J	F	M	A	M	J	J	A	S	O	N	D
Pradosia schomburgkiana (A. DC.) Cronq.													
	flowering	0	2	0	0	0	0	0	0	0	1	1	1
	fruiting	0	0	0	0	4	3	0	0	1	1	0	0
Simaroubaceae													
Quassia multiflora (Adr. Juss.) Nooteboom													
	flowering	0	2	4	1	0	0	0	0	0	0	0	0
	fruiting	0	0	2	4	0	0	0	0	0	0	0	0
Quassia simaruba L.f.													
	flowering	0	1	0	0	3	3	1	1	4	3	3	0
	fruiting	4	2	2	1	1	0	0	0	0	0	0	0
Sterculiaceae													
Sterculia priuriens (Aubl.) Schumann													
	flowering	11	19	13	5	2	3	2	5	0	0	0	0
	fruiting	0	0	0	1	4	8	7	1	0	0	0	0
Xylosterculia rugosa (R. Br.) Kosterm.													
	flowering	0	0	0	0	0	1	5	1	1	0	0	0
	fruiting	1	5	6	4	3	1	0	0	0	0	1	1
Tiliaceae													
Apeiba echinata Gaertner													
	flowering	5	3	1	1	1	1	1	3	8	9	12	8
	fruiting	1	1	1	1	1	2	5	4	3	2	0	1
Verbenaceae													
Vitex stahelii Mold.													
	flowering	1	3	13	13	4	1	1	0	0	2	1	0
	fruiting	0	0	0	1	4	7	5	0	0	0	0	0
Vochysiaceae													
Vochysia tetraphylla (G. Meyer) DC.													
	flowering	1	0	1	10	11	8	3	1	6	17	21	13
	fruiting	1	5	8	2	1	0	2	3	3	1	1	0

Tropical rain forest types and soils of a watershed in Guyana, South America

Hans ter Steege, Victor Jetten, Marcel Polak & Marinus Werger

Abstract

An inventory was made of the vegetation and soils of a watershed area in the tropical rain forest of Guyana. In a watershed of 480 ha 252 plots of 0.05 ha were sampled. In the total 111 tree species ≥20 cm were recorded. Seven main forest associations can be recognized. Most areas in the watershed are characterized by the dominance of one or a few species. Species distribution pattern is strongly determined by soil type and drainage class.

Keywords: Soil hydrology; Vegetation Analysis.
Nomenclature: See Appendix 1. Names are according to Mennega et al. (1988). In the text no further reference is made to the sub-specific level.

Introduction

Tropical rain forest is a term that may cover a wide array of forest types. In South America in general and in Guyana in particular, several distinct forest types such as mangrove, marsh forest, swamp forest and muri shrub, are clearly related to edaphic factors, such as flooding regime or excessive drainage (Fanshawe 1952). Within the so-called mixed forests of Guyana, associations can also be distinguished but the relation between forest types and soil factors is far from clear and this seems to hold for many tropical mixed forests (e.g. Fanshawe 1952, Knight 1975, Baillie et al. 1987). Mixed rain forests are rich in tree species and in many areas no single species accounts for more than a few percent of all individuals and thus most species are rare (Richards 1952, Ashton 1969). Occasionally, dominance of a group of species or even a single species can also be found (Richards 1952). Evidence is growing that dominance of a few species, often belonging to one family, or a single species can be found in all major rain forest blocks. To name a few: some Dipterocarpaceae in SE Asia (Richards 1952, Ashton 1969), Myrtaceae in SE Brazil (Mori et al. 1983), Leguminosae in Africa (Gartlan et al. 1986, Newberry et al. 1988, Hart et al. 1989) and Lecythidaceae and Leguminosae in many neotropical forests (Richards 1952, Schulz 1960, Whitton 1962). Hart et al. (1989) and Connel & Lowman (1989) provide many more examples and references.

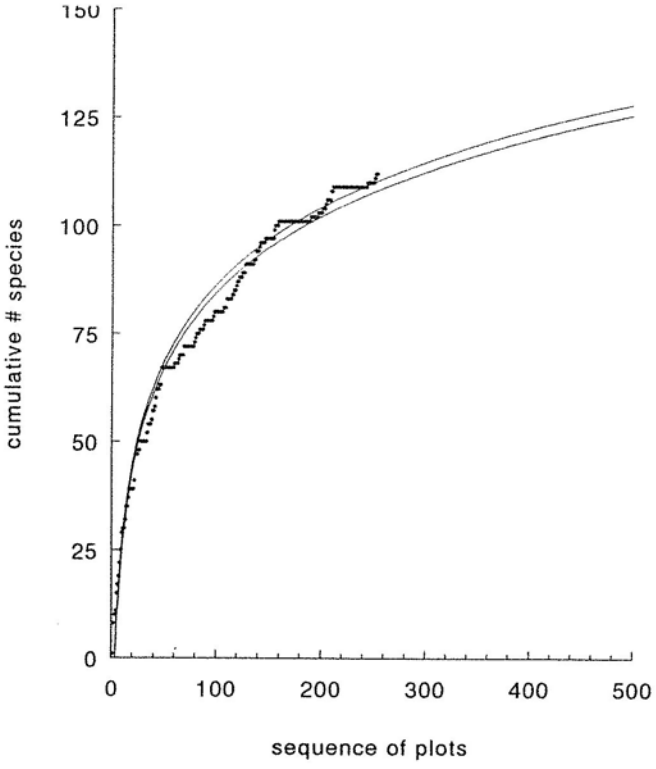

Figure 1. Species area curve for 252 plots in the Waraputa Compartment Inventory Watershed. Smooth upper line indicates the 'hypothetical species area curve' (see text), the lower line indicates a non-linear regression based on the actual data points.

Often 'single-dominance' has been related to edaphic factors such as poor drainage or extreme drainage and/or extreme nutrient poverty (Richards 1952). While this may be the case in for instance the *Eperua* forests in Guyana, not in all cases of single-dominance edaphic factors could be identified, that account for it. Hart et al. (1989), for instance, found no differences in soil factors under *Gilbertiodendron dewevrei* forest and adjacent mixed forest.

In Guyana several authors realized early this century that much of the forest is dominated by one or a few species (Davis & Richards 1933, 1934, Richards 1952, Fanshawe 1952, Whitton 1962). These authors also suggested the link between soil types and forest types. However, this correlation has never been quantified.

In this paper we describe the woody vegetation of a watershed of 480 ha in Guyana. We used many (252) plots of 0.05 ha instead of a few hectare size plots. This large number enables us to quantify both relations among tree species as well as between tree species and soils. Of special interest are a few common species for which the relation with soil types will be described in more detail.

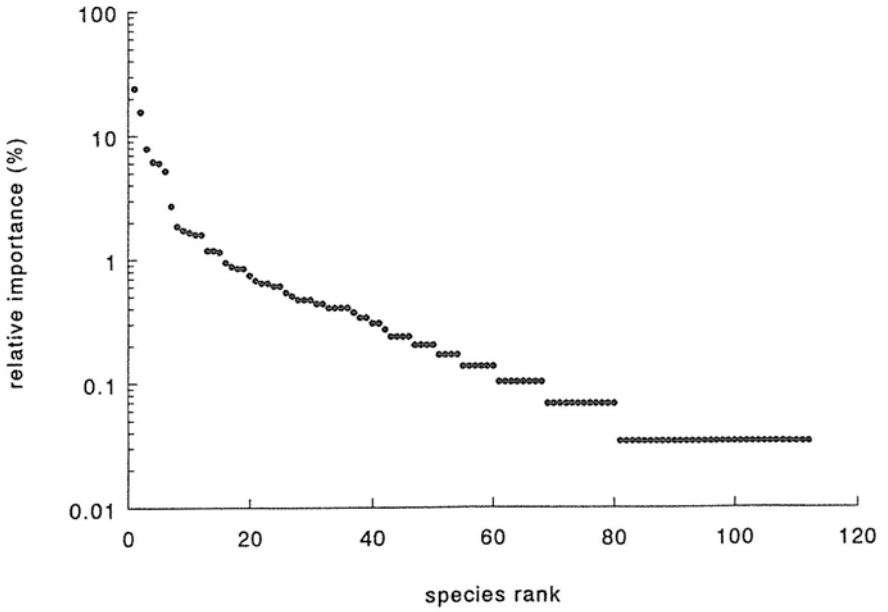

Figure 2. Species importance curve for 111 species on the Waraputa Compartment Inventory Watershed. Relative importance is the percentage of individuals a species of the total number of individuals.

The project was carried out within the framework of the TROPENBOS Programme in Guyana.

Study site

Guyana is situated in NE South America. Our study was conducted in a watershed area in the 'Waraputa Compartment' near Mabura Hill (5°13'N, 58°48'W). The area is designated as Waraputa Compartment Inventory Watershed and hereafter will be referred to as 'the watershed'. The climate is tropical with high rainfall, between 2500 and 3400 mm per year. There are two distinct dry periods: January to March and August to September. Mean daily average temperature over the year is 25°C (ter Steege and Persaud 1991). Soils of the watershed are mainly sandy. Following the FAO-classification they can be classified as Haplic Arenosols, referred to in Guyana as 'white sands', and Haplic Ferralsols and Ferralic Arenosols, also referred to as 'brown sands'. In lower areas and areas with impeded drainage Fibric and Terric Histosols, Gleyic Arenosols and Dystric Fluvisols are found (Khan et al. 1980, Khan & Jetten 1992, Jetten et al. accepted). For a detailed description of the soil types in the area the reader is referred to Khan et al. (1980)

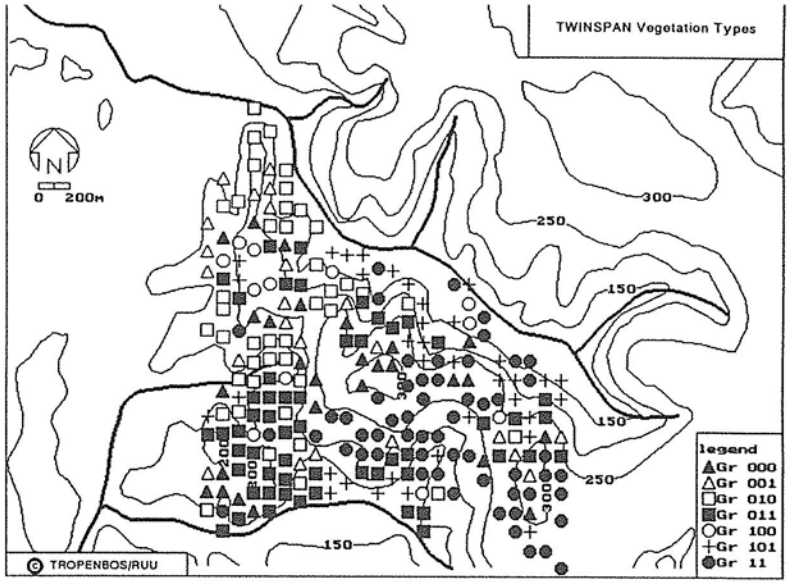

Figure 3. Map of plots on the Waraputa Compartment Inventory Watershed. Types are TWINSPAN 'forest' types according to tables 1 and 2. N.B. distances on the map are in meters, height contours are given in feet!

Methods

The watershed is bordered by a creek in the north and one in the south. Twenty nine lines were cut by an inventory crew of Demerara Woods Ltd. in a south to north direction, with a distance of 100 meters between the lines. Circular plots of 0.05 hectare were established on these lines, again at a distance of 100 meter - thus creating a grid of 100 x 100 m. Due to time limitation lines 1 to 5 were not covered. On all other lines all plots were sampled except in the central part, where the construction of a road damaged some of the plots. In total 252 plots were used.

In all plots trees with a DBH ≥20 cm were identified and recorded with their DBH. The forest type (sensu Fanshawe 1952), soil type, and slope were noted. Soil types were determined by augering up to 1.20m in 87 of the plots and by shallower inspection in all other. The trees were identified by a well trained tree spotter and by the two botanists of the team with the aid of a checklist of the area (ter Steege 1992). Most trees were identifiable to the species level, but some problem groups remained, notably in the Chrysobalanaceae, in the Sapotaceae, *Swartzia* spp. and *Catostemma* spp.

Data for the 53 most common species (more than 10 individuals in the inventory, 48% of the number of species) were processed with TWINSPAN (Hill 1979b) and DECORANA (Hill, 1979a). Input for both TWINSPAN and DECORANA was in the form of the number of individuals per plot in six classes: 1, 2, 3-4, 5-8, 9-16, >16. With DECORANA both an ordination with detrended correspondence analysis and one with basic reciprocal averaging was calculated, in both cases with down-weighting of rare spe-

Table 1. TWINSPAN divisions with the respective indicator species (Eigenvalues of the divisions between brackets) .

			group *			
			(.529)			
			group 0	group 1		
			E.sagotiana	*E.grandiflora*		
			C.rodiei	*E.falcata*		
			(.305)	(.409)		
	group 00		group 01	group 10		group 11
			E.rubiginosa	*E.rubiginosa*		*E.grandiflora*
				Diospyros		*D.altsonii*
				ierensis		
	(.392)		(.239)	(.352)		
group 000	group 001	group 010	group 011	group 100	group 101	
Swartzia	*Mora*	*Mora*	*D.altsonii*	*Chamaecrista*	*D.altsonii*	
leiocalycina	*gonggrijpii*	*gonggrijpii*	*C.rodiei*	*apoucouita*	*E.rubiginosa*	
D.altsonii	*C.rodiei*	*Tapura*		*E.falcata*	*Tabebuia*	
Sloana	*E.rubiginosa*	*guianensis*			*insignis*	
guianensis						

cies (Hill 1979a) but see Gartlan et al. (1986). TWINSPAN 'vegetation types' were compared on their basal area, number of trees per hectare, and main soil type. To compare species and soil distributions, a simple mapping program was written, which was able to plot distribution patterns on maps. For the seven most common species the relation with soil type, drainage of the area and distribution pattern was examined in more detail. Soil drainage was classified in seven drainage classes ranging from excessively drained soils to very poorly drained soils, following the FAO guidelines for soil description (FAO 1977).

Results

Floristic diversity

In the 252 plots 111 tree species of ≥20 cm DBH (2952 individuals) were found. Full names and authorities can be found in Appendix I. The species area curve for the plots in

Table 2. Synoptic vegetation table of canopy trees on the 'Waraputa Compartment Inventory Watershed'. Presence is indicated in steps of 10 by the length of the bar for each species under a type (10 characters long is 100%). The height of the bar give a measure of average abundance in the plots. —1-2 per plot, ▬ 3-4 per plot and ■ 5-8 per plot. ▶

nr plots	27	23	42	55	12	36	57
nr trees/plot	10.85	9.78	10.83	10.89	12.17	15.17	12.07
basal area	1.61	1.65	1.75	1.79	1.05	1.62	1.54
main soil type	FRh,ARo	FRh,ARo	FRh,ARo	FRh,ARo	ARg,FLd	HSs, HSt	ARh
average drainage	++	++	++	+-	-	--	+++
group	000	001	010	011	100	101	11
Chlorocardium rodiei	▬	▬	▬	▬		—	—
Mora gonggrijpii	—	▬	▬	—	—		
Maburea triplinevis	▬	—	—	—		—	
Clathrotropis sp.	—			—	—		
Eschweilera sagotiana	▬	▬	▬	▬	■	■	—
Pouteria melinonii	—			—			
Carapa guianensis	—	—	▬				
Mora excelsa			—				
Tapura guianensis	▬	—	▬	—		—	
Aspidosperma cruentum	—	—	—				—
Lecythis corrugata	▬	▬	▬	—	—	—	—
Chaetocarpus schomburkianus	—	▬	—	—		—	—
Lecythis confertiflora	▬	▬	▬	—	▬		—
Eschweilera alata	▬	▬		▬	—		—
Swartzia leiocalycina	▬	—	▬	—	▬	—	
Eugenia arawakorum	▬				—		
Sloanea guianensis	▬		—		▬	—	
Licania sp.	▬	—		—	▬		
Goupia glabra	▬	—	—			—	—
Pouteria filipes	—	—	—	—	—		—
Chamaecrista apoucouita	▬	▬	▬	▬	▬	—	—
Licania sp.	▬		—	—	—	▬	—
Pera sp.		—		▬	▬	—	—
Diospyros dichroa	—	—	—	—	—	—	
Eperua rubiginosa	—	▬	■	■	■	■	■
Lecythis zabucajo			—	—	—	—	
Tallisia sp.			—	—	—		

Table 2. Continued. Dominant species are given in bold. Soiltypes : FRh = haplic Ferralsol, ARo = ferric Arenosol, ARg = gleyic Arenosol, FLd = dystric Fluvisol, HSs = terric Histosol, FSf = fibric Histosol, ARh = haplic Arenosol. Drainage : +++ = excessive, ++ = well, +- = moderately well, - = poor, -- = very poor.

nr plots	27	23	42	55	12	36	57
nr trees/plot	10.85	9.78	10.83	10.89	12.17	15.17	12.07
basal area	1.61	1.65	1.75	1.79	1.05	1.62	1.54
main soil type	FRh,ARo	FRh,ARo	FRh,ARo	FRh,ARo	ARg,FLd	HSs, HSt	ARh
average drainage	++	++	++	+-	-	--	+++
group	000	001	010	011	100	101	11
Inga sp.			-	-		-	-
Terminalia sp.			-	-	-	-	
Eperua falcata	-	-	-	-	-	-	-
Catostemma sp.	-	-	-	-	-	-	-
Diplotropis purpurea	-	-				-	-
Licania sp.	-	-	-	-	-	-	-
Aspidosperma excselsum	-		-	-	-	-	-
Licania	-	-	-	-	-	-	-
Protium guianensis	-				-		-
Tallisia squarrosa	-	-		-		-	-
Swartzia sp.		-	-	-	-	-	-
Dycimbe altsonii	-	-	-	-	-	-	-
Eperua grandiflora				-	-	-	-
Luehopsis rugosa							-
Swartzia sp.				-	-		-
Tovomita sp.				-	-		
Ormosia coutinhoi			-	-	-	-	-
Ocotea puberula	-				-	-	-
Chamaecrista pteridophylla				-	-	-	-
Tabebuia insignis						-	-
Iryanthera lanceifolia			-			-	-
Symphonia globulifera						-	
Couratari guianensis	-		-			-	-
Saccoglotis obovata						-	-
Diospyros ierensis		-		-	-	-	
Hevea cf. *pauciflora*						-	-
Chaetocarpus sp.	-			-	-	-	

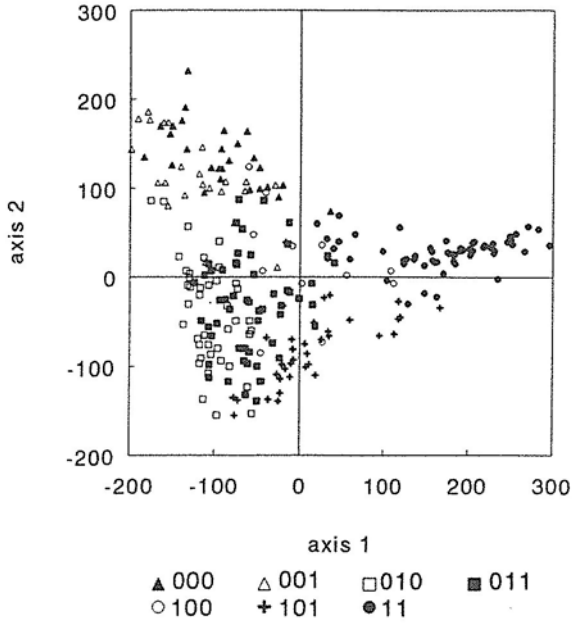

Figure 4. Representation of reciprocal averaging of 252 plots of the Waraputa Compartment Inventory Watershed. Symbols indicate TWINSPAN 'forest' types according to tables 1 and 2.

random order is given in Figure 1. The curve does not deviate much from the hypothetical species area curve for randomly distributed species (Coleman in Hubbel & Foster 1983). Inspection of the hypothetical curve shows that a reasonable sample level has been reached - doubling the number of plots would have resulted in approximately 125 species instead of 111. The species importance curve is given in Figure 2. The high abundance of the first seven species causes a very steep beginning of the species importance curve. These species are in sequence *Eperua rubiginosa, Dicymbe altsonii, Eperua grandiflora, Eperua falcata, Eschweilera sagotiana, Chlorocardium rodiei,* and *Mora gonggrijpii.* Although these seven species comprise only 7% of the total number of species, they account for 68% of all individuals and for 76% of the total basal area.

The most common families in the inventory are Lecythidaceae (11 species), Caesalpiniaceae (10 species), Papilionaceae (10 species), Sapotaceae (8 species), Chrysobalanaceae (>7 species). Leguminosae s.l. account for 25 species, or 23% of the total number. In terms of individuals Leguminosae s.l. account for 64% of all individuals (Caesalpiniaceae 59%, Mimosaceae <1%, Papilionaceae 5%), Lecythidaceae for 11%, Chrysobalanaceae for 4% and Sapotaceae for only 1%.

Classification and ordination

Table 1 summarizes the first three levels of divisions made by TWINSPAN. Since seven species are so common and most others are comparatively rare these seven species

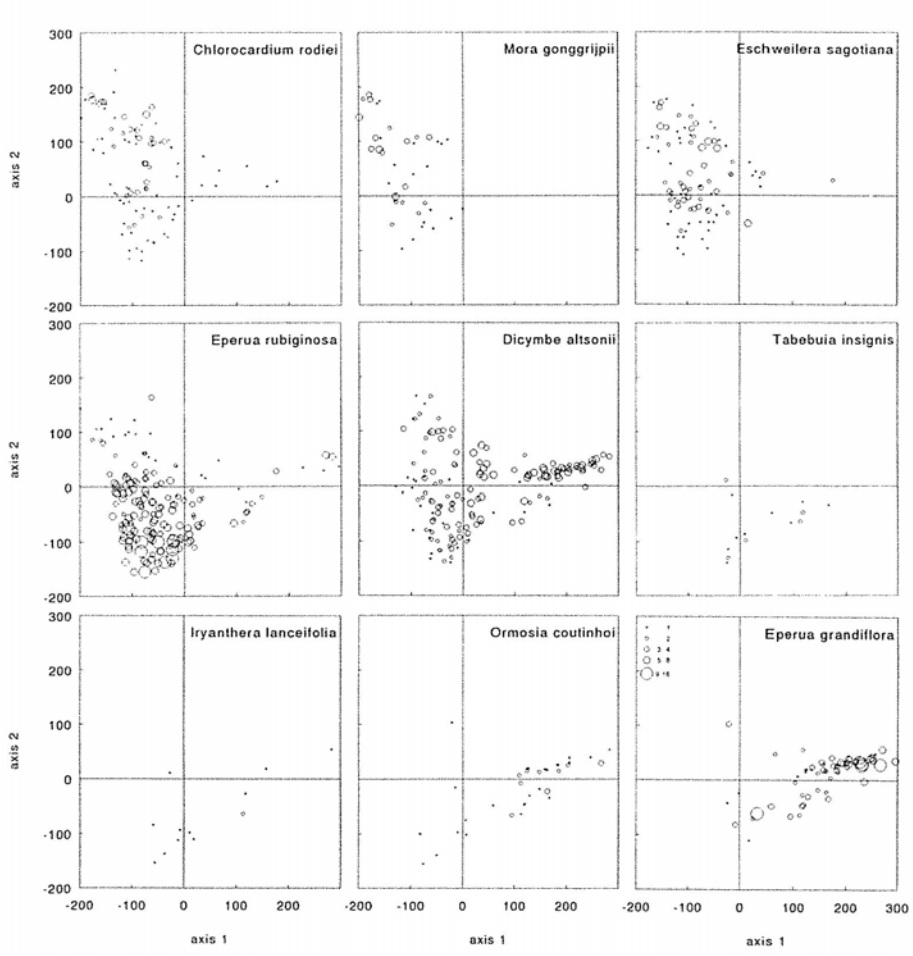

Figure 5. Species occurrence and abundance on plots plotted on the DECORANA reciprocal averaging ordination of the 252 plots along the first two axes. Species are given in approximate order of occurrence along the first gradient. Legend of the number of trees per plot is found in the graph of *Eperua grandiflora*.

have a large influence on the TWINSPAN classification (Table 2).

The first division is based on four species, *Eschweilera sagotiana* and *Chlorocardium rodiei* for group 0 and *Eperua grandiflora* and *Eperua falcata* for group 1. The plots are roughly divided into a group (0) of plots mainly occurring on brown sands (Haplic Ferralsols and Ferralic Arenosols, $\chi^2_{[1]}=113.425$, $p<0.001$) and a group (1) of plots mainly occurring on white sands and on soils with poor drainage (Haplic Arenosols and Histosols, $\chi^2_{[1]}=48.846$, $p<0.001$).

within group 1 TWINSPAN makes a division based on *Eperua rubiginosa* and *Diospyros ierensis* for group 10 and *Eperua grandiflora* and *Dicymbe altsonii* for group 11. The plots of group 10 are mainly plots on poorly drained soils, whereas the plots of group 11 are found on excessively drained white sands. A further subdivision in group 10 was based upon *Eperua falcata* and *Chamaecrista apoucouita* for group 100 and *Dicymbe altsonii*, *Eperua rubiginosa* and *Tabebuia insignis* for 101. This division splits the plots on poorly drained soils into those along creeks on Dystric Fluvisols and Gleyic Arenosols (group 100) and the true swamp plots on Histosols (group 101)

Within group 0, that is the plots on brown sands, the picture is a somewhat less clear. The major subdivision into groups 00 and 01 is based only upon the high presence and abundance of *Eperua rubiginosa* in group 01. It appears that the plots of group 01 occur on less well drained soils than do the plots of group 00. The third division within the 'brown sand plots' is influenced by a nearly perfect exclusive occurrence of *Dicymbe altsonii* and *Mora gonggrijpii* within group 0. Both groups 000 and 011 show high occurrence of the first species, while the latter is found mainly in groups 001 and 010. It appears that the classification within the 0 group also indicates a moisture gradient, as indicated by an increase of *Eperua rubiginosa* from 000 to 011.

Within the mixed forest plots on brown sands (groups 000-011), whether well or poorly drained a rather constant mix of non-dominant species is present. Our current data set does not allow us to go into detail on their distinct correlations

The distribution pattern of the seven TWINSPAN groups on the watershed is given in Figure 3. The white sand soils with their related forest types (11) are mainly found on the south eastern part of the watershed. Brown sand soils and their related forest types occur mainly on the western part and a few small patches are found in the eastern area. Swamp plots are, obviously, found in the lower lying areas.

The results of the DECORANA analysis are given in Figures 4 and 5. Ordination with basic reciprocal averaging produced better interpretable results than with detrended correspondence analysis. This is mainly due to the fact that the central part of the first axis contains some mixed plots and wide amplitude species. In such a case the arch distortion can be quite useful (Gauch 1982, cited in Teixera et al. 1989). Obviously the first axis of the DECORANA ordination for all species and all plots does not differ much from the 'ordination' of plots of TWINSPAN and seems to represent a soil type gradient. Plots on brown sands (000 to 011) are found on the left part of the axis and plots/species on the white sands (100 to 11) on the right (Fig. 4A). The second axis may be regarded as a gradient of hydrology. Plots of well drained soils (000, 001 and 11) have a high score on this axis, while plots from poorly drained areas (010, 011 and 101) have a low score an this axis. Group 100, plots on alluvial soil, poorly drained, takes a weakly defined position in the graph.

Species abundance within the plot ordination shows good correspondence for some common species (Figure 5) and these patterns are distinct on the map of the watershed (Figure 6). *Chlorocardium rodiei*, *Mora gonggrijpii* and *Eschweilera sagotiana* are species of

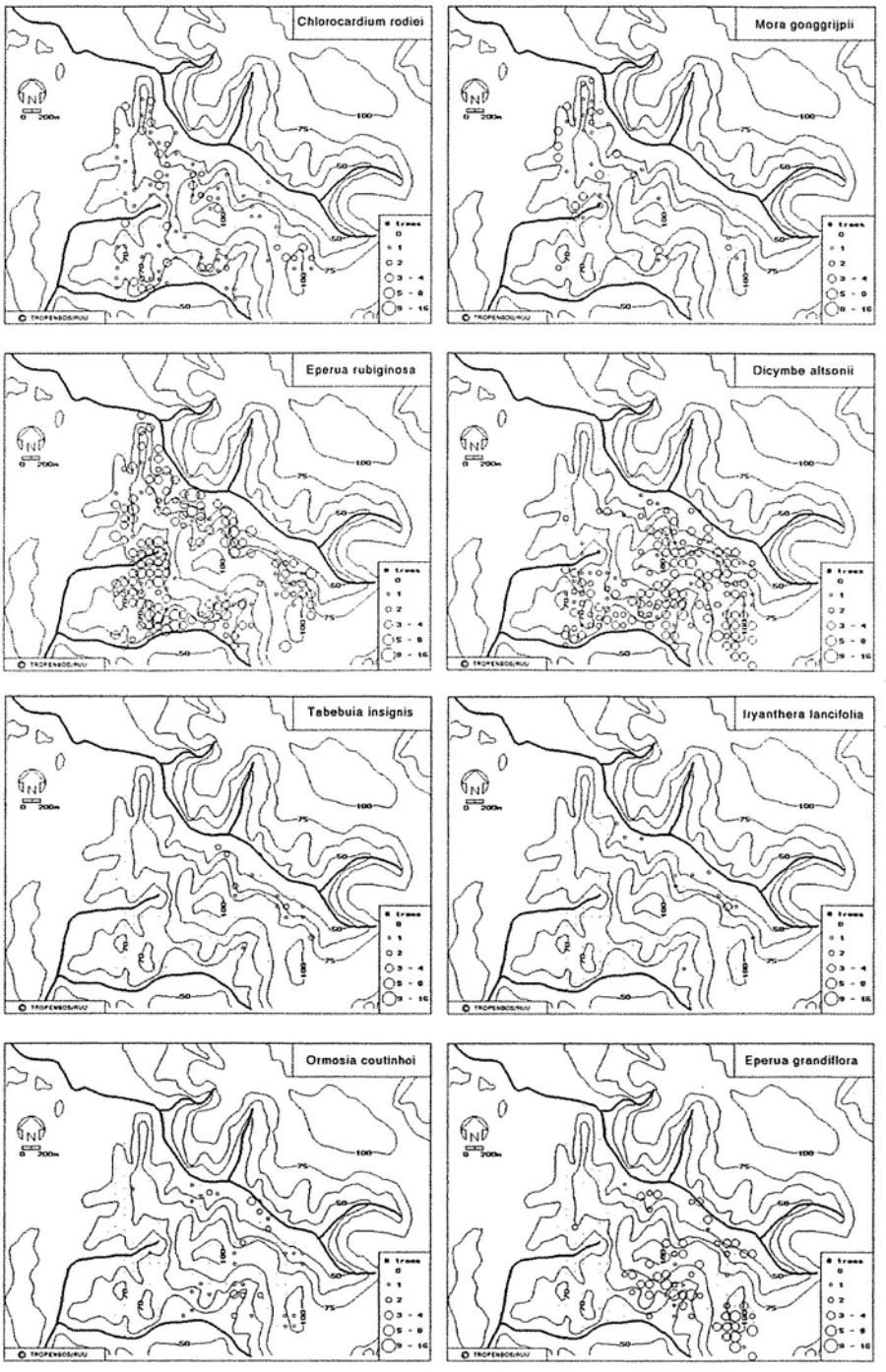

Figure 6. Species occurrence and abundance on the Waraputa Compartment Inventory Watershed. Species are given in approximate order of occurrence along the first DECORANA/TWINSPAN gradient (see figure 5).

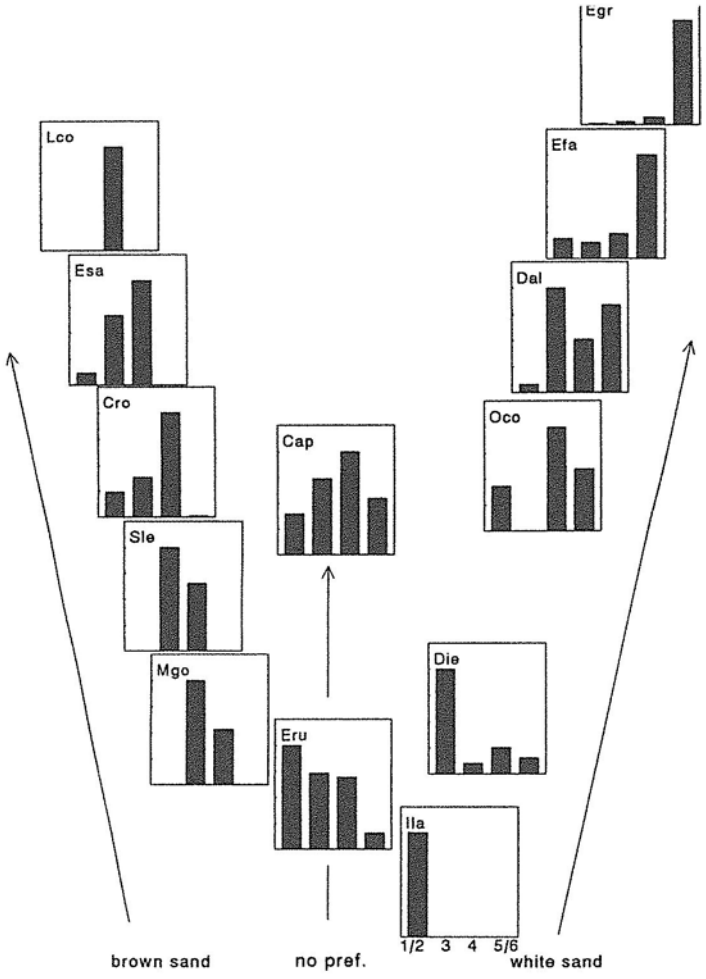

Figure 7. Average basal area of selected tree species per plot per drainage class. Classes 1 and 2, and classes 5 and 6 have been pooled because of low numbers. Species significantly more present on brown sand and with basal area of more than 1% of the total basal area in the inventory are on the left in order of occurrence from wet to dry. White sand species, using the same criteria are on the right. *Iryanthera lancifolia* has been added for completeness, in spite of the low total basal area (but sign. more on white sand). Abbreviations (and value of the highest bar m^2 / 0.05 ha^{-1});

Lco=*Lecythis confertiflora* (0.0293);
Cro=*Chlorocardium rodiei* (0.2806);
Mgo=*Mora gonggrijpii* (0.1480);
Cap=*Chamaecrista apoucouita* (0.0322);
Die=*Diospyros ierensis* (0.0380);
Dal=*Dicymbe altsonii* (0.7065);
Egr=*Eperua grandiflora* (0.3816).
Esa=*Eschweilera sagotiana* (0.1114);
Sle=*Swartzia leiocalycina* (0.0456);
Eru=*Eperua rubiginosa* (0.6382);
Ila=*Iryanthera lancifolia* (0.0077);
Oco=*Ormosia coutinhoi* (0.0761);
Efa=*Eperua falcata* (0.1978);

the brown sands. *Eperua rubiginosa* is a widespread species with preference for the slightly lower lying, wetter plots. *Dicymbe altsonii* is a widespread species with a preference for somewhat drier plots and is also common on the pure white sands. *Tabebuia insignis* and

Iryanthera lancifolia are both characteristic of the swamp plots with Histosols, along the creeks and in gully heads. Finally, *Eperua grandiflora* and *Ormosia coutinhoi* are both species of the white sand, the latter of which often occurs along the edges of swamps.

Dicymbe altsonii and *Mora gonggrijpii* appear to be spatially segregated (Figure 6, $\chi^2_{[1]}=29.837$, $p<0.001$). This segregation is reflected also in the TWINSPAN classification (Table 2) and the DECORANA ordination (Figure 5).

Based upon both analyses the following five 'associations' were distinguished, beginning with the dry white sands:

- **dry evergreen forest** on excessively drained Haplic Arenosols. Dominant species are *Eperua falcata* and *Eperua grandiflora*. Other common species are *Tovomita* sp., *Swartzia* sp., *Aspidosperma excelsum* and *Catostemma* cf. *fragrans*. *Ormosia coutinhoi* is found near the borders with lower, swampy areas.
- **palm-swamp forest** on Histosols. Dominant species are *Eperua falcata, Eperua rubiginosa*. Common species are *Diospyros ierensis, Jessenia bataua, Tabebuia insignis, Iryanthera lancifolia, Symphonia globulifera*, and *Couratari* cf. *gloriosa*. The forest is very open and a dense herb layer of *Rapatea paludosa* may be present.
- **creek forest** on alluvial Gleyic Arenosols and Dystric Fluvisols. Dominant species are *Eperua falcata* and *Catostemma* sp.. *Eperua rubiginosa, Chamaecrista adiantifolia* and *Diospyros ierensis* are often found.
- **poorly drained mixed forest** in low-lying small creek heads and valleys. Soils are mainly Ferralic Arenosols and Haplic Ferralsols. *Eperua rubiginosa* is strongly dominant here. *Eschweilera sagotiana* and *Chlorocardium rodiei* and *Mora gonggrijpii* may be co-dominant.
- **well drained mixed forest** on Ferralic Arenosols and Haplic Ferralsols but better drained than the former type. *Chlorocardium rodiei, Eschweilera sagotiana* (plus other Lecythidaceae) and *Dicymbe altsonii* dominate these areas, alone or in combination.

TWINSPAN types differ in their average basal area and number of trees per plot (Table 2). Basal areas are especially low in creek forests (group 100), but these forest as well as the swamp forests have a higher average number of trees per plot.

Distribution patterns and population structure

Several species are clearly linked to one of the two main soil types. Species significantly (χ^2, $p<0.05$) more present in plots on white sand (with ≥1% of the total basal area) are: *Eperua grandiflora, Eperua falcata, Dicymbe altsonii, Ormosia coutinhoi*, species significantly more present on brown sand plots are *Eschweilera sagotiana, Chlorocardium rodiei, Swartzia leiocalycina* and *Mora gonggrijpii*. Other species, such as *Chamaecrista apoucouita* and *Eperua rubiginosa* are not more present on either. Some of these species may become dominant and it is therefore not surprising to find that their distribution pattern is far from uniform or random (Table 3). Most of those species are also clumped on the soil type of their preference (brown or white sands). Thus *Chlorocardium rodiei, Mora*

Table 3. Distribution patterns of tree species on the Waraputa Inventory Watershed. Patterns are tested against a poisson distribution. ▶

nr of ind/plot species	0	1	2	3	4	5	6	7	8	9	>10
C. rodiei all	161	60	12	8	9	2	-	-	-	-	-
on Brown Sands	62	40	10	5	7	1	-	-	-	-	-
E. falcata all	156	41	37	8	7	2	1	-	-	-	-
on White Sands	20	12	15	3	1	-	-	-	-	-	-
E. grandiflora all	191	9	16	10	11	3	2	3	2	2	3
on White Sands	20	4	7	4	5	2	2	2	2	1	2
E. rubiginosa all	97	22	17	25	12	26	19	11	14	2	7
M. gonggrijpii all	213	20	8	6	2	1	1	1	-	-	-
on Brown Sands	100	12	6	4	1	-	1	1	-	-	-
E. sagotiana all	163	43	22	14	5	3	1	-	1	-	-
on Brown Sands	68	24	12	13	4	2	1	-	1	-	-
D. altsonii	101	28	42	25	27	16	9	-	4	-	-

gonggrijpii and *Eschweilera sagotiana* are clumped on brown sands and *Eperua grandiflora* is clumped on white sand. *Chamaecrista apoucouita* and *Eschweilera alata* have random distributions in our plots on brown sands, while *Eperua falcata* and *Ormosia coutinhoi* have random distributions on white sands.

Species occurrence is also determined by soil drainage class. Figure 7 shows species (with ≥1% of the total basal area) in order from poorly drained sites to well and excessively sites. Although the classes one to six are not a single soil characteristic, in a way they represent a sort of direct gradient. The gradient is longer on the white sand, running from the swamp forests up to the excessively drained parts. There were no swamps on the brown sand and brown sands were seldomly classified as excessively drained. *Eperua rubiginosa* can be found on all drainage classes but highest numbers are reached on plots with poor drainage. Although the latter species is does not show a preference for one of the two main soil types, all poorly drained brown sand areas have a high presence of the species. Thus a gradient on brown sand will typically start with *Eperua rubiginosa.*

Size class distributions of all and the seven most common species are given in Figure 8. Although forests on white sands appear to have more (thinner) stems per area there is

Table 5. Continued. Avg = average on plots, cd = coefficient of dispersion, *** = p < .001, ** = p < .01, * = p < .05. A pattern is random if p is > .05 (n.s.).

nr of ind/plot species	avg	var	cd	χ^2	p	distribution
C. rodiei all	.61	1.11	1.82	45.36	***	clumped
on Brown Sands	.86	1.35	1.56	11.89	*	clumped
E. falcata all	.73	1.29	1.78	43.58	***	clumped
on White Sands	1.08	1.09	1.01	3.91	n.s.	random
E. grandiflora all	.90	4.04	4.49	193.46	***	clumped
on White Sands	2.57	8.64	3.64	15.55	**	clumped
E. rubiginosa all	2.78	8.71	3.13	642.99	***	clumped
M. gonggrijpii all	.32	.88	2.78	37.20	***	clumped
on Brown Sands	.42	1.20	2.84	21.25	**	clumped
E. sagotiana all	.71	1.53	2.17	63.78	***	clumped
on Brown Sands	1.02	2.19	2.16	38.24	***	clumped
D. altsonii	1.83	3.93	2.15	177.15	***	clumped

no difference between the population structures of the different soil types. Therefore all plots of all soil types are pooled. Several species show a positive stand table indicating good regeneration and recruitment. *Chlorocardium rodiei* and *Mora gonggrijpii* show a deficiency of trees in the lower size classes, which may indicate irregular recruitment. *Dicymbe altsonii* produces different populations structures on white and brown sands. On brown sands the number of individuals in the smaller size classes is far lower than on white sand. On brown sand the species also reaches larger dimensions.

Discussion

Floristic diversity

The total number of 111 tree species encountered in a total sample of 12.6 hectare may be considered relatively low if compared with other inventories (Boom 1986, Campbell et al. 1986 and many references therein, Balslev et al. 1987, Mori & Boom 1987, Bongers et al. 1987). Difficulties in comparison exist, since the area sampled here is far from homogeneous. In fact it consisted of several forest types but so did a few of

the above mentioned. Based on the hypothetical species area curve, we are confident that the area sampled gave a good representation of the species present in the watershed.

Classification and Ordination

It was possible to distinguish five 'forest types' with TWINSPAN and DECORANA. Seven dominant species had a disproportional influence on this classification. The plot size used in the classification is very small and a large part of the variation may be attributable to sampling error linked to such a small size. Particularly, the subdivisions on brown sands may have been influenced by the small size. Even so, the groups obtained with TWINSPAN are readily comparable to the field situation. Especially the first division into plots on brown sands and white sands and the second division of the white sands in dry and wet ones are very clear. The separation of species along the environmental gradient, reflected by axis 1 and 2 of DECORANA, closely corresponds to a direct gradient analysis on both white and brown sand (Figure 7). The classification agrees with earlier reports on the forest associations in Guyana (Davis & Richards 1934, Fanshawe 1952). The 'Dry evergreen forest on white sands' here is synonymous with the wallaba forest of Davis & Richards (1933) and Fanshawe (1952). Swamp forest (Palm marsh forest sensu Fanshawe 1952), with dominance of *Symphonia*, *Virola*, *Tabebuia*, and *Euterpe* occurs from the Orinoco mouth to French Guiana (Fanshawe 1952). Our data do not support a robust subdivision of mixed forests on brown sands into associations, as suggested by Fanshawe (1952), a more or less similar mix of other species co-occur with the dominant species in most associations (but see above). It may be more appropriate to describe this type as a mixed forest where various species may become dominant. Hart et al. (1989) encountered similar problems in classifying *Gilbertiodendron* forests in Africa, which shared all tree species with the mixed forest, but at different densities. In their case neither soil quality, successional status, herbivory, nor differences in disturbance level could account for the difference between mixed and single-dominant forest. Local dominance as it occurs on the Waraputa Compartment Inventory Watershed is more rule than exception in the forests of the near interior of Guyana (Richards 1952, Fanshawe 1952, Whitton 1962). Low disturbance levels (Hart et al. 1989) and association of dominant species with ectomycorrhiza (Connel & Lowman 1989) have been proposed as possible mechanisms for single dominance. Our data offer no further explanation as why dominance occurs in these forests.

Locally dominant canopy trees may be generalists with respect to soil conditions, such as *Eperua rubiginosa* or *Eperua falcata*, occurring on many soil types and a range of soil drainage classes, or specialists like *Eperua grandiflora*. Most of the variation between the white sands and the brown sands may be attributable to low nutrient contents (Kahn et al. 1980), low field capacity (Simpson 1989), or excessive drainage of the white sand areas (Fanshawe 1952). Differences in habitat preference between *Eperua falcata* and *Eperua grandiflora* have also been noted by Schulz (1960), Lescure & Boulet (1985), and Barthes (1991). All these authors found *Eperua falcata* on both extreme ends of catenas from wet valleys to dry hill tops, and *Eperua grandiflora* in the middle part. In our area,

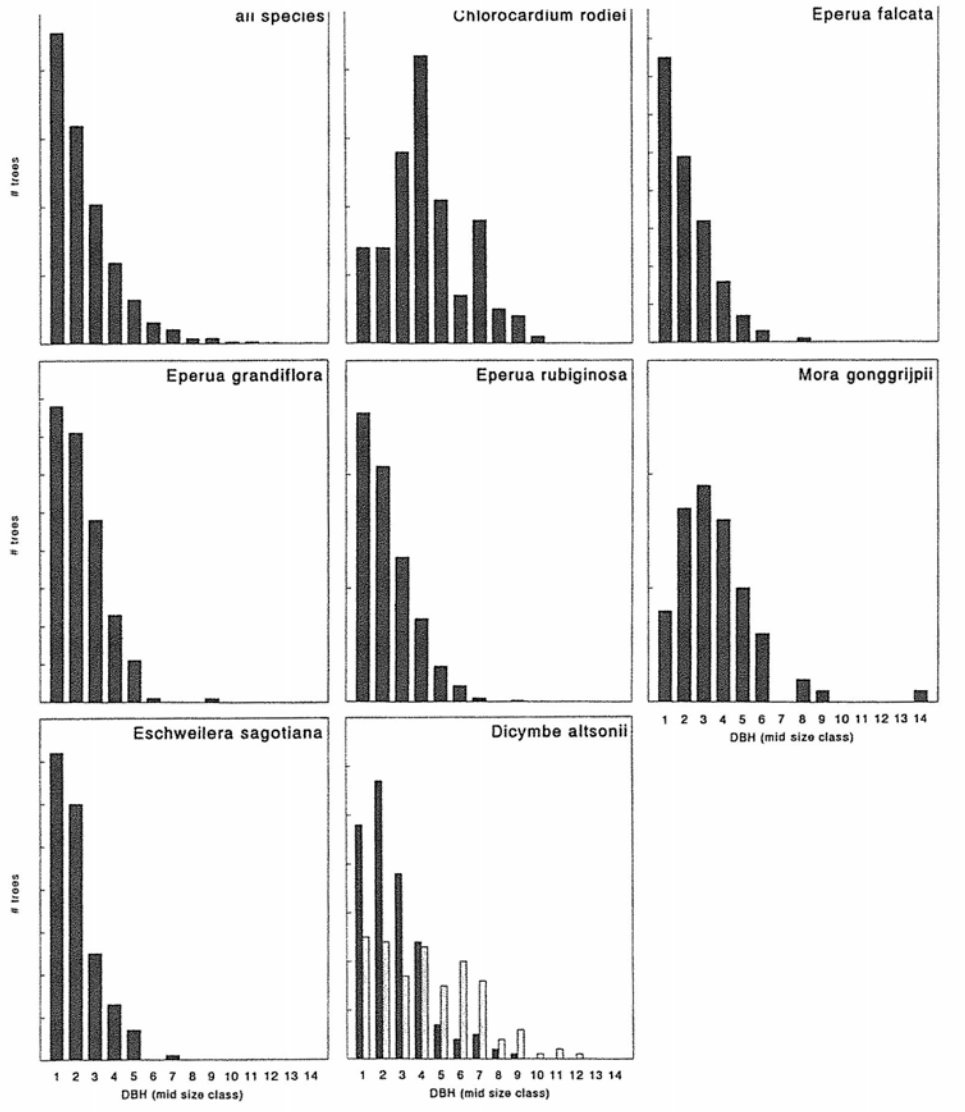

Figure 8. Size class distributions of all species and the seven most common ones on the Waraputa Compartment Inventory Watershed. Note the difference in scaling of the Y-axes. *Dicymbe altsonii*: black bars, on white sand; hatched bars, on brown sand.
X-axis legend: 1=20-29, 2=30-39, 3=40-49, 4=50-59, 5=60-69, 6=70-79, 7=80-89, 8=90-99, 9=100-109, 10=110-119, 11=120-129, 12=130-139, 13=140-149, 14=≥150.

however, *Eperua rubiginosa* is the main dominant in low areas. Our data furthermore suggest that *Eperua grandiflora* tolerates similar or more excessive drainage than does *Eperua falcata*. Fanshawe (1947) also noted this.

On the watershed most dominant and sub-dominant tree species have a clear association with a distinct soil type or hydrology class. This information may be helpful in forest and/or soil classification. However, to be able to produce a complete system for Guyana, similar to provisional one proposed by Fanshawe (1952), but based upon vegetation samples, a huge amount of actual field data will be required.

Distribution patterns and population structure

Several species show good regeneration and recruitment but the population structures of a few, such as *Chlorocardium rodiei* and *Mora gonggrijpii,* indicate irregular recruitment (Bongers et al. 1987). In the case of *Chlorocardium rodiei* this agrees with former findings (Fanshawe 1947, Richards 1952). The population structure of *Mora gonggrijpii,* usually classified as an extreme shade tolerant species with good regeneration and recruitment, differs much from previously published ones (e.g. Richards 1952, Maas 1971). Possibly our sample size has not been large enough for this particular species.

The difference in population structure of *Dicymbe altsonii* on white sands and brown sands is striking. It may suggest that different modes of regeneration prevail on different soil types. This species produces a large number of root/stem suckers ('clumps') on living, healthy adults (the Guyanese name is Clump wallaba). Since most *Dicymbe altsonii* adults die as a result of snapping rather than of uprooting (pers. obs.), these suckers may benefit faster from gaps. Equipped with the large root system of their 'parent' they may grow much faster and pass through middle size classes faster than seedlings, with lower mortality, creating a relative shortage of lower and middle sized trees. Based on the difference in population structures one would expect clumping to be more common on brown sands. Limited field observations (Zagt pers. communication) suggest that this may be true.

Acknowledgments

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Appendix I. Species List.
Complete species list off all species recorded during the inventory of the Waraputa Compartment Inventory Watershed. Species are sorted alfabetically under their family. Names are according to Mennega et al. (1988). Although with the aid of our knowledgeable treespotter and our excisting checklist (ter Steege 1992) most trees could be identified to the species level, some problems in determining the right name for some species remained, notably in the families of Myrtaceae, Chrysobalanaceae and Sapotaceae and the genus *Swartzia* (Papilionaceae). Percentages less than 0.5% are given as -.

	nr of indiv.	% of indiv.	basal area	% of B.A.
Annonaceae				
Oxandra asbeckii (Pulle) R.E. Fries	2	-	.07	-
Unonopsis spp.	1	-	.03	-
Apocynaceae				
Aspidosperma excelsum Benth.	12	-	2.33	1
Aspidosperma cruentum Woodson	5	-	.66	-
Parahancornia fasciculata (Lam.) Benoist	3	-	.65	-
Araliaceae				
Schefflera spp.	2	-	.33	-
Arecaceae				
Jessenia bataua (Mart.) Burret	3	-	.12	-
Mauritia flexuosa L.f.	1	-	.06	-
Bignoniaceae				
Jacaranda copaia (Aubl.) D. Don	1	-	.09	-
Tabebuia insignis (Miq.) Sandw. var *monophylla* Sandw.	19	1	2.90	1
Bombaceae				
Catostemma altsonii Sandw.	5	-	.81	-
Catostemma commune Sandw./				
C. fragrans Benth	55	2	3.70	1
Boraginaceae				
Cordia exalta Lam. var *melanoneura* I.M. Johnston	1	-	.06	-
Burseraceae				
Protium guianense (Aubl.) Marchand	9	-	.43	-
Tetragastris altissima (Aubl.) Swart	3	-	.18	-
Trattinickia rhoifolia Willd.	2	-	.41	-
Caesalpiniaceae				
Chamaecrista apoucouita (Aubl.) Irwin & Barneby	51	2	4.91	1
Chamaecrista adiantifolia (Benth.) Irwin & Barneby				
var *pteridophylla* (Sandw.) Irwin & Barneby	19	1	1.66	-
Dicymbe altsonii Sandw.	461	16	100.66	24
Eperua falcata Aubl.	183	6	20.75	5

Appendix 1. Continued.

	nr of indiv.	% of indiv.	basal area	% of B.A.
Eperua grandiflora (Aubl.) Benth.	233	8	27.46	7
Eperua rubiginosa Miq.	711	24	85.34	21
Hymenaea courbaril L.	1	-	.06	-
Mora excelsa Benth.	2	-	.87	-
Mora gonggrijpii (Kleinh.) Sandw.	80	3	18.04	4
Peltogyne venosa (Vahl) Benth.	2	-	.36	-
Caryocaraceae				
Caryocar nuciferum L.	4	-	3.12	1
Celastraceae				
Goupia glabra Aubl.	12	-	3.02	1
Maytenus myrsinoides Reissek	1	-	.10	-
Chrysobalanaceae				
Licania sp1	18	1	.93	-
Licania sp2	47	2	3.64	1
Licania sp3	26	1	2.54	1
Licania sp3	1	-	.04	-
Licania/Couepia	35	1	1.97	-
Parinari excelsa Sabine	1	-	.13	-
Parinari cf. *rodolphi* Huber	2	-	.67	-
Combretaceae				
Buchenavia fanshawei Exell & Maguire	1	-	.28	-
Terminalia sp.	7	-	2.57	1
Dichapetalaceae				
Tapura guianensis Aubl.	35	1	1.83	-
Ebenaceae				
Diospyros dichroa Sandw.	13	-	.89	-
Diospyros ierensis Britt.	22	1	1.84	-
Elaeocarpaceae				
Sloanea sp.	20	1	1.96	-
Euphorbiaceae				
Chaetocarpus schomburgkianus (Kuntze) Pax & K.Hoffm.	14	-	1.28	-
Chaetocarpus sp.	14	-	1.26	-
Hevea cf. *pauciflora* (Spruce ex Benth.) Muell. Arg.	10	-	.93	-
Pera sp.	18	1	1.70	-
Guttiferae				
Callophyllum lucidum Benth.	1	-	.06	-

Appendix 1. Continued.

	nr of indiv.	% of indiv.	basal area	% of B.A.
Clusia cf. *fockeana* Miq.	2	-	.07	-
Symphonia globulifera L.f.	11	-	1.38	-
Tovomita sp.	12	-	.67	-
Humiriaceae				
Humiriastrum obovatum (Benth.) Cuatr.	5	-	.39	-
Lauraceae				
Aniba sp.	3	-	.14	-
Chlorocardium rodiei (5chomb.) Rohwer, Richter & v.d. Werff (syn. *Ocotea rodiaei* (Schomb.) Mez)	154	5	43.98	11
Ocotea cf. *puberula* Nees	10	-	1.73	-
Ocotea sp.	1	-	.07	-
Lecythidaceae				
Couratari cf. *gloriosa* Sandw.	16	1	1.78	-
Eschweilera alata A.C. Smith	25	1	1.41	-
Eschweilera cf. *grata* Sandw.	1	-	.06	-
Eschweilera coriacea (DC) C. Mart. ex O Berg/*decolorans* Sandw.	25	1	2.36	1
Eschweilera sagotiana Miers	178	6	18.43	5
Eschweilera wachenheimii (Benoist) Sandw.	1	-	.26	-
Lecythis confertiflora (A.C. Smith) Mori	49	2	4.38	1
Lecythis corrugata Poit.	4	-	.40	-
Lecythis holcogyne (Sandw.) Mori	4	-	.16	-
Lecythis zabucajo Aubl.	8	-	1.21	-
Lecythidaceae sp.	1	-	.10	-
Meliaceae				
Carapa procera DC.	12	-	1.85	-
Mimosaceae				
Inga alba (Sw.) Willd.	1	-	.05	-
Inga sp.	6	-	.44	-
Parkia cf. *nitida* Miq.	2	-	.19	-
Pithecelobium jupunba (Willd.) Urban	3	-	.71	-
Pithecelobium pedicellare (DC.) Benth.	1	-	.06	-
Moraceae				
Cecropia angulata I. Bailey	3	-	.12	-
Myristicaceae				
Iryanthera lancifolia Ducke	14	-	.90	-
Iryanthera sp.	1	-	.04	-

Appendix 1. Continued.

	nr of indiv.	% of indiv.	basal area	% of B.A.
Virola surinamensis (Rolander) Warb.	1	-	.07	-
Myrtaceae				
Eugenia cf. *arawakorum* Sandw.	6	-	.33	-
Eugenia patrisii Vahl	1	-	.12	-
Myrcia/Myrciaria sp.	1	-	.07	-
Myrtaceae sp.	1	-	.03	-
Olacaceae				
Minquartia guianensis Aubl.	1	-	.08	-
Maburea trinervis Maas	15	1	.65	-
Papilionaceae				
Acosmium praeclarum (Sandw.) Yakovlev	2	-	.20	-
Alexa leiopetala Sandw.	1	-	.04	-
Clathrotropis macrocarpa Ducke	9	-	.75	-
Clathrotropis brachypetala (Tul.) Kleinhoonte	1	-	.08	-
Diplotropis purpurea (Rich.) Amshoff	7	-	.55	-
Ormosia coccinea (Aubl.) B.D. Jackosno	3	-	.40	-
Ormosia coutinhoi Ducke	47	2	6.18	2
Swartzia leiocalycina Benth.	34	1	3.53	1
Swartzia benthamiana Miq./*S. xanthopetala* Sandw.	28	1	3.38	1
Swartzia cf. *oblanceolata* Sandw.	7	-	.40	-
Quiinaceae				
Quiina cf. *indigofera* Sandw.	1	-	.20	-
Rosaceae				
Prunus myrtifolia (L.) Urban var. *accumulans* Koehne	1	-	.09	-
Sapindaceae				
Matayba spp.	4	-	.16	-
Talisia furfuracea Sandw.	2	-	.11	-
Talisia squarrosa Radlk.	13	-	1.53	-
Talisia sp.	4	-	.55	-
Sapotaceae				
Pouteria cf. *jenmanii* (Pittier) Sandw.	2	-	.13	-
Pouteria filipes Eyma	7	-	.53	-
Pouteria melinonii (Engl) Baehni	5	-	.36	-
Pradosia schomburgkiana (DC.) Cronq.	4	-	.59	-
Sapotaceae sp1	1	-	.09	-
Sapotaceae sp2	1	-	.05	-

Appendix 1. Continued.

	nr of indiv.	% of indiv.	basal area	% of B.A.
Sapotaceae sp3	3	-	.24	-
Simaroubaceae				
Quassia simarouba L.f.	1	-	.05	-
Sterculiaceae				
Sterculia guianensis Sandw.	1	-	.10	-
Tiliaceae				
Apeiba cf. *echinata* Gaertner	1	-	.04	.01
Lueheopsis rugosa Willd.	6	-	2.15	1
Family Indet				
spec 1	2	-	.16	-
spec 2	6	-	.50	-
Total	2952	100	411.48	100

The effects of man made gaps on germination, early survival, and morphology of *Chlorocardium rodiei* seedlings in Guyana

Hans ter Steege, Carla Bokdam, Miranda Boland, José Dobbelsteen & Ivo Verburg

Abstract

Germination success of Chlorocardium rodiei is low in large gaps. High light levels, however are beneficial for the survival of seedlings. (Partial) removal of cotyledons has a large negative impact on survival especially under low light conditions. Seedlings from large gaps are larger but not taller than those from the understorey, due to differential internode growth. Although growth of seedlings is improved by higher light levels caused by e.g. logging, great care should be taken with logging intensity, which may increase seed mortality.

key words: light climate, logging, tropical rain forest.

Introduction

Chlorocardium rodiei (Schomb.) Rohwer, Richter & van der Werff (Greenheart, synonym *Ocotea rodieai*, LAURACEAE) is Guyana's best known timber species. It is of high commercial value and is confined to an area almost entirely within Guyana (ter Steege 1990). Although it amounts to only 1.5% of the standing volume of total commercial species, it makes up more than 70% of all exported timber (GNRA 1989). In Guyana 'selective logging' of *Chlorocardium rodiei* is practised. 'Selective logging' means that all individuals larger than 25 cm can be felled. This forest practice is probably not detrimental to the environment on a large scale, but leads to 'clear felling' on a smaller scale. As in the case of selective felling of teak (*Tectona grandis* L.) in Thailand (Gajaseni & Jordan 1990), selective logging of *Chlorocardium rodiei* may lead to decline of the species. At present *Chlorocardium rodiei* is considered over-exploited (GNRA 1989).

Gaps are common in the lowland tropical forests (Brokaw 1982, Sanford et al. 1986, Popma et al. 1988). They play an important role in the maintenance of species diversity in rain forests (Hartshorn 1980). Most natural gaps are small, however (Sanford et al. 1986). Man made gaps usually differ in various ways from natural ones. Felling a single tree results in a gap formation similar to the natural situation. But usually more trees are felled in a small area and thus the gaps are larger, resulting in far higher light levels.

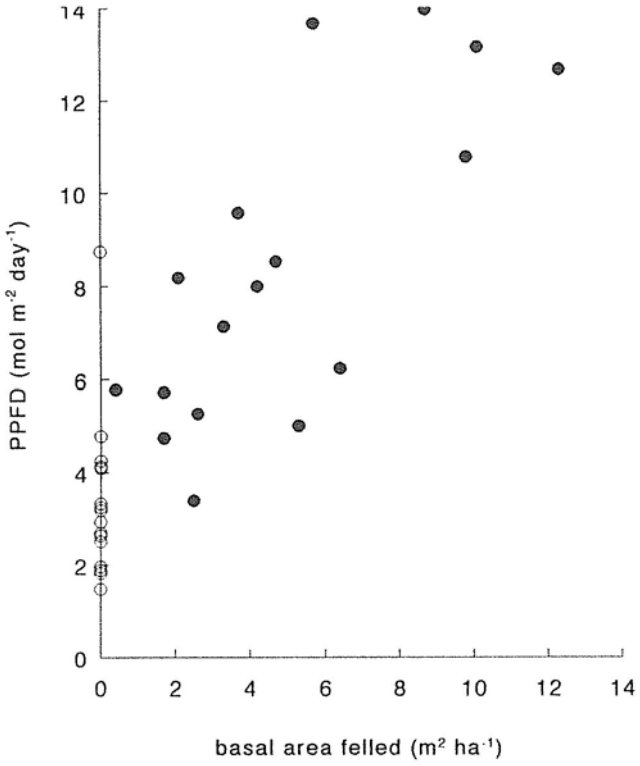

Figure 1. The relation between basal area felled and daily average PPFD of 37 plots in a variably logged over area. Open circles: unlogged plots, filled circles : logged plots.

Mechanized extraction of the logs is unlike any natural event, resulting in disturbance of the litter layer and compaction of the soil (Allen 1985, Hendrison 1990). Mechanized extraction also takes a high toll of small trees (Jonkers 1987).

Several factors may improve survival and growth rates for tropical tree seedlings after logging, e.g. higher light levels (Augspurger 1984). *Chlorocardium rodiei* seedlings and saplings respond well to openings in the canopy (Fanshawe 1948, Clarke 1956). Older individuals also respond favorably to the openings in the canopy and diameter growth in logged forest is higher than in natural forest (ter Steege 1990). Silvicultural treatments may further stimulate growth (Prince 1971). On the other hand seeds of many tropical climax species do not tolerate dry environments (Richards 1952) and germination in *Chlorocardium rodiei* too, seems inhibited by drought (Fanshawe 1948).

Finally insect attack on *Chlorocardium rodiei* seeds in the forest is high (ter Steege 1990) and may be an important factor in the survival of the seedlings.

Little quantitative information on factors affecting germination of seeds and growth and survival of seedlings of *Chlorocardium rodiei* is available. In this study we investigated: 1) the germination of buried and unburied *Chlorocardium rodiei* in the understorey

of an undisturbed forest and in gaps; 2) the effect of cotyledon removal, simulating insect attack on early survival and growth, in different light environments, and 3) the effect of light intensity on the morphology of seedlings. The study was conducted within the framework of the TROPENBOS programme in Guyana.

Study site and species

Guyana is situated in north eastern South America. The climate is tropical with high rainfall, between 2500 and 3400 mm per year. There are two distinct dry periods; January to March and August to September. Mean average temperature over the year is 25°C (ter Steege & Persaud 1991). *Chlorocardium rodiei* is a canopy tree in mixed evergreen forest on brown sandy soils and is confined to an area almost entirely within Guyana (ter Steege 1990). Locations with a dominance of the species are usually referred to as Greenheart forest, or 'Greenheart reefs' (Richards 1952, Fanshawe 1952). The species flowers on a regular yearly basis from February to May (Fanshawe 1947, ter Steege 1990). Maturation of the fruits takes approximately one year, after which the fruits have an average fresh weight of 65.5 g ± 22.3 SD (ter Steege 1990). Germination starts 2-4 months after seed fall.

Our study was conducted in Mabura Hill, on two sites on the timber concession of Demerara Timbers Ltd., near the center of distribution of *Chlorocardium rodiei*. One site is near the Ecological Reserve (5°13'N, 58°48'W) of the TROPENBOS Programme in Guyana, the other 5 km further south in a logged-over area of the concession: the Waraputa compartment.

Methods

Light climate

Hemispherical photographs of the sky were taken, using a camera with a fish eye lens. The pictures were taken in the middle of an area where experiments were carried out (see below) at a standard height of 1 meter. The camera was mounted on a tripod, fixed horizontally, with the top to the geographical north. The black and white photographs were scanned and digitized with a LochiTech Handheld Scanner at 100 DPI and subsequently analyzed with PPFDCALC (ter Steege, 1992) on a Hyunday AT computer. PPFDCALC calculates maximum diffuse and direct sunlight. Direct sunlight is calculated from the solar radiation (see Gates 1980) and is corrected for atmospheric transmissivity and path lenght through the atmosphere (Gates 1980, Pearcy 1989), PAR (Photosynthetic Active Radiation) fraction (51% of total radiation), solar declination, latitude of the site, and obstructions in the canopy, assuming there will be no transmission or reflection. Diffuse sunlight is calculated using the Uniform Overcast Sky (UOC, see Pearcy 1989), which makes the assumption that every part of the sky is equally bright. The total amount of diffuse light is taken as 15% of the calculated direct light (Gates 1980). For formulas

Table 1. PPFD estimates for forest sites in germination and survival study.

	% canopy openness	PPFD (mol m^{-2} day^{-1})
Germination		
forest understorey	6.6	1.29
forest edge	13.2	2.02
large gap	87.5	21.37
Survival		
forest understorey	9.8	1.60
forest edge	9.8	1.76
large gap	88.6	21.56

used see Gates (1980) and Pearcy (1989). In direct light calculations PPFDCALC can make corrections for average cloudiness. Average sun-hours per day in the forestry belt in Guyana amount to 5.2 hours per day (calculated with data from Persaud 1982). Since the sun-recorders used in Guyana can effectively measure 11 hours of sunshine on a cloudless day (the first and last half hour of the day having too little radiation to be registered, Persaud 1982), direct PPFD (Photosynthetic Photon Flux Density) as calculated from PPFDCALC was multiplied by 5.2/11 to estimate corrected average direct PPFD. Hereafter, maximum (daily) PPFD is the total uncorrected amount in mol m^{-2} day^{-1}. Average (daily) PPFD means total daily PPFD, corrected for cloudiness in mol m^{-2} day^{-1}.

To describe the effect of logging intensity on canopy openness and resulting total PPFD, we used basal area removed (m^2 ha^{-1}). There are two reasons for this choice: 1) Crown area is usually linearly related to basal area of a tree (e.g. Swellengrebel 1959, Heinsdijk 1953) and this is also the case in *Chlorocardium rodiei* (ter Steege et al. unpubl. data). Thus there exist a relationship between DBH (Diameter at Breast Height) and gap size of a felled tree (Hendrison 1990); 2) basal area harvested per hectare is a common unit used in logging prescriptions.

Germination

In the end February 1989, one month after the start of seed fall, 1200 seeds were randomly selected from a large batch of seeds varying in weight between 60 to 70 grammes, collected within the Ecological Reserve at Mabura Hill. At three sites; centre of a large gap, forest edge, forest understorey, 20 plots were established (see Table 1 for PPFD of the sites). In ten plots on each site 20 seeds were laid out in a square pattern, with the seeds 20 cm apart on the soil surface. In ten plots 20 seeds were buried just below the surface, again 20 cm apart. Germination was recorded every two weeks. After 88 days the experiment was terminated and all seeds were collected. The seeds were opened subse-

Table 2. ANOVA table for angular transformed germination data of *Chlorocardium rodiei* in three light climates * buried or not buried.

source of var.	df	SS	MS	Fs
Subgroups	5	9608	1922	
Site	2	876	438	10.26 **
Burying	1	6491	6491	152.08 ***
Interaction	2	2241	1120	26.25 ***
Error	54	2305	43	
Total	59	11913		

quently: a large number showed clear signs of germination and were also considered germinated at that time. Damage (fungal attack, predation and dehydration) were noted. The percentages of germination were arcsine transformed and analyzed with a two way ANOVA (Zar 1984).

Survival

180 a few month old seedlings were collected from within the Ecological Reserve. Shoot height of all seedlings was between 35 and 40 cm. All seedlings had at least two and no more than eight leaves. The seedlings were placed in 2.5 litre pots filled with yellow loamy sand. Seedlings were transferred to three light climates: large gap, forest edge, and forest understorey (see Table 1 for PPFD of the sites). In 1/3 of all seedlings both cotyledons were removed, in 1/3 one cotyledon, and 1/3 was left intact. The cotyledons, remaining on the seedlings, were covered with yellow sand to prevent dehydration. Watering of the plants was done regularly. Every week shoot height, measured from soil surface, number of leaves, and length of the longest leaf were measured. The experiment lasted for eight weeks. Survival data were arcsine transformed and analyzed with two way ANOVA (Zar 1984), with two samples of ten plants per plot per site.

Morphology

Within the Waraputa compartment an area of 480 ha was chosen. A timber inventory of this area had been executed slightly over a year (December 1988) before the start of the experiment in March 1990. On roughly 250 circular plots, 100 m apart, all trees >30 cm DBH had been enumerated. Out of the 480 ha, 220 ha were *Chlorocardium rodiei* bearing mixed forest. Logging took place shortly after the inventory (March 1989), and one year after logging 37 circular plots from the 250 were selected in *Chlorocardium rodiei* bearing mixed forest. Since felling had occurred somewhat haphazardly (but mainly along the main timber roads) the whole continuum from no logging to very intense logging was available within the 220 ha area. The only criterion for the selection of a plot for this study was the presence of one year old *Chlorocardium rodiei* seedlings. Such seed-

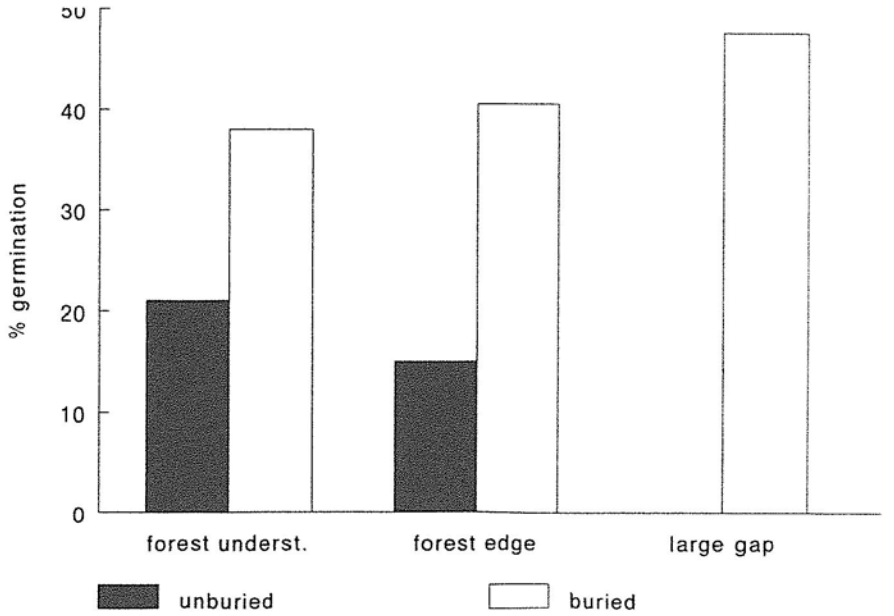

Figure 2. Germination percentages for *Chlorocardium rodiei* in the understorey (US), forest edge (FE), and large gap (LG), in buried and unburied condition.

lings can be identified by the intact cotyledons. At each 0.1 ha circular plot the number of trees >25 cm DBH was noted, as well as the number of trees logged. A uniform set of 5 to 10 one year old seedlings was sampled. The following parameters were measured: number of leaves, stem diameter at the base, stem height, length of all stem internodes. Leaf area was measured with a leaf area meter (TFDL, The Netherlands). Afterwards the seedlings were split up 4 fractions: 1) roots, 2) leaves, 3) petioles + stems and 4) cotyledons, and the fractions were dried in a field stove at 85-105°C for 24 hours. The small woody stems were cut in small pieces to ensure drying within this time. From the dry weights and leaf area the following parameters were calculated: average leaf size (leaf area/ nr of leaves, m^2), LAR (leaf area/plant dry weight, $cm^2\ g^{-1}$), SLA (leaf area/leaf weight, $cm^2\ g^{-1}$), LWR (leaf dry weight / plant dry weight g g^{-1}), StWR (stem dry weight / plant dry weight g g^{-1}), ShWR (shoot dry weight / plant dry weight g g^{-1}), RWR (root dry weight / plant dry weight g g^{-1}), SStW (stem height / stem weight cm g^{-1}).

To estimate growth we calculated RGR following Hunt (1978):

$$RGR = \frac{(\ln W_1 - \ln W_0) * 1000}{t_1 - t_0}\ mg\ g^{-1}\ day^{-1}$$

W_0 is the average initial dry seed weight (28 g), W_1 is the final dry seedling plus final dry seed weight. For t_1-t_0 we used two time intervals to present the maximum difference in age in seedlings due to unequal germination (see above).

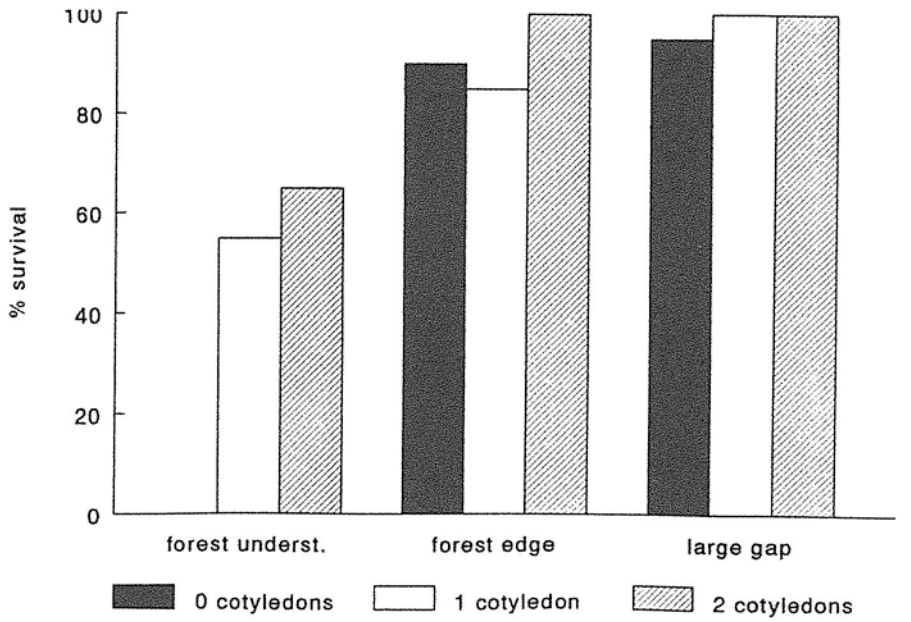

Figure 3. Survival percentages for *Chlorocardium rodiei* in the understorey (US), forest edge (FE), and large gap (LG), with no, one or two cotyledons removed.

Results

Light climate

Logging intensities in the 0.1 ha plots in the Waraputa compartment ranged from 0-13.7 m^2 ha^{-1} basal area removed, with an average of 4.4 m^2 ha^{-1}. The canopy openness in the unlogged plots ranged from 4.4- 16.6% with one extreme value of 29.2%. In the logged plots canopy openness ranged from 11.9-52.2%. Calculated average daily PPFD on the unlogged plots ranged from 1.48-4.78 mol m^{-2} day^{-1} in the unlogged plots and from 3.39-14.07 mol m^{-2} day^{-1} in the logged plots, or in total between 6-56% of total average daily PPFD above the canopy. Calculated average maximum total daily PPFD (100% openness, no cloudiness) for the site is 43.6 mol m^{-2} day^{-1}. Average (calculated and corrected) PPFD amounts to approximately 22.6 mol m^{-2} day^{-1}. Estimated total corrected PPFD increases with increased logging intensity (figure 1). Both direct and diffuse light are dependent on the location of the openings in the canopy, but both have a very high correlation with the canopy openness ($r=0.95$, $p<0.001$ and 0.99, $p<0.001$ respectively). Light intensities for both germination plots and survival plots are given in Table 1.

Germination

Germination of unburied *Chlorocardium rodiei* seeds decreased from the darkest, probably moistest site to the lightest one (Figure 2). Germination of unburied seeds in

Table 3. ANOVA table for angular transformed survival rates of *Chlorocardium rodiei* in three different light climates, with varying number of cotyledons.

source of var.	df	SS	MS	Fs
Subgroups	8	2319	290	
light	2	1328	664	171.84 ***
cotyledons	2	392	196	50.68 ***
Interaction	4	599	150	38.73 ***
Error	9	35	4	
Total	17	2354		

the large gap was nil. All seeds remaining on this site showed signs of damage as a result of drought and cracking. A few seeds had been washed away by heavy rain. Germination of seeds buried in the soil increased from the darkest to the lightest site. The resulting interaction site*treatment was significant (Table 2). Treatment (buried or unburied), however, seems to be more important than site, since germination of buried seeds was always higher than of seeds on the soil surface.

Survival

Survival percentages after 8 weeks are given in Figure 3. Survival was highest with two cotyledons in both forest edge and large gap. Survival was nil in the understorey with no cotyledons. The factor site had a significant effect on the survival of the seedlings as had the number of cotyledons (Table 3). Due to the very high mortality in the understorey for plants with no cotyledons there was also a significant interaction. There was a large difference in PPFD between the large gap and forest edge (Table 1) but only a small effect on the survival of the seedlings. There is a small difference between PPFD of the forest edge and the understorey but a large effect on the survival. In all treatments seedlings lost leaves in the course of the experiment.

Morphology

Within the range of light climates, the average total dry weight of one year old *Chlorocardium rodiei* seedlings was positively related to average PPFD ($r=0.69$, $p<0.01$). Average dry weight on the plots varied from 7 g (in the understorey) to 34 g (in a large gap). Stem diameter, number of leaves and leaf area were all higher in seedlings in gaps compared to seedlings in the understorey (r with average PPFD = : 0.58, $p<0.05$, 0.79, $p<0.01$, and 0.71, $p<0.01$ respectively). Table 4 summarizes the characteristics for three contrasting sites. The average leaf size was not affected by the light climate, but ranged largely within all habitats. Shoot height did not differ along the light gradient. The length of the first internode (epicotyl) decreased with increasing PPFD (Figure 4). The length of all other internodes did not change over the light gradient (Figure 4), but the

Table 4. Some characteristics of *Chlorocardium rodiei* seedlings from three contrasting light climates. Standard errors of the averages are given between brackets.

	Large Gap		intermediary		Understorey	
PPFD (mol m^{-2} day^{-1}	13.66		6.23		1.82	
n	6		10		5	
stem diameter (cm)	1.08	(0.03)	0.75	(0.04)	0.62	(0.01)
stem height (cm)	83.6	(4.3)	66.2	(4.6)	56.2	(3.3)
length 1st int. (cm)	23.9	(2.1)	34.5	(2.7)	34.8	(3.6)
n internodes on stem	8.0	(0.4)	5.7	(0.5)	4.4	(0.2)
avg lenght i.o.s.	7.3	(1.4)	6.7	(0.4)	6.2	(0.7)
stem weight (g)	19.8	(1.4)	8.5	(0.7)	3.1	(0.3)
leaf weigt (g)	22.9	(2.6)	6.9	(0.7)	1.3	(0.2)
shoot weight (g)	42.7	(3.4)	15.4	(1.3)	4.5	(0.3)
root weight (g)	14.2	(2.0)	5.6	(0.7)	1.6	(0.3)
n of leaves	79	(4.0)	37	(2.4)	9	(1.2)
leaf area (cm^2)	2792	(282)	928	(76)	206	(25)
LAR (cm^2 g^{-1})	48.7	(2.7)	44.4	(1.7)	33.8	(2.4)
SLA (cm^2 g^{-1})	120	(3.0)	140	(0.47)	155	(3.9)
LWR (g g^{-1})	0.40	(0.02)	0.33	(0.01)	0.22	(0.02)
SWR (g g^{-1})	0.76	(0.02)	0.74	(0.02)	0.74	(0.03)
RWR (g g^{-1})	0.24	(0.02)	0.26	(0.02)	0.26	(0.03)
R/S (g g^{-1})	0.33	(0.02)	0.36	(0.02)	0.36	(0.03)

number of internodes per plant increased. After 1 year of growth the higher number of internodes on plants in light environments compensated for their shorter epicotyl, so that seedlings from all environment equaled each other in height. SLA increased with decreasing light ($r=0.73$, $p<0.01$) and LWR decreased ($r=0.73$, $p<0.01$). The decrease in the latter was of such magnitude that the product of both, the LAR, also decreased with decreasing PPFD ($r=0.52$, $p<0.05$). Plants in the understorey and plants in a large gap invested equal proportions of their biomass in roots and shoots (Figure 5). StWR, however decreased with increasing PPFD, while LWR showed the opposite relationship (Figure 6). Cotyledon dry weight after one year did not differ along the light gradient. RGR is only positive in the large gap. Neither in the understorey nor in the intermediary situations are seedlings able to grow in excess of their cotyledon reserves.

Discussion

Estimated average PPFDs for our forest sites fall within the range measured in other tropical forests (Chazdon & Fetcher 1984 - max 33 mol m^{-2} day^{-1}, Oberbauer & Strain

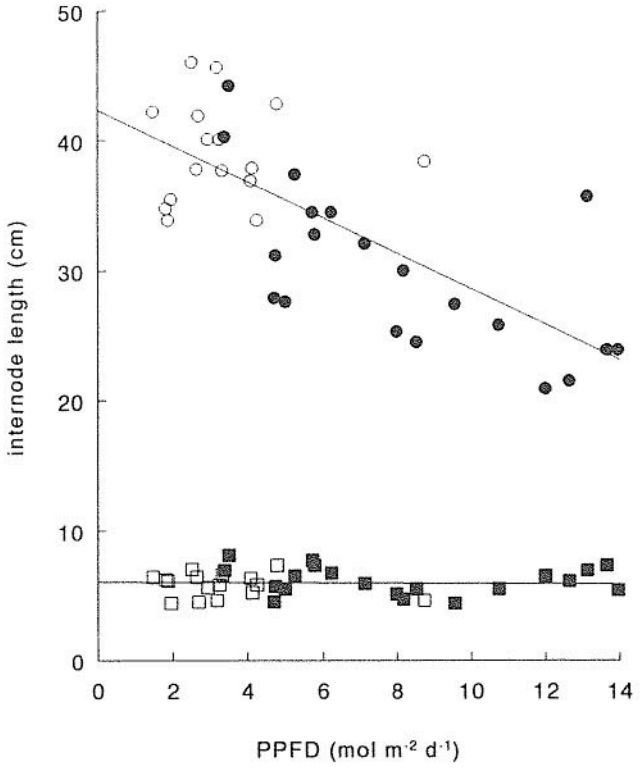

Figure 4. Average length of first internode and all other stem internodes of *Chlorocardium rodiei* on plots under varying average daily PPFD in natural and logged forest. Cirlces: 1st internode, squares: mean of other internodes, open symbols: unlogged plots, filled symbols: logged plots.

1985 - avg 27 mol m^{-2} day^{-1} in a large clearing, Raich 1989 - average 31.2 mol m^{-2} day^{-1}). Raich (1989) furthermore found that mean PPFD was linearly correlated with canopy openness. Diffuse light and direct sunlight were highly correlated in our study. A similar observation was made by Turner (1990b).

Germination of *Chlorocardium rodiei* differed strongly between sites. Large forest seeds, with high moisture content, often do not germinate in the open (Richards 1952, Raich & Gong 1990). The results for *Chlorocardium rodiei* are in agreement with these findings. Sork (1985) found similar results in *Gustavia superba* (Kunth) Berg. Germination of buried seeds is always higher than of unburied seeds in all light climates. For those seeds in the forest, which have a long dormancy this may be beneficial if the seeds get covered with litter during their seeming inactivity. While low relative humidity and high insolation may kill the seeds, high temperature may not necessarily be harmful and seeds are able to survive and germinate in the soil in a large gap. Sufficient soil moisture may be a factor here. Under 'normal conditions', however, large gaps decrease the germination of *Chlorocardium rodiei* significantly.

Short term mortality in *Chlorocardium rodiei* is mainly influenced by the amount of

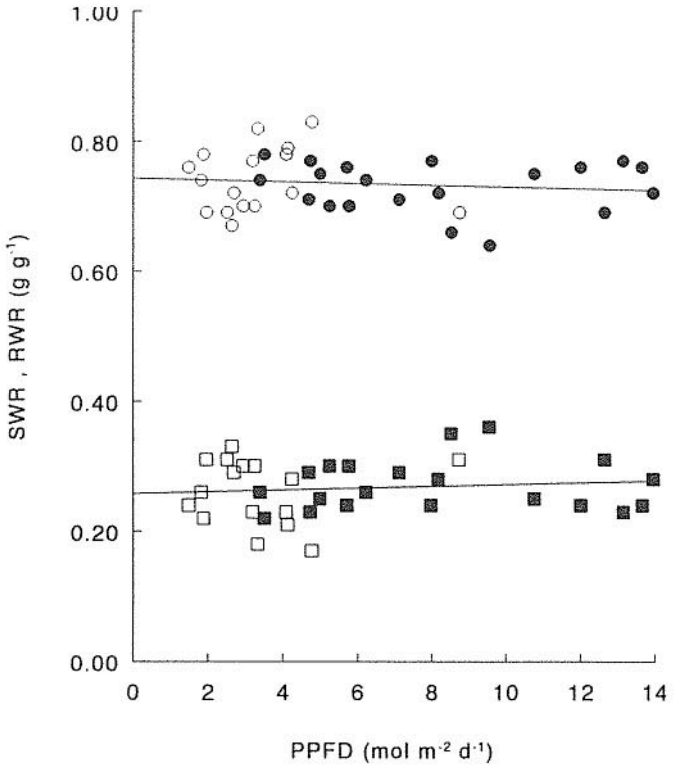

Figure 5. Average shoot weight ratio (SWR) and root weight ratio (RWR) of *Chlorocardium rodiei* on plots under varying average daily PPFD in natural and logged forest. Cirkes: SWR, squares: RWR, Open symbols: unlogged plots, filled symbols: logged plots.

light in the environment. This agrees with findings of Augspurger (1984) and Turner (1990b). Light seems even more important for survival than the amount of seed reserves left on the plant. Although the forest edge and the understorey differed only slightly in light intensities, differences in mortality were large. We do not know if differences in high coverage were not appropiately distinguished by PPFDCALC, or that a PPFD of 2 mol m^{-2} day^{-1} is the lower limit for survival in *Chlorocardium rodiei*.

Apart from low light levels, fungal attack (Augspurger 1984) or insect attack (Augspurger 1984, Turner 1990a) are common causes of death for seedlings in the forest understorey. Although mortality may have been increased by taking seedlings from soil into pots, the results clearly show the potential effect of seed predation in the forest.

Growth of *Chlorocardium rodiei* is enhanced by increasing light intensity. Seedlings in the sun are larger, heavier, have more branches (data not shown), more leaves and larger leaf area, but are not taller, mainly due to a shorter epicotyl. Climax species are often regarded as R/FR insensitive as compared to pioneer species (e.g. Kwesiga & Grace 1986). In Dipterocarp climax species, however, especially epi- and hypocotyl elongation were shown to be highly influenced by R/FR (Sasaki & Mori 1981). Since R/FR decreases steadily with decreasing light intensity (Lee 1987 and as also indicated by calculations with PPFDCALC) the epicotyl elongation in *Chlorocardium rodiei* in darker sites might

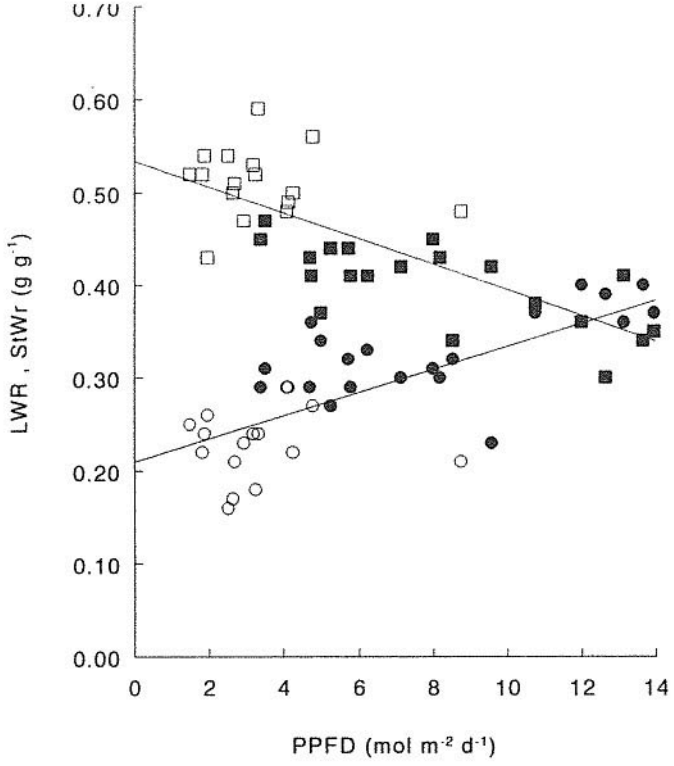

Figure 6. Average leaf weight ratio (LWR) and stem weight ratio (StWR) of *Chlorocardium rodiei* on plots under varying average daily PPFD in natural and logged forest. Cirlces: StWR, squares: LWR, Open symbols: unlogged plots, filled symbols: logged plots.

be attributable to low R/FR ratio or to low light intensity or both.

SLA of the seedlings increased with decreasing light. This is in agreement with Fetcher et al. (1983), Oberbauer & Strain (1985), Bongers et al. (1988), Popma & Bongers (1988). An increase in SLA seems beneficial since more leaf area is constructed with the same amount of biomass. Increase in SLA may indeed to a certain degree compensate for a decrease in PAR (Mitchell & Woodward 1988). LAR of *Chlorocardium rodiei* seedlings decreases with decreasing light, this result contrasts with most of the above mentioned studies, where an increase in SLA is mostly accompanied by an increase in LAR. The low LAR in *Chlorocardium rodiei* can only be explained by a very low LWR in the understorey (since the SLA increased). A low LAR in shade was also found by Popma and Bongers (1988) in 3 out of 10 species studied. The 3 species involved also had a very low to negative RGR. Low LWR can be the result of high leaf loss rates in relation to production rates. Short leaf duration (read: high turn over) was found in *Pentaclethra macroloba* in full shade but also in full sun (Oberbauer & Strain 1985). Popma & Bongers (1988) found shorter leaf duration in full sun, but this was more than compensated for by growth. The number of internodes on our plants in shade (each node had two leaves) indicates indeed that leaf loss has been substantial in *Chlorocardium rodiei* seedlings in the

Table 5. RGR of *Chlorocardium rodiei* in three light climates. Since absolute age of seedlings can range between 12 and 8 months RGR is calculated for two periods.

	PPFD	RGR[a]	RGR[b]
	mol m^{-2} day^{-1}	mg g^{-1} day^{-1}	
Large gap	13.66	2.42	4.21
intermediary	6.23	-0.17	-0.29
understorey	1.82	-2.45	-4.25

[a] time period of 365 days
[b] time period of 240 days

understorey. Leaf turn over may be influenced by a low R/FR (Mitchell and Woodward 1988).

Root/shoot ratios did not differ significantly in plants over the PPFD continuum, contrary to most other experiments (see references above). The fact that *Chlorocardium rodiei* has no clearly lower R/S in the understorey is due to a very low LWR in those plants. Undoubtedly some roots have been lost while digging up the seedlings. However in the forest the rootsytems are small and losses are also small. In the open areas root sytems were easy to obtain as the root density (of other individuals) is far lower. The small amount of secondary roots lost in the forest will probably did not change the RSR greatly.

After 1 year of growth plants in the sun had a higher total biomass and leaf area than plants in shade. Due to high leaf loss, resulting in a low LAR, plants in the understorey did not produce much biomass. Although maximum and minimum RGR differ considerably within site (Table 5), there is no overlap in RGR between sites. Strong positive growth over a year is found only in the large gap. In that same year cotyledon dry weight decreased from 28 to 8.6 g, with no differences between the sites. In the understorey growth is negative. When the reserves stored in the seed are exhausted, either by the seedlings own use or by predation, the seedlings (sensu stricto) in the understorey will not grow anymore and die, as indicated by the mortality experiment.

Chlorocardium rodiei has been classified as shade tolerant (Fanshawe 1948) but would respond fast on canopy openings. Our findings suggest that while seedlings may persist at least one year in the understorey, they are not shade tolerant for many years. The observed light levels in natural, unlogged forest are probabely not high enough to promote positive growth. Large gaps such as those caused by logging are big enough to increase growth and survival of *Chlorocardium rodiei* seedlings. In mature Greenheart forest such canopy openings do not occur very often and seedlings grow slowly. While seedlings may be conservative with their reserve food, predators are not and overall seedling mortality is high in *Chlorocardium rodiei*. Establishment of saplings will only occur in the rare case of a large gap. This may help to explain the relative uncommonness of middle sized trees in size class diagrams (Richards 1952, see also Clark & Clark 1987 and ter Steege 1990).

Although seedlings of *Chlorocardium rodiei* can tolerate full sunlight at a young stage, caution in logging activity should be taken. The seeds of *Chlorocardium rodiei* do not germinate in too open habitats, as are often created in felling the gregariously growing *Chlorocardium rodiei* individuals. In logged areas some mature trees should remain to provide seeds and, shade and moisture.

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Seedling growth of *Mora gonggrijpii*, a large seeded climax species, under different soil and light conditions

Hans ter Steege

Abstract

Mora gonggrijpii seedlings were harvested on two soil types in small gaps and in the forest understorey. The seedlings appear to be intolerant of lateritic soil with poor drainage either as a result of poor aeration or reduction of the soil which is rich in iron and aluminium. Biomass allocation is not greatly affected on the lateritic soil as compared to the better drained sandy soil. During the initial growth of two months light has no effect on the growth of the seedlings but soil type does. In the same period cotyledon depletion is equal, suggesting higher turnover rates or respiration rates on the poorly drained lateritic soil. From the second to the seventh month light stimulates growth, but *Mora gonggrijpii,* seedlings are not plastic in their morphology. Leaf area remains constant during this period, and no branching is observed in the higher light environment. Specific leaf area, leaf area ratio, net assimilation rate and relative growth rate are all among the lowest thus far reported for tree seedlings. Evidence is presented that these characteristics are found often in large seeded (climax) species.

Introduction

The genus *Mora* (CAESALPINIACEAE) is among the dominant tree genera in Guyana (Fanshawe 1952, Richards 1952). Within the Guianas two species are found, *Mora excelsa* Bentham and *Mora gonggrijpii* (Kleinhoonte) Sandwith. *Mora excelsa* occurs from eastern Surinam to Trinidad (ter Steege 1990), while *Mora gonggrijpii* has a slightly more restricted distribution from mid Surinam to eastern Venezuela (ter Steege 1990). Both *Mora* species are thought to be strongly shade tolerant in their seedling stage, and show abundant regeneration and recruitment (Richards 1952, Bell 1969, ter Steege et al. in prep).

The genus *Mora* is currently thought to be comprised of four species on the South American mainland (Ragonese 1973), three of which occur mainly along creeks and rivers and depend at least partly on surface water for their dispersal (Mayo-Melendez 1965, Bell 1969, Roosmalen 1985, ter Steege 1990). *Mora gonggrijpii* is the only *Mora* species that is common, in fact may be dominant, on higher, drier ground.

In December 1988 *Mora gonggrijpii* produced a large seed crop at Mabura Hill, Guya-

na. Most seeds germinated and produced healthy seedlings. Large seedling populations were present in January 1989 along a newly built road on both well-drained sandy soil and poorly-drained lateritic soil, the latter occasionally saturated with water. This situation created an opportunity to observe growth and morphological plasticity of *Mora gonggrijpii* seedlings on different soil (drainage) types as well as in contrasting light climates. Since *Mora gonggrijpii* seedlings are rare along creeks, where *Mora excelsa* is dominant, it was expected that *Mora gonggrijpii* seedlings would grow better on well drained soil compared to poorly drained soil. Furthermore it was expected that *Mora gonggrijpii*, being very shade tolerant, would show little plasticity in its behaviour related to light increases.

This is the first in a series of studies on flooding and drought tolerance of *Mora* spp. The study was carried out within the framework of the Forest Project Mabura Hill, a joint research project between the University of Utrecht and the University of Guyana. This project is now incorporated in the TROPENBOS Programme Guyana.

Site and study species

The study was carried out near the Ecological Reserve of the Forest Project Mabura Hill in the near interior of Guyana, 05°13' N 58°48' W. Climate in Guyana is tropical with high rainfall (2400-3400 mm per year), concentrated in two rainy seasons, and high average temperatures (25°C) (ter Steege & Persaud 1991).

Mora gonggrijpii is a tall evergreen canopy species of the mixed rain forest of Guyana and surroundings. Seeds are produced at irregular intervals but seedfall is in the rainy season of either December or May (ter Steege & Persaud 1991). Mean fresh seed weight is high, 106 g (sd=38, n=438) and one or sometimes two seeds are found in a pod. The range in seed weight observed is huge but the distribution is not different from normal (Figure 1). Germination is immediate and almost 100% and seedling mortality is very low in the first half year.

Materials and methods

Growth and biomass allocation

Seedlings of *Mora gonggrijpii* were harvested on four sites along a newly built road, 1) in the forest understorey on well drained sandy soil (Ferralic Arenosol), 2) in a small gap near the road on the same soil, 3) in the forest understorey on poorly drained lateritic soil (Dystric Leptosol, Rudic Phase) and 4) in a small gap near to the road on the same soil. All four sites were within 200 m of each other, the lateritic sites at a slightly lower elevation than the sandy sites (*Mora gonggrijpii* was abundantly present in the canopy on all four sites. Within the very large, fairly homogeneous seedling populations at each site the ten largest seedlings were harvested at the end of January 1989 (many seedlings of equal size remained). Seedlings were again sampled at the end of June 1989, when again

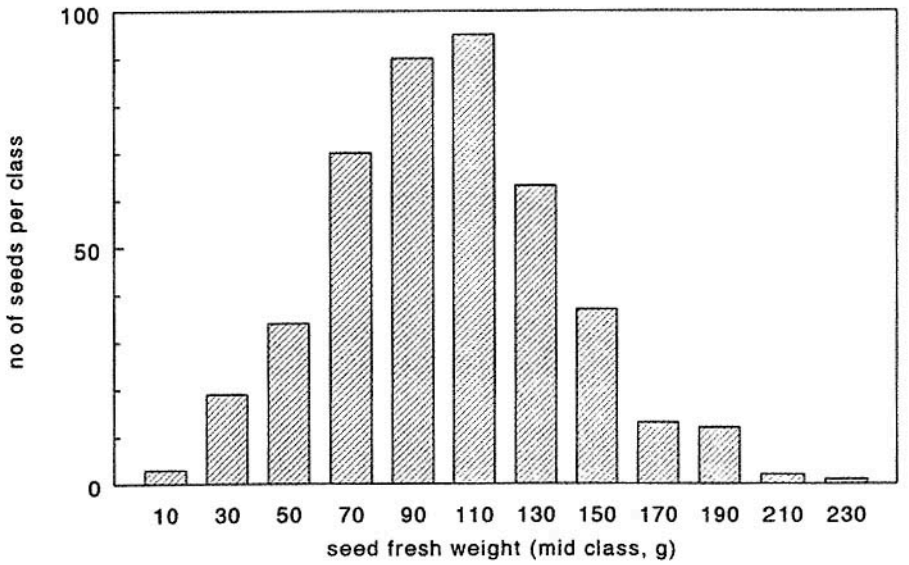

Figure 1. Seed fresh weight distribution of *Mora g onggrijpii*. Average seed weight is 106 g (sd=38, n=438). The distribution is not different from normal.

the largest ten seedlings were harvested. At harvest, height (cm) and number of leaves of each seedling were recorded. At harvest seedlings were carefully dug out by hand and cutlass and care was taken to collect as many roots belonging to a plant as was possible in the dense root mat. The seedlings were separated into roots, stems and leaves. Leaf area (cm^2) was measured with a Li-3000 area meter (Licor, Lincoln, Nebraska). Length and width (cm) of all leaves was recorded and the leaf shape index (LSI) calculated as length/width. The plant fractions were oven-dried at 75°C for 48 hours and weighed with an electronic scale to 0.1 g. From these measurements leaf area ratio (LAR: $cm^2\ g^{-1}$), specific leaf area (SLA: $cm^2\ g^{-1}$), leaf weight ratio (LWR: $g\ g^{-1}$), stem weight ratio (SWR: $g\ g^{-1}$), root weight ratio (RWR: $g\ g^{-1}$) and root shoot ratio (R/S: $g\ g^{-1}$) were determined.

Data were processed with factorial (2^3) ANOVA (Zar 1984). The three factors were soil (sand or laterite), light climate (gap or understorey), and time (January or June). Growth of seedlings is significant if a significant portion of the existing variance is explained by the factor time. The relative growth rate (RGR) can then be expressed as:

$$RGR = \frac{[Ln(W_{t2}) - Ln(W_{t1})]}{t_2 - t_1} * 1000\ (mg\ g^{-1}\ day^{-1})$$

where W_{t1} and W_{t2} are the total dry plant weight, without cotyledons, in January and in June respectively, t_2-t_1 the duration in days between the harvests. Net Assimilation Rate (NAR) was calculated as:

Table 1. Percentage cover and estimated photosynthetic photon flux density (PPFD) on the two sites in the forest understorey and two in small gaps. PPFD is an average dayly amount from January till June corrected for average cloud cover.

site	cover (%)	PPFD mol m^{-2} day^{-1}
Sand, understorey	90.4	2.02
Sand, gap	61.5	10.82
Laterite, undestorey	97.1	0.92
Laterite, gap	64.2	12.49

$$NAR = \frac{W_{t2} - W_{t1}}{t_2 - t_1} * \frac{Ln(A_2) - Ln(A_1)}{A_2 - A_1} * 1000 \text{ (mg cm}^{-2} \text{ day}^{-1})$$

(Hunt 1978), where A is leaf area.

Since the amount of storage in the cotyledons is large compared to the seedling weight, RGR is also calculated for seedling dry weight plus cotyledon dry weight (W_{t+c}). This may indicate if, apart from the uptake of cotyledon reserve, growth due to photosynthesis has taken place. Since seeds had fallen in the beginning of December, the first growth interval was 60 days, from the beginning of December until the end of January. The second growth interval was 150 days, from the end of January until the end of June.

Relative cotyledon use (RCU), the rate at which cotyledons are depleted, is expressed as:

$$RCU = \frac{[Ln(W_{c1}) - Ln(W_{c2})]}{t_2 - t_1} * 1000 \text{ (mg g}^{-1} \text{ day}^{-1})$$

where W_c is the dry weight of the cotyledons. (note that the order of W_{c1} and W_{c2} is altered)

Light climate on the sites was characterized with the aid of hemispherical photographs (Pearcy 1989; ter Steege 1992). One picture was taken in the centre of each site at a height of approximately 1 m. The pictures were scanned with a hand-held scanner (Lochitech, Fremont CA 94555, USA). The digitized images were subsequently analyzed by PPFDCALC (ter Steege 1992, ter Steege et al. submitted). PPFDCALC estimates PPFD (photosynthetic photon flux density) for any day and any site in steps of 3 min. An average PPFD for the duration of the experiment was obtained by calculating the PPFD for each 15th day of the months from January until June for each of the four sites, with correction for cloudiness (ter Steege et al. submitted).

Results

Light climate

Canopy coverage and estimated PPFD for the four sites are given in Table 1. Both small gaps had similar coverage and resulting average PPFD. The forest understorey site on sand was slightly more open than the forest understorey site on laterite, resulting in a slightly higher average daily PPFD.

Growth and biomass allocation

The main results of the sampling are given in Table 2. In January as well as in June seedlings of *Mora gonggrijpii* were taller and heavier and produced more leaf area on sand than on laterite. On average, seedlings of *Mora gonggrijpii* grew faster on well drained sandy soil than on poorly drained lateritic soil. The factor soil had a significant effect on all size related characteristics. However, no differences in biomass allocation between soil types were found, except for a slightly lower LWR and slightly higher SLA on laterite compared to sand.

Light had a strong effect on both size characteristics and biomass allocation but not until June. In January seedling weight and leaf area were not significantly affected by the light climate. In June seedlings in the small gaps were taller, heavier and had more leaf area than those from the understorey. LWR was higher in plants in the gaps, except in June on sand. Here seedlings in the understorey had a higher LWR. This resulted in an interaction between the factors light and soil. No difference in LAR among seedlings of different light climates was found. SLA was higher in seedlings from the forest understorey. Leaf shape index was constant on all sites and both harvests.

Seedlings on all plots showed net growth in the period from January to June, indicated by a significant portion of variance in total plant dry weight accounted for by the factor time. However leaf area decreased in the plots in the understorey. Average RGRs for the sites are given in Table 3. RGR and NAR were highest in the small gap on sand. Although final dry weight of the seedlings on laterite was lower than on sand, RGRs from January to June were comparable to the plants of the small gap on sand. Leaf weight and leaf area did not change from January to June. Consequently LWR, LAR and SWR decreased, while RWR and R/S increased.

Cotyledon weight of the seedlings of the four sites did not differ significantly among sites in January. This suggests that cotyledon use from December until January has been equal in all sites. In June the weight of the cotyledons in the forest understorey was lower than of those in the gaps, suggesting an higher cotyledon use in the understorey environments. Although the cotyledons had retained some dry weight at the end of June, they were rotten in most cases on all four sites and had probably lost their function. Only seedlings in the gap on sand showed a net increase in weight in excess of their cotyledon use (Table 3).

Table 2. Final results and 2^3 ANOVA analyses, for *Mora gonggrijpii* seedlings grown in contrasting light climates and different soil types. ▶

		January		June	
		s.gap	f.und.	s.gap	f.und.
shoot height (cm)	sand	65.4	93.9	101.7	97.9
	laterite	45.5	75.9	66.3	111.5
stem weight (gr)	sand	13.6	14.9	29.7	14.8
	laterite	5.2	7.2	9.2	11.3
leaf weight (gr)	sand	24.3	15.9	29.6	15.5
	laterite	8.3	6.0	10.1	5.2
shoot weight (gr)	sand	37.9	30.8	59.3	30.2
	laterite	13.5	13.1	19.3	16.5
root weight (gr)	sand	6.7	5.1	27.4	6.3
	laterite	2.0	2.5	7.5	5.5
plant weight (gr)	sand	44.6	35.8	86.6	36.5
	laterite	15.4	15.6	26.9	22.0
cotyl weight (gr)	sand	23.8	27.7	13.0	7.5
	laterite	24.6	28.2	10.2	9.2
leaf lenght (cm)	sand	24.2	21.5	19.9	18.2
	laterite	14.0	13.7	11.9	12.5
leaf width (cm)	sand	8.7	7.8	7.3	7.1
	laterite	5.6	5.2	4.3	4.8
leaf area (cm^2)	sand	2635	2133	2955	2016
	laterite	988	840	1090	749
leaf shape index	sand	2.77	2.76	2.74	2.58
	laterite	2.68	2.68	2.78	2.60
LAR ($cm^2\ g^{-1}$)	sand	59.0	60.9	34.7	55.0
	laterite	64.4	55.1	40.7	32.9
SLA ($cm^2\ g^{-1}$)	sand	108.3	134.4	100.2	131.2
	laterite	118.7	141.6	108.1	141.4
LWR	sand	.54	.45	.35	.42
	laterite	.54	.39	.38	.23
SWR	sand	.85	.86	.69	.83
	laterite	.87	.84	.72	.74
RWR	sand	.15	.14	.31	.17
	laterite	.13	.16	.28	.26
R/S	sand	.18	.16	.46	.21
	laterite	.15	.19	.39	.35

Table 2. Continued. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; n.s. not significant. Each cell represents the average of ten seedlings.

		among	soil	month	light	s*m	s*l	m*l	l*s*m
shoot height (cm)	Fs	8.13	7.16	18.78	20.21	.52	5.20	.62	4.46
	p	***	*	***	***	n.s.	n.s.	n.s.	*
stem weight (gr)	Fs	13.48	47.80	17.10	2.69	1.82	9.29	7.78	7.87
	p	***	***	**	n.s.	n.s.	**	*	*
leaf weight (gr)	Fs	21.99	109.61	1.25	31.54	.50	8.33	2.38	.35
	p	***	***	n.s.	***	n.s.	*	n.s.	n.s
shoot weight (gr)	Fs	18.99	88.24	8.64	14.90	1.30	10.50	5.72	3.63
	p	***	***	**	**	n.s.	**	n.s.	n.s
root weight (gr)	Fs	14.60	21.50	25.70	16.28	4.82	12.57	13.38	7.93
	pp	***	***	***	**	*	**	**	*
plant weight (gr)	Fs	22.39	79.82	19.07	21.12	3.21	15.41	11.23	6.90
	p	***	***	***	***	n.s.	**	**	*
cotyl.weight (gr)	Fs	6.33	.00	41.82	.01	.06	.18	2.01	.23
	p	***	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.
leaf lenght (cm)	Fs	18.36	106.31	15.82	2.79	1.14	1.51	.84	.09
	p	***	***	***	n.s.	n.s.	n.s.	n.s.	n.s
leaf width (cm)	Fs	15.08	90.57	10.85	.82	.18	1.17	1.94	.05
	p	***	***	**	n.s.	n.s.	n.s.	n.s.	n.s
leaf area (cm^2)	Fs	15.05	92.37	.11	9.34	.09	2.27	.99	.15
	p	***	***	n.s.	**	n.s.	n.s.	n.s.	n.s
leaf shape index	Fs	.39	.10	.32	.96	.48	.00	.84	.01
	p	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s
LAR ($cm^2\ g^{-1}$)	Fs	6.87	1.39	32.26	.10	1.58	8.41	2.50	1.85
	p	***	n.s.	***	n.s.	n.s.	**	n.s.	n.s
SLA ($cm^2\ g^{-1}$)	Fs	11.06	6.64	2.55	66.85	.00	.00	1.23	.15
	p	***	*	n.s.	***	n.s.	n.s.	n.s.	n.s
LWR	Fs	10.07	5.41	35.74	12.18	1.21	8.78	3.65	3.50
	p	***	*	**	**	n.s.	**	n.s.	n.s
SWR	Fs	8.89	.37	43.33	4.41	.62	5.33	6.98	1.16
	p	***	n.s.	***	n.s.	n.s.	*	*	n.s
RWR	Fs	8.89	.37	43.33	4.41	.62	5.33	6.98	1.16
	p	***	n.s.	**	n.s.	n.s.	*	*	n.s
R/S	Fs	7.45	.19	34.58	4.66	.28	4.52	6.38	1.52
	p	***	n.s.	***	*	n.s.	n.s.	n.s.	n.s

Table 3. Relative growth rate (RGR, mg g^{-1} d^{-1}, net assimilation leaf rates (NAR, mg cm^{-2} d^{-1}) and relative cotyledon use (RCU mg g^{-1} d^{-1}) of *Mora gonggrijpii* seedlings (dry weights from table 2, $t_{De\text{-}Ja}$ = 60 days, $t_{Ja\text{-}Ju}$ = 150 days). W_{Dec} for cotyledons is for seeds slightly higher than average.

plant weight	W_{Jan}	W_{Jun}	$RGR_{J\text{-}J}$	NAR		
sand gap	44.64	86.62	4.42	1.00		
sand forest	35.84	36.47	.12	0.02		
laterite gap	15.44	26.85	3.69	0.54		
laterite forest	15.63	22.03	2.29	0.74		
cotyledon weight	W_{Dec}	W_{Jan}	$RCU_{De\text{-}Ju}$	W_{Jun}	$RCU_{Ja\text{-}Ju}$	
sand gap	65.00	23.77	6.71	12.98	4.03	
sand forest	65.00	27.74	5.68	7.50	8.72	
laterite gap	65.00	24.56	6.49	10.19	5.86	
laterite forest	65.00	28.24	5.56	9.18	7.49	
plant +cot. weight	W_{Dec}	W_{Jan}	$RGR_{De\text{-}Ja}$	W_{Jun}	$RGR_{Ja\text{-}Ju}$	$RGR_{De\text{-}Ju}$
sand gap	65.00	68.41	.85	99.60	2.50	2.03
sand forest	65.00	63.58	-.37	43.97	-2.46	-1.86
laterite gap	65.00	40.00	-8.09	37.04	-.51	-2.68
laterite forest	65.00	43.87	-6.55	31.21	-2.27	-3.49

Discussion

In general plants grew well and appeared little affected by herbivory (estimated at <5% of the leaf area) or fungal infections on all sites, this is especially true for the largest and most vigourous seedlings, which were used.

Soil conditions have a large overall effect on the performance of *Mora gonggrijpii* seedlings. Seedlings do better on (well drained) sandy soil compared to (poorly drained) lateritic soil. Reduction of growth under poorly drained conditions is normal for temperate plant species not adapted to waterlogged conditions (e.g. Hook & Brown 1973, see Kozlowski 1984 for a review). Not much is known of tropical species, but in those species studied so far growth completely stopped (Joly & Crawford 1982), continued (Joly & Crawford 1982, Sena Gomes & Kozlowski 1988) or even increased under flooded conditions (Hartshorn 1972). In many temperate cases root adaptations (Kozlowski 1984) or alteration in R/S (Keely 1979) allowed plants to survive waterlogged conditions . Adaptations, such as adventitious roots or a difference in root/shoot ratio were not exhibited by *Mora gonggrijpii* seedlings in this study and the species may be considered poorly adapted to imperfectly drained soils. Other factors such as reduction of the soil and subsequent toxicity of e.g. iron or aluminium ions (Kozlowski 1991), both of which are generally abundantly present in lateritic soil, may also be important factors in the poor perfor-

mance of *Mora gonggrijpii* seedlings on poorly drained lateritic soil. Although there were no visible signs of pathogens on any of the sampled seedlings, differences in infection between the sites cannot be excluded. Preliminary data of Zagt et al. (pers comm.) for instance indicate that other species in the area may show infection with different fungal pathogens on different soils.

During the first two months after seed fall (December-January) seedling dry weight was not significantly affected by light climate. The main source of carbon for the seedlings in this period was probably the carbon stored in the cotyledons with little additional from carbon assimilation. While cotyledon use was not significantly affected by soil type, growth was affected by soil type (lower on laterite), suggesting higher (root?) turnover rates and/or respiration rates under poorly drained conditions. Initial seed weight may play an important role in the total plant weight during growth associated with cotyledon depletion. For instance the rate in seedling dry weight of three *Eperua* spp.was in close accordance with the rate in initial seed fresh weight (10 : 35 : 60 g, ter Steege unpublished data). Seeds of *Mora gonggrijpii* collected from these four and two other sites show a normal distribution (Figure 1) and it is likely that average weight differs little between the sites. The small differences in cotyledon dry weights both in January and in June are another indication that initial cotyledon weights were most likely in the same order for all sites. The largest seedlings of each site, however, most likely originated from seeds of more than average weight. To compensate for this effect seed dry weight in Table 3 is taken slightly higher than average.

In the following period (January-June) seedlings of *Mora gonggrijpii* grew faster and produced more leaf area per unit time in the small gaps. SLA was higher in the understorey and the understorey plants lost some of their leaf area, possibly due to a somewhat higher leaf loss (ter Steege et al. submitted). These findings are in full agreement with earlier reports of growth in tropical seedlings (Fetcher et al. 1983, Oberbauer & Strain 1985, Bongers et al. 1988, Popma & Bongers 1988). Seedlings on all sites showed growth in the period from January to June (Table 3). In the same period cotyledon usage was slightly higher in the understorey. Growth was very low in forest on sand, although initial growth, associated with the use of the cotyledon reserves, from December to January of seedlings in forest on sand was high and unaffected by the amount of light. Maintenance costs of the relatively larger seedlings in January may have caused a drop in RGR from January to June.

RGR of *Mora gonggrijpii* seedlings in the small gaps is the lowest RGR found in a tropical tree species under such light conditions reported so far (cf. Okali 1971, Okali 1972, Oberbauer & Strain 1985, Oberbauer & Donnelly 1986, Kwesiga & Grace 1986, Popma & Bongers 1988). A low RGR can be explained by a low NAR and/or a low LAR (cf. Poorter 1989), both of which occurred in *Mora gonggrijpii.*

How is the low NAR and LAR in *Mora gonggrijpii* to be explained? A low NAR in shade may be caused by 1) an inherently low maximum rate of photosynthesis, 2) a high maximum rate of photosynthesis, resulting in an increased dark respiration lowering

Table 4. Seed dry weight of several tropical woody species in relation to LAR, SLA and LWR of seedlings in forest understorey conditions.

species	seed dry weight(g)	LAR $cm^2 g^{-1}$	SLA cm^2	LWR g^{-1}	
Heliocarpus appendiculatus [2]	.0005	490	847	.58	pioneer
Myriocarpa longipes [4]	.0009	316	588	.53	pioneer
Cecropia obtusifolia [4]	.009	213	476	.45	pioneer
Poulsenia armata [4]	.09	150	345	.44	sub canopy tree
Cordia megalantha [4]	.11	288	588	.48	small gap species
Ceiba pentandra1 [1]	.45	141	n.a.	n.a.	pioneer
Pseudolmedia oxyphyllaria [4]	.50	126	250	.51	sub canopy tree
Amphitecna tuxtlensis [4]	.60	182	385	.47	shade tolerant
Psychotria simiarum [4]	.83	200	400	.50	shade tolerant
Brosimum alicastrum [4]	.90	135	270	.50	sub canopy tree
Lonchocarpus guatemalensis [4]	.95	171	370	.46	sub canopy tree
Pethaclethra macroloba [3,7]	5.01	147	288	.51	shade tolerant
Eperua falcata [5]	5.05	58	181	.37	small gap species
Omphalea oleifera [4]	5.15	150	588	.26	sub canopy tree
Dipteryx panamensis [2]	16.00	140	439	.32	small gap species
Eperua grandiflora [5]	17.45	42	135	.31	shade tolerant
Chlorocardium rodiei [5]	28.00	25	216	.21	small gap species
Eperua rubiginosa [5]	30.10	55	164	.34	shade tolerant
Mora gonggrijpii [6]	52.00	55	131	.42	shade tolerant

[1]) Okali 1972, [2]) Fetcher et al. 1983, [3]) Oberbauer & Strain 1985, [4]) Popma & Bongers 1988, [5]) ter Steege unpublished, [6]) this study, [7]) courtesy David Hammond.

NAR especially in shade (Konings 1989), or 3) production of 'costly' products such as wood or secondary compounds (cf. Poorter 1989). The first cause is commonly found in shade tolerant species (Langenheim et al. 1984, Oberbauer & Donnelly 1986, Konings 1989), the second mainly in light demanders. However, Raaijmakers et al. (pers. comm.) found an intermediate maximum photosynthesis in *Mora excelsa*, a species closely related to *Mora gonggrijpii* with similar growth strategy and low LAR (ter Steege unpublished data). *Mora gonggrijpii* does produce large woody stems (50% of the shoot weight in shade) and the production of which certainly may have influenced the NAR.

Both SLA and LWR may independently influence LAR (Poorter 1989). LWR in *Mora gonggrijpii* is not particularly low (Table 4), so apparently the low LAR is caused by the low SLA (Table 4) The thick leaves (241 µm, ter Steege in prep; cf. Fetcher et al. 1983; Oberbauer & Strain 1985, Bongers & Popma 1988) and high content of silica grains both contribute to a low SLA.

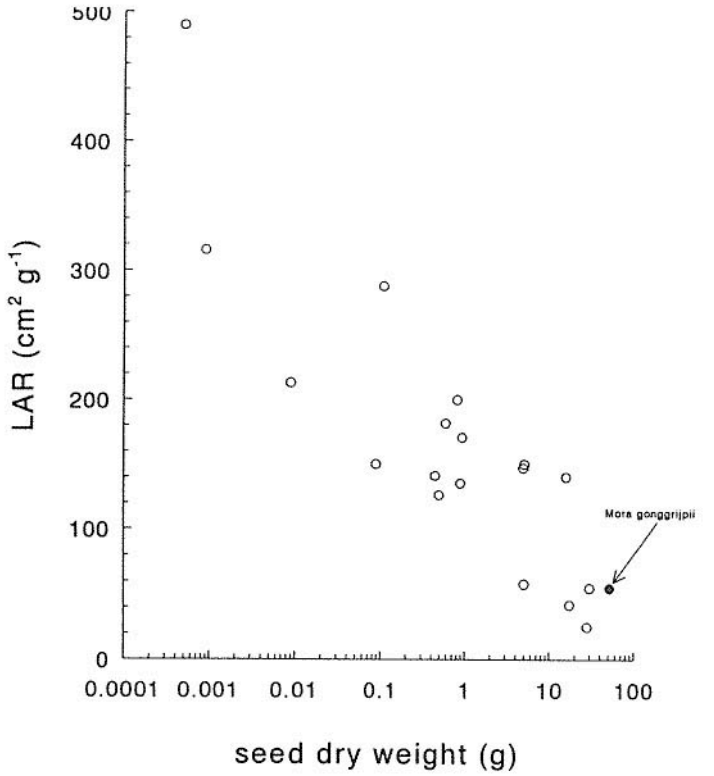

Figure 2. LAR of selected tropical seedlings grown in full shade or understorey conditions against seed dry weight note log scale. For sources see Table 4.

In *Mora gonggrijpii* leaf area was rather constant over a six month period, although total dry weight increased. This caused LAR and LWR to decrease over the same period. Even in the small gaps leaf area did not increase from January to June. This suggests a resistance by *Mora gonggrijpii* in changing its shade strategy to one commonly found in many species under high light levels - branching and high leaf production rates relative to leaf loss rates.

In shade tolerant climax species, seedlings with a tall stem, and an investment in relatively few (thick) leaves may be beneficial. A few leaves on a narrow high structure avoids self-shading. Pioneers on the other hand react to shade by an increase of SLA, producing 'large' thin leaves; see e.g. Fetcher et al. (1983). A low SLA and consequently low LAR appear to be general features in shade tolerant species (Table 4). Possibly slow growing, shade tolerant, climax seedlings invest in long lived leaves with a relatively low SLA (both thicker leaves and more secondary compounds). In this respect they would resemble the slow growing herbs from nutrient poor sites in temperate areas (Poorter 1989). A low SLA and the high percentage of woody tissue result in a particularly low LAR in large climax seedlings. In Figure 2 the LAR of seedlings of several tropical tree species, grown in

shade, is shown against initial seed dry weight. This can be regarded as a good indicator of pioneer-climax status. LAR is strongly negatively correlated with log seed weight (r=-0.88). LWR on the contrary is not correlated with seed weight (see Table 4). Thus within this array of species *Mora gonggrijpii* is not an exception, with its low LAR and RGR, but rather an extreme of the spectrum.

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Segregation of two *Mora* species along a water availability gradient: I occurrence and flooding tolerance

Hans ter Steege

Abstract

Mora excelsa and *Mora gonggrijpii* are well segregated along a soil hydrological gradient. *Mora excelsa* is positively associated with soil hydrological characteristics, whereas *Mora gonggrijpii* is negatively associated with these characteristics. Growth and mortality were studied in both species in occasionally flooded forest and dryer uphill forest. In a moderate year, such as 1992 (no flooding, no drought), there is no difference in growth or mortality between the forest types in any of the two species. *Mora gonggrijpii* was larger in both forest types. Tolerance to flooding and waterlogging was studied in seeds and seedlings of both species. Seeds of *Mora gonggrijpii* are very intolerant to flooding. Germination in this species drops to 50% after only 11 days of flooding. Seeds of *Mora excelsa* float and 80% of the seeds is viable after as much as 50 days of flooding. Artificially submerged seeds of the latter species have intermediate survival response. Flooding in seedlings resulted in a halt of RGR in both species. No mortality occurred, except in all *Mora gonggrijpii* individuals after eight weeks of continuous flooding. Hypertrophied lenticels were observed in both species and appeared to be more abundant in *Mora excelsa*. The latter species also showed higher root porosity. It is concluded that *Mora excelsa* is more tolerant to (moderate) flooding. The floating (and survival) of the seeds during flooding periods, which are especially common just after seedfall, is of significance for the dispersal and establishment of this species in riverine forest.

Key words: *Mora excelsa*, *Mora gonggrijpii*, seedlings, tropical rain forest

Introduction

The genus *Mora* (Caesalpiniaceae) is among the dominant canopy tree genera in the Guianas. Currently *Mora* is thought to comprise four species (Ragonese 1973, 1982), two more species are present on Hispaniola (Liogier 1985). The occurrence of the genus appears to be associated with running water, and at least two species, both with floating seeds, may depend on water for their dispersal (Mayo-Melendez 1965, Bell 1969, v Roosmalen 1985). Two species of *Mora* occur in the Guianas; *Mora excelsa* Bentham is a tall evergreen species with a distribution range from the centre of Surinam to Trinidad (ter Steege 1990), *Mora gonggrijpii* (Kleinhoonte) Sandwith is found from western Surinam to eastern Venezuela. The two species are very hard to distinguish by their flowers or fruits, but easily by the number of leaflets per leaf and form of the leaflets (6-8 in *Mora excelsa* and 3.5 times as long as wide, 4 in *Mora gonggrijpii* 2.5 times as long as

Mora excelsa is a common to dominant tree along large and smaller streams in the near interior of Guyana (Richards 1952, Fanshawe 1952). *Mora gonggrijpii* can be found more frequently on higher well-drained ground (Richards 1952, ter Steege et al. submitted). It was recently shown that soil hydrology is a main determinant of the occurrence of canopy trees in Guyana (ter Steege et al. submitted), but there is little experimental evidence for adaptation to flooding or drought in seedlings of canopy trees from this area. The two taxonomically closely related *Mora* species give a good opportunity to start a study on this theme.

Although there is substantial knowledge on the flooding tolerance in temperate plants, rather little is known on this subject for tropical plants (Sena Gomes & Kozlowski 1988, Joly & Kramer 1982, v Donselaar 1989, Joly 1990). However, Mori & Becker (1991) recently demonstrated that sporadic flooding may have a significant effect on the mortality of canopy tree species and thus influence canopy tree composition.

Plants may adapt morphologically to flooding by the formation of e.g. hypertrophied lenticels, adventitious roots, and better aerated tissues (see Kozlowski 1984 or 1991 for a review) or physiologically (Keely 1979, Crawford 1982, Joly & Crawford 1982, Joly 1990). Usually flooding tolerance will include a morphological as well as a physiological component (Joly & Crawford 1982, Joly 1990). Recently Worbes et al. (1992) argued that many flood tolerant species are not strictly flood tolerant but more tolerant to seasonally poor growing conditions in general.

In the study area both *Mora excelsa* and *Mora gonggrijpii* are abundantly present and occur mostly in distinct separate patches, often not more than 200 metres apart.

To investigate the success of *Mora excelsa* and *Mora gonggrijpii* I studied the occurrence of the two species along a soil hydrological gradient. Germination success, growth rate and survival of seedlings were studied in a wet, *Mora excelsa* dominated, forest and a drier, *Mora gonggrijpii* dominated, forest. In a moderate year the 'dry' forest may not be really dry and the 'wet' forest may not be flooded and overall differences in growth and mortality may be small or even absent. Extreme conditions were, therefore, simulated in flooding experiments both for seeds as well as seedlings. Apart from the general responses, such as germination rates and growth rates, some more attention was paid to the morphological changes of seedlings during the flooding experiments. Drought tolerance will be described in an other paper.

This study was conducted within the framework of the TROPENBOS Programme in Guyana.

Methods

Study area and species

This study was conducted in the near interior of Guyana, South-America, in and around the Ecological Reserve of the TROPENBOS Programme in Guyana (05°13' N 58°48' W). The climate in Guyana is tropical with high rainfall and high average temperatures. Rainfall is seasonal with two rainy seasons, one from May to June and one

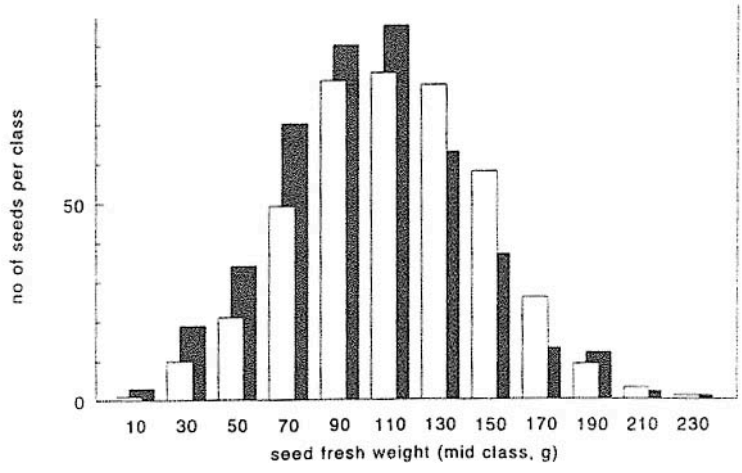


Figure 1. Seed weight distribution of *Mora excelsa* and *Mora gonggrijpii*. Black bars represent *Mora gonggrijpii*, open bars *Mora excelsa*.

from October to December though average rainfall is higher than 100 mm for each month (ter Steege & Persaud 1991). Both *Mora* species can produce abundant seeds shortly before either one of the rainy seasons (ter Steege 1990, ter Steege & Persaud 1991). Seed fall on average occurs every one and a half to two years (Richards 1952). Both species may become locally dominant in the canopy (Davis & Richards 1934, Richards 1952, Fanshawe 1952, ter Steege et al. submitted). These local patches are named after the vernacular name of the two species: *Mora excelsa* = Mora => Mora forest, *Mora gonggrijpii* = Morabukea => Morabukea forest.

Seed collection

In May 1991 seeds of both species were collected shortly after peak seed fall. From these seeds a random set was selected and weighed to the nearest gram. The average initial fresh seed weight of *Mora excelsa* thus obtained was 111.7 g (se=1.8, n=422) and for *Mora gonggrijpii* 101.6 g (se=1.8, n=438). The range in seed size encountered is huge, from 5 g up to 240 g, but is perfectly normally distributed (Figure 1). The difference in average seed weight between the two species is significant ($F_{s[1,859]}=15.68$, $p<0.001$). For the experiments a range in seed weight from 90-120 g is used. This range is sufficiently small to limit the effects of seed size on seedling size and sufficiently large to include the averages of both species.

Transect study

Three transects were laid out perpendicular to the Maiko creek, the main creek in the Ecological Reserve. Transects ran from mixed forest with high abundance of *Mora gonggrijpii* down to the creek into forest with dominance of *Mora excelsa*. Two transects started in one patch of mixed forest with an angle of 40 degrees between them, the third tran-

sect was laid out one km north of the first two. At 20 m intervals circular plots with a radius of 10 m were established.

Slope correction for distance between the plots and height difference between plots were obtained with a Suunto clinometer. The height of a plot relative to the creek water level was obtained by summing the height differences of all plots from the creek up to the plot in question.

In 52 plots the presence of *Mora excelsa* and *Mora gonggrijpii* seedlings as well as adults was noted. In each plot a soil augering down to 1.20 meter was done. Colour, consistence, gleyic features, mottling and the presence of ground water were recorded per 10 cm depth. The presence of the two species in the plots in relation to height above creek level was processed with logistic regression (CSS StatSoft Tulsa Oklahoma, see ter Braak 1987). Association of the species with respect to soil characteristics was tested with χ^2 (Zar 1984).

Survival and growth rates

Seeds of narrow weight range (see above) were laid out in a forest plot in forest along the Maiko creek with dominance of *Mora excelsa* (=Mora forest) and in mixed forest with dominance of *Mora gonggrijpii* (= Morabukea forest). Ten seeds of each species were randomly selected out of this seed batch. They were fresh weighed, cut in small pieces to enable fast drying, dried at 70-80°C and re-weighed. Canopy cover at the two plots was estimated with the aid of hemispherical photographs (ter Steege 1992) and did not differ much among the two sites. Cover for the Mora forest plot was 94% and cover for the Morabukea forest plot 95% (resulting calculated average photon flux densities in the order of 3 mol m^{-2} day^{-1}). To avoid competition between the experimental seedlings and established undergrowth, the latter was removed from the plots. Seeds were laid out in rows 50 cm apart alternating in species. Planting distance between the seeds on the lines was also 50 cm. Plants were harvested four times at three months intervals, giving a total growing time of one year. At each harvest germination and survival since the last harvest was noted. Only aboveground biomass was harvested as the collecting of the horizontally spreading roots is virtually impossible in the dense root mat of the rain forest and would damage the soil in the plot too much. At harvest the following characteristics were measured: plant height (height from cotyledon to apical meristem, cm), stem diameter 5 cm above the cotyledon (cm), leaf area (with Digitizer Tablet and custom-made Pascal program and later with Licor 3100 area meter, cm^2). Plants were separated in 1) leaves and 2) stems plus petioles, dried 48 hours at 70-80°C, and subsequently weighed on a Sartorius mg scale. From the total leaf area and leaf dry weight the specific leaf area (SLA, cm^2 g^{-1}) was calculated.

Differences in weight were analyzed with ANOVA (Zar 1984). If differences in shoot weight between harvests were significant, there has been a significant increase in dry matter. The relative growth rate (RGR_s) of the shoot can then be expressed as:

$$RGR_s = \frac{[\ln(W_{s,t2}) - \ln(W_{s,t1})]}{t_2 - t_1} * 1000 \quad (mg\ g^{-1}\ day^{-1})$$

(Hunt 1978), where W_s is the shoot dry weight at time t. Relative cotyledon use, the rate at which the cotyledons are depleted (RCU, mg g^{-1} day^{-1}) is calculated with the same formula, with $W_{c,t1}$ and $W_{c,t2}$ interchanged. NAR was calculated according to Hunt (1978). Differences in RGR between species were tested according to Poorter & Lewis (1984). In this method significant interactions of group x time in ANOVA on ln-transformed data indicate differences in RGR.

Seed sizes and floating

Twenty seeds distributed over the seed weight range of each species were selected and weighed. Volume of the intact seed and volume of the two opened cotyledons were measured with a fixed cylinder completely filled with water. The seed or cotyledons were submerged in the cylinder with the aid of a needle. Volume was defined as the amount of displaced water, measured with a Sartorius balance (resolution 1 g or 1 cm^3) as the weight difference before and after submergence of a seed. The size of the air pocket between the cotyledons (cm^3) was taken as the difference between the measurement of the total seed and the measurement of the cotyledons.

Flooding and germination

Ungerminated seeds of both species were randomly selected from the large seed batch. Seeds of both species were assigned to the following treatments in lots of 20 seeds: no water treatment, flooding for 4 days, flooding for 1 week, for 2 weeks, for 4 weeks, for 6 weeks and for 8 weeks respectively. Seeds were allowed to float but *Mora gonggrijpii* seeds sank and were always under water during the treatment time. To allow for comparison with the submerged *Mora gonggrijpii* seeds, additional lots of *Mora excelsa* seeds were artificially submerged for the same periods. During treatment the floating *Mora excelsa* seeds of the floating treatment were counted twice per week. After the treatment seeds were laid out on the forest floor of a Mora forest (*Mora excelsa* seeds from the submerged treatment were first checked on their floating ability) and monitored bi-weekly on their germination and survival. Ten weeks after seeds of a lot had been laid out, the seedlings were measured. Characteristics measured were stem diameter at 5 cm above the cotyledon (mm), stem height (cm), leaf area (cm^2). After the first two harvests, however, a caterpillar pest defoliated most of the seedlings present. This created series of seedlings without herbivory and seedlings with total defoliation and made subsequent comparison impossible. Measurements of size parameters of the seedlings was therefore not continued.

Flooding of seedlings

Another batch of seeds were potted in 5 l black plastic bags with white sand and left to germinate in a small nursery with gray nylon shade mesh, which produced 55% shade (as measured with a Licor Li-1000 data logger and quantum sensors). Two months after germination plants were randomized and assigned to flooded, waterlogged or control treat-

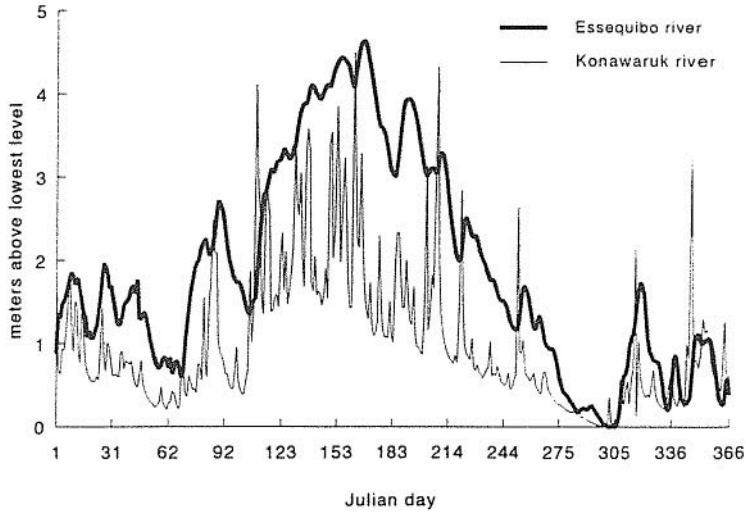


Figure 2. Water levels of two rivers near the Mabura Hill area in 1972. The Konawaruk, at its measuring point, drains approximately 200 km^2, the Essequibo, at its measuring point, drains approximately 66600 km^2. Data are taken from surface water tables 1972 (Anon. 1985). Note the frequent short rising of water level in the Konawaruk river as compared to less frequent but more prolonged rising of water level of the Essequibo river. *Mora excelsa* occurs along both rivers near the measuring points.

ments in sets of five. Plants were waterlogged and flooded in large galvanized containers. The waterlogging treatment consisted of creating a water level just at the soil surface. Cotyledons were not flooded in the waterlogged treatment as they are lying on top of the soil surface. Flooding consisted of creating a water level at 10 cm above soil level, except for the tip of a few of the lowest leaves all leaves were above the water level in this treatment. Flooding may differ considerably in duration and frequency in rivers of different size (see Figure 2). Large rivers may flood once or a few times per year but for a prolonged period of time, while small rivers may flood more often but for short periods. Such differences may be of significance to the response of seedlings (cf. van der Sman et al.). To simulate this difference flooding and waterlogging was constant for eight weeks in one set of treatments (treatments W8 and F8) and intermittent (2 weeks flooded/ waterlogged then 4 weeks normal and finally 2 weeks flooded/waterlogged again, treatments W2 and F2). Water in the F8 and W8 treatment was refreshed after four weeks. Control plants (treatment C) were kept well watered at all times. The harvesting scheme is presented in Table 1.

At harvest plants were washed free of sand and divided in primary roots, secondary roots, adventitious roots (if present), stems plus petioles, leaves, and cotyledons. Stem diameter, stem height, and leaf area were measured as above. The plant fractions were dried at 70-80°C for 48 hours and subsequently weighed to the nearest mg. From the dry weights and leaf area, leaf area ratio (LAR, leaf area / total plant dry weight, $cm^2\ g^{-1}$), specific leaf area (SLA, leaf area / leaf dry weight, $cm^2\ g^{-1}$), leaf weight ratio (LWR, leaf dry weight / total plant dry weight, $g\ g^{-1}$), stem weight ratio (StWR, stem dry weight /

Table 1. Harvesting scheme of *Mora excelsa* and *Mora gonggrijpii* seedlings in the flooding and waterlogging experiment. The control of week 0 serves as starting value for each series. Each harvest consisted of 5 seedlings.

week 0	Week 2	Week 4	Week 8	code
control		control	control	C
	waterlogged	waterlogged	waterlogged	W8
	flooded	flooded	flooded	F8
			waterlogged 2x	W2
			flooded 2x	F2

total plant dry weight, g g^{-1}), root weight ratio (RWR, root dr weight / total plant dry weight, g g^{-1}), root shoot ratio (R/S, root dry weight / shoot dry weight, g g^{-1}) and primary root / secondary root ratio (PSR, primary root dry weight / secondary root dry weight, g g^{-1}) were calculated.

If differences in weights between harvests were significant, RGR was calculated as above.

Of each individual two small pieces of the lower stem and two small pieces of the upper root part were stored in FAA (5 parts formaline 5% and 5 parts acetic acid in 90 parts ethanol 96%). A correction was made for the loss of dry stem and root weight. Microscopic slides of the root and stem samples were prepared as follows: the samples were flushed with ethanol 70% and transverse sections of 15-20 µm were made with a microtome. The sections were then bleached with hypochlorite, stained with safranan, flushed with a series of increasing alcohol solutions, xylol and fixed with Canada Balsam. These slides were examined qualitatively on bark and wood structure (porosity, lenticels and other characters if present).

Results

Transect study

Both *Mora* species were well segregated along the transects from the creek up hill (Figure 3). Soils along the creek belonged to the Dystric Fluvisols and Gleyic Arenosols, both with impeded drainage. Stagnant water was often found within 1.20m of the soil surface and in some places water was found at the ground surface in small depressions. Gley and mottling were frequently encountered. *Mora excelsa* was positively associated with these hydromorphic characteristics (Table 2). Seedlings of this species were abundantly present in the Mora forest, but were almost absent in depressions (often flood channels with stagnant water). *Mora gonggrijpii* was found mainly on the somewhat higher hill slopes

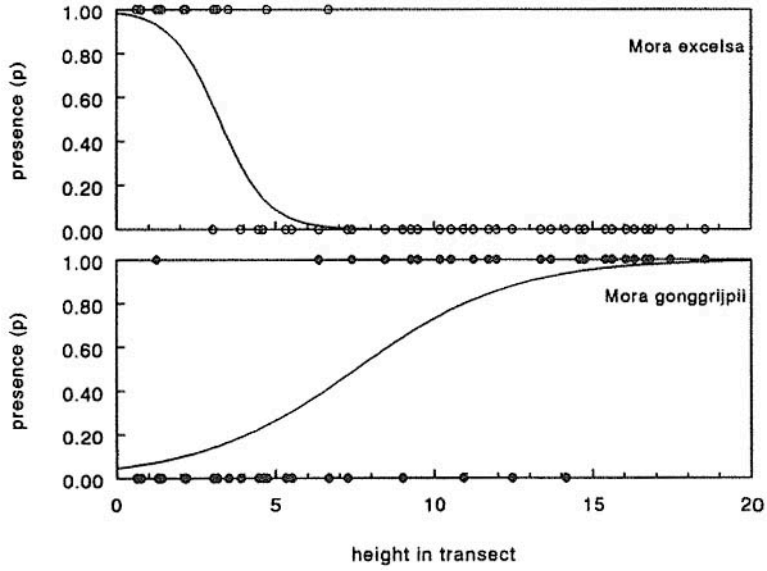


Figure 3. Occurrence (absence-presence data) of *Mora* spp. seedlings along three transects perpendicular to the Maiko creek. The X-axis represents the height of a plot relative to water level of the creek on the day of measurement.
The sigmoid lines are the logit functions ($y = e^{(b+ax)}/(1 + e^{(b+ax)})$), indicating the chance of finding a seedling of a species on that particular height above the creek level. Both sigmoid's are highly significant, $p<<0.001$.

Table 2. Two by two tables of *Mora* spp. in relation to soil hydrology. Hydromorphic characters are: presence of gley, presence of mottling or visual presence of ground water within 1.20 m of soil surface. *Mora excelsa* is positively associated with soil hydromorphic characters (χ^2=33.417, $p<0.001$), *Mora gonggrijpii* is negatively associated with soil hydromorphic characters (χ^2=28.285, $p<0.001$)

		hydromorphic characters	
		absent	present
Mora excelsa	absent	30	4
	present	1	17
Mora gonggrijpii	absent	8	20
	present	23	1

on slightly loamy sands, Ferric Arenosols and Haplic Ferralsols. These sites were never flooded and there were no indications of stagnant water nor of an impermeable layer within 1.20m. *Mora gonggrijpii* was negatively associated with soil hydromorphic characteristics (Table 2). *Mora excelsa* and *Mora gonggrijpii* were negatively associated with each other on the 52 plots studied (χ^2=18.942, $p<0.001$).

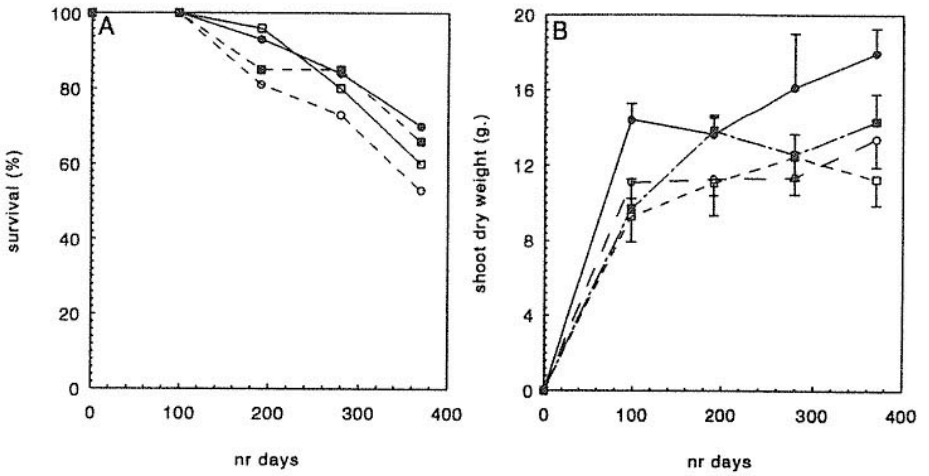


Figure 4 a). Survival of *Mora* species in Mora- and Morabukea forest. Open symbols represent *Mora excelsa*, closed symbols *Mora gonggrijpii*, circles Morabukea forest, squares Mora forest.
b) Shoot dry weight of *Mora spp.* seedlings in Mora and Morabukea forest.

Survival and growth rates

Fresh seed weight of the ten selected seeds was not different for both species (104.4 for *Mora gonggrijpii* and 103.8 for *Mora excelsa*). Proportion dry matter was significantly different (0.49, se=0.009 and 0.45, se=0.008 respectively, $F_{s[18,1]}=10.00$, $p<0.01$, arcsine transformed data and one *Mora gonggrijpii* with an outlyer of 0.78 omitted).

Seed dry weight was slightly higher in *Mora gonggrijpii* but not significantly different ($F_{s[18,1]}=3.28$, $0.05<p<0.1$). Germination and survival of both species was 100% after 3 months in both forest types and declined slowly but steadily after that in both species (Figure 4a). There were no differences in survival for any combination of species and forest type after 1 year ($\chi^2=1.78$, $p>0.1$). RGR_s was not different between species or forest types from the second to the last harvest, as indicated by very low interactions in ANOVA tests (results not shown, but see 4b). At the final harvest there were significant differences in shoot weight both among species and among the forest types (Table 3). *Mora gonggrijpii* showed greater shoot dry weight in both forest types and both species produced more shoot dry weight in the Morabukea forest. Leaf weight and leaf area differed both among the two species and two forest types in a similar manner. SLA differed significantly between the two species only (Table 3). RGR_ss differed widely in all treatments but were low for all treatments and sometimes even negative (Table 4). There were no significant differences in RGR_s between the two species. The NAR was lower in *Mora gonggrijpii* the first period as compared to *Mora excelsa* : 0.23 and 0.44 mg cm^{-2} day^{-1} respectively. In the second period the NAR was approximately 0.25 mg cm^{-2} day^{-1} in both species. RCU was equal for each species in either forest type (Table 4).

Table 3. Shoot characteristics of *Mora excelsa* and *Mora gonggrijpii* seedlings after one year of growth in Mora and Morabukea forest (se between brackets). Anova shows the final results of the 2^2 analysis of variance (forest x species): n.s.=not significant, *=p<0.05, **=p<0.01, ***=p<0.001.

	Morabukea forest				Mora forest				ANOVA		
	M. gong.		*M. exc.*		*M. gong.*		*M. exc.*		forest	species	int.
stem diameter (cm)	8	(0.4)	7.9	(0.3)	8.6	(0.4)	7.6	(0.3)	*	n.s.	n.s.
stem height (cm)	78.6	(3.0)	68.1	(4.5)	76.0	(3.9)	87.3	(6.4)	n.s.	n.s.	*
shoot weight (g)	17.9	(1.3)	13.4	(1.5)	14.3	(1.5)	11.3	(1.4)	*	*	n.s.
stem weight (g)	9.3	(0.5)	8.0	(0.9)	8.5	0.8)	7.8	(0.9)	n.s.	n.s.	n.s.
leaf weight (g)	8.6	(1.0)	5.4	(0.8)	5.8	(0.7)	3.4	(0.1)	**	*	n.s.
leaf area (cm^2)	1094	(123)	799	(115)	718	(93)	484	(89)	**	*	n.s.
SLA ($cm^2\ g^{-1}$)	127	(3.3)	148	(1.7)	125	(5.6)	141	(3.7)	n.s.	***	n.s.

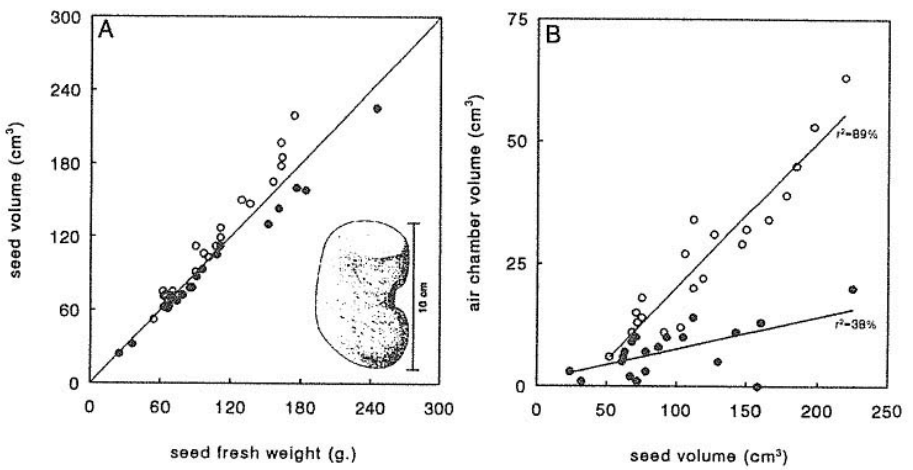


Figure 5. a) Relation between seed fresh weight and seed volume of *Mora excelsa* (open symbols) and *Mora gonggrijpii* (closed symbols). Inset: seed of *Mora excelsa.* b) The relation between the seed volume and the size of the air pocket between the cotyledons of the two *Mora* species. Note the lower r^2 for *Mora gonggrijpii.*

Seed sizes and floating

Over the complete range of seed weight all *Mora excelsa* seeds but one had a 'density' lower than 1 g cm^{-3}, whereas all *Mora gonggrijpii* seeds but one had a 'density' higher than 1 g cm^{-3} (Figure 5a). The size of the air pocket was closely related to the size of the seed in *Mora excelsa* (Figure 5b), a feature expected if seeds of all weight classes are to float. In *Mora gonggrijpii* the correlation between size and air pocket was far less, but still significant (Figure 5b). In both species the density of the cotyledon mass was higher than 1 (*Mora excelsa* : 1.14 ± 0.19; *Mora gonggrijpii* : 1.17 ± 0.17).

Table 4. RGRs of shoots and RCU (mg g^{-1} day^{-1}) of *Mora excelsa* and *Mora gonggrijpii* seedlings in forest plots in Mora- and Morabukea forest. The plants are the same as those of figure 4.

harvesting date	29/5/91	3/9/91	5/12/91	2/3/92	1/6/92
		period 1	period 2	period 3	period 4
		RCU	RGR		
Morabukea forest					
Mora gonggrijpii		12.2	-0.59	2.06	1.08
Mora excelsa		14.7	2.19	-1.66	0.27
Mora forest					
Mora gonggrijpii		10.7	0.16	0.11	1.66
Mora excelsa		13.1	1.00	-0.45	-0.27

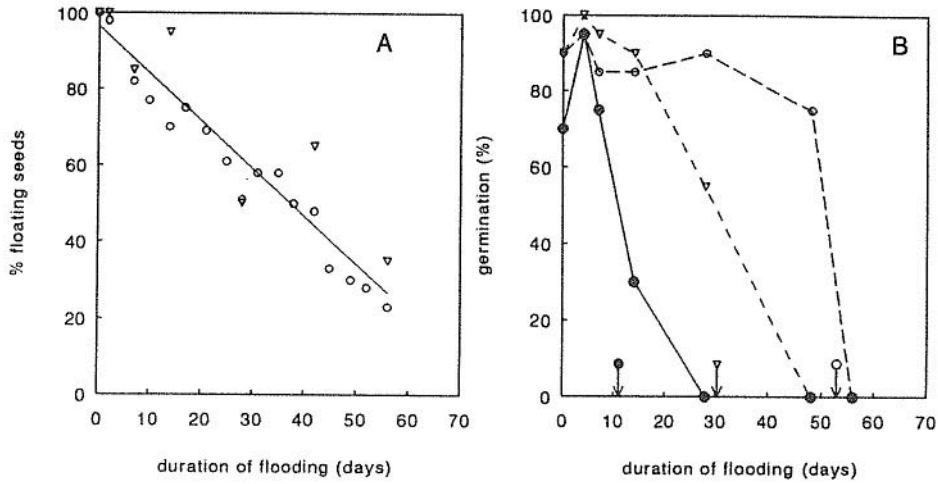


Figure 6. a) Floating ability of *Mora excelsa* seeds as a function of time of flooding. The 'floating half life' is approximately 35 days. There is no difference for seeds that were allowed to float (open circles) and those forced under water (open triangles). The line given is for pooled data, r=0.95, p<0.001. b) Percentage of germination of *Mora* spp. seeds as a function of the duration of the flooding period. Open circles represent *Mora excelsa* floating seeds, open triangles *Mora excelsa* submerged seeds, filled circles *Mora gonggrijpii* submerged seeds. Arrows indicate LD50 of flooding for each.

Flooding and germination

Seeds of *Mora excelsa* lost their floating ability slowly but steadily (Figure 6a). Fifty percent of the seeds had sunk after approximately 35 days. After 60 days some 20% of tthe seeds still floated. There was no difference in this respect between seeds that were allowed to float during the flooding period and seeds that had been artificially submerged.

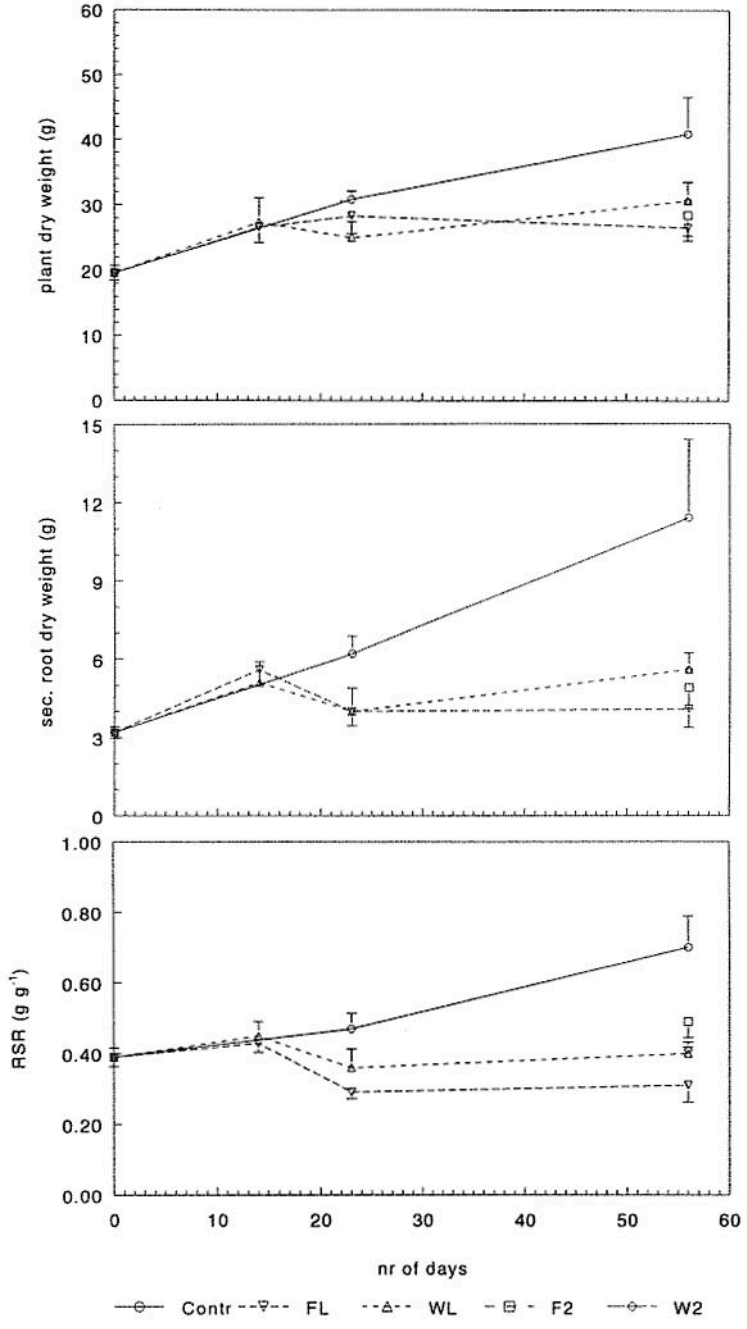


Figure 7. Plant dry weight, secondary root dry weight, and root shoot ratio of *Mora excelsa* seedlings during flooding treatments. C, control; F8, W8, continuously flooded or waterlogged for eight weeks respectively; F2, W2 intermittently flooded or waterlogged during the eight week period respectively.

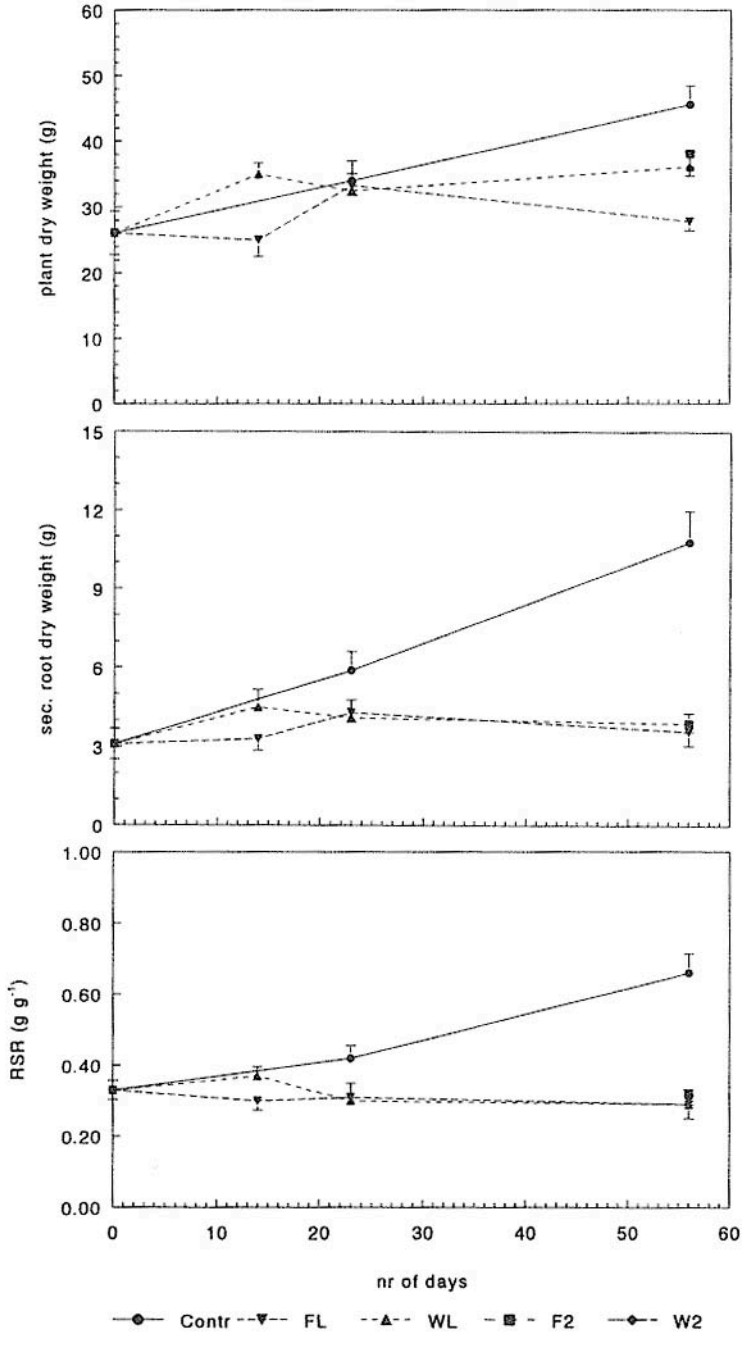


Figure 8. Plant dry weight, secondary root dry weight, and root shoot ratio of *Mora gonggrijpii* seedlings during flooding treatments. Abbreviations and symbols see figure 7.

Germination was fast; final percentages were reached about two weeks after the seeds had been put out on the forest floor (data not shown). Flooding of the seeds had an impact on the germination of both species (Figure 6b). In all cases germination was increased after four days of flooding treatment. In *Mora gonggrijpii* this increase was significant (χ^2=4.329, p<0.05). After the first four days germination percentage declined sharply for *Mora gonggrijpii* seeds. LD50 was reached after only 10-11 days of flooding, while 27 days of flooding killed all seeds. Floating *Mora excelsa* seeds kept their germination potential longer. In these seeds success was almost 80% even after 50 days of flooding. After that germination success also declined sharply. In submerged *Mora excelsa* seeds LD50 was approximately 32-33 days.

Flooding of seedlings

Flooding caused few morphological changes in both species. Swelling of lenticels was observed in most waterlogged plants just above the water level. Adventitious roots were observed only once on a *Mora gonggrijpii* (!) individual in the F8 treatment. These (two small) roots had disappeared within one week. Adventitious roots in the soil (succulent in appearance) were formed by several plants of both species, but due to their very scarce occurrence were pooled with secondary roots.

Growth of both species was negatively affected by flooding and waterlogging treatments (Figures 7 and 8). While the controls showed significant growth during the eight weeks, growth was positive for all water regimes only up to about two to three weeks. After that period growth stopped in all treatments and may have been negative for secondary roots, as indicated by some mortality among these roots. RGRs were low; in the control plants it was 11.8 mg g^{-1} d^{-1} for *Mora gonggrijpii* and 19.8 mg g^{-1} d^{-1} for *Mora excelsa* for the first period of four weeks, in the second period the values were 9.58 and 9.34. Neither difference is significant.

Apart from the control treatment, there were no significant differences in plant dry weights among the other treatments after eight weeks, except for a slightly lower plant weight in W8 *Mora gonggrijpii* seedlings. These seedlings died during the last week but while all leaves had turned brown they still all remained on the plants. Root shoot ratio increased in the control plants during the eight weeks, but declined in all water treatments (Figure 7c and 8c), due to death of some secondary roots (Figures 7b and 8b) and the lack of overall growth. Stem diameter, plant height and leaf area did not show any significant differences between treatments (data not shown). SLA did not differ among treatments, but hardly any new leaves had been formed.

Mora excelsa had more lenticels on the lower stem part than did *Mora gonggrijpii*. Root porosity, especially in the newly formed bark, appeared to be more extensive in *Mora excelsa*, especially in the roots of the waterlogged (W8) seedlings (Figure 9). In most flooded and waterlogged seedlings of *Mora gonggrijpii* parenchyma cells adjacent to vessels .

Discussion

Mora excelsa and *Mora gonggrijpii* are well segregated along transects perpendicular to the creek. This confirms earlier findings of e.g. Davis & Richards (1934) and Fanshawe (1952). Both species are significantly associated with different soil hydrological properties and this justifies to further investigate their flooding (and drought) tolerances.

Survival rates in the growth plots do not differ among species and fall within the range of previously reported ones (e.g. Forget 1989, 1990, 1992, Howe 1990, Turner 1990). After one year both species were larger in the Morabukea forest, while *Mora gonggrijpii* was larger than *Mora excelsa* in both forest types, but no significant differences in RGR were found The size difference between the species may be the result of the slightly higher dry matter content of the seeds in *Mora gonggrijpii*. This was also observed in three *Eperua* spp., differing widely in seed weight (10.1, 34.9 and 60.2 g): seedling weight after three months reflected almost identical ratios between the three species as did the seed weights (ter Steege unpublished data). RGR of both species is low after the cotyledon has been depleted, one reason probably being the low light levels in the understorey. RGR is slightly higher in the control plants grown in the half shade in the nursery but is still low compared to many tropical seedlings (Fetcher et al. 1983, Oberbauer & Strain 1985, Oberbauer & Donnely 1986, Popma & Bongers 1988). RGR is probably intrinsically low in these shade adapted species, due to both a low LAR and a low NAR (ter Steege submitted).

As mentioned in the introduction the 'wet' Mora forest does not necessarily flood in average years and the 'dry' Morabukea forest is moist in average years. Thus both forests may create favorable conditions for germination and establishment for both species. Flooding (pers obs.) and drought (Brouwer, unpublished rain data) did indeed not occur within the time span of the experiments. The result is important since it suggests that the occurrence of the two *Mora* species may be limited more by the extreme soil hydrological conditions of a habitat than by the average soil hydrology. A similar observation was made by Davis & Richards (1934) with respect to drought and geographical occurrence of species.

Mora excelsa seeds float (and survive it!) for a relatively long time. Seeds with better flood tolerance do exist. *Parkia auriculata* seeds show 84% germination after six months submersion, as high as control seeds stored for the same time in a dark place (Coutinho and Struffaldi 1971). The floating of the seeds of *Mora excelsa* is mainly due to the size of the air pocket in relation to the total seed weight, as the cotyledon mass has a density of over 1 g cm^{-3}. As *Mora excelsa* often grows along running water and seeds are dropped shortly before the rainy (=flooding) season, the floating of the seeds coupled to a high survival rate may contribute significantly to the dispersal and establishement of the species. Floating fruits or seeds are not uncommon in species of riverine forest in Guyana. It

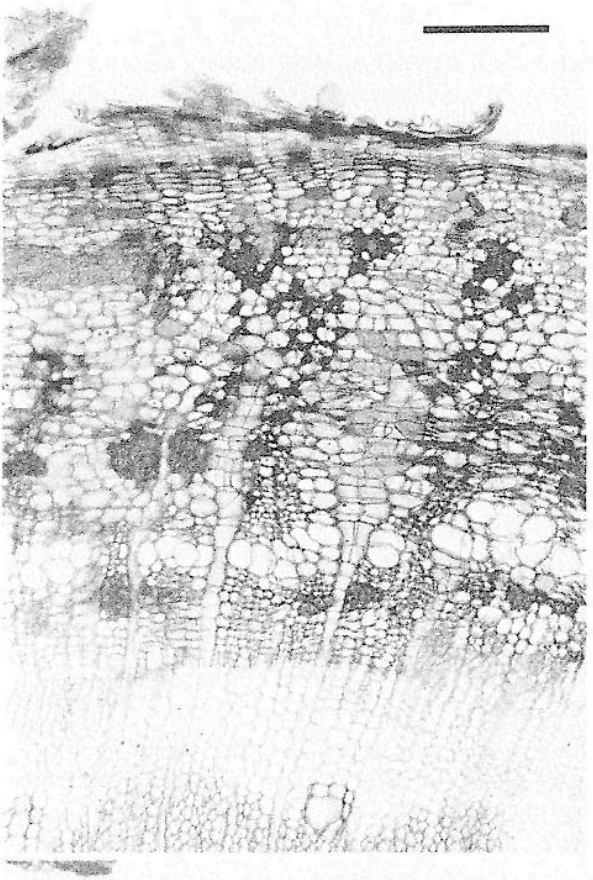
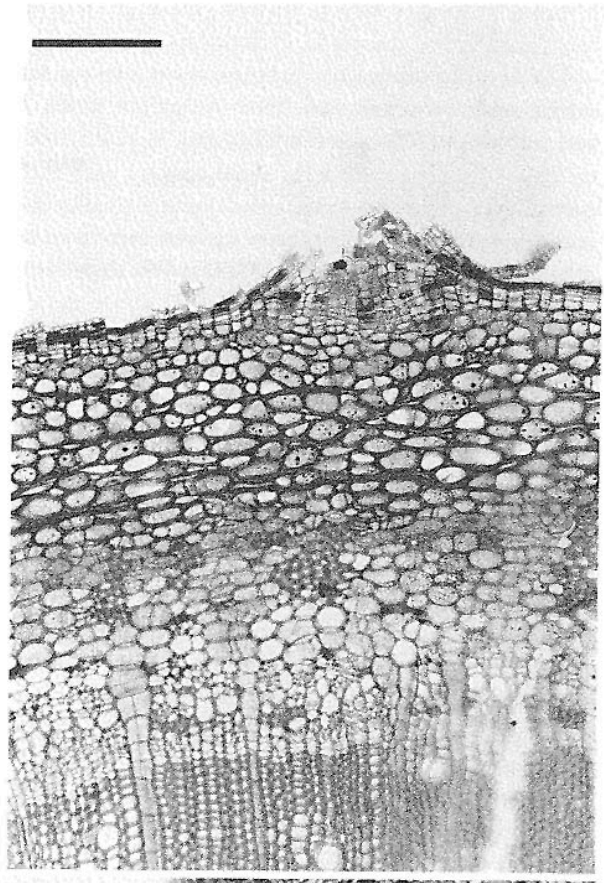


Figure 9. Transverse root sections of *Mora excelsa* and *Mora gonggrijpii*.
Note the higher porosity in the bark of *Mora excelsa*.
In both species but especially in *Mora gonggrijpii* cells adjacent to vessels are filled with a solid substance.

◀ bar = 200 µm

Mora excelsa

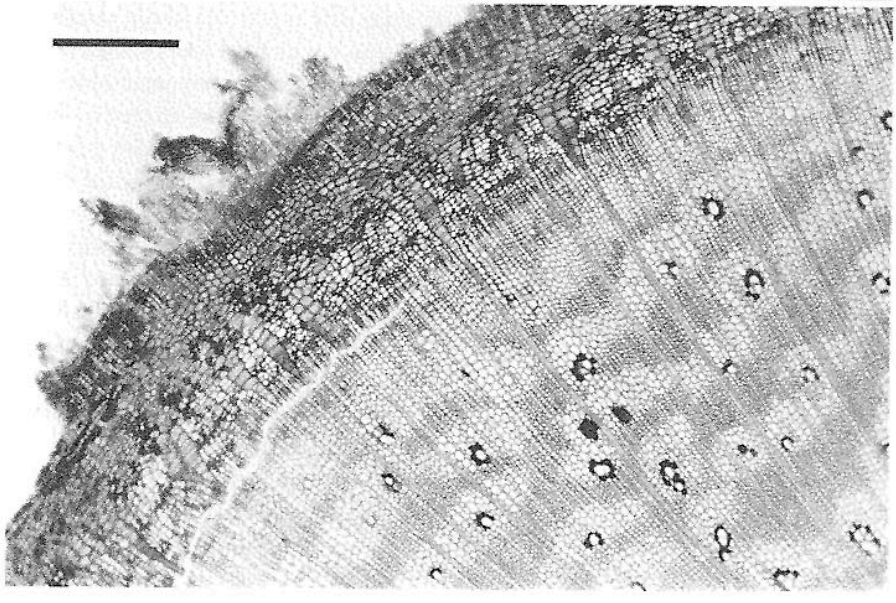
▼ bar = 500 µm



▶ bar = 200 µm

Mora gonggrijpii

▼ bar = 500 µm



is found in species such as *Carapa guianensis, Machaerium lunatum, Macrolobium bifolium, Pentaclethra macroloba, Pterocarpus officinalis.*

LD50 of flooding days decreases from floating *Mora excelsa* seeds to submerged *Mora excelsa* seeds to submerged *Mora gonggrijpii* seeds. The difference between the floating and submerged *Mora excelsa* seeds may be due to the lower oxygen availability in the latter case - floating seeds have some contact with the air and float in a more oxygen enriched layer. *Mora gonggrijpii* seeds have a smaller air pocket in relation to their seed size and this may explain their lower survival compared to submerged *Mora excelsa* seeds. Another explanation may be that *Mora excelsa* seeds can either lower their metabolism in anaerobic conditions (cf. Crawford 1977) or are more tolerant to the end products of anaerobic respiration, such as ethanol or lactate (see Joly & Crawford 1982), or a combination of both, but data to proof this hypothesis are lacking.

Both species show higher germination rates if seeds are flooded for only four days. This suggests that, although the seeds are considered 'wet seeds', some imbibition may still take place before or during germination. This may be of more significance for *Mora gonggrijpii* as its seeds have a higher dry matter percentage.

Flooding and waterlogging lowered the growth rates of both species, which classifies both as flooding intolerant sensu Joly & Crawford (1982). Worbes (1986), however, showed that most floodplain trees showed strongly reduced growth under flooded conditions. The seedlings also lacked adventitious roots and may be viewed as flooding intolerant sensu Kozlowski (1984, 1991). However if flooding occurs frequently and not for prolonged periods of time the formation and subsequent loss of adventitious roots may be too wasteful. Moreover, in deep anaerobic water (e.g. the Essequibo when really flooded) adventitious roots probably serve no purpose at all (Crawford 1982). In such a case flood tolerant seedlings might lower their metabolism and/or tolerate to some extent the products of anaerobic respiration (Joly & Crawford 1982, Joly 1990). Saving of carbohydrates may be a significant aid in survival, especially under the shady conditions of the forest understorey. Increased stem and root porosity may help *Mora excelsa* to survive waterlogged conditions, but again are probably no great help in deep anaerobic water.

Seedling survival after eight weeks was 100% for all treatments except in flooded *Mora gonggrijpii* seedlings. Still, eight weeks is a short period compared to the extreme flooding regimes of the Amazon and Rio Negro (Junk 1989), where seedlings (of other species) can survive seven months of total submergence (Coutinho & Struffaldi 1971).

Mora gonggrijpii has been classified before as a 'flood intolerant' species (ter Steege submitted), based on the performance of the species on a poorly drained soil compared to a well drained soil. The death of all F8 seedlings was not unexpected. However, the mortality may have been enhanced strongly by the higher vapour pressure deficits of the large gap, (in which the nursery was situated), compared to the forest understorey. All leaves were brown and dry and drying out may have been the cause of mortality. High vapour pressure deficits (VPD) and low root activity may have resulted in a 'physiological drought' in the leaves. As the VPD in the forest understorey is usually small such a 'physiological drought' would probably not have occurred that fast in flooded seedlings in the forest. There growth of both species would probably still be hampered but long

term mortality for flooded seedlings under natural conditions is unknown. As both *Mora* species are extremely slow growing and very shade persistent (see ter Steege submitted), long term survival rates may be more relevant to compare than RGRs.

Conclusions

Mora gonggrijpii appears to be less tolerant to flooding than *Mora excelsa*. The flooding intolerance is very clear in the seed germination stage. *Mora excelsa* seeds are moderately well adapted to flooding, or well adapted to moderate flooding regimes, and may well benefit from flooding in their seed dispersal. Seedlings of *Mora gonggrijpii* also are intolerant to flooding, but the same may be said of *Mora excelsa* seedlings. The higher number of lenticels and higher root and stem porosity of *Mora excelsa* may enhance survival on the long term.

We gained some insight in the question as to why *Mora gonggrijpii* is absent in flood prone areas. The growth and survival rates of both species were comparable in both forest types and give no additional information on differences in drought tolerance between the two species (as drought was probably absent). We need additional drought experiments to further understand the absence of *Mora excelsa* on higher ground. This will be the subject of part II.

Acknowledgments

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Segregation of two *Mora* species along a water availability gradient: II transpiration rates and drought tolerance

Hans ter Steege

Abstract

Drought tolerance of seedlings of *Mora excelsa* and *Mora gonggrijpii* were studied in a lysimeter experiment. Seedlings of approximately equal size of both species differed widely in a number of characteristics such as: total leaf area and leaf dry weight, leaf thickness, leaf size, stomatal density, SLA and LAR. Seedlings did not differ in stem hydraulic conductivity nor in pressure-volume relationships. Contrary to the expectations *Mora excelsa* showed lower osmotic potential at full hydration, which may be related to the higher adult tree size. Turgor points were not nearly approached in the forest during the mid dry season in either of the two species. Seedlings of the two species differed greatly in their stomatal conductance, due to differences in stomatal density. Boundary layer resistance contributed in a large extent to the total leaf resistance. Total plant transpiration in the drying out experiment was higher in *Mora gonggrijpii* as the lower conductance in this species is compensated for by its larger leaf area. No difference in the response to drought was observed. *Mora gonggrijpii* may be able to utilize its higher leaf water content under moderate drought in the forest understorey. Based upon leaf characteristics, a higher water use efficiency was assumed in the latter species but carbon isotope discrimination did not indicate any difference in this respect.

Keywords: conductance, lysimeter, *Mora excelsa*, *Mora gonggrijpii*, seedlings, tropical rain forest.

Introduction

The role of light, herbivory, and pathogens in the establishment of seedlings has received considerable attention. More recently drought has also been considered as an important factor in the mortality of seedlings from the wet tropics (Rankin 1979, Howe 1990, Turner 1990, Fisher et al. 1991, Forget 1991). Ter Steege (submitted) showed that two species of *Mora* were well segregated along a water availability gradient. The absence of *Mora gonggrijpii* in periodically flooded areas could be explained in part by the intolerance of seeds and seedlings of this species to flooding. As yet no comparative data are available on the drought tolerance of the *Mora* species. Rankin (1979) suggested early water-stress-related mortality in *Mora excelsa* seedlings in Trinidad. However, Davis and Richards (1933) reported heavy mortality among *Mora gonggrijpii* seedlings and some other canopy trees in 1925-1926. Those years were exceptionally dry and Davis and Richards suggested "*It is therefore likely that these droughts prevent the vegetation from be-*

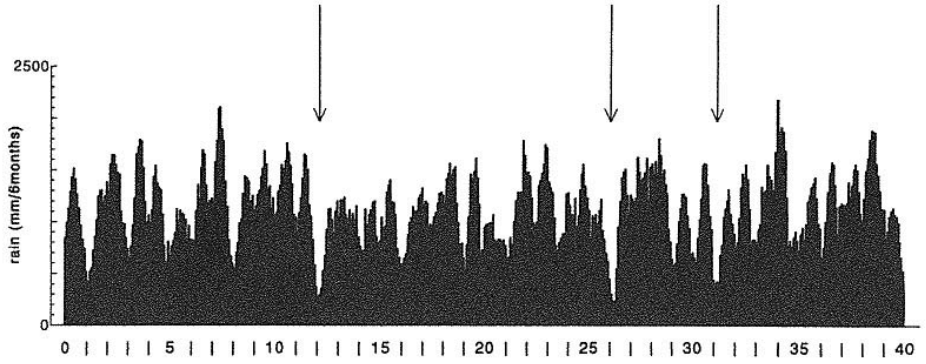

Figure 1. Rainfall for Georgetown, Guyana in the period 1900 to 1980, given as moving totals for 6 months. Data from the Dept. of Hydrology and Meteorology, Ministry of Works, Guyana.

ing as hygrophilous a type as is allowed by the average climate". Severe droughts such as in 1925-1926 also occurred in 1911-1912 and 1931-1932 and are not uncommon in Guyana (Figure 1) -as probably in most wet tropical countries.

Drought-induced water deficits may influence a number of processes in plants, including photosynthesis and growth. Since changes of turgor pressure may be among the most important factors influencing plant metabolism (Bradford & Hsiao 1982), changes in turgor should ideally be kept small (Turner & Jones 1980, Robichaux 1984). Turgor maintenance of leaves is importantly affected by the osmotic and elastic properties of the leaves (Tyree & Jarvis 1982). By lowering the tissue elastic modulus, that is the change in turgor pressure for a change in fractional water loss, turgor can be kept above zero at lower leaf water potentials. Secondly, a lower (more negative) bulk osmotic potential at full hydration increases the bulk turgor at full hydration and consequently values of turgor pressure at lower leaf water potentials (Robichaux 1984). However, Lo Gullo & Salleo (1987) and Salleo & Lo Gullo (1990) argued that a high elastic modulus, coupled to high hydraulic stem conductivity could result in fast recovery of water losses and could then also be considered adaptive to drought.

The hydraulic conductivity of stems is affected by the area of xylem in the stem (A_x), the number of vessels per area and the size of the vessels (e.g. Zimmerman & Milburn 1982). The size of the vessels is of great importance since conductivity increases with the fourth power of the radius (Ewers & Zimmerman 1984, Nobel 1991). Larger vessel diameters are thought to be more prone to blockage, due to embolism (e.g. Elmore & Ewers 1985, Baas pers. comm.), when the water potential gradients are large (i.e. under water stress). However, more recently Sperry & Tyree (1988) and Sperry & Sullivan (1992) demonstrated that vessel diameter is not an important factor in embolism for plants that never experience freezing.

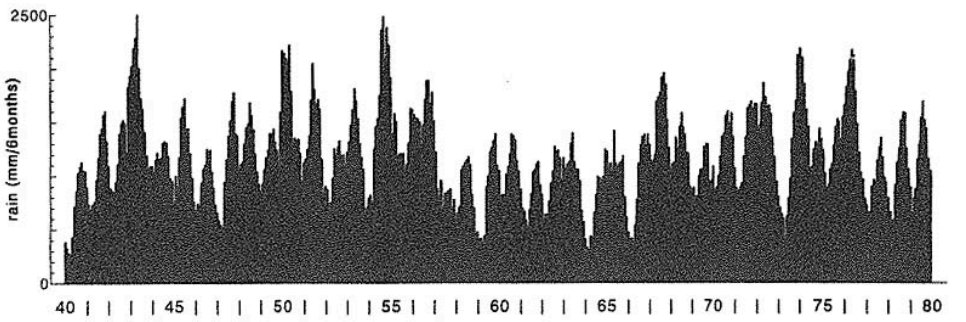

Figure 1. Continued. Note the dip in rain in the winters of 1911-1912, 1925-1926 and 1930-1931, which were reported by Davis & Richards (1933). Heavy mortality was mentioned by the same authors for the drought of 1925-1926.

To assess the comparative drought tolerances of *Mora gonggrijpii* and *Mora excelsa*, both species were subjected to drying soil, while stomatal conductance and total plant transpiration were monitored for one month. Morphological (e.g. the root system, the water-supplying part and leaf area, the water-spending part), wood anatomical (supply conductivity) and leaf anatomical (including the amount of stomata) and leaf physiological parameters were measured to gain insight in the comparative plant parameters, that may influence differential drought tolerance between the seedlings of the two species. Because in logging practices, commonly applied in the study area, the light intensity also increases (see e.g. ter Steege et al. in press) and irradiation levels and water supply might interact, the factors drought and light were combined in a lysimeter experiment. I expected *Mora gonggrijpii* to be more drought tolerant and thus expected, lower osmotic potentials at full hydration, lower tissue elastic modulus, and/or better control of transpiration during drying out of the soil. Furthermore, if any mortality due to drought would occur, I expected it to be lower in *Mora gonggrijpii.*

This study was conducted within the framework of the TROPENBOS Programme in Guyana.

Materials and methods

Plant material

Study site and species are described in ter Steege (Part I submitted). The drying out experiment was conducted in lath houses in the Mabura Hill township 20 km north of the TROPENBOS Ecological Reserve. Seedlings of both species were grown from seeds of a narrow weight range of 90-120 g (ter Steege submitted). Seeds were planted at the end of May 1991 in 5 l black plastic bags, filled with white sand. The plastic bags were

placed on low benches in the understorey of a Mora forest and Morabukea forest next to the forest-plots, described in ter Steege (submitted). Seeds were left to germinate and seedlings to grow for 5 months. Since the cotyledons contain a substantial amount of storage, plants were fertilized only once. Rain during the first three months in combination with low vapour pressure deficits (VPD) of the forest understorey made watering of the seedlings unnecessary. Insect herbivory on the seedlings was negligible, but seedlings grown in the pots in the Mora forest seemed to suffer from drainage problems and were taller with far less and smaller leaves than their counterparts in the Morabukea forest. Therefore, only seedlings from the Morabukea forest were used in the rest of the experiments.

Leaf physiology

Leaves of both species were severed from the seedlings in the pots in the Morabukea forest in the late afternoon. They were immediately re-cut under distilled water and transferred to Mabura. Here they were stored overnight with their petioles still in distilled water, under dark, humid conditions. Pressure volume curves were determined with a pressure bomb (PMS inc., Corvalis, USA), using the bench drying technique (e.g. Koide et al. 1989). ψ_l at the start of the measurements should be near zero. A great many leaves failed to meet this criterion and were rejected. Finally five leaves per species produced accepTable starting conditions. The relative water content was calculated as RWC = (fresh weight - dry weight)/(full turgid weight - dry weight). Leaf osmotic potential at full hydration (π_{ftw}, MPa) was determined by plotting the inverse of ψ_l against RWC values between 95 and 75%. All pressure volume curves per species were lumped and π_{ftw} and its standard error were determined with linear regression analysis (Sokal and Rolph 1969), where π_{ftw} is the inverse of the y-intercept (Koide et al. 1989). The apoplasmic water fraction (RWC_a) and its confidence intervals were determined with the x-intercept. Turgor pressure (P, MPa) were derived from ψ_l and π_l according to Koide et al. (1989). Bulk elastic modulus at full hydration (E_{ftw}, MPa) was calculated according to Koide et al. (1989). Since turgor fell almost linearly to zero with a small decrease in RWC, average bulk modulus of elasticity over the full turgid range is calculated as

$$\bar{\varepsilon}_{ftw} = (100\text{-}RWC_a)^*(P_{ftw}\text{-}0)/(100\text{-}RWC_{tlp}).$$

Where P_{ftw} is the turgor pressure at full hydration and RWC_{tlp} is the relative water content at the turgor loss point. Leaf water potentials of seedlings in the forest were measured once, during the dry period, with a pressure bomb (PMS inc., Corvalis, USA).

Transpiration and leaf conductance

Plants were transferred to the Mabura township on November 3, 1991, the soil in the bags was saturated and left to drain overnight. Field capacity was determined by extracting 5 soil rings (100 cm^3) with soil from the centre of five bags. The rings were weighed, dried at 105°C for 48 hours and weighed again, after which the percentage of water after

1 night draining, as well as bulk density of the soil, were calculated. The plastic bags with plants were placed (after one night draining) in white buckets to avoid further loss of water. The soil in the bags was covered with polystyrene foam chips. A silver plastic bag was loosely tied around the stem of the seedlings and loosely fitted over the top of the bucket to avoid further transpirational losses. Plants were randomly assigned to drought and control treatments in half-shade and full-shade treatments (4 November), before 7:00h at which time the initial weight of pots plus plants was determined. The total weight of one seedling plus pot was approximately 10 kg. The half shade treatment was created in a lath-house with one layer of neutral 50% shade cloth, the full shade treatment was created in a lath house with two layers of 50% neutral shade cloth and two layers of green shade cloth. Both lath houses were covered on the roof with clear plastic to avoid wetting of the plants by rain. Photosynthetic photon flux densities, as measured with a Licor Li-1000 datalogger and quantum sensors were 50% and 12% of the flux on top of the lath houses.

Plants in both lath houses were weighed every day at 7:00h and 19:00h to the nearest gram, at 19:00h control plants were refilled to the exact weight they had at the start of the experiment. Alternating among the two lath houses each day more accurate measurements were done in one of them. These measurements consisted of; weight of all plants at 7:00, 10:00, 13:00, 16:00 and 19:00 hours. Between the weight measurements leaf conductance was measured twice for each plant with a Licor Li-1600 steady state porometer if ambient relative humidity (RH) was below 80%. Measurements of the plants started at the full hours between the weight measurements. Most measurements are from 11:00, 12:00, 14:00 and 15:00h, however, as RH was often over 80% before 10:00 and resistance was often near 100 cm s^{-1} after 16:00h. Relative humidity and air temperature were noted each full hour of the day.

Leaves of the plants of the half shade lath house were harvested at 30 November and those from the full shade lath house at 1 December. At this harvest day measurements of leaf water potential (ψ_l) were made with a pressure bomb (PMS Inc., Corvalis, USA) starting at 6:00, 8:00, 9:00, 11:00, 13:00, 15:00, and 17:00h. Each series consisted of 3 leaves per species per treatment. From 9:00h conductance was measured with the Li-1600 of those leaves of which the water potential was determined. After the conductance measurement the leaf was wrapped in a plastic bag, cut off with a razor blade and placed in the pressure bomb within seconds. The fresh leaf was then weighed to the nearest mg, leaf area was determined with a Licor Li-3100 leaf area meter, leaf length, leaf width (mm) were measured. The leaves were dried for 48 hours at 70°C and reweighed. Plants were finally harvested at 2 December (half shade) and 3 December (full shade). At harvest the weight of the plant/pot system was determined, a soil sample of the droughted plants was taken and processed as described above. The plants were washed free of soil and separated in stems plus petioles, remaining leaves, primary roots, and secondary roots. Measured were; plant height (H, cm), stem diameter at 5cm height (D, cm), remaining leaf area (LA, cm^2). One leaf per plant was stored in FAA (5 parts Formalin 33%, 5 parts Acetic acid 98% and 90 parts Alcohol 70%) or anatomical measurements, dry weight corrections were made through the relation LA and SLA (see below). A part

of the lower stem of the control plants was cut off under 5 mM KCl (Ellmore and Ewers 1985) and stored for a few hours in a refridgerator to be used in the hydraulic conductivity measurements. Plant fractions were dried at 70°C for 48 hours and weighed with a Sartorius balance to the nearest mg. A weight correction was made for the small section of the lower stem stored in FAA. From the dry weights the following ratios were determined; leaf area ratio (total leaf area /plant weight, LAR $cm^2\ g^{-1}$), specific leaf area (leaf area / leaf weight, SLA $cm^2\ g^{-1}$), leaf area per secondary root dry weight (LASR $cm^2\ g^{-1}$), leaf weight ratio (leaf weight / plant weight, LWR), stem weight ratio (stem weight / plant weight, StWR), root weight ratio (root weight / plant weight, RWR), and root shoot ratio (R/S) all these ratios being expressed in $g\ g^{-1}$. From leaf length and leaf width the leaf shape index (length / width, LSI) was calculated.

Transpiration rates per three hours and per day were expressed per secondary root weight and leaf area. Since there may be a difference in average plant size between the treatment sets, changes in the transpiration rates throughout the course of the experiment were expressed as a percentage of the transpiration of each plant on the first day of the experiment. Average conductance of the total leaf area, g_{st+bl} (i.e. conductance of stomata and conductance of the boundary layer, $cm\ s^{-1}$) per three hours was calculated from the transpirational weight loss (E), RH and air temperature measured during the three hours. The absolute humidities $\rho_{ambient}$ and ρ_{intern} were calculated from the respective temperatures and relative humidities, converted to vapour pressures (Unwin 1980) . Vapour pressure is converted to absolute humidity according to Rundel and Jarrel (1989). Total plant conductance is then

$$g_{st+bl} = E/(\rho_{intern} - \rho_{ambient})$$

and this can be converted to leaf conductance using the total leaf area of each plant.

Hydraulic conductivity

Stem segments from the control plants (see above) were re-cut with new razor blades after storage in the refridgerator and, still submerged under 5 mM KCl (Ellmore and Ewers 1985), kept at 0.03 MPa for several minutes to remove surface air bubbles from the tissue (Chiu and Ewers 1992). Under water, water-filled tubes were connected to both ends of the stem parts. A solution of 5 mM KCl was perfused through these stem segments under gravity, with a maximum pressure of 16.6 kPa. Volumetric flow was determined with a pipette and stopwatch. Diameter and length of the stem segment were recorded and K_h, the hydraulic conductivity is calculated as the volumetric flow rate per pressure gradient per length ($kg\ s^{-1}\ MPa^{-1}$ m, Ewers and Zimmerman 1984, Tyree et al. 1991, Chiu and Ewers 1992). The stem segments were stored in FAA for further anatomical analysis. Microscopic slides of the stem segments were prepared as follows: the samples were flushed with ethanol 70%and transverse sections of 15-20 µm were made with a microtome. The sections were than bleached with hypochlorite, stained with safranine, dehydrated with a series of increasing alcohol solutions, xylol and fixed with Canada Balsam. The sections were examined at various magnifications. The area of xylem

(A_x)was determined at 250x, by averaging radii of pith (r_p) and pith + xylem (r_{p+x}) measured in four directions. A_x is then $\pi r^2_{p+x} - \pi r^2_p$. Specific conductivity is calculated as K_h/A_x. Leaf specific conductivity is defined as K_h/LA (kg s^{-1} MPa^{-1} m^{-1}, Ewers and Zimmerman 1984). Finally the Huber value was calculated as A_x/LA (Ewers and Zimmerman 1984). As no dye was available in Mabura and it was too difficult to distinguish vessels from surrounding parenchyma in these young plants, no further attempt was made to measure vessel diameters, or count the number of vessels.

Leaf anatomy

Transverse sections of 15-20 μm were made of one leave of all 10 control plants. The sections were bleached and stained with Astra blue and safranine. They were dehydrated and mounted as above. Slides were examined with an Olympus microscope at 400x. Thickness of upper epidermis, hypodermis (in the case of *Mora gonggrijpii*), palisade parenchyma, spongy parenchyma and lower epidermis were measured with a calibrated ocular micrometer (all measurements in μm). Upper epidermis and lower epidermis were removed. Hereto the leaves were kept in 1:1 hydrogen peroxide 35% and acetic acid 98% for 48 hours at room temperature. They were cleaned with a soft brush, stained with safranine and dehydrated and mounted as above. The number of stomata (mm^{-2}) was determined by counting the number in 5 microscope fields of each individual at 400x. The size of the stomatal pore was measured from photographs taken at 1000x.

Leaf Nitrogen content and carbon isotope analysis

Total leaf nitrogen content was used as a relative measure of maximum photosynthetic capacity (Evans 1989, Pons et al. 1989). In January 1993 the youngest full grown leaf of 20 individuals of *Mora gonggrijpii* and 18 *Mora excelsa* were collected. Leaf area and dry weight were determined as above. Leaf nitrogen and carbon content were determined on four samples of four leaves (total 16 leaves) with an element analyzer. Leaf nitrogen concentration was expressed per leaf area (LNC_A, mg g^{-1}) and dry weight (LNC_W, mg cm^{-2}). Carbon isotope discrimination values ($\delta^{13}C$ in ppm) were determined by mass spectrometry (Farquhar et al. 1982). Since all individuals were growing near to each other these values were taken as a measure of water use efficiency (Farquhar et al. 1982, Farquhar and Richards 1984).

Results

Plant material

Seedling characteristics are given in Table 1. All data are from the plants actually used in the lysimeter experiment. The seedlings of both species were equal in height, stem diameter, and secondary root weight. Total plant dry weight, leaf dry weight, primary root dry weight, and fresh leaf area were all larger in *Mora gonggrijpii*. As a result LWR, LAR

Table 1. Seedling characteristics of *Mora gonggrijpii* and *Mora excelsa* used in drought experiments, standard errors in parentheses. n=20 for seedling characteristics and biomass allocation. n=167 in *Mora gonggrijpii* and 170 in *Mora excelsa* respectively in leaf size, length, width and LSI. n=10 in leaf thickness and its sudivision and in hydraulic parameters. Finally, n=5x5 in the nr of stomates (see text).

	Mora gonggrijpii		*Mora excelsa*		
seedling characteristics					
stem height (cm)	79.1	(2.5)	79.8	(3.0)	n.s.
stem diameter (cm)	8.9	(0.2)	8.4	(0.2)	n.s.
plant weight (g)	31.16	(5.03)	24.23	(1.17)	***
stem weight (g)	9.24	(1.12)	9.18	(0.54)	n.s.
leaf weight (g)	11.78	(0.57)	6.69	(0.41)	***
root weight (g)	10.14	(0.43)	8.36	(0.41)	**
prim. root weight (g)	5.17	(0.31)	4.03	(0.24)	**
sec. root weight (g)	4.97	(0.36)	4.33	(0.29)	n.s.
leaf area (cm^2)	1424	(69)	920	(56)	***
biomass allocation					
LWR ($g\ g^{-1}$)	0.38	(0.01)	0.28	(0.01)	***
StWR ($g\ g^{-1}$)	0.30	(0.01)	0.38	(0.01)	***
RWR ($g\ g^{-1}$)	0.33	(0.01)	0.35	(0.01)	n.s.
LAR ($cm^2\ g^{-1}$)	45.6	(1.4)	38.2	(1.3)	***
SLA ($cm^2\ g^{-1}$)	122	(2)	141	(3)	***
LA/sec RW ($cm^2\ g^{-1}$)	320	(29)	224	(16)	**
R/S ($g\ g^{-1}$)	0.49	(0.02)	0.54	(0.03)	n.s.
Leaf Characteristics					
leaf size (cm^2)	64.2	(2.5)	29.6	(1.2)	***
leaf length (cm)	16.4	(0.4)	12.4	(0.3)	**
leaf width (cm)	5.8	(0.1)	3.4	(0.1)	***
leaf shape index	2.8	(0.03)	3.7	(0.1)	***
leaf thickness (µm)	241.4	(6.0)	152.6	(5.0)	***
upper epidermis (µm)	8.8	(0.7)	12.1	(0.5)	n.s
hypodermis (µm)	19.0	(0.8)			(***)
pallisade parenchyma (µm)	33.6	(1.2)	36.6	(1.3)	n.s.
spongy parenchyma (µm)	170.9	(6.4)	95.1	(5.0)	***
lower epidermis (µm)	9.1	(0.4)	9.1	(0.4)	n.s.
nr stomata (mm^{-2})	177	(5)	329	(15)	***
stomatal pore length (µm)	9	(n.a.)	9	(n.a.)	n.s.
hydraulic conductivity					
K_h($kg\ s^{-1}\ m\ MPa^{-1}\ 10^{-4}$)	6.17	(1.95)	7.90	(2.63)	n.s.
K_s ($kg\ s^{-1}\ m^{-1}\ MPa^{-1}$)	25.5	(8.1)	28.0	(9.3)	n.s.
LSC ($kg\ s^{-1}\ m^{-1}\ MPa^{-1}\ 10^{-3}$)	4.25	(4.25)	8.5	(9.03)	n.s.
HV ($m^2\ m^{-2}\ 10^{-4}$)	1.96	(0.62)	3.08	(0.98)	**

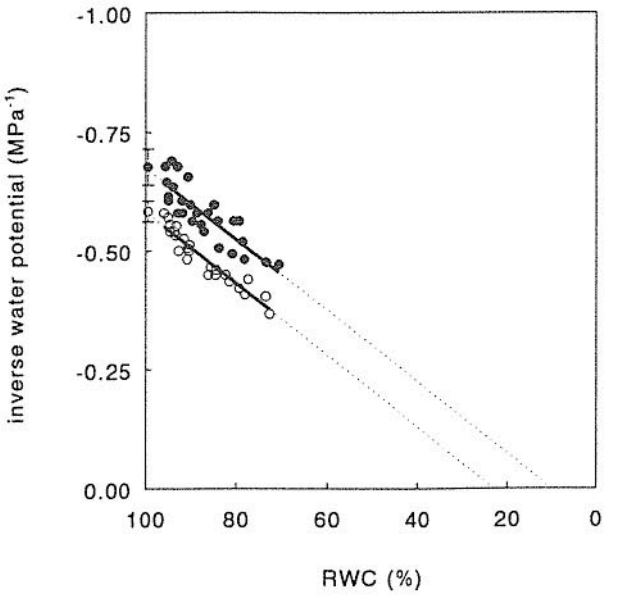

Figure 2. Inverse water potential as a function of relative water content and the estimation of $1/\pi_{ftw}$. Open circles *Mora excelsa* , filled circles *Mora gonggrijpii* . In both species values of five leaves are used.

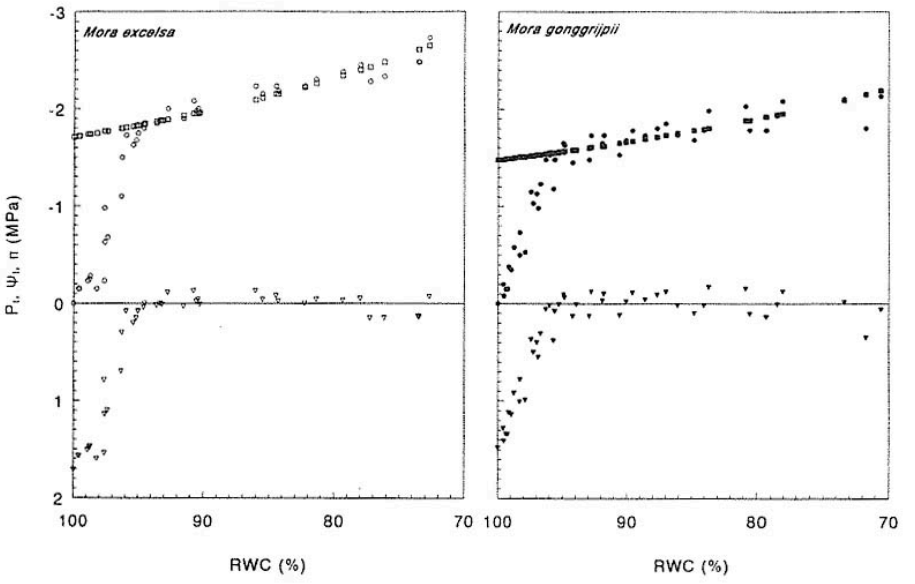

Figure 3. Average pressure volume curves of *Mora excelsa* and *Mora gonggrijpii*, with breakdown of leaf water potential (Ψ_{leaf}) in leaf osmotic potential a (π_{leaf}) and turgor pressure (P).

Table 2. Leaf physiology data for *Mora gonggrijpii* and *Mora excelsa* seedlings. n=5 for each measurement, standard errors in parentheses.

	Mora gonggrijpii		*Mora excelsa*		
π_{ftw} (MPa)	-1.481	(0.014)	-1.702	(0.007)	***
ψ_{tlp} (MPa)	-1.560	(0.010)	-1.848	(0.005)	***
RWC_{tlp} (%)	95.4	(n.a)	94.6	(n.a)	n.s.
RWC_a (%)	9.9	(n.a)	22.1	(n.a)	n.s.
$\bar{\varepsilon}_{ftw}$ (MPa)	28.72	(n.a)	26.65	(n.a)	n.s.
WC_{ftw} (%)	64.9	(0.76)	60.0	(0.98)	**

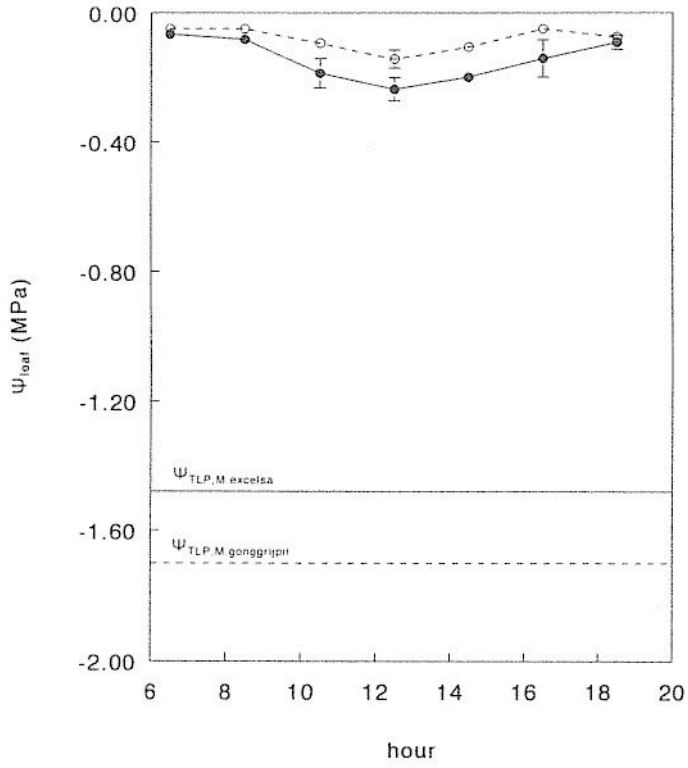

Figure 4. Leaf water potential of *Mora excelsa* and *Mora gonggrijpii* seedlings in Morabukea forest. The lower lines are the ψ_l values at which turgor is lost (ψ_{tlp}). Means are given with their standard error.

and LASR were higher, and root/shoot ratio and SLA were lower in the latter species. Individual leaves were larger in *Mora gonggrijpii*, both in width and length but the LSI also differed for both species. *Mora excelsa* had longer leaves relative to its width.

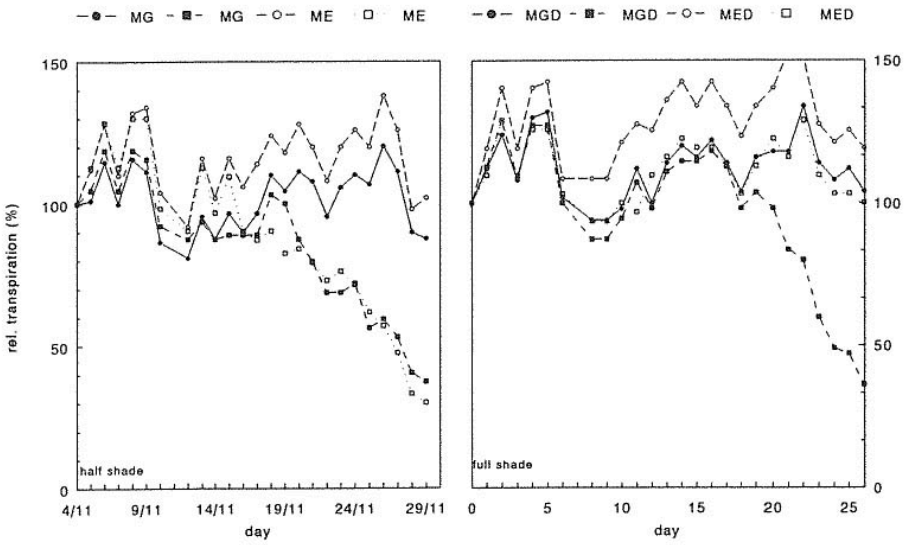

Figure 5. Relative average daily transpiration of *Mora excelsa* (ME) and *Mora gonggrijpii* (MG) seedlings in the lysimeter experiment. Transpiration on the first day (g plant^{-1}), in half shade: MGD0, 89; MGD1, 64; MED0, 50; MED1 63;in full shade: MGDO, 47; MGD1, 50; MED0, 31; MED1, 55. D0=control plants, D1=droughted plants

Leaf physiology

The estimation of π_{ftw} is given in Figure 2. Pressure-volume curves for both species are given in Figure 3. Water potential,ψ_l, is broken down into the osmotic potential, π_l, and bulk averaged turgor P. *Mora excelsa* exhibited lower osmotic potentials at full hydration than did *Mora gonggrijpii* (Table 2). This resulted in a higher π_l over the full range of RWC studied. Turgor pressures dropped quickly in both species, and turgor was lost in both at a RWC of about 95%. A high elastic modulus was found for both species, 26.7 MPa for *Mora excelsa* and 28.7 MPa for *Mora gonggrijpii.* Leaf water potentials at turgor loss point were -1.70 MPa for *Mora excelsa* and -1.48 MPa for *Mora gonggrijpii* (Table 2). Turgor loss points, however, were not even nearly approached in the forest in the mid dry season (September 3rd, Figure 4).

Transpiration and leaf conductance

Gravimetric soil water percentage was approximately 45% after one night draining. Corresponding soil water potential was near zero MPa (based on a pF curve for white sand, Jetten unpublished data). Transpiration was high in both species with average daily values in half shade for *Mora gonggrijpii* of 90 g per plant per day and for *Mora excelsa* of 58 g per plant per day. Typical transpiration per secondary root weight was 20 g g^{-1} and 15 g g^{-1} and per leaf area 58 mg cm^{-2} day^{-1} and 68 mg cm^{-2} day^{-1}, respectively. The water content of fully turgid leaves was 65% in *Mora gonggrijpii* and 60% in *Mora excelsa*

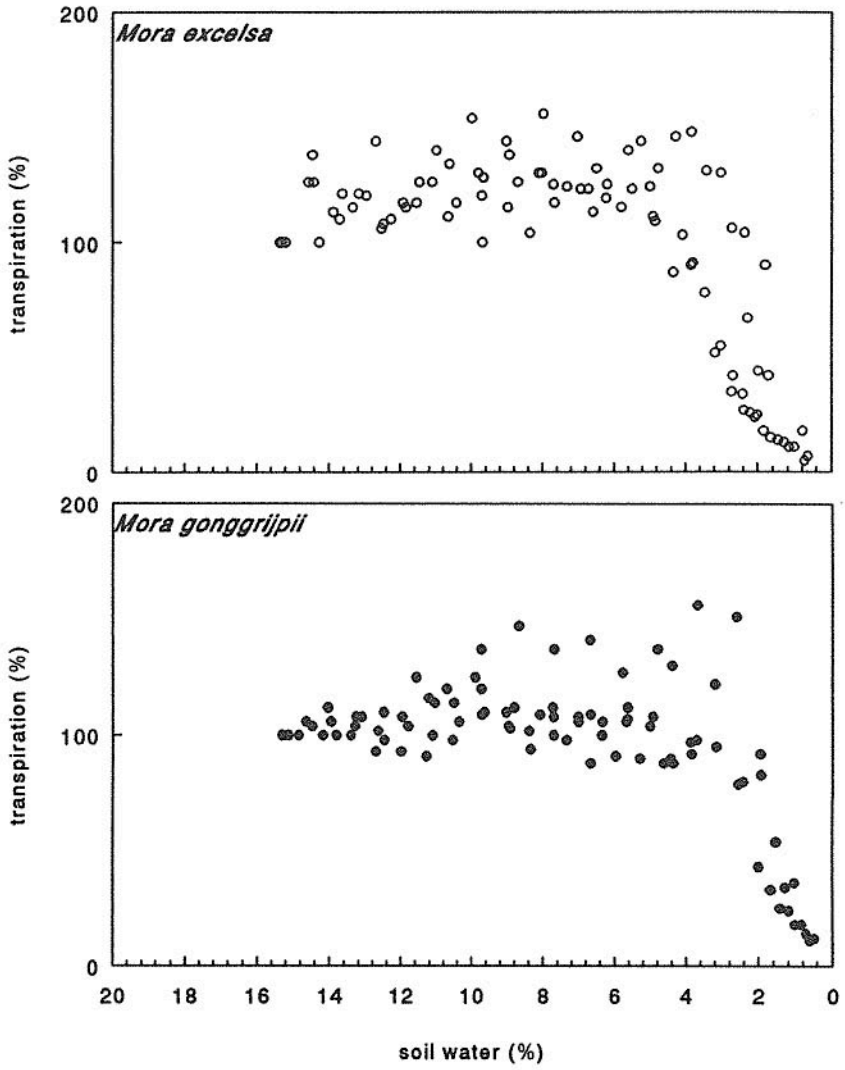

Figure 6. Relative average daily transpiration of *Mora excelsa* and *Mora gonggrijpii* seedlings in the lysimeter experiment, as a function of soil water content.

(Table 1) and consequently the total leaf water was 21.9 and 10 g. Thus, *Mora excelsa* transpired about six times its leaf water content per day, while *Mora gonggrijpii* transpired about 4 times its leaf water content. Total daily transpiration differed substantially between days (Figure 5), due to different VPDs on the different days (data not shown). In the full shade lath house transpiration was lower than in the half shade lath house, but the patterns were similar (Figure 5). Here average daily transpiration for control plants was 42 g per plant per day for *Mora gonggrijpii* and 51 g for *Mora excelsa*. Soil water percentages measured at the end of the experiment were consistent with the total amounts of water lost by all plants.

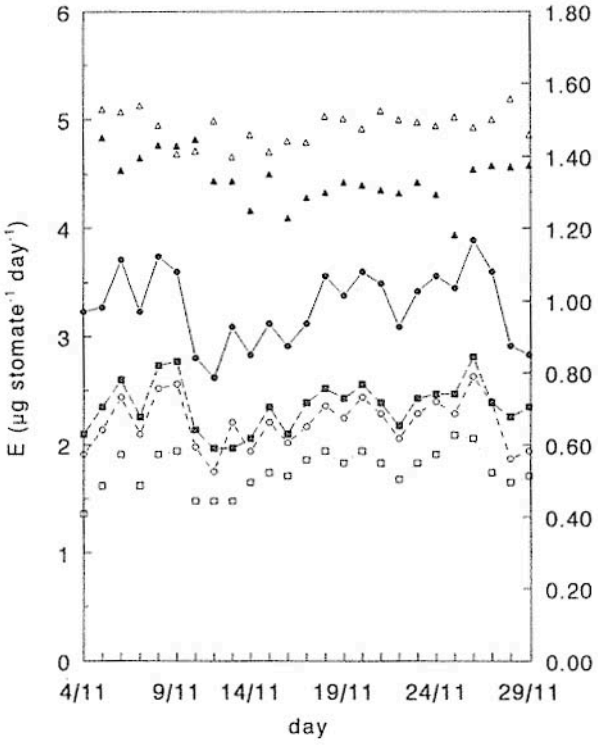

Figure 7. Average daily transpiration of *Mora excelsa* and *Mora gonggrijpii* seedlings in the lysimeter experiment per stomate. Open circles and squares *Mora excelsa* in half shade and full shade conditions, filled circles and squares *Mora gonggrijpii*, same. Open triangles ratio Mg/Me in half shade, closed triangles same in full shade.

In the half shade lath house transpiration declined from the 18th of November and both species reacted in a similar manner. This decline started for both species at a soil water percentage (on weight basis) of 2-4% (Figure 6). These soil water percentages correspond to soil water potentials of approximately -0.3 MPa. In the full shade lath house there was only a visible decline in the transpiration of *Mora gonggrijpii*. The droughted *Mora excelsa* plants transpired on average only 30 g per plant per day, due to their smaller size and never reached low soil water potentials.

Transpiration per stomate per day in the control plants in the half shade lath house was higher for *Mora gonggrijpii* (Figure 7). The ratio between the two species in this respect was rather constant during the course of the experiment.

Calculated total leaf conductance, g_{st+bl} was variable for the period from 7:00 to 10:00h (data not shown) and decreased in each subsequent period of three hours (Figures 8 and 9). Calculated conductances were always higher for *Mora excelsa* and were constant during the course of the experiment, except g_{st+bl} for 16:00-19:00h, which declined towards the end. Measured r_{st} (Figure 8) is lower for both species than r_{st+bl}, the difference being due to r_{bl}. The size of the boundary layer (r_{st+bl} - r_{st}) was constant during the day for both species and was apparently rather equal in both species.

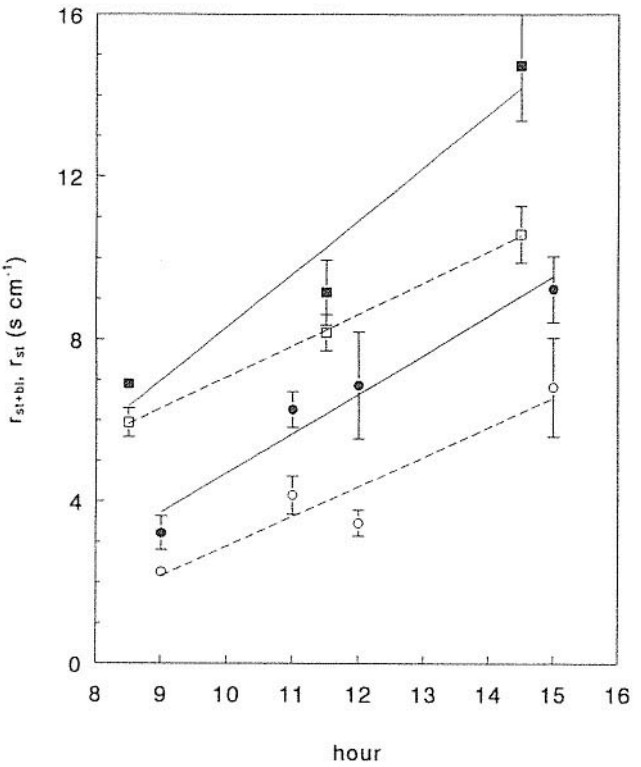

Figure 8. Calculated r_{st+bl} (squares), and measured r_{st} (circles) values on November 5 in the half shade lath house. Open symbols and broken lines *Mora excelsa* , filled symbols and solid lines *Mora gonggrijpii.* Means are given with their standard error.

Table 3. Leaf size, SLA, dry matter, leaf carbon content, leaf nitrogen content and carbon isotope discrimination for leaves of seedlings of *Mora excelsa* and *Mora gonggrijpii*, standard errors in parentheses. n=4 bulk samples of 4 leaves per sample.

	Mora gonggrijpii		*Mora excelsa*		
leaf size (cm^2)	64.6	(4.0)	44.1	(4.5)	**
SLA (cm^2 g^{-1})	155.4	(5.2)	163.8	(5.9)	n.s.
dry matter (%)	35.6	(3.4)	42.1	(2.8)	***
leaf carbon (%)	46.5	(0.80)	50.5	(0.61)	***
leaf nitrogen (mg g^{-1})	16.33	(0.54)	17.66	(0.58)	n.s.
leaf nitrogen (mg cm^{-2})	0.107	(0.0041)	0.107	(0.0022)	n.s.
$\delta^{13}C$ (‰)	-30.9	(0.64)	-30.4	(0.09)	n.s.

Stomatal conductance and leaf water potentials for the days of harvest are given in Figure 10. Stomatal conductance was higher for *Mora excelsa* in both lath houses, and this is consistent with the calculated values. ψ_l declined during the day in both species and both

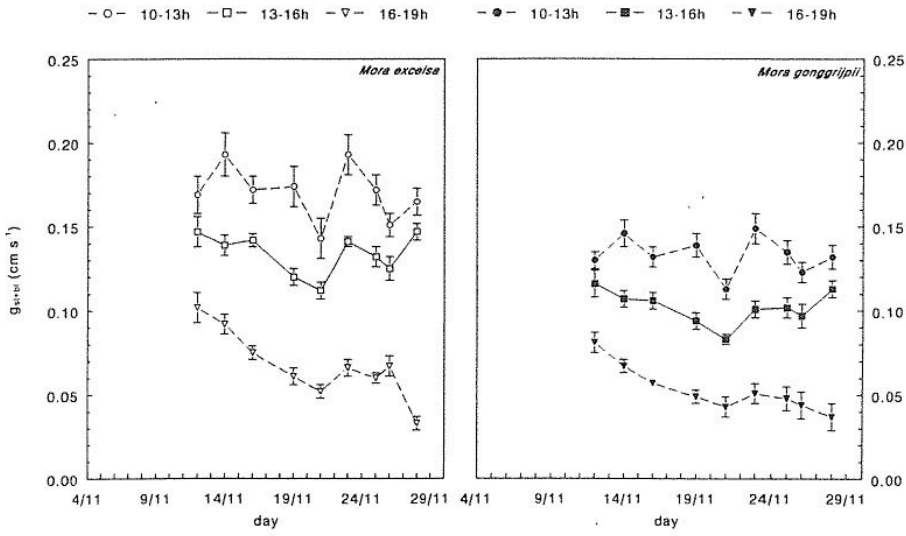

Figure 9. Calculated total leaf conductances (g_{st+bl}) in the lysimeter experiment in the half shade lath house. Means are given with their standard error.

lath houses but full recovery of ψ_l was gained in both species before 20:00h. As in the forest individuals, ψ_{tlp} was not reached in the full shade plants, but due to the higher VPD in the Mabura township, values were lower than in the forest. In the half shade lath house both species may have lost turgor around 17:00h. The low value at this time, when stomatal conductance was especially low, was mainly due to a high VPD (data not shown).

Hydraulic conductivity

Hydraulic conductivity, specific conductivity and leaf specific conductivity were the same for both species (Table 1). There was no relation between hydraulic conductivity, specific conductivity and stem diameter. Huber values were smaller for plants of *Mora gonggrijpii*, due to their larger leaf area.

Leaf anatomy

Leaf anatomical data are given in Table 1 and transverse sections are presented in Figure 11. *Mora gonggrijpii* had thicker leaves than *Mora excelsa*. The reasons for this difference were a thicker spongy parenchyma in *Mora gonggrijpii* and the presence of a hypodermis, which was completely lacking in *Mora excelsa*. Many cells in the leaves of *Mora gonggrijpii* are filled particles, which are probably silica grains (Ragonese 1973). Such particles are almost absent in *Mora excelsa* leaves. The number of stomata per area in *Mora gonggrijpii* was about half of that of *Mora excelsa* (Table 1). The size of stomatal pore length was approximately 9 µm in both species.

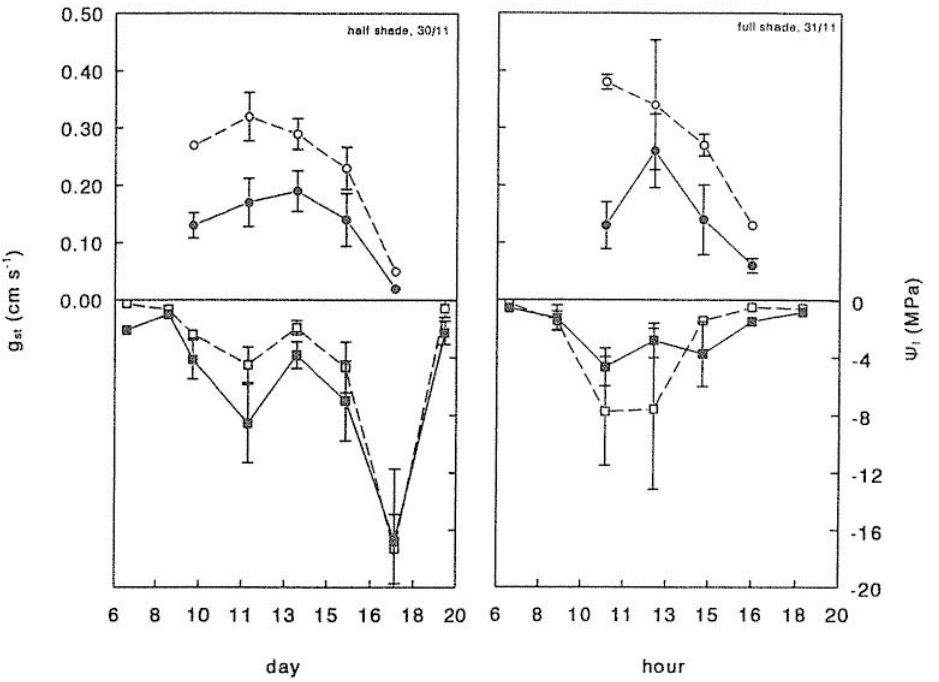

Figure 10. Stomatal conductance (g_{st}) and leaf water potential (Ψ_l) on the last but one day of the lysimeter experiment. Open symbols *Mora excelsa* , filled symbols *Mora gonggrijpii.* Means are given with their standard error.

Leaf nitrogen content and carbon isotope analysis

Leaf nitrogen content for both species are presented in Table 3. LNC, both on a weight base as well as on an area base, was equal for both species. SLA for these leaves, collected in January 1993, were higher than the ones collected in October 1991 (cf. Table 1) and not different for both species. Water content was higher in the leaves of *Mora gonggrijpii* and the latter showed a lower leaf carbon content (per dry weight). Carbon isotope discrimination values of *Mora excelsa* were rather constant around -30.4. The values in *Mora gonggrijpii* ranged from -29.7 to -31.9. Consequently there were no significant differences.

Discussion

Plants were about equal in size, which makes comparison of transpiration rates per plant more valid. Still *Mora gonggrijpii* showed a slightly higher total biomass, probably due to a slightly higher initial dry seed weight (ter Steege submitted).

The values found for π_{ftw} and Ψ_{tlp} are within the range of these parameters reported

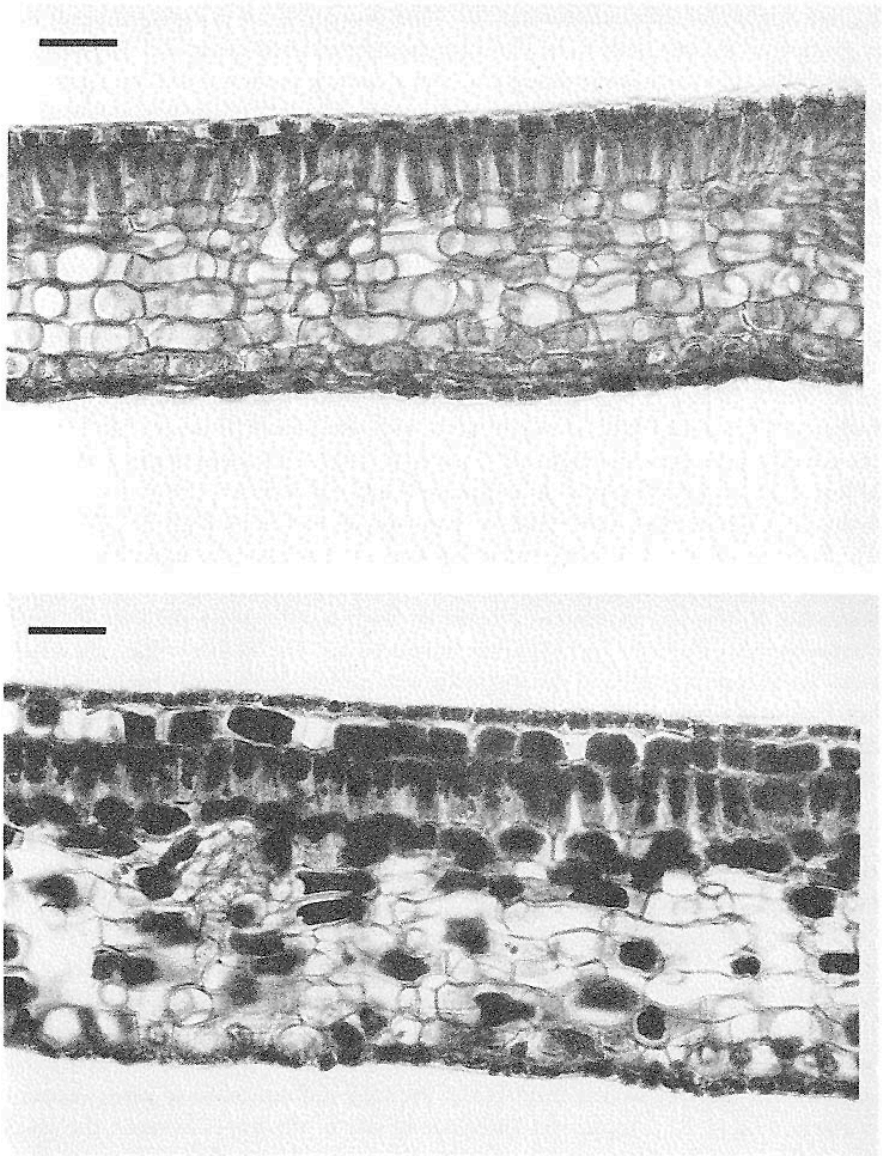

Figure 11. Transverse sections of leaves of *Mora excelsa* and *Mora gonggrijpii*. The dark particles in the cells of *Mora gonggrijpii* are probably silica grains. Also note the presence of a hypodermis in the latter species. (The size of the bar is 50μm).

for tropical seedlings thus far (Robichaux & Canfield 1985, Oberbauer & Strain 1985, Myers et al. 1987, Oberbauer et al. 1987, Alexandre 1991, Tyree et al. 1991, Medina & Olivares 1992).

π_{ftw} was higher for *Mora excelsa* than for *Mora gonggrijpii*, an unexpected result since *Mora gonggrijpii* was supposed to be the more drought-adapted species (cf. Robichaux & Canfield 1985). However severe drought is rare in average years and will limit growth in seedlings less often than light does in the understorey. The lack of drought in the understorey in an average year is illustrated by the fact that turgor loss points of plants in the forest were not even nearly approached during the mid dry season (but data for the end of the dry season are lacking). The higher π_{ftw} in *Mora excelsa* may then be related to the larger size these trees attain in the forest (>60 vs 40 m) and may then be viewed as an intrinsic offset to overcome a larger $\psi_{gravitation}$ (cf. Oberbauer et al. 1987). Interestingly, 20 m would correspond with the approximately 0.2 MPa difference found in π_{ftw}. The elastic modulus at full hydration is high and equal for both species and comparable to the one reported for *Pentaclethra macroloba* seedlings, another wet-forest species (Oberbauer & Strain 1985). A high elastic modulus has been regarded as drought sensitive (Robichaux & Canfield 1985), as turgor is lost with small losses of water . However, hydraulic conductances are fairly high (cf. Tyree et al. 1991) and could result in fast recovery of lost water, if soil drought is not persistent (Lo Gullo & Salleo 1988).

Hydraulic conductances were equal for both species and fairly high (cf. Tyree et al. 1991). Some error may have been caused by water conductance through pith and bark. The highly variable pith size was not related to stem diameter in this set of seedlings, consequently A_x was also unrelated to diameter. Both could explain the lack of correlation between stem diameter and hydraulic conductivity. The Huber value, the relation between the transpiring area and the supplying area, differs significantly between the two species, due to the higher leaf area of *Mora gonggrijpii*. However, since the latter species has only half the amount of stomates per unit leaf area and the number of vessels per xylem area is unknown the usefulness of the parameter is doubtful.

The lysimeter experiment showed considerable differences in conductances between the two species, but no differences in the reaction to drying of the soil. The problem lies in the fact that soil water potential remains high until there is only a few percent water left. Then it drops quickly to, what could be considered 'wilting points', in a few days. Since both species transpired approximately equal amounts this point appeared at the same time for both. The *Mora excelsa* seedlings in full shade transpired considerably less than the *Mora gonggrijpii* seedlings, due to their smaller sizes and thus never reached low soil water potentials. The boundary layer resistance is large compared to the stomatal resistance in both species and may form 2/3 of the total leaf resistance to water vapour in *Mora excelsa* (Figure 8). Despite the difference in size of the leaves between the species the size of the boundary layers were approximately equal. This result is not in accordance with current theories on boundary layer resistances (Nobel 1991).

Total leaf water content is low in comparison to transpirational losses in half shade, but may be of more significance in the forest where VPD are lower than in the lath houses.

Both species lost turgor at a RWC of approximately 95%. An average *Mora gonggrijpii* seedling, as used in the experiment, may thus loose slightly over a gram of water before losing turgor, an average *Mora excelsa* will loose its turgor with the loss of half a gram of

water. With a RH of 90%, a temperature of 30°C, a stomatal resistance of 4 s cm^{-1} for *Mora gonggrijpii* and 2.7 s cm^{-1} for *Mora excelsa* (this difference of a factor one and a half was often observed) and a boundary layer resistance of 3 s cm^{-1} for both, the transpiration rates for *Mora gonggrijpii* would be 0.043 g min^{-1} and 0.033 g min^{-1} for *Mora excelsa*. With these transpiration rates *Mora gonggrijpii* can transpire 30 minutes before losing turgor and *Mora excelsa* 17 minutes. In the understorey where plants have to utilize light flecks, the loss of turgor during those flecks has been observed in other species (Pearcy 1990) and response times of stomates in relation to light flecks are in the order of the above mentioned time periods (Tinoco-Ojanguren and Pearcy 1992). The 13 minutes more of transpiration (and assimilation) may be of benefit for *Mora gonggrijpii*, certainly if between sunflecks leaf water loss could be recovered fast (see above). The higher water content at full turgor for *Mora gonggrijpii* is probably due to the thicker layer of spongy parenchyma, as the hypodermis is small and its cells are to a high degree filled with particles, probably silica grains (Ragonese 1973, ter Steege submitted). The grains are also found in a number of other cells and this probably explains the lower carbon content of the leaves in *Mora gonggrijpii*, as in *Mora excelsa* silica grains were far less observed. Some of the differences in leaf characteristics between the seedlings are also found in the adult trees of the two species: *Mora excelsa* has a higher SLA than *Mora gonggrijpii* (141 and 71 g cm^{-2} respectively, Raaymakers unpublished data) and in adult *Mora gonggrijpii* leaves a hypodermis of two cell layers was observed (Ragonese 1973). Differences observed in some of the leaf-characteristics may thus be species specific but possibly related to leave life in the upper canopy.

Due to the high VPD in Mabura and fast loss of soil water potential in the last few days of the experiment it is difficult to compare the drought tolerance of both species. Possibly *Mora gonggrijpii* can utilize its higher leaf water content under moderate drought in the understorey. Furthermore *Mora gonggrijpii* may exhibit a higher WUE than does *Mora excelsa* based on its larger leaf area and lower stomatal density. Water use efficiency (WUE) at the leaf level can be written as

$$WUE = A/E = (P_a - P_i)/1.6 \bullet (e_i - e_a)$$ (Farquhar & Richards 1984)

where A is carbon assimilation, E is transpiration, P_a and P_i the external and internal CO_2 pressures and e_i and e_a the internal and external vapour pressures. It can also be shown that a lower conductance will generally lead to a lower P_i (Farquhar & Sharkey 1982) and consequently to a higher WUE (see above, in the latter case P_a-P_i will be larger). This may also be the case in *Mora gonggrijpii* as opposed to *Mora excelsa*, since the former has a lower conductance but equal LNC_A and probably equal potential assimilation per unit leaf area. On total plant basis the higher leaf area in *Mora gonggrijpii* compensates for the lower conductance, giving equal or even higher total assimilation rates.

In full light the large leaves may either lead to excessively high temperatures or water loss as predicted by leaf energy balance models (Parkhurst & Loucks 1972, Gates 1980). This is consistent with the observation that the water loss per stomate in *Mora gonggrijpii* in comparison to *Mora excelsa* was higher in half shade compared to full shade and with

observations in medium to large gaps where *Mora gonggrijpii* seedlings suffered high leave mortality due to sun damage (unpublished observations). In full shade such a model would predict a benefit for larger leaves, but this benefit is probably negligible (Chiariello 1984). As canopy trees the two *Moras* appear to behave as expected from the model: *Mora gonggrijpii* has smaller leaves as an adult-sized tree (ter Steege 1990, Polak 1992).

The $\delta^{13}C$ values did not indicate a higher WUE in any of the two species. The values found are rather high for understorey species, however, which are typically around -34 to -35 ‰ (Medina & Minchin 1980, Medina et al. 1986, Sternberg et al. 1989). The high values may suggest that the carbon in the seedlings is to some extent still derived from the seed reserves (Medina & Minchin 1980, Medina et al. 1986), which should exhibit a value around -27 to -30 ‰, depending on parent discrimination characteristics. This would be surprising since the cotyledons loose their function in the forest after 6 months (ter Steege submitted), while the seedlings used for the carbon isotope determinations were one and a half year old. Secondly, light flecks may have increased the $\delta^{13}C$ values (Pearcy & Pfitsch 1991) but probably not to such a large extent, since PPFD estimated from hemisperical photographs (see ter Steege submitted) is low (appr. 3 mol m^{-2} day^{-1}). The argument that seedlings in the understorey experience high internal CO_2 concentrations, due to low rates of CO_2 uptake in the understorey and thus have a high $\delta^{13}C$ (Farquhar et al. 1982, Mulkey 1986) is probably not valid here as most assimilation will take place during sunflecks. Using the discrimination values of both Mora species and a $\delta^{13}C$ for forest air at 1 m of -10.4 ‰ (Sternberg et al. 1989) a average C_a/C_i during photosynthesis of 0.64 can be calculated (Farquhar et al. 1982). This is a low value for shade adapted plants (e.g. Pfitsch & Pearcy 1989, Tinoco-Ojanguren & Pearcy 1992). The case clearly needs further research for definite conclusions.

Conclusions

Mora excelsa and *Mora gonggrijpii* differ in a great number of seedling characteristics. Some characteristics such as thicker leaves, more water at full hydration, larger leaves and lower stomatal conductance in *Mora gonggrijpii* may have a significance in the WUE of this species. However, neither the results of a drying out experiment nor the results of carbon isotope determination give evidence of a higher WUE in this species as opposed to *Mora excelsa*.

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Summary and conclusions

In the rain forest in Guyana there exists a small scale spatial pattern in which forest types may alternate within less than a 100 metres. Several forest types are linked to a particular soil condition. Factors that may lead to spatial heterogeneity are differences in soil characteristics, gap dynamics, irregular disturbances, such as drought or flooding, and the interaction of the latter with soil types. This is discussed in the introduction.

Chapter 2 discusses the temporal pattern in the Guyanese rain forest. The climate is strongly linked to the movement of the intertropical convergence zone (ICZ). This gives rise to two flowering and fruiting peaks in some species, but one main flowering peak for the forest as a whole. As predicted by v Schaik and Terborgh (msc) peak flowering is linked to the peak in sunshine hours, that is the long dry season. Peak leaf-fall and subsequent flushing are approximately around the same time or slightly earlier (Sabatier & Puig 1985, Puig & Delobelle 1988, Brouwer pers. comm.). Assuming that young leaves have a high photosynthetic potential (see e.g. Harper 1989), flushing just before flowering may ensure a high seed production, if rainfall is not limiting. In average years this will be the case: on average no month receives less than 100 mm of rain. Maturation of the fruits takes between 3 to 6 months and most fruits/seeds fall shortly before either one of the two the wet seasons. Timing of fruiting in respect to the rainy season may be beneficial in many climax species, which often lack seed dormancy (Richards 1952). Rain provides the extra moisture necessary for germination and establishment in this critical period.

Occasional drought may take a heavy toll of seedlings (Davis & Richards 1933) and as discussed in the introduction of Chapter 7, drought is a factor in mortality in many tropical rain forest seedlings. Irregular weather conditions can also influence the maturation of seeds as was observed in 1990. In that year both *Mora excelsa* and *Mora gonggrijpii* flowered in January. However the dry period between January and May was extremely wet and cloudy and in March and April both species aborted their fruits. As a consequence there was no seed crop in May. Both species flowered again in January 1991 and produced seeds in May 1991.

Masting had been reported for Lecythidaceae in French Guiana. There was no evidence of mast fruiting in our data on the three most common tree families, Lecythida-

ceae (Kakaralli family), Chrysobalanaceae (Kauta family) and Sapotaceae (Asepoko family). Flowering is too regular on a yearly base in these common families to be linked to irregular weather events, as in the case of Dipterocarpaceae (Ashton et al. 1988). In Lecythidaceae flowering is strongly linked to the dry periods and the physiology of flowering is probably not unlike that of *Tabebuia* as described by Borchert (1983): here drought serves as the causal trigger for flowering.

Chapter 3 describes the relation between soil types and forest types. Two main soil groups were found on a watershed of 480 hectare, white sands (Haplic Arenosols; Tiwiwid sand) and brown sands (Ferric Arenosols and Haplic Ferralsols; Tabela sand and Kasarama loamy sand). Several species are more commonly found on either one of these two soil groups. Within each soil group a gradient exists from wet to dry on which several species have a distinct optimum. A few forest types were distinguished. On the white sands dry evergreen forest, dominated by *Eperua* spp. (Wallabas), is found. There is a clear sub-set of species associated with two dominant *Eperua's*, e.g. *Ormosia coutinhoi* (Korokororo), *Swartzia* sp. (Itikiboroballi) and *Tovomita* spp. (Awasokule). Where drainage is blocked, e.g. when a layer of brown sand is found near the surface or when a hard pan is present (Gleyic Arenosol; Ituni sand), swamp forest may occur. Under very wet conditions a peaty soil (Histosols; pegasse) is found. Swamp forests on those soils are often dominated by palm species, notably *Jessenia bataua* (Turu), *Mauritia flexuosa* (Ité) and also *Euterpe oleracea* (Manicole). The situation on brown sands is complex. Several species may become locally dominant. Such dominant species are *Chlorocardium rodiei* (Greenheart), *Eschweilera sagotiana* (Black kakaralli), *Mora gonggrijpii* (Morabukea), *Eperua rubiginosa* (Watapa) and *Dicymbe altsonii* (Clump wallaba). The sub-set of species associated with these dominants is similar in most cases. This makes the recognition of clear-cut associations difficult. It can be concluded that the objective recognition of 'forest types' such as Greenheart forest and Morabukea forest (=patches dominated by Greenheart or Morabukea) are not supported by our data. However, since patches in which a species is dominant are so easily recognised in the field, the use of these 'forest types' will be perpetuated by foresters and scientists alike.

Chapter 4 describes the various aspects of gap size on germination, survival and morphology of *Chlorocardium rodiei* seedlings. Large gaps have a strong negative effect on the germination of seeds on the soil surface (the natural situation). Seedlings respond favourable to the creation of gaps by showing less mortality and more growth. *Chlorocardium rodiei* is relatively plastic in its seedling morphology. Seedlings in gaps show different biomass allocation patterns, more branching and far more leaf area than those in closed forest. Cotyledon reserves are of paramount importance under a closed canopy. Mortality is 100% if the both cotyledons are removed, suggesting that such seedlings cannot maintain a positive carbon balance in the understorey. Our results show that *Chlorocardium rodiei* can be considered a gap dependent species. While in our study total biomass of the seedlings was linearly related to canopy openings up to 52% , this does one say that large gap sizes are in all circumstances beneficial for the survival of the seedlings. Firstly Richards (1952) notes that *Chlorocardium rodiei* seedlings in gaps (no size mentioned)

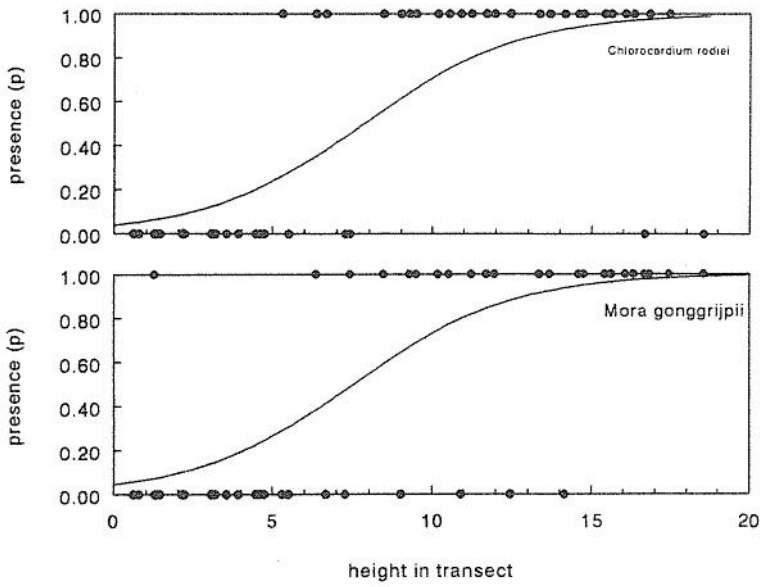

Figure 1. Occurrence (absence-presence data) of *Chlorocardium rodiei* and *Mora Gonggrijpii* seedlings along three transects perpendicular to the Maiko creek. The X-axis represents the height of a plot relative to water level of the creek on the day of measurement. The sigmoid lines are the logit functions ($y = e^{(b+ax)} / (1 + e^{(b+ax)})$), indicating the chance of finding a seedling of a species on that particular height above the creek level. Both sigmoid's are highly significant, $p<<0.001$. *C. rodiei* is positively associated with *M. Gonggrijpii*: $\chi^2=19.81$ $p<0.001$.

grow little and appear stunted by drought. Secondly *Chlorocardium rodiei* is a slow grower, far slower than pioneers such as e.g. *Cecropia* spp. (Congo pump) and will be overtaken by fast growers in larger gaps. Within a few years light conditions under such a pioneer canopy may resemble those of the climax understorey, with all negative effects for the *Chlorocardium rodiei* seedlings. Thus there may be an optimal gap size in which seeds of *Chlorocardium rodiei* can germinate, seedlings can grow favourably, and secondary vegetation is not favoured too much. At present we can not define such an optimal gap size.

The high commercial value and small scale dominance of *Chlorocardium rodiei* on small brown sand patches surrounded by forest regarded non-commercial creates the ideal circumstances for local overharvesting. Forestry in Guyana should recognise the threat of depletion of an ecologically and commercially interesting species and deemphasize the logging of greenheart timber in favour of other species. Comparison of soil types, standing volume and growth rates of timber trees with those of areas where sustainable systems have been developed (Jonkers 1989) suggest that, with less emphasis on one single species, logging could be sustainable in Guyana (ter Steege 1990). Such systems should be implemented soon. Long term monitoring will then allow fine tuning of the harvesting schemes for the Guyanese forests.

Chapters 5, 6 and 7 investigate the occurrence of *Mora excelsa* and *Mora gonggrijpii* along a water availability gradient. Chapter 5 also discusses the response of *Mora gong-*

grijpii to different light conditions. In contrast to *Chlorocardium rodiei, Mora gonggrijpii* is rather rigid in its morphology as regards to light availability. Plants of *Mora gonggrijpii* are larger and have more leaf area in small gaps as compared to the forest understorey but show little differentiation in biomass allocation. Branching, so pronounced in *Chlorocardium rodiei* in gaps, is completely absent in *Mora gonggrijpii.* Leaf area remained constant from the first month up to the third month and reflects the upward oriented growth of *Mora gonggrijpii* seedlings, which is clearly adaptive in shade tolerant seedlings. *Mora gonggrijpii* and *Chlorocardium rodiei* appear to prefer identical soil conditions (compare Figure 1 of this Chapter with Figure 2 of Chapter 6) and are found to co-occur in areas as far apart as Mabura Hill (this thesis) and western Surinam (Maas 1971). Due to its shade persistence *Mora gonggrijpii* could have the potential of replacing *Chlorocardium rodiei* under stable conditions. Whether this is the case or whether disturbance mechanisms maintain the mixture of the two species is unknown.

Relative growth rate in *Mora gonggrijpii* is low, even in small gaps, which is the result of a low NAR as well as a low LAR. The low LAR can be explained by a low SLA, due to the fairly thick leaves (Chapter 7) and a high amount of silica grains in the leaves (Chapter 5 and 7) and the presence of large woody stems. The low NAR can possibly be explained by the production of a high amount of woody tissue (and the possibly production of secondary compounds). A low LAR is probably common in shade adapted climax species with large seeds (Chapter 5). Perhaps slow growers at dark sites show a low RGR because they invest in durability of their leaves, as is the case in slow growers at nutrient poor sites (Poorter 1991),

Mora gonggrijpii and *Mora excelsa* are well segregated along a water availability gradient (Chapter 6). *Mora excelsa* is found exclusively on soils with a high water table along creeks. *Mora gonggrijpii* is found mainly on higher ground and hardly ever experiences flooding. Growth of the latter is negatively influenced by poorly drained soils (Chapter 5). Flooding greatly affects the germination of *Mora gonggrijpii.* Half of the seeds are killed after as few as 11 days. *Mora excelsa* seeds float and survive far longer. Floating of the seeds in the latter species promotes dispersal by water. Flooding and waterlogging affect growth of both species negatively. Mortality is nil except in seedlings of *Mora gonggrijpii,* where all seedlings die after 8 weeks of flooding. The observations of Chapter 6 suggest that *Mora excelsa* is tolerant of moderate flooding. Two other observations are in agreement with this finding 1) the length of flooding periods lowers the survival of the seedlings (Fanshawe 1948, no data); 2) seedlings are notably absent in shallow drainage channels with stagnant water (pers. obs.).

Mora gonggrijpii and *Mora excelsa* differ in a number of seedling characteristics. Leaf area and leaf dry weight are much higher in *Mora gonggrijpii,* resulting in a higher LWR. SLA is lower in *Mora gonggrijpii,* due to thicker leaves and more silica grains. The LAR (LWR*SLA) is still larger in *Mora gonggrijpii.* As we were unable to find differences in RGR, we must conclude that *Mora gonggrijpii* has a lower NAR. The lower LAR could be related to the lower SLA and higher root weight ratio. Both species do not differ in hydraulic conductivity and related parameters, except in the amount of leaf area per area of xylem. They differ little in leaf physiology and contrary to our expectations *Mora ex-*

celsa showed a lower osmotic potential at full hydration than did *Mora gonggrijpii* (Chapter 7). It was suggested that this difference could reflect an intrinsic offset for the larger size of adult trees in *Mora excelsa*. It would indeed be interesting to compare leaves of adults in this respect. No difference in RGR and mortality was found in both species and in both forest types. This is consistent with the suggestion that differences in moderate years, in the sense of flooding and drought, are not responsible for the differences in the occurrence of these species.

Both species performed similar in a drying out experiment but this may have been due to the characteristics of the soil used in the pots in combination with the high transpiration rates. Several seedling characteristics, such as leaf width, leaf thickness, stomatal density and conductance, may lead to differences in water use efficiency (WUE) and on the basis of theoretical considerations *Mora gonggrijpii* should be the more efficient species. However, there is no proof as yet for a higher WUE in any of the species. Proof in this respect might be gathered in more precise growth experiments in which water use is closely monitored. Alternatively, other soil characteristics may be important to explain the absence of *Mora excelsa* on sites where *Mora gonggrijpii* is dominant.

Mora excelsa and *Mora gonggrijpii* seedlings both are intolerant of sudden large changes in the light climate and suffer heavy losses in leaf area. Low conductances coupled to high irradiation loads may lead to intolerably high leaf temperatures. Even after several months of acclimatization seedlings remain stunted in full light (unpublished observations). Observations (unpublished) made in several gaps in Morabukea forest also indicated that *Mora gonggrijpii* seedlings are not very tolerant of high irradiation.

Mora gonggrijpii shows a very positive stand table and may well be harvested sustainably with care (ter Steege 1990). However, the intolerance of high irradiance loads may have consequences for the regeneration capacity of the species and consequently for the size of gaps that harvesting is allowed to create.

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Samenvatting

Patronen in het tropisch regenbos in Guyana

Het tropisch regenbos in Guyana, Zuid Amerika, bestaat uit een kleinschalig mozaïek, waarin verschillende bostypen elkaar afwisselen binnen een straal van 100 m. De verschillende bostypen zijn gebonden aan bepaalde bodemcondities. Factoren die invloed hebben op de ruimtelijke variabiliteit in bostypen zijn verschillen in bodemkarakteristieken, bosdynamiek, onregelmatig terugkerende verstoringen zoals droogte en overstromingen, en de interactie van deze laatste met de bodem. Dit is besproken in de inleiding.

Hoofdstuk 2 behandelt patronen in de tijd. Het klimaat in Guyana is in sterke mate afhankelijk van de Intertropische Convergentie Zone. Dit houdt in dat er twee duidelijke natte en droge periodes per jaar zijn. Bij verschillende boomsoorten treden twee duidelijke periodes van bloei en vruchtzetting op. Het bos in zijn geheel genomen vertoont echter één bloeipiek. De meeste bloei vindt plaats in de lange droge tijd, wanneer er ook een piek in het aantal zonne-uren is. Rond deze tijd treedt ook de meeste bladval en de daaropvolgende nieuwe bladgroei op. Aangenomen dat jonge bladeren een hoge assimilatiecapaciteit hebben en water niet beperkend is, is op deze manier een hoge zaad produktie mogelijk. De rijping van de zaden neemt ongeveer drie tot zes maanden in beslag en de meeste zaden vallen juist vóór de korte of lange regentijd. Dit kan van groot belang zijn voor de vestiging van zaailingen, omdat regen het extra aan vocht levert dat nodig is in deze kritieke fase van kieming en vestiging. Onregelmatige droogte kan een hoge tol eisen onder de jonge zaailingen, zoals is waargenomen in verschillende gebieden en ook bij de soorten waaraan in deze studie verder gewerkt is.

Massa bloei, dat is het verschijnsel dat verschillende soorten op dezelfde zeer onvoorspelbare tijdstippen tot bloei komen, was beschreven voor Frans Guiana. Bloei in Guyana blijkt echter te regelmatig, op jaarbasis, om massabloei aannemelijk te maken.

In hoofdstuk 3 wordt de relatie tussen bodemsoorten en bostypen beschreven. Twee hoofdbodemsoorten werden aangetroffen op een waterscheiding van 480 hectare, witte en bruine zandgronden. Verscheidene boomsoorten werden uitsluitend op één van deze twee bodems gevonden. Binnen beide bodemsoorten bestaat er een gradiënt in het voor-

komen van soorten, van de natte plaatsen onder aan de hellingen tot de drogere plaatsen op de top van de waterscheiding. Een aantal bostypen werd onderscheiden. Op de extreem gedraineerde witte zanden groeit droog altijdgroen loofbos, gedomineerd door twee Eperua soorten. Op plaatsen met geblokkeerde drainage vormt zich moerasbos, vaak met een venige bodem. In dit bostype zijn palmen erg algemeen. Op de bruine zandgronden konden niet echt bostypen beschreven worden, omdat hier wel enkele soorten domineren, maar deze worden bijna altijd vergezeld door dezelfde begeleidende soorten. Bostypen als 'Groenhart bos' en 'Morabukea bos' zijn dan ook mogelijk geen echte bostypen. Door hun opvallende uiterlijk zullen deze 'bostypen' toch gebruikt blijven worden door zowel bosbouwers als wetenschappers.

Hoofdstuk 4 beschrijft verschillende effecten van openingen in het kronendak van het bos op de kieming, overleving en morfologie van Groenhart zaailingen. Grote openingen, zoals ontstaan door houtkap, hebben een sterk negatief effect op de kieming van zaden. Zaailingen reageren positief op openingen in het bosdak: er vindt minder sterfte plaats en meer groei. De zaadreserve blijkt van uitermate groot belang voor zaailingen in het intakte bos. Zaailingen gaan in het algemmen dood als ze vroegtijdig hun zaad verliezen. Dit zou erop kunnen duiden dat de zaailingen van Groenhart onvoldoende assimilatie kunnen vertonen in de donkere omstandigheden onder het gesloten bosdak. Voor het voortbestaan van de soort zijn dan ook waarschijnlijk gaten in het kronendak nodig. Een verwijdering van meer dan 50 procent van het kronendak had een positief effect op de groei van zaailingen. Dit betekent echter niet dat zo'n grote verstoring in alle opzichten gunstig is. In de eerste plaats lijken ook zaailingen van Groenhart gevoelig voor de grotere droogte, die in zulke open plekken kan optreden. Verder zij vele zogenaamde pioniersoorten veel beter aangepast aan zulke open plekken en zij zouden wel eens voor te grote concurrentie kunnen zorgen in grote open plekken. Waarschijnlijk bestaat er dus een optimale opening in het kronendak, waarbij Groenhart zaden nog kunnen kiemen, de zaailingen voldoende kunnen groeien en pioniersoorten niet te veel bevoordeeld worden. Op dit moment kunnen we nog niet goed de optimale grootte aangeven.

De grote commerciële waarde van Groenhart en het feit dat de soort in kleine concentraties voorkomt, vaak omringd door bos met een lage commerciële waarde, schept de ideale omstandigheden voor lokale kaalkap. De bosbouw in Guyana moet de uitputting van een ecologisch en economisch interessante soort dan ook serieus nemen en minder nadruk leggen op de kap van Groenhart. Vergelijking van bodems, bosopstanden en groeisnelheden van houtsoorten uit die gebieden waar duurzaam bosbeheer is ontwikkeld, doet vermoeden dat met minder nadruk op één enkele soort duurzaam bosbeheer mogelijk moet zijn. Een dergelijk systeem zou zo snel mogelijk moeten worden toegepast. Lange-termijn-onderzoek kan dan aangeven waar aanpassingen aan de typisch Guyanese omstandigheden nodig zijn.

De hoofdstukken 5, 6 en 7 beschrijven het voorkomen van Mora (Mora excelsa) en Morabukea (Mora gonggrijpii) langs een water beschikbaarheids-gradiënt. Hoofdstuk 5 behandelt ook de respons van Morabukea op verschillende lichtomstandigheden. In tegenstelling tot Groenhart is Morabukea erg star in zijn morfologie. Morabukea is een goed aan de schaduw aangepaste soort en houdt zelf onder relatief hoge lichtomstandig-

heden vast aan een strategie, die typisch is voor een schaduwsoort. Zo blijft gedurende lange tijd de totale bladoppervlakte gelijk en vertakken de zaailingen niet. Morabukea en Groenhart komen op identieke bodems vaak naast elkaar voor. Dankzij zijn hoge schaduw tolerantie zou Morabukea Groenhart langzaam kunnen verdringen in ongestoord bos. Of dit ook werkelijk het geval is, is niet duidelijk.

Morabukea en Mora komen ruimtelijk duidelijk gescheiden voor. Mora word bijna uitsluitend langs kreken en rivieren aangetroffen, op bodems die tijdelijk onder water kunnen staan. Morabukea groeit voornamelijk op iets hogere gronden, waar overstromingen vrijwel uitgesloten zijn. De gedachte bestond dan ook dat Mora beter bestand zou zijn tegen wateroverlast, terwijl Morabukea beter bestand zou zijn tegen droogte. Dit werd in een aantal experimenten getest. Groei van Morabukea wordt in negatieve zin beïnvloed door slecht gedraineerde bodem (hoofdstuk 5). Kunstmatige overstromingen hebben een groot effect op de kieming van deze soort. De helft van de zaden gaat dood na slechts 11 dagen. De zaden van Mora drijven en zij overleven meer dan 50 dagen overstroming. Overstromingen in het oeverbos, direct na de zaadval, dragen waarschijnlijk bij tot de verspreiding van de soort langs rivieren. De groei van beide soorten wordt in negatieve zin beïnvloed door overstromingen. Mora lijkt iets beter bestand te zijn tegen de effecten van overstromingen, maar lijkt niet bestand tegen langdurige overstromingen.

Met betrekking tot de droogte werden geen grote verschillen gevonden tussen de twee soorten. In stamanatomie, bladfysiologie lijken de soorten erg veel op elkaar. Wat betreft bladmorfologie zijn er grote verschillen. Morabukea heeft grotere en dikkere bladeren. Toch werden er in een droogte-experiment geen grote verschillen gevonden tussen beide soorten. Op theoretische gronden kan men aannemelijk maken dat Morabukea efficiënter met zijn water om zou gaan, maar dit werd door geen van de metingen bevestigd. Er bestaat dan ook nog geen duidelijk antwoord op de vraag waarom Morabukea zo algemeen is op drogere gronden, terwijl Mora daar vrijwel volledig ontbreekt.

Beide soorten bleken erg slecht tegen hoge instraling te kunnen. Zelfs na vele maanden aanpassing blijven de zaailingen van Morabukea in grote open plekken er zeer slecht uit zien. Gecombineerd met het feit dat de drainage van de bodem ook vaak verslechterde en dit ook geen positief effect op de groei van Morabukea had (hoofdstuk 5) betekent dat ook bij de exploitatie van deze voor de bosbouw interessante soort, de richtlijnen voor kap nauwkeurig dienen te worden uitgezocht.

Curriculum vitae

Hans ter Steege werd geboren op 28 november te Schiedam. In 1978 behaalde hij het diploma Atheneum B aan het Kottenpark College in Enschede. In datzelfde jaar startte hij de studie Biologie aan de Rijksuniversiteit in Utrecht. Het kandidaats-programma werd in 1981 afgerond en de studie werd voltooid in 1987. In de doctoraal fase van de studie bewerkte hij een hoofdonderwerp bij de vakgroep Zoölogische Oecologie en Taxonomie in samenwerking met het Rijksinstituut voor Natuurbeheer over de relatie tussen de vogelstand met de vegetatie en recreatie in het Nieuwkoopse Plassen gebied. Een tweede bijvak betrof een stage bij de Interfacultaire Werkgroep Milieukunde. Hierna behaalde hij zijn onderwijs aantekening bij de vakgroep Didactiek van de Biologie. Een laatste hoofdvak betrof een onderzoek naar de verticale verspreiding van epiphyten in staande bomen in het regenbos van Guyana, bij de vakgroepen Systematische Plantkunde en Botanische Oecologie.

In September 1987 volgde een aanstelling bij de Rijksuniversiteit Utrecht als coördinerend onderzoeker van het 'Forest Project Mabura Hill' in Guyana. Gedurende deze tijd werd een ecologisch reservaat met veldstation opgezet en tevens een start gemaakt met het promotie onderzoek. Van 1988 en 1989 was hij ook verbonden aan de Universiteit van Guyana als gastdocent. Van 1989 tot 1992 werkte hij vervolgens als Project Leider voor het Tropenbos programma in Guyana. Vanaf Oktober 1992 werkt hij als toegevoegd onderzoeker bij de Vakgroep Botanische Oecologie en Evolutiebiologie.