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Variability and Grouping of Tree Leaf Traits in Multi-Species Reforestation (Leyte, Philippines)

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Dissertation
zur Erlangung des akademischen Grades Doctor of Philosophy (PhD)
der Fakultät für Forstwissenschaften und Waldökologie
der Georg-August-Universität Göttingen

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VARIABILITY AND GROUPING OF TREE LEAF TRAITS IN MULTI-SPECIES REFORESTATION (LEYTE, PHILIPPINES)

Natural rainforests in the tropics are mostly highly diverse in tree species. Continuous loss of these forests and subsequent replanting leads to the creation of large areas of planted forests which primarily rely on few species creating stands of low functional diversity. A different approach to reforestation, the so called rainforestation, has been developed in Leyte, Philippines in the mid-1990s. This scheme to reforestation emphasizes mixed stands and the preferential use of native species supplemented by fruit trees. The approach is considered promising and future extensions are planned. Characterization of reforestation species through their leaf traits and other related physiological parameters is crucial for the assessment of the systems´ ecological functioning. Leaf traits guide us to understand the function of specific species in an ecosystem and to predict their performance through growth and survival. Limited studies are available on the leaf traits assessment of species in mixed reforestations. In this study, I investigate species-specific functional leaf traits i.e. stomatal conductance for water vapour (g_s), leaf morphology and chemistry.

The general objective of this research was to assess rainforestation as a scheme to reforest degraded sites, in terms of the functional diversity of the co-occurring species. Specific objectives were outlined as follows: (1) to assess the species-specific variation of leaf traits and in particular of maximal leaf stomatal conductance (g_{smax}), (2) to search for relationships between g_{smax} and tree variables i.e. tree architecture, leaf morphological and chemical traits (3) to group species according to their distinct foliar traits.

The study was conducted in three rainforestation sites established near the villages Cienda, Patag and Marcos, Leyte, Philippines. Stands were less than three kilometers distant from each other and with comparable stand characteristics i.e. tree density, soil characteristics and topography. At the time of the study, the three stands were 11 to 12 years old. Four nurseries located near the mixed reforestation stands were also selected to study the leaf traits of seedlings of various species. These nurseries were established to produce planting materials mainly for reforestation purposes.

This dissertation consists of five chapters. Chapter one gives an overview of the forest resources in the Philippines. This chapter describes the history of the forest cover loss in the country from land being previously covered with rain forest to being one of the mostly heavily deforested tropical countries. Various reforestation strategies to restore the degraded state are also presented including the `rainforestation´ approach to reforestation. The materials and methods

used for studying leaf traits are explained in Chapter 2. This includes the use of porometry for measuring the stomatal conductance (g_s) or the loss of water from plant leaves through their stomata. Methods of leaf samples collection for leaf morphological and chemical analyses were also described in this chapter. In Chapter 3, sixteen broad-leaved species were studied, with five individual trees per species. Measurements of g_s in ten fully expanded sunlit leaves per individual tree in the upper canopy were made possible with the use of movable bamboo towers. Diurnal measurements of g_s were conducted in an hourly interval in the morning until late afternoon. Mature and healthy sun-exposed leaves were collected for morphological and chemical analysis. Chapter 4 focuses on the study of leaf characterization of tree species belonging to different canopy layers in the rainforestation. This is an extension of the earlier study including more species (in total 26) but fewer traits. The last chapter deals with the study on seedling morphology and leaf traits of 25 species grown in the nurseries. Seedling stage is the most vulnerable phase in the whole plant development. Mortality is very high at this stage due to many factors such as water, light and nutrients which may limit seedling growth and survival. Hence, leaf characteristics in seedlings could be decisive on the determination of tree species performance at the later stage of development.

The following are the major findings:

- Species-specific leaf traits differ between the sixteen broad-leaved species studied. The g_{smax} differed five-fold between species (165 to 772 mmol m^{-2} s^{-1}). Among the measured tree variables, only carbon isotope ratio ($\delta^{13}C$) showed a simple linear correlation with g_{smax}. Dipterocarp species indicated a strong negative relationship between g_{smax} to specific leaf area (SLA, measure of leaf thinness) which may indicate slightly different characteristics in these species. In a multivariate analysis all native dipterocarps species, a native Guttiferae and the durian tree (*Durio zibethinus*) were associated with more depleted $\delta^{13}C$, small leaves and low leaf width to length ratio (WLR). Two exotic species frequently used for reforestation (*Gmelina arborea* and *Swietenia macrophylla*) and the native early successional *Terminalia microcarpa* were separated from other species by their high SLA and high leaf nitrogen content per leaf area basis (N_{area}). Both species of *Artocarpus* (*A. blancoi* and *A. odoratissima*) were also separated and had large leaves with low SLA and low N_{area}. These associations of species with leaf traits as variables indicate that species have different leaf investment strategies, which may influence whole plant performance.

- Significant variation was found in the leaf morphological and chemical traits of 26 species studied with sun-exposed (18) and shaded (8) crowns. Comparison of leaf morphological and chemical traits between exposed and shaded species showed no significant differences. Among the measured tree variables, leaf $\delta^{13}C$ showed simple linear correlation to tree height, diameter at breast height, leaf width to length ratio (WLR) and nitrogen content in the leaves. Most species studied were characterized by more depleted in leaf $\delta^{13}C$ and low leaf WLR. However, two native pioneer species (*Pterocarpus indicus* and *Melia dubia*), an exotic species (*Gmelina arborea*) and both species of *Artocarpus* (*A. blancoi* and *A. odoratissimus*) were found to be more enriched in $\delta^{13}C$ and with high WLR. Other studied species (i.e. *Pterocapus indicus, Melia dubia, Dracontomelon dao, Teminalia microcarpa, Swietenia macrophylla* and *Vitex turczaniinowii*) grouped together because of their high SLA and N_{mass}. Most shaded crown species were grouped together with more depleted leaf $\delta^{13}C$. Significant variation in leaf morphological and chemical traits found in the species studied showed characteristics similar to species growing in lowland tropical forests.

- Seedling morphology, g_{smax} and leaf morphological traits varied between the 25 species studied at seedling stage. Species-specific g_{smax} differed nine-fold (72 to 643 mmol m^{-2} s^{-1}). For studied leaf traits, only WLR showed a simple linear correlation with g_{smax}, but the explained variance was low. Results of a principal component analysis (PCA) showed that two axes still explain 68 percent of variance in the tested leaf traits. A number of species (e.g., *Artocarpus heterophylla, Sandoricum koetjape, Samadera indica* and *Samanea saman*) were associated with high g_{smax}, and high WLR or round leaves. Others however, (e.g., *Calophyllum blancoi, Terminalia microcarpa, Diplodiscus paniculatus, Diospyrus philippinensis, Lithocarpus luzoniensis* and *M. altissima*) showed low g_{smax} values and have low WLR or oblong leave shape. Species e.g. *N. lappaceum, V. parviflora, D. dao, P. indicus, and S. saman* were grouped according to their low SLA while *Durio zibethinus, Swietenia macrophylla, Artocarpus heterophylla, Dipterocarpus grandiflorus, Palaquium luzoniense* and *Samadera indica* were all separated by their distinct characteristics of having high SLA. Overall, most of the species were grouped together in the centre or with intermediate values of leaf traits. Results from cluster analysis using leaf traits suggested six distinct clusters of species at seedling stage. Leaf traits of adult trees of thirteen species showed no relationship with leaf traits of the same species at seedling stage except for WLR. Findings from this study showed that seedling characteristics in some species change as they mature. Thus, an assessment of leaf traits and performance at mature states may not necessarily be indicative for leaf traits and performance at the seedling stage, which may be of great importance for reforestation success.

Overall, association of species with distinct leaf traits in rainforestation may indicate leaf investment strategies, which may be critical to whole plant performance such as growth and mortality. Leaf traits information may help to adjust the species combination in further developments of the reforestation scheme to specific goals. The relatively high variability in leaf traits among co-occurring tree species suggests that the multi-species reforestation is already quite successful in – at least partly - restoring the functional variability of the former natural forest.

CHAPTER 1

Introduction

1.1 Overview of forest resources in the Philippines

The Philippines is one of the few countries in the world which was originally and thoroughly covered by rain forest (Schulte, 2002). It is considered as one of the mega diverse countries in the world in terms of its large share of endemic flora and fauna however, it is now on the list of biodiversity hotspots (Myers et al. 2000). The replacement of natural forests to various unproductive lands worsens the country´s condition in terms of massive forest loss. In fact, the decline of its old growth forest cover from 70% to 7% in less than a century is considered as one of the most severe in the world (Heaney, 1998). Countrywide, Philippines has only three percent primary forest cover remaining, with very few of these forests found in the lowlands (ESSC, 1999; Myers et al., 2000). Forest cover loss was attributed to intensive logging (both illegal and legal), upland migration and agricultural expansion; and unsustainable practices such as shifting cultivation (Heaney, 1998; Pulhin et al. 2006). These activities have created 13M hectares of open grassland areas and 5.2 M hectares of this figure need immediate rehabilitation (FAO, 2005) (see Figures).

Protection of the remaining forest cover and the adoption of necessary schemes for the rehabilitation of huge barren land in the country have been put forward. In fact, reforestation efforts in the country have started one hundred years ago (since 1910) through various projects initiated by the government (Pulhin et al. 2006). However, success in terms of the area coverage by rehabilitation efforts was poorly seen on the ground (Esteban, 2003). In addition, a huge gap between the rate of reforestation and deforestation with a ratio of 1:23 hectares, favouring the latter was evident (FAO, 2005). Lack of technical expertise to rehabilitate the land and poor species-site matching are among the many constraints identified in most of the reforestation in the country (Pulhin et al. 2006, Carandang and Cardenas, 1991).

Conversion of many natural forests in the Philippines through shifting cultivation leaving large areas of open grasslands and degraded land. (Middle and last photos were taken by J. Quimio).

1.2 Reforestation strategies in the Philippines

The situations mentioned earlier had brought the government to lead various programs that could rehabilitate the country's degraded forest lands. One of the biggest forest restoration activities in the Philippines happened during the period of 1987 to 1995 through National Forestation Program which targeted to reforest 1.4 M hectares (Magno, 1994). Another project was reforestation through an organized communities and also known as Community-Based Forest Management. Communities were contracted by the government to reforest and have occupancy over the lands that they have developed (Pulhin et al. 2006). This approach is one of the most promising strategies to reforest large areas that promote sustainable forest management not only in the Philippines, but also to some other southeast Asian countries (Shulte, 2002).

However, a limited number of species are being used in reforestation. These species particularly come from the genera *Pinus*, *Eucalyptus* and *Acacia* (Lamb et.al 2005). In the Philippines alone, about 80% of the established plantations were planted with *Gmelina arborea, Swietenia macrophylla, Acacia auriculiformis, Acacia mangium* and *Eucalyptus* species (Pulhin et al. 2006). These species were introduced to the country and favoured by most farmers due to the availability of resources and established methods on how to grow them successfully in the field. Studies have shown that areas planted in a monoculture approach are less good in terms of their productivity and ecological gains compare to mixed-species stands (Erskine et al. 2006). In fact, many traditional plantations have supplied goods but have made minor contributions to the restoration of the ecological functions and biodiversity (Lamb et.al. 2005).

1.3 Rainforestation approach to reforestation

In the tropics, recent approaches to reforestation emphasize the establishment of native species in mixed stands (Lamb et al. 2005, Montagnini et. al 1995). Stands planted with mixture of indigenous species perform well in terms of biomass productivity and carbon sequestration than pure stands (Redondo-Brenes and Montagnini, 2006). In the mid-90s a farming technology called "rainforestation" on the island of Leyte, the Philippines was envisioned. The working hypothesis in the creation of rainforestation was "The closer a farming system in the humid tropics is to a natural rainforest ecosystem, the more sustainable it is" (Margraf and Milan, 1996). In addition to its goal, rainforestation will serve as a buffer to remaining protected areas by planting species that are native in areas such as public degraded forest lands, in other tenurial instruments including Community-based Forest Management, ancestral domain sites and protected areas. It aims to restore degraded areas and farms planted with old coconut stands through a highly diverse and economically future-oriented and sustainable tree farm (Margraf and Milan 1996). The proposed planting scheme to rainforestation establishment was to initially plant native pioneers at a close distance of 2m x 2m and planting of shade tolerant species in the second year. Shade tolerant species are composed on highly values timber tree species in the Philippines, mostly belong to Dipterocarpaceae family. Planting of fruit trees were also suggested in the second year (Margraf and Milan, 1996). The scheme aims to restore one million hectares of rainforests by year 2020 using tree species native to a particular forest in the area (Rainforestation Primer, 2007).

1.4 Significance of the study

Land restoration in the tropics in the form of reforestation is commonly objected due to high evapotranspiration rates of the created stands which could lead to decrease in stream flows and ground water recharge (Bruijnzeel, 1997). In many cases of reforestation in the Philippines, empirical evidence is scarce on how these efforts affect the water and soil properties (Chokkalingam et al. 2006). Recent study in reforestation in Leyte revealed a significant variation in the water use depending on the species, tree size and biomass (Dierick and Hölscher, 2009).Their results suggested that species selection plays an important role in the control of water consumption in reforestation. Similar studies addressing more appropriate tree species selection and species mixtures are currently underway (Wishnie et al., 2007; Potvin and Dutilleul, 2009). An assessment of the functional diversity in such mixed stands for example on the basis of leaf traits appears relevant.

Characterization of reforestation species through their leaf traits and other related physiological parameters is crucial for the assessment of the systems´ecological functioning. Leaf traits lead to understanding the functional leaf ecology of species (Castro-Diez, et. al. 2000) and to predicting plant performance though their growth and survival (Poorter and Bongers 2006; Martinez-Garza et.al 2005) especially when planted to an early-successional environment like in most areas needing immediate restoration.

In this study, investigation was done on the leaf water conductance of the most common species used in reforestation in Leyte. Stomatal conductance (g_s) is a significant physiological parameter which provides the capacity of the species in terms of its rate of water turn over through its leaves. It is closely associated with the CO_2 assimilation rate (Farquhar and Sharkey, 1982). Juhrbandt et al. (2004) compiled a list of the maximal stomatal conductance (g_{smax}) rates of various tree species belonging to early and late successional groups from humid tropical forests. To my knowledge, this study is a pioneering work with respect to this topic in a reforestation setting in the Philippines. It is deemed necessary and timely to assess the relationship of these parameters to species which co-exists in a new course of restoring previously degraded areas. Results could serve as a baseline data for further research activities related to reforestation and forest management, in broadening the pool of species with known stomatal conductance rates and leaf traits and to recommend species combination to attain specific goal to restoration.

1.5 Research objectives

The general objective of this research was to assess rainforestation as a scheme to reforest degraded sites, in terms of the functional diversity of the co-occurring species. Specific objectives were outlined as follows:

(1) to assess the species-specific variation of leaf traits and in particular of maximal leaf stomatal conductance (g_{smax})

(2) to search for relationships between g_{smax} and tree variables i.e. tree architecture, leaf morphological and chemical traits

(3) to group species according to their distinct foliar traits.

CHAPTER 2

Methodology

2.1 Study site

This study was conducted on the island of Leyte, the eighth largest in the Philippines. It is located in Region 8, the Eastern Visayas region. The island consists of two provinces namely: Leyte and Southern Leyte which covers a total land area of about 750,000 hectares. The three reforestation sites were located in the lowlands adjacent to the Leyte Cordillera near the villages Marcos (10°45'55''N, 124°47'25''E), Patag (10°44'10''N, 124°48'16''E) and Cienda (10˚44' 16'' N, 124˚ 48'25'' E). The studied stands were no more than three kilometres distant from each other and near the Visayas State University (VSU) (Figure 1). Site selection was motivated by the proximity to Mt. Pangasugan as the nearby natural vegetation and being the early stands established using “rainforestation” approach to reforestation. At the time of the study, the three stands were 11 to 12 years old.

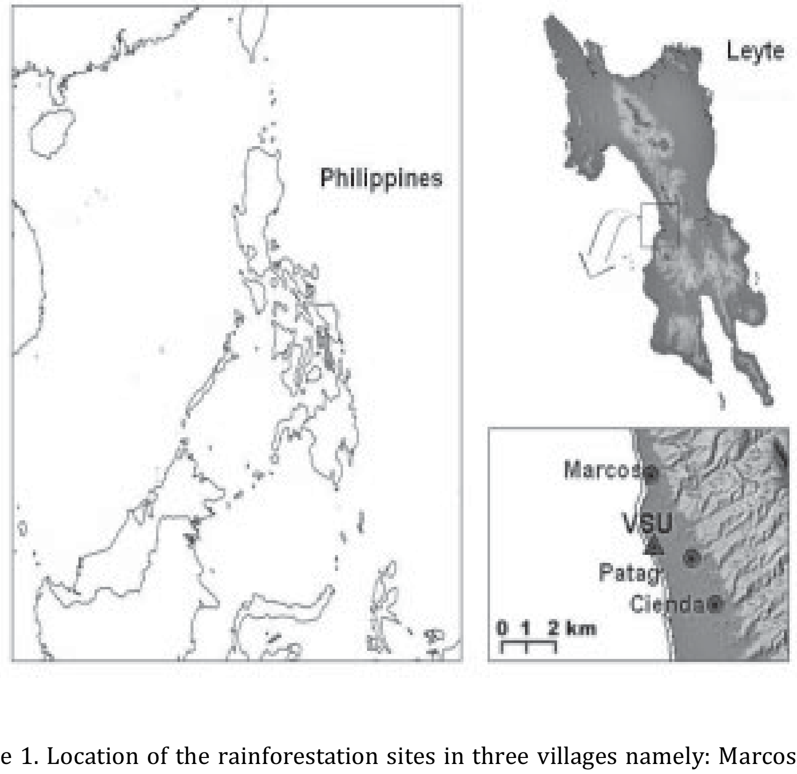

Figure 1. Location of the rainforestation sites in three villages namely: Marcos, Patag and Cienda on Leyte, Philippines. Map shows the proximity of the study sites to Visayas State University (VSU).

Leyte experiences two types of climate. In the east, climate is characterized by very pronounced rainfall from November to January, while the climate affecting the west is characterized by more or less evenly distributed rainfall throughout the year. Average rainfall in the region amounts to 2753 mm y^{-1} as measured at the nearby weather station in the Visayas State University (PAGASA, 2007) Average annual air temperature is 27.5 °C and no prolonged drought was observed during the study period and variation in precipitation regime was very little (Figure 2).

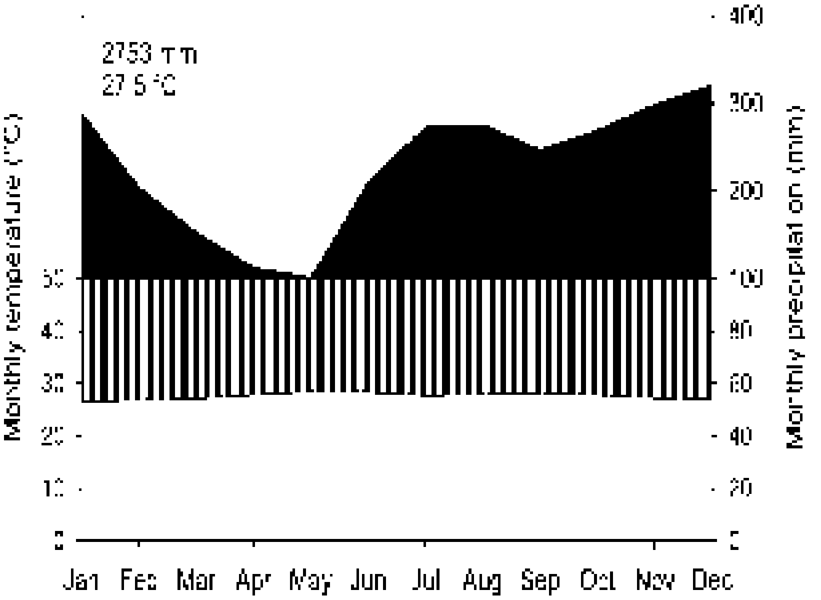

Figure 2. Climatic diagram showing the average annual precipitation and temperature in Leyte (PAGASA, 2007).

The area is described as a species-rich low land forest, where dipterocarps dominate the forest (ESSC, 1999). Only few undisturbed part of the forests are to be found on less accessible slopes of Leyte´s central cordillera (Langenberger, 2006). Land areas located at the foothills of Mt. Pangasugan which are more accessible were encroached and cleared with vegetation mostly through shifting cultivation and were converted to land uses particularly to agricultural and coconut stands. Reforestation plot in Barangay Marcos is owned by private individuals while stands in Cienda and Patag are owned and managed by community farmers association. These sites were found to be unproductive with grasses (*Saccahrum spontaneum* and *Imperata cylindrica*) dominating the understorey (Ceniza et.al 2004). After deforestation and intermittent cultivation of annual crops, coconut plantations were established. In a degraded state, the study sites were reforested following the rainforestation approach while maintaining the coconut present at the site.

The three study sites were found to have deeper rooting profile (Fischer, 2008). Fine root mass taken from the top centimetre of the soil was found to be high (49-74%) but decreasing with a decreasing depth from the floor (range, 528 g m^{-2} to 60 g m^{-2}). General overview of soil properties of the study sites including the pH, base saturation, cation exchange capacity and soil bulk density was described in details by Fischer (2008). Soils were found slightly acidic at 0 to 10 cm depth. Moreover, soils of the sites were developed from volcanic origin and were classified as Luvisol (Marcos), Cambisol (Patag) and Nitisol (Cienda) (Marohn, 2007). Nutrient supply ranged from moderate to high and C/N ratio ranged from 10.2 to 10.9 (Marohn, 2007). During the study, soil moisture was measured at 0 to 30 cm soil depth with a hand held time domain reflectometer or TDR probe (CS616, Campbell Scientific Inc., Logan, UT, USA), which was calibrated for local site conditions (Dierick and Hölscher, 2009). Soils were usually quite wet with an average soil moisture content of 52 percent (range: 43 to 68 percent).

Leaf area index (LAI, m^2) of the three stands was estimated from six hemispherical photos taken at regularly spaced locations within the plots. Photos were taken at low sun elevation using a digital camera (Coolpix 4500 and FC-E8 fisheye lens, Nikon Coop., Tokyo, Japan). The camera was positioned horizontally using a tripod with one meter distance from the ground. Analysis was done using the program CanEye version 4.1 (INRA, 2007). Analysis showed that minimal varability in LAI was observed from the three sites during the period of study (see Table).

Four nurseries located in the lowlands adjacent to the Leyte Cordillera, and near the campus of VSU were selected to study the leaf traits of seedlings. Three of these nurseries are managed by the staff of VSU namely: College of Forestry and Natural Resources nursery (CFNR), Institute of Tropical Ecology-Deutsche Gesselschaft für Technische Zusammenarbeit (ITE-GTZ) and Department of Horticulture (DOH). Another nursery is located in the nearby village Patag and is under operation through an organized farmers association.

2.2 Tree inventory and study species

A full inventory of trees with more than 7 cm dbh found in the each stand was conducted. Tree species identified in the sites belonged to 24 (Cienda), 28 (Marcos) and 17 (Patag) families (see Appendix tables 1 to 3). Most of the native pioneer species were initially planted in 2m x 2m spacing at the beginning of the site establishment. Shade tolerant species such as Dipterocarps and fruit trees were interplanted after the second year in between pioneers with the spacing of 1m x 1m (Margraf and Milan, 1996) (Figure 3). Fruit trees and crops were incorporated in the farm for the economic purpose of providing early income to the farmers.

Species which are commonly planted in reforestation sites were selected for this study (see Appendix tables 4 to 6). Species selection represented tree species belonging to different categories mentioned in the guidelines of rainforestation which are based on biogeographic origin, main use, and successional status (Margraf and Milan, 1996). Studied species were described in details in the respective chapters were they were selected for study. Important species which belong to Dipterocarpaceae namely: *Hopea malibato, Hopea plagata, Parashorea malaanonan, Shorea contorta* and *Shorea polysperma* were represented to study their leaf traits. A total of sixteen species were investigated in Chapter 3.

Figure 3. Mixed species reforestation site in Barangay Marcos. The area of the stand is less than one hectare but comprised of 50 tree species. Coconuts and pineapples were also present in the area.

Table on the site characteristics of the three rainforestation sites.

Site	Age (year)	Area (ha^{-1})	Elevation (m asl)	Slope (°)	Exposition	Tree stem density (n ha^{-1})	Tree species number	Tree basal area (m^2 ha^{-1})	LAI (m^2 m^{-2})
Cienda	11	1.0	50	0-5	-	1027	41	23.0	6.7
Patag	12	0.3	28	5-20	WNW	1503	30	26.4	6.0
Marcos	12	0.4	23	5-15	W	990	50	23.0	5.2

An additional two species were added to the 16 species studied in Chapter 3, these were *Myrica javanica* and *Melia dubia* making a total of 18 species with crown-exposed individuals. Eight more species with shaded crowns namely: *Dipterocarpus kerrii*, *Dracontomelon dao*, *Annona muricata*, *Pterocarpus indicus*, *Garcinia mangostana*, *Artocarpus heterophylla*, *Theobroma cacao* and *Vitex turczaninowii* were included in the list, summing 26 species studied for one chapter (Chapter 4).

The fifth chapter focused on the investigation of leaf traits of 25 species in their seedling stage. They were grown in polybags in the nursery. List of species are found in table 1 of this chapter.

2.3 Field set up and porometry

Mature and healthy leaves of individual trees per species were studied. Access to the sun-exposed crown of the study trees was provided by movable bamboo towers (Figures 4a and 4b). Stomatal conductance (g_s) was measured with a Delta-T Porometer Type AP4 (Delta-T Devices Ltd., Cambridge, England, UK) to determine the rate of water loss from plant leaves through their stomata (Figure 5a). The equipment was calibrated prior to g_s measurement. This was done by using a calibration plate wetted with distilled water and allowed to stabilize in a plastic envelope for an hour prior to the calibration in the field (AP4 Porometer manual, 2004). Relative humidity was set in the porometer according to the prevailing condition in the field during time of measurement. In cases like the occurrence of rain, postponement of data collection until the onset of the normal weather condition in the area was done.

Each of the leaf was labeled to make sure that the same leaves were monitored throughout the measurement period (Figure 5b). Diurnal measurements were conducted in an hourly interval in the morning when the dew had completely evaporated around 9:00 am and until late afternoon at 3:00 pm before the rain occurs, mostly in the afternoon. Other parameters such as leaf temperature and average photosynthetically active photon flux density were also recorded in the porometer. Measurements of g_s in seedlings in the nurseries were a lot easier than adult trees in the field.

Figure 4 (a) Bamboo tower to access sun-exposed leaves from the upper canopy of trees.
(b) Stomatal conductance measurement on sunlit leaves of tree species during sunny days.

Figure 5 (a) Delta-T Porometer type AP4 (Delta-T Devices Ltd., Cambridge, England, UK) (b) Stomatal conductance measurement on mature leaves of *Artocarpus heterophylla* in the nursery. Measurements were taken from the widest width of the leaf approximately 1-2 cm from the leaf edge.

2.4 Leaf morphological and chemical traits measurements

Fully expanded mature leaves of all species were collected as samples to ensure stable leaf traits. To ensure that leaf age is not variable within and across species, leaves of the individual trees were sampled from different branches just behind the new leaves to select for similar leaf ages. In cases of species with compound leaves, one leaflet at the same position was sampled (see Appendix figures). Morphological leaf traits of collected leaves were measured including the leaf size, specific leaf area, and width to length ratio. Fresh leaves samples were scanned and analyzed using Winfolia software (Winfolia 2004a). After measurement, leaves were oven-dried at 70°C for 48 hours and were weighed with a precision balance. The specific leaf area (SLA, m^2 kg^{-1}) was calculated as the leaf blade area divided by the leaf dry mass. Dried leaf samples were ground into a fine powder using a plant sample mill for the carbon isotope signature (δ^{13} C) and leaf nitrogen content determination (Figure 6). Samples were analyzed for mass spectroscopy at the Centre for Stable Isotope Research, University of Göttingen.

Figure 6. Dried leaves samples were prepared for chemical analysis. Carbon, nitrogen and stable carbon isotopes in the leaves were analyzed at the Center for Stable Isopes, University of Göttingen.

CHAPTER 3

Variability and grouping of leaf traits in 16 species, including maximal stomatal conductance

Introduction

In the tropics, natural rainforests are mostly highly diverse in tree species and also comprise a substantial functional variability. In contrast, current conventional reforestation primarily relies on few species commonly planted in monospecific stands. Such stands contribute little to ecological functioning and to conservation of biodiversity (Lamb et al., 2005). Thus, studies addressing more appropriate tree species selection and species mixtures are currently underway (Wishnie et al., 2007; Potvin and Dutilleul, 2009). An assessment of the functional diversity in such mixed stands for example on the basis of leaf traits appears topical.

Forests and their trees play an important role in the exchange of water vapour with the atmosphere through leaves and stomates. Leaf stomatal conductance (g_s) has for example been used to estimate stand transpirational water loss and to delineate differences among species (Khamzina et al., 2009). Maximal leaf stomatal conductances (g_{smax}) of sun leaves of tropical tree species varies widely and there is much evidence that early and late successional species differ in leaf traits (Bazzaz, 1991; Strauss-Debenedetti and Bazzaz, 1996, Juhrbandt et al., 2004). Based on a worldwide analysis of leaf trait data, Wright et al. (2004) described a universal spectrum of leaf traits that runs from quick to slow return of invested resources and works independently of plant functional types. Thus, relatively easy to assess leaf traits, such as specific leaf area, leaf size per leaf dry weight (SLA, m^2 kg^{-1}) may be used to predict other functional leaf traits such as stomatal conductance. Also plant performance, for example, growth and survival, may be predicted based on leaf traits. This was apparent from a study on 53 rainforest species in Bolivia by Poorter and Bongers (2006). They found a high variability in leaf traits and demonstrated that, for example, species with short-lived, physiologically active leaves have high growth but low survival rates, thus illustrating that leaf traits can be used to predict plant performance. Another important trait that can be measured from the leaves of various species is the stable carbon isotope signature ($\delta^{13}C$). Leaf $\delta^{13}C$ allows the assessment of the functional diversity and ecophysiological differences among the co-occurring species in given stand (Bonal et al., 2000, Guehl et al., 1998).

The Philippines are very important biodiversity hotspots of the world with a large share of endemic species (Myers et al., 2000). On Leyte, Philippines, a multi-species reforestation scheme, the so called rainforestation, was developed and implemented. This scheme emphasizes the use of native species and, combines early and late successional species, planted in mixed stands with fruit trees (Margraf and Milan, 1996). This approach to reforestation in the Philippines is considered promising and future extensions are planned. However, as in many other regions of the tropics, species-specific information on life history and other ecological characteristics of many of the native species is presently not available. From the existing data from various biomes, Reich et al. (1999) found that leaf traits suggest which successional position certain species may occupy (i.e. early or late succession). Species for example with high SLA, high leaf nitrogen content and short leaf life span are more likely to be classified as early successional species which occupy high light microsites and performs fast growth rate. This could serve as a guide to assess species with unknown successional classification.

In three of such rainforestation stands, we measured the maximal stomatal conductance (g_{smax}) and morphological and chemical leaf traits of 16 tree species. The objectives of the study were: (1) to assess the species-specific variation of leaf traits and in particular of maximal leaf stomatal conductance (g_{smax}), (2) to search for relationships between g_{smax} and other tree variables, and (3) to assess whether leaf traits group the species studied. The results may help to learn more about ecological characteristics of the involved tree species and to assess the degree of functional diversity created in rainforestation.

Methods

Study site

Three rainforestation stands were selected for this study (see Figure 1, Chapter 2 Methodology). The stands were small (0.3 to 1 ha) but comprised of an impressive number of tree species (30 to 50 species per stand) (see Appendix tables 4 to 6). At the time of the study, the three stands were 11 to 12 years old (Table in Chapter1). The soils developed from volcanic parent material and were slightly acidic with a pH (KCl) at 0 to 10 cm depth of 4.9 in Cienda, 4.1 in Patag and 4.3 in Marcos (C. Fischer, pers. comm., 2008). Nutrient supply in the soil ranged from moderate to high and C/N ratio ranged from 10.2 to 10.9 (Marohn, 2007).

For this chapter, we selected sixteen tree species belonging to nine families. Species selection was guided by the requirement for five tree individuals per species with well-exposed crowns for sun leaves measurement. We further wanted to represent trees from the different categories mentioned in the guidelines of rainforestation based on their biogeographic origin, main use, and successional status (Margraf and Milan, 1996). Five of the selected species belonged to the family Dipterocarpaceae, (*Hopea malibato* Foxw., *Hopea plagata* S. Vidal, *Parashorea malaanonan* Merr.*, Shorea contorta* S.Vidal*, Shorea polysperma* Merr.*)*, three to Meliaceae (*Lansium domesticum* Corr. *, Sandoricum koetjape* Merr.*, Swietenia macrophylla* King), two to Moraceae (*Artocarpus blancoi* Merr., *Artocarpus odoratissimus* Blanco), two to Verbenaceae (*Gmelina arborea* Roxb.*, Vitex parviflora* A. Juss.), one to Combretaceae (*Terminalia microcarpa* Decne.), one to Guttiferae (*Calophyllum blancoi* Pl. and Tr.) and one to Sapindaceae (*Nephelium lappaceum* L.)*.* Eleven species were considered native to the region, while five were exotic, wherein three are domesticated fruit trees. The major uses of these species are listed in Table 1. Most of them have high value timber for construction (nine species); some are fruit trees (five species) or are favoured for furniture-making (two species). Most species, particularly dipterocarps, were listed as late successional species; while *C. blancoi, T. microcarpa* and *V. parviflora* were classified as early successional species according to Margraf and Milan (1996).). In addition, *S. macrophylla* also occupies the latter successional position (Whitmore, 1996) and *G. arborea* is a light-demanding species. The five fruit tree species were classified as shade-tolerant at least in their early stage of development (Margraf and Milan, 1996). *A. blancoi* has an intermediate successional position (E. Fernando, pers.comm. 2007). All the dipterocarp species and *A. blancoi* are classified as critically endangered and are threatened to habitat loss (IUCN, 2009).

Table 1. Characteristics of the sixteen species studied in mixed reforestation stands. Tree architecture included total height, diameter at breast height (dbh) and crown projection area (CPA). Mean with standard deviation values in parentheses are per species, n = 5. Significant differences are indicated by different letters (analysis of variance, $p < 0.05$).

Species	Species code	Family	Study sites	Native or Exotic	Main uses	height	dbh	CPA
						(m)	(cm)	(m^2)
Hopea malibato Foxw.	Hm	Dipterocarpaceae	Patag	Native	All purpose*	8.2 (1.4)^{ab}	10.4 (3.0)^{bcd}	15.9 (5.8) ^{abcd}
Hopea plagata S.Vidal	Hp	Dipterocarpaceae	Patag	Native	All purpose	7.1 (1.0)^{b}	7.0 (0.5)^{d}	7.4 (1.4) ^{d}
Parashorea malaanonan Merr.	Pm	Dipterocarpaceae	Cienda	Native	All purpose	10.0 (1.2)^{ab}	10.1 (2.0)^{bcd}	9.3 (3.1) ^{d}
Shorea contorta S.Vidal	Sc	Dipterocarpaceae	Cienda	Native	All purpose	10.0 (1.7)^{ab}	9.6 (1.7)^{cd}	6.6 (2.5) ^{d}
Shorea polsyperma Merr.	Sp	Dipterocarpaceae	Patag	Native	All purpose	8.5 (1.0)^{ab}	10.6 (3.4)^{bcd}	11.6 (4.3) ^{bcd}
Lansium domesticum Corr.	Ld	Meliaceae	Marcos	Native	Fruit	8.4 (0.5)^{ab}	10.7 (3.0)^{bcd}	12.0 (7.2) ^{bcd}
Sandoricum koetjape Merr.	Sk	Meliaceae	Marcos	Native	Fruit	11.5 (2.2)^{a}	24.8 (4.6)^{a}	29.5 (7.6) ^{abc}
Swietenia macrophylla King	Sm	Meliaceae	Patag	Exotic	All purpose	8.5 (1.5)^{ab}	11.2 (2.2)^{bcd}	10.5 (4.6) ^{cd}
Artocarpus blancoi Merr.	Ab	Moraceae	Patag	Native	All purpose	9.2 (3.7)^{ab}	17.0 (9.4)^{abcd}	20.9 (16.7) ^{abcd}
Artocarpus odoratissimus Blanco	Ao	Moraceae	Marcos	Exotic	Fruit	10.9 (1.7)^{ab}	20.5 (5.1)^{abc}	36.8 (12.1) ^{a}
Gmelina arborea Roxb.	Ga	Verbenaceae	Marcos	Exotic	light construction	10.6 (3.0)^{ab}	25.1 (11.4)^{a}	30.9 (12.6) ^{abc}
Vitex parviflora A. Juss.	Vp	Verbenaceae	Marcos	Native	All purpose	11.1 (0.9)^{ab}	21.7 (3.8)^{ab}	37.4 (18.2) ^{a}
Durio zibethinus L.	Dz	Bombacaceae	Marcos	Exotic	Fruit	10.9 (1.2)^{ab}	18.4 (8.5)^{abcd}	36.7 (28.6) ^{ab}
Terminalia microcarpa Decne.	Tm	Combretaceae	Cienda	Native	light construction	10.2 (1.9)^{ab}	12.7 (4.3)^{bcd}	20.6 (15.2) ^{abcd}
Calophyllum blancoi Pl. and Tr.	Cb	Guttiferae	Cienda	Native	All purpose	9.5 (1.1)^{ab}	11.3 (1.5)^{bcd}	10.8 (2.6) ^{bcd}
Nephelium lappaceum L.	Nl	Sapindaceae	Marcos	Exotic	Fruit	10.2 (1.8)^{ab}	17.8 (4.6)^{abcd}	43.0 (19.1) ^{a}
Mean						**9.7 (1.3)**	**14.9 (5.8)**	**21.2 (12.5)**

*use as general construction material

Most of the species studied have simple leaves while *L. domesticum*, *N. lappaceum* and *S. macrophylla* have compound leaves. Leaf shapes vary from oblong, elliptic, obtuse, lanceolate and acuminate. A few species, such as *G. arborea, S. koetjape* and *T. microcarpa,* possess pubescent leaves, and most have glabrous to shiny leaves. Leaves of *A. odoratissimus* have a distinct sandy-like texture on top and are hairy at the underside, with hairs extending up to the petioles.

Stomatal conductance of leaves

Five individual trees per species and ten fully expanded sunlit leaves per individual tree were studied. Leaflets were considered as samples for species with compound leaves. Species with pinnate leaves were *L. domesticum*, *N. lappaceum* and *S. macrophylla*, with trifoliate leaves, *S. koetjape* and *V. parviflora*, and with closely alternate leaves (*T. microcarpa*). Ten leaflets from these specific leaf arrangements were taken per tree per species. Access to the sun crown of the study trees was provided by movable bamboo towers. Stomatal conductance was measured on the lower leaf side using a Delta-T Porometer type AP4 (Delta-T Devices Ltd., Cambridge, England, UK). Prior to g_s measurement in the field, the porometer was calibrated with a calibration plate wetted with distilled water (AP4 Porometer manual, 2004). Diurnal courses of g_s were measured on sunny days. Measurements were taken at hourly intervals, starting in the morning when the dew had completely evaporated, around 9:00 am, until 3:00 pm before the usual afternoon rain occurs. The average leaf temperature during the study days was 31°C and average photosynthetically active photon flux density was 878 µmol m^{-2} s^{-1}. Soil moisture was measured at 0 to 30 cm soil depth with a hand held time domain reflectometer or TDR probe (CS616, Campbell Scientific Inc., Logan, UT, USA), which was calibrated for local site conditions (Dierick and Hölscher, 2009). Soils were usually quite wet with an average soil moisture content of 52 percent (range: 43 to 68 percent).

Tree architecture

Diameter at breast height (1.3 m, dbh) was measured using a diameter tape. Tree heights were assessed using an Abney-hand level or a standard meter stick, 3 meters long. The crown projection area (CPA, m^2) was calculated from the canopy extension measured in four cardinal directions. The CPA was computed by summing the area from the four quadrants using a standard equation for a quarter ellipse (Pi*x*y/4) centred at the origin.

Leaf morphological and chemical traits

Ten sun leaves per tree from five individuals per species were taken. Fresh leaves were scanned and the leaf size and width to length ratio (WLR) of the sample leaves or leaflets were analyzed from the images using Winfolia software (Winfolia, 2004a). The leaves were then oven-dried at 70°C for 48 hours for dry weight determination. The specific leaf area (SLA, $m^2\ kg^{-1}$) was calculated as the leaf size divided by the leaf dry mass. The dried leaves were ground into a fine powder using a plant sample mill and analyzed in five replicates per species for stable carbon isotope signature ($\delta^{13}C$) and leaf nitrogen content. The $\delta^{13}C$ was determined with a gas isotope mass spectrometer (Delta Plus, Finnigan MAT, Bremen, Germany) and results were reported in parts per thousand (‰) referring them to the international standard (Pee Dee Belemnite). Leaf nitrogen content was determined with an elementar analyser (NA 2500, CE-Instruments, Rodano, Milano, Italy). All chemical analyses were done at the Centre for Stable Isotope Research, University of Göttingen.

Data analysis

Descriptive statistics including the mean and standard deviation of measured tree variables were computed from five individual trees per species. To determine the species-specific g_{smax}, we selected the daily maxima of g_s ($g_s$high) for the 10 leaves measured per tree and calculated the species average of $g_s$high from the five tree individuals per species. Tree species variables were tested for normal distribution using the Shapiro-Wilk test. Data not normally distributed was log-transformed prior to statistical analysis. The relationship between g_{smax}, tree architecture and leaf traits was analyzed using simple and multiple linear regressions. One-way analysis of variance (ANOVA) was applied to test for significant differences among the 16 species and a post-hoc Honest Significant Differences (HSD) Tukey´s test was used to assign species to statistically different groups. The significance level was set at $p \leq 0.05$. Multivariate association of leaf traits (g_{smax}, leaf size, WLR, SLA, $\delta^{13}C$ and leaf nitrogen content) was analyzed with a principal component analysis (PCA) based on a correlation matrix. Species-specific leaf trait values used for PCA were standardized prior to analysis. Most calculations were performed with the R Programming Software version 2.7.1 (2008), while for the multivariate analysis PC-ORD version 5.12 (2006) was used.

Results

Leaf traits

The g_{smax} varied significantly among the species by a factor of five (165 to 772 mmol m^{-2} s^{-1}, Figure 1). The highest g_{smax} was found in *A. blancoi* whereas low values were observed for dipterocarp species, *S. contorta* and *H. malibato* in particular.

The mean size of exposed sun leaves showed significant differences among the species with *A. blancoi* having the largest leaf size (763 cm^2) and *H. malibato* the smallest (17 cm^2) (Table 2). The SLA of sun exposed leaves also varied significantly from 9.2 m^2 kg^{-1} (*L. domesticum*) to 17.5 m^2 kg^{-1} (*G. arborea*). A significant difference in $\delta^{13}C$ species belonging to the Dipterocarpaceae was found and were more depleted in $\delta^{13}C$ (-33.2 to -31.2‰) when compared to *A. blancoi* and *G. arborea* species with less negative values (more enriched in $\delta^{13}C$) (-28.7‰) (Table 2). Leaf nitrogen content per unit area (N_{area}) and per unit mass (N_{mass}) among the species studied varied by twofold range.

Correlations between leaf traits, tree variable and g_{smax}

A weak, but significant relationship was found between g_{smax} and dbh of the species studied ($r^2 = 0.25$, $p = 0.05$, $n = 16$, Table 3). No relationship was found between tree architectural variables such as height and CPA. A significant positive relationship was obtained between g_{smax} and log-transformed leaf size ($r^2 = 0.40$, $p = 0.01$, $n = 15$), when *A. odoratissimus* was excluded from the analysis due to its hairy leaf characteristics. Over all species, no significant relationship was found between SLA and leaf nitrogen concentration and g_{smax}. However, a separate analysis for dipterocarp species on the g_{smax} and SLA showed a highly significant inverse relationship result ($r^2 = 0.96$, $p < 0.01$, $n = 5$).

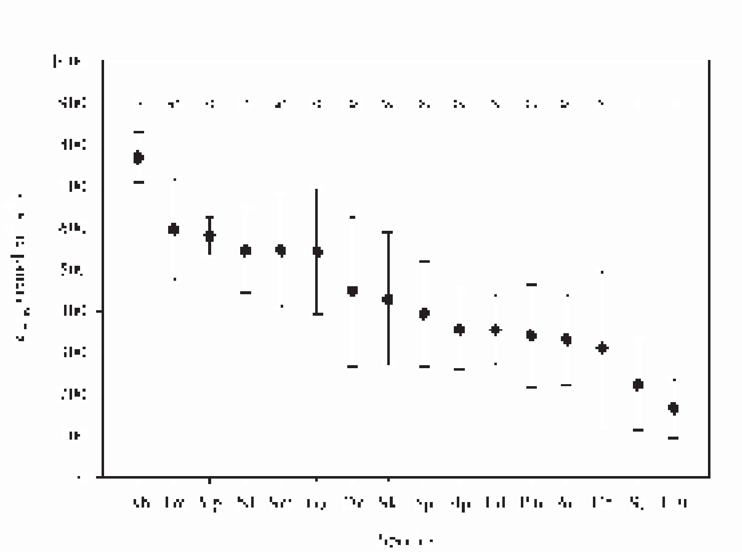

Figure 1. Maximal stomatal conductance (g_{smax}) of sixteen species studied. Means are shown with standard deviations given by vertical bars. Significantly different means are indicated by different letters (analysis of variance, $p < 0.05$, $n = 5$). Species abbreviations are found in Table 1.

Table 2. Maximum stomatal conductance (g_{smax}) and leaf morphological and chemical traits of the sun leaves in the sixteen species studied. Full names of species are listed in Table 1. Means with standard deviations in parentheses are given per species. Significantly different means are indicated by different letters (analysis of variance, $p < 0.05$, $n = 5$).

Species code	g_{smax} (mmol m^{-2} s^{-1})	Leaf size (cm^2)	Leaf length (cm)	Leaf width (cm)	WLR (cm cm^{-1})	SLA (m^2 kg^{-1})	N_{mass} (g kg^{-1})	N_{area} (g m^{-2})	$\delta^{13}C$ (‰)
Hm	165.2 (70.7) ^{d}	16.5 (5.1) ^{g}	7.8 (1.1) ^{c}	3.6 (0.6) ^{d}	0.46 (0.04) ^{cde}	14.8 (1.5) ^{abc}	18.6 (1.7) ^{bcd}	1.9 (0.2) ^{bcd}	-31.4 (1.4) ^{bc}
Hp	355.6 (97.3) ^{abcd}	49.2 (9.0) ^{ef}	12.2 (1.0) ^{c}	6.3 (0.7) ^{cd}	0.51 (0.02) ^{bcd}	10.8 (0.8) ^{defg}	15.6 (1.1) ^{de}	1.6 (0.1) ^{de}	-33.2 (0.4) ^{c}
Pm	339.1 (124.2) ^{bcd}	76.9 (18.1) ^{de}	15.6 (1.8) ^{c}	7.7 (1.1) ^{cd}	0.50 (0.06) ^{bcd}	12.0 (1.4) ^{cdefg}	20.4 (1.9) ^{bc}	2.0 (0.2) ^{bc}	-31.2 (0.5) ^{bc}
Sc	222.6 (110.8) ^{cd}	59.7 (4.9) ^{def}	17.4 (0.9) ^{c}	7.6 (2.4) ^{cd}	0.44 (0.02) ^{cde}	14.4 (1.9) ^{abcde}	18.4 (0.5) ^{bcd}	1.8 (0.1) ^{bcd}	-31.3 (0.7) ^{bc}
Sp	393.0 (126.1) ^{abc}	66.7 (6.2) ^{def}	16.2 (0.7) ^{c}	6.5 (0.5) ^{cd}	0.39 (0.03) ^{ef}	10.4 (0.9) ^{efg}	17.8 (0.8) ^{cde}	1.8 (0.1) ^{cde}	-31.8 (1.0) ^{bc}
Ld	354.6 (86.2) ^{abc}	94.8 (20.2) ^{cd}	17.7 (2.4) ^{c}	7.7 (0.7) ^{cd}	0.44 (0.06) ^{cde}	9.2 (1.3) ^{g}	23.4 (2.5) ^{ab}	2.3 (0.3) ^{ab}	-31.4 (0.4) ^{bc}
Sk	428.5 (160.9) ^{abc}	159.1 (18.3) ^{c}	23.8 (1.2) ^{bc}	12.3 (0.9) ^{cd}	0.52 (0.03) ^{bc}	13.9 (1.0) ^{abcdef}	19.4 (2.2)^{bcd}	1.9 (0.2) ^{bcd}	-30.7 (2.4) ^{ab}
Sm	544.7 (137.4) ^{ab}	77.2 (13.6) ^{de}	17.9 (1.5) ^{c}	6.4 (0.6) ^{cd}	0.36 (0.01) ^{fg}	16.3 (3.1) ^{ab}	19.0 (3.7) ^{bcd}	1.9 (0.4) ^{bcd}	-30.4 (0.5) ^{ab}
Ab	772.1 (63.3) ^{a}	762.9 (494.3) ^{a}	36.0 (7.4) ^{a}	27.1 (8.0) ^{a}	0.74 (0.08) ^{a}	10.1 (0.9) ^{fg}	20.4 (1.8) ^{bc}	2.0 (0.2) ^{bc}	-28.7 (0.7) ^{a}
Ao	329.8 (108.5) ^{bcd}	601.0 (156.8) ^{a}	34.6 (2.2) ^{b}	23.7 (2.1) ^{ab}	0.67 (0.08) ^{a}	10.1 (1.2) ^{fg}	18.2 (1.9) ^{cde}	1.8 (0.2) ^{cde}	-30.8 (1.0) ^{ab}
Ga	542.7 (150.1) ^{ab}	291.3 (48.2) ^{b}	24.0 (3.3) ^{bc}	13.2 (1.6) ^{bc}	0.55 (0.06) ^{b}	17.5 (1.8) ^{a}	26.4 (4.2) ^{a}	2.6 (0.4) ^{a}	-28.7 (0.9) ^{a}
Vp	580.3 (46.9) ^{ab}	51.2 (12.7) ^{ef}	13.9 (1.3) ^{c}	5.7 (0.8) ^{cd}	0.41 (0.03) ^{def}	11.0 (1.4) ^{cdefg}	18.2 (2.2) ^{cde}	1.8 (0.2) ^{cde}	-30.9 (1.5) ^{abc}
Dz	446.9 (180.7) ^{abc}	83.7 (27.6) ^{de}	19.9 (2.4) ^{c}	6.2 (1.2) ^{cd}	0.31 (0.03) ^{g}	12.1 (3.1) ^{cdefg}	19.4 (2.5) ^{bcd}	1.9 (0.3) ^{bcd}	-32.5 (1.2) ^{bc}
Tm	595.4 (122.5) ^{ab}	39.3 (3.9) ^{f}	13.3 (0.5) ^{c}	5.0 (0.3) ^{cd}	0.38 (0.01) ^{ef}	14.6 (2.9) ^{abcd}	22.0 (1.6) ^{abc}	2.2 (0.2) ^{abc}	-30.6 (0.9) ^{ab}
Cb	309.4 (187.8) ^{abcd}	17.7 (1.5) ^{g}	10.0 (0.4) ^{c}	3.0 (0.1) ^{d}	0.29 (0.01) ^{g}	12.3 (1.8) ^{bcdefg}	14.4 (0.9) ^{e}	1.4 (0.1) ^{e}	-31.6 (0.7) ^{bc}
Nl	545.1 (103.6) ^{ab}	69.1 (6.8) ^{de}	14.2 (0.9) ^{c}	6.9 (0.2) ^{cd}	0.49 (0.02) ^{bcd}	10.0 (1.3) ^{fg}	19.0 (1.6) ^{bcd}	1.9 (0.2) ^{bcd}	-31.6 (0.6) ^{bc}
Mean	**432.6 (150.4)**	**157.3 (150.4)**	**18.4 (7.9)**	**9.3 (6.8)**	**0.47 (0.12)**	**12.5 (2.4)**	**19.4 (2.8)**	**1.9 (0.3)**	**-31.1 (1.2)**
Min	**165.2**	**16.5**	**7.8**	**3.0**	**0.29**	**9.2**	**14.4**	**1.4**	**-33.2**
Max	**772.1**	**762.9**	**36.0**	**27.1**	**0.74**	**17.5**	**26.4**	**2.6**	**-28.7**

Data shown in abbreviations are width to length ratio (WLR), specific leaf area (SLA), leaf nitrogen content per unit leaf mass (N_{mass}), leaf nitrogen content per unit leaf area (N_{area}), stable carbon isotope ratio ($\delta^{13}C$).

Table 3. Linear regression analysis between maximum stomatal conductance g_{smax} (in mmol m^{-2} s^{-1}) and tree variables (tree height, diameter at breast height (dbh), crown projection area (CPA)), leaf traits (leaf size, width to length ratio (WLR), specific leaf area (SLA), leaf nitrogen content per area basis (N_{area}) and stable carbon isotope signature ($\delta^{13}C$)). Significant relationships ($p < 0.05$, n = 16) are indicated in bold.

Variables	Unit	r^2	p
height	m	0.06	0.36
dbh	cm	**0.25**	**0.05**
CPA	m^2	0.22	0.06
leaf size	cm^2	0.23	0.06*
WLR	cm cm^{-1}	0.02	0.59
SLA	m^2 kg^{-1}	0.00	0.88
N_{area}	g m^{-2}	0.12	0.18
$\delta^{13}C$	‰	**0.33**	**0.02**

A multiple linear regression analysis with leaf size and tree height as independent variables explained 57 percent of the variation in g_{smax} (p = 0.01, n = 16). A significant result was also found with the combination of leaf size and CPA, which explained 55 percent of the variation of g_{smax} (p = 0.02, n = 16).

Coordination of leaf traits

Results of the principal component analysis (PCA) showed a high percentage of explained variance (75 percent) among the tested variables from all the species studied. The first and second principal component axes (PCA 1 and PCA 2) explained 49 and 26 percent of the total variance of leaf traits, respectively (Figure 2a). Higher loadings along PCA 1 indicated species which are more depleted in $\delta^{13}C$, with low leaf size and low leaf width to length ratio (WLR), while higher loadings on PCA 2 indicated species with higher specific leaf area (SLA) and higher leaf nitrogen content per area basis (N_{area}). Most species were closely associated with high scores on PCA 1 or more depleted in $\delta^{13}C$, small leaf sizes and low WLR (e.g., *H. malibato*, *H. plagata*, *S. contorta, S. polysperma, C. blancoi* and *D. zibethinus*) (Figure 2b). *A. blancoi, A. odoratissimus* and *G. arborea* however showed low scores on PCA 1 and thus reflect that they are more enriched in $\delta^{13}C$, with big leaf size and high WLR. High scores on PC 2 for *G. arborea, S. macrophylla* and *T. microcarpa* reflected high SLA and high N_{area} of these species. The two *Artocarpus* species (*A. blancoi* and *A. odoratissimus)* however were both separated by their distinct characteristics of having low SLA and low N_{area} (PCA 2). The g_{smax} as one of the variables used was more reflected on the third axis of the PCA however we found less variance (12%) in this axis.

Discussion

The species-specific variability in maximal stomatal conductance in the studied reforestation stands (165 to 772 mmol m^{-2} s^{-1}) was considerably high but on the higher and the lower side less than revealed in an earlier literature review covering trees from very different locations and life histories (Juhrbandt et al., 2004). For a given site in Indonesia, in co-occurring early successional species in secondary forests g_{smax} values between 393 and 734 mmol m^{-2} s^{-1} were found; in near-by natural old-growth forests variability was more pronounced and also very low values were reported (68 to 583 mmol m^{-2} s^{-1}) (Hölscher et al., 2006). The highest g_{smax} in our study was recorded for *A. blancoi*, which has a large leaf size (763 cm^2) and is considered as an intermediate species (species in between early and late succession, E. Fernando, pers. comm., 2008). This species has a lobed leaf shape, formed with a deeply indented margin that probably prevents a thick continuous boundary layer that is common to large leaves (Stokes et al., 2006; Grace, 1983). Such interrupted boundary layer may allow the leaf to absorb more CO_2 or release more water from the stomata, which may explain high g_{smax} values obtained in *A. blancoi*, despite its large leaves. On the other hand, *A. odoratissimus*, another species with large leaves (601 cm^2) exhibited an intermediate g_{smax}, which can be attributed to an intact boundary layer and the presence of hairs on the abaxial surface of the leaf. One of the physiological roles of leaf hairs is to reduce the boundary layer conductance and protect the plant against excessive transpiration from the stomata (Wuenscher, 1970; Schreuder et al., 2001). Leaf hairs also enhance water use efficiency, especially in dry conditions as often experienced by trees subjected to high midday vapour pressure deficits in degraded tropical secondary forest (Kenzo et al., 2008).

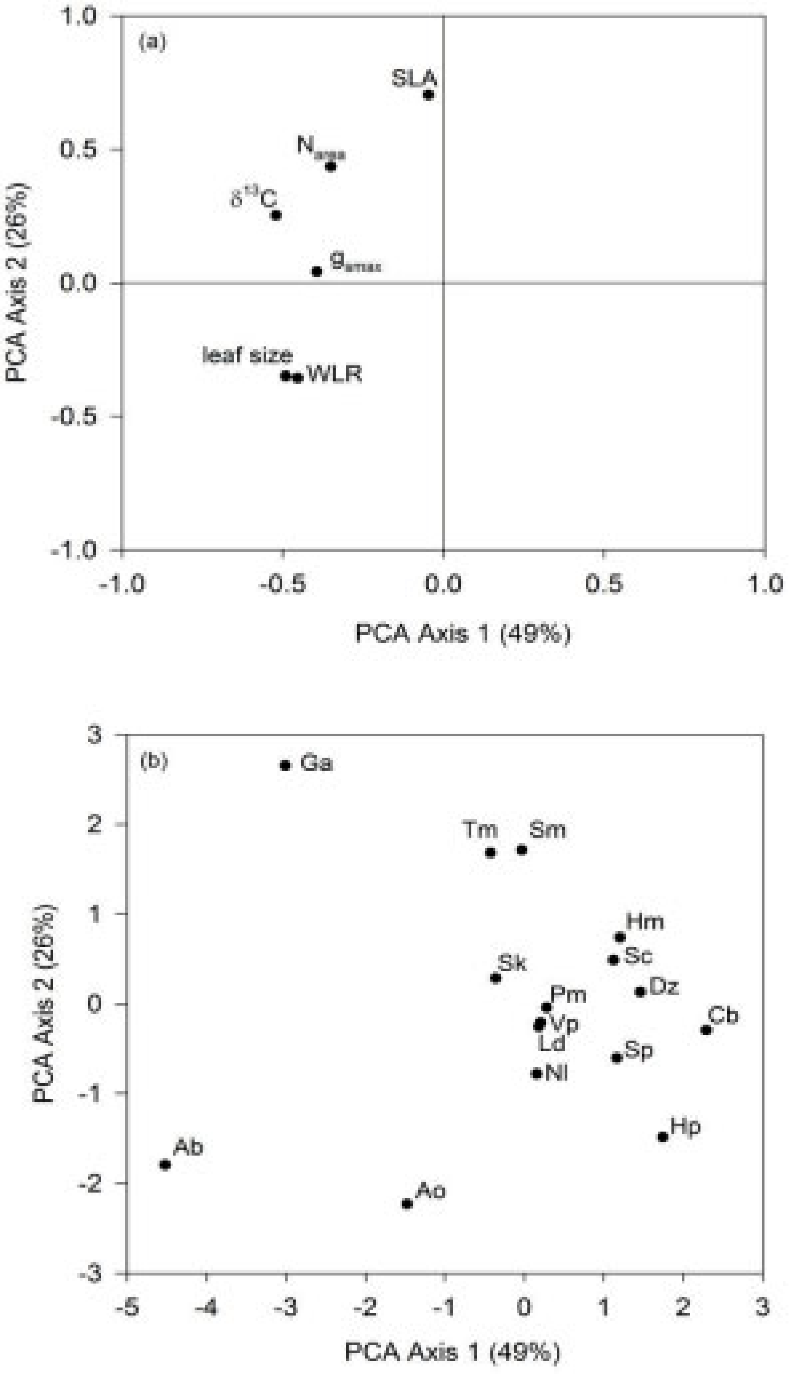

Figure 2. Principal component analysis of six leaf traits of sixteen species studied. (a) Loading plots for the PCA 1 (explained variation is 49 percent) and PCA 2 (explained variation is 26 percent). (b) Species loadings on the first and second axes. Leaf traits and species abbreviations are found in Tables 1 and 2.

Our study showed a positive relationship between log- transformed values of leaf sizes and g_{smax}, if the hairy-leafed species *A. odoratissimus* is excluded from the analysis. This relationship is opposite to the findings on eight early-successional tree species from Indonesia, where leaf sizes were negatively correlated with g_{smax} (Juhrbandt et al., 2004). The relationship leaf size to g_{smax} found in our data was strongly influenced by the large leaf size and special features of the two *Artocarpus* species. We found no significant correlation at all when both species were excluded. We therefore suggest that, although the relationship leaf size to boundary layer conductance is quite clear, that there was no general relationship because other leaf traits such as leaf shape and hairiness also have a strong influence.

In the rainforestation stands, a significant relationship was found between log-transformed dbh and g_{smax} of the co-occurring trees but the explained variance was low. Investigations made by Andrade et al. (1998) on the whole-tree water use from five tree species growing in a Panamanian seasonal forest revealed that the differences in g_s of these species was closely associated with the variation in the leaf area-specific total hydraulic conductance of the soil/leaf pathway. Their findings also suggested that differences in stomatal regulation of transpiration on a leaf area basis seemed to be controlled by tree size and hydraulic architectural features (i.e. leaf area, sapwood area) rather than physiological traits that affect the sensitiveness of stomata. Although we could not provide a better comparison using our data as we did not investigate the sapwood area of the species studied. The variation in g_{smax} along with the differences in tree size was indeed reflected in the mixture of the species grown in rainforestations. Studied dipterocarps which had lower g_{smax} values could have lower CO_2 assimilation and relatively lower growth rate compare to big diameter and fast-growing species (e.g. *G. arborea* and *A. blancoi*).

In dipterocarp species from rainforestation sites on Leyte, wood anatomical trait like vessel diameter in particular, was correlated with the stem hydraulic conductivity (k_s) (Rana et al., 2008). A recent study from China documented a linkage between k_s and vessel diameter and other leaf structural and functional traits including g_s in dipterocarps (Zhang and Cao, 2009). Thus, lower g_{smax} of dipterocarp species from our study, along with their low dbh, may be related to a lower k_s among the species in this group.

No significant correlation was found between g_{smax} and SLA from all the species studied. A strong inverse relationship however was found among dipterocarps species with SLA as predictor variable to g_{smax}. A study on successional classification of tropical rainforest species in French Guiana suggests a classification of late successional species into fast-growing and slow-growing (Bonal et al., 2007). Our data implies that *H. plagata* and *S. polysperma* have leaf traits that characterize slow-growing species while *H. malibato* and *S. contorta* may be grouped as fast- growing late succesional species with low g_s and high SLA, and *P. malaanonan* in between (Bonal et al., 2007). High relationship found between predictor variable SLA to g_{smax} suggests that this group of species could possess a special physiological leaf traits that differentiate them from other species studied in the rainforestation. Further investigation however is necessary because the inverse relationship between g_{smax} and SLA does not conform with the reported general continuum of leaf traits i.e. higher SLA, higher g_s, shorter leaf life span which is common to early successional and fast growing species.

We found a significant variation of sun exposed leaf $\delta^{13}C$ values among the co-occurring species in rainforestation stands (-33.2 ‰ to -28.7 ± 1.2). Mean species $\delta^{13}C$ signature varied by 4.5 ‰ range among the species studied. This variability is lower than the $\delta^{13}C$ values obtained from various tropical rainforest species in French Guiana with 7.3‰ range (-34.8 to -27.5 ‰) (Bonal et al., 2000) and also lower when compared to the canopy tree species in Amazonian rainforest in Rondônia, Brazil with 5.5‰ range (-34.3 to -28.8 ‰) (Martinelli et al., 1998). Our data however is similar to the $\delta^{13}C$ values obtained by Guehl et al. (1998) from the similar study site in French Guiana but including only 18 species. Successional position of species (i.e. early and late) was separated according to the leaf $\delta^{13}C$ signature i.e. early successional species are more enriched in $\delta^{13}C$ that late successional species which are more depleted in $\delta^{13}C$ (Bonal et al., 2000; Martinelli et al., 1998; Bonal et al., 2007). *A. blancoi* and *G. arborea* are more enriched in $\delta^{13}C$ which could be related to high intrinsic water use efficiency (WUE) of these species compare to dipterocarps species. A consistently more negative $\delta^{13}C$ (low WUE) values obtained from the studied dipterocarp species suggests that this trait may be controlled genetically within this group (Farquhar et al., 1989; Bonal et al., 2000). This could be explained by the phylogenetic close relationship of the genera *Hopea*, *Shorea* and *Parashorea*, which were all represented in our study (Zhang and Cao, 2009).

A weak but significant correlation was found between g_{smax} and $\delta^{13}C$ among the species studied. No relationship was found between g_{smax} and $\delta^{13}C$ among eight co-existing species in natural forest (Bohman, 2004) and eight early successional species in second-growth forest in Sulawesi (Juhrbandt et al., 2004). Substantial physiological variation among all the studied species may exist and remarkable variation in $\delta^{13}C$ could be attributed to species-specific physiological diversity (Leffler and Enquist, 2002). A precise ecophysiological explanation for the variation of $\delta^{13}C$ among species however, needs further clarification as was also suggested by previous studies in various tropical forest ecosystems (Guehl et al., 1998; Bonal et al., 2000).

In our multivariate analysis (PCA), the sixteen species studied in rainforestation plots were ordinated according to six variables (g_{smax}, leaf size, width to length ratio (WLR), stable isotope signature ($\delta^{13}C$), specific leaf area (SLA) and leaf nitrogen content per area basis (N_{area})). The main contributors to high values of PCA 1 (explained variance 49 percent) were the species which are more depleted in $\delta^{13}C$ (more negative values); low leaf size and low WLR. Thus, in the PCA run all dipterocarps species, *D. zibethinus* and *C. blancoi* seem to form a group having similar leaf traits that were mentioned above. The two *Artocarpus* species from our study reflected a unique strategy compared to most species studied, showing an overlapping traits known to early and late successional species (i.e. large leaves, high WLR, more enriched in $\delta^{13}C$ but low SLA and low N_{area}) (Poorter and Bongers, 2006; Wright et al., 2004). The separation of species in our study according to their life history (early or late successional) was not clear as most of them, especially fruit trees were domesticated and some are exotics. Based on their close relatives and origin, all of them can be considered late successional species with *A. blancoi* which falls in between early and late successional stage (E. Fernando, pers. comm., 2008).

The high scores along the PCA 2 of the two exotic species (*G. arborea* and *S. macrophylla*) and a fast-growing native (*T. microcarpa*) was influenced by their high

SLA and high N_{area}. The first two species are known for being fast growing exotics that performs very well in the tropics. These species share the same leaf traits and were described as physiologically active species with fast leaf growth rates but short leaf lifespan which could indicate the same successional position as early successional species (Reich et al., 1991, 1992, 1999). We also observed high leaf conductance facilitating high assimilation rates that enable them to capture and utilize more light thus encouraging high growth (Poorter and Bongers, 2006). Leaf senescence from older leaves give way to more sun exposed and more valuable younger leaves (Ackerly et al., 1995). This characterizes *G. arborea*, *S. macrophylla* and *T. microcarpa* species which shed their leaves. One of the many advantages of the introduction of such species in a mixed reforestation is the increase in productivity and the quick leaf turn over, the disadvantage could be the invasive characteristic of few species that may have negative impact on the biodiversity of the stands.

In contrast, dipterocarps species have low SLA which in general is producing tougher leaves (Reich et al., 1991) and low leaf N content as their strategy to minimize damage caused by leaf herbivores (Coley et al., 1985). Late successional species like dipterocarps used up minimal resources (i.e. light, water) (Wright et al., 2004; Poorter and Bongers, 2006) and utilise high irradiances and are more tolerant of water and nutrient deficiency exhibiting slow and long time leaf investment to produce longer leaf life span for their higher chance of survival under shade (Reich et al., 1991; 1999; Poorter and Bongers, 2006).

Conclusions

Overall there were only minor correlations between leaf traits and g_{smax} but in the important dipterocarp family a high correlation was indicated. Thus, along the successional gradient, dipterocarps may show slightly different characteristics. Further, some of the species were grouped according to their leaf traits which may indicate differences in overall plant performance such as growth and mortality. Such information may also help to adjust the species combination in further developments of the reforestation scheme to specific goals.

CHAPTER 4

Variability and grouping of leaf traits in 26 co-occurring species

Introduction

Tropical forests and other forest types have considerable variations both within and among, in terms of the leaf structural characteristics of tree species found therein i.e. leaf mass per unit leaf area, the inverse of specific leaf area, anatomical features and nutrient contents (Turner et al. 2000; Turner, 2001; Sandquist and Cordell, 2007). There is much evidence that early and late successional species differ in leaf traits (Bazzaz, 1991; Strauss-Debenedetti and Bazzaz, 1996, Juhrbandt et al., 2004). Moreover, plant performance, for example, growth and survival, may be predicted based on their leaf traits (Poorter and Bongers, 2006). A global study presenting the importance of leaf traits to evaluate the nutrient availability in the soil has been established from the work of Ordoñez et al. (2009). To my knowledge, information on leaf traits of co-existing species in mixed reforestation is presently limited.

A new approach to reforestation called rainforestation, is gaining more attention nowadays by being widely promoted to reforest many degraded areas in the Philippines. Pioneer rainforestation sites for more than a decade have created highly diverse stands with impressive number of species (average, 40) per hectare (see Table in Chapter 1). Functional diversity of trees in these stands could be assessed for example on the basis of leaf traits of co-existing species. This important step may lead us to a conclusion that the new scheme is indeed successful in imitating the natural forest, as conceptualized.

This study is an extension work of the previous chapter dealing with the investigation of leaf morphological and chemical traits of ten additional species from the initial 16 broad-leaved species in Chapter 3. The study focused on the characterization of species belonging to different canopy layers in the rainforestation. Relatively easy to assess leaf morphological traits such as specific leaf area, leaf size per leaf dry weight (SLA, m^2 kg^{-1}), leaf size and leaf width to length ratio (WLR) may be used to predict other important traits for example stable carbon isotope ($\delta^{13}C$).

Plant carbon isotope composition ($\delta^{13}C$) is a tool that has been increasingly popular in many ecophysiological studies to assess the functional variability of the multitude of trees in most tropical rainforests (Bonal et al 2000, Guehl et al. 1998, Huc et al. 1994, Leffler and Enquist 2002, Martinelli et al. 1998) and mixed species stands in temperate forests (Hölscher 2003, Chevillat et al. 2005). It helps us to understand the performance of C3 species in terms of photosynthesis and their coordination with water use in physiological and ecological studies (Farquhar et al. 1989). Moreover, $\delta^{13}C$ signature has a link to the time-integrated water use efficiency (WUE), defined as the ratio of the CO_2 assimilation to stomatal conductance for water vapour (g_s) of the leaf area (Farquhar et al. 1982). Understanding the species-specific $\delta^{13}C$ has an implication on the responses of trees to climate change, origin and maintenance of species diversity within and across tropical communities (Leffler and Enquist, 2002). In the case of the rainforestation scheme, balance between biodiversity and economic gains are the concern to be more attractive to target smallholders. Thus, this study was conducted (1) to assess leaf morphological and chemical traits variability of sunlit and shade leaves of co-existing species in mixed-species stands, and to determine if the variability was related to crown exposure (2) to find out correlation among measured leaf variables (3) and to investigate possible grouping of species according to their important leaf traits. The results from this study could help evaluate the functional variability as well as the determination of ecophysiology of wide range of species use in reforestations in Leyte.

Materials and methods

Study site and species studied

The study was conducted in Leyte, Philippines situated about 9°45' N latitude and 123°50'- 126°00' E longitude with an extension of 214 kms from north to south. Characteristics of the studied mixed-species stands were described in Chapter 2, Methodology.

Species selection was guided by the requirement for five tree individuals per species with well-exposed crowns and another group of species with shaded crowns, also with five sample trees. Crown exposed species are with sunlit leaves usually found in the upper canopy layer while shaded crown are species with fully shaded leaves occupying the lower canopy layer. These terms were consistently used in the text to separate the two groups. Species investigated belonged to a wide variety of tree families (Table 1). Six species are from Dipterocarpaceae, (*Hopea malibato* Foxw., *Hopea plagata* S. Vidal, *Parashorea malaanonan* Merr*.*, *Shorea contorta* S.Vidal*, Shorea polysperma* Merr., *Dipterocarpus kerrii* King*)*, four to Meliaceae (*Lansium domesticum* Corr.*, Sandoricum koetjape* Merr.*, Swietenia macrophylla* King., *Melia dubia* Cav.), three to Moraceae (*Artocarpus blancoi* Merr., *Artocarpus odoratissimus* Blanco, *Artocarpus heterophylla* Lmk.), three to Verbenaceae (*Gmelina arborea* Roxb.*, Vitex parviflora* A. Juss., *Vitex turczaninowii* Merr.), two to Guttiferae (*Calophyllum blancoi* Pl. and Tr., *Garcinia mangostana* L.), one each to Anacardiaceae (*Dracontomelon dao* Merr. & Rolfe), Annonaceae (*Annona muricata* L.), Bombacaceae (*Durio zibethinus* L.), Combretaceae (*Terminalia microcarpa* Decne.), Fabaceae (*Pterocarpus indicus* Willd.), Myricaceae (*Myrica javanica* Blume), Sapindaceae (*Nephelium lappaceum* L.) and Sterculiaceae (*Theobroma cacao* L.).

For all the species studied, 18 were considered native to the region, while eight were exotic. Major uses of species are listed in Table 2. Most of them have high value timber for construction (fifteen species); some are fruit trees (nine species) or are favoured for furniture-making (two species). All dipterocarps were classified as late successional species. *C. blancoi, T. microcarpa, V. parviflora, M. dubia, M. javanica, P. indicus, D. dao, V.turczaninowii, G. arborea* and *S. macrophylla* are classified as early successional species. *A. blancoi* is considered in between early and late successional stage according to E. Fernando, pers. comm., 2008. However, the life history of other species that we studied was unknown. All dipterocarp species and *A. blancoi* are classified as critically endangered and are threatened to habitat loss (IUCN, 2009).

Most of the species studied have simple leaves while *L. domesticum*, *N. lappaceum, S. macrophylla*, *D. dao*, *P. indicus, S. koetjape, V. parviflora* and *V. turczaninowii* have compound leaves. In addition, *T. microcarpa* has closely alternate leaf arrangement which bunch at the end of the twig. Leaf shapes vary from oblong-obovate, elliptic, obtuse, ovate-lanceolate and acuminate.

Table 1. Characteristics of the twenty six species studied in mixed reforestation stands. Tree height and diameter at breast height (dbh) of sample individuals, n = 5. Means are reported ± standard error. Significant differences are indicated by small letters (analysis of variance, $p < 0.05$) and capital letters for the differences between crown-exposed and shaded crown species (unpaired t-test, $p < 0.05$).

Species	Species code	Family	Study sites	Native or Exotic	Main uses	Tree height (m)	dbh (cm)
Crown-exposed species							
Hopea malibato Foxw.	Hm	Dipterocarpaceae	Patag	Native	Timber	8.2 ± 0.6 ^{bc}	10.4 ± 1.3 ^{bcd}
Hopea plagata S.Vidal	Hp	Dipterocarpaceae	Patag	Native	Timber	7.1 ± 0.4 ^{c}	7.0 ± 0.2 ^{d}
Parashorea malaanonan Merr.	Pm	Dipterocarpaceae	Cienda	Native	Timber	10.0 ± 0.5 ^{abc}	10.1 ± 0.9 ^{bcd}
Shorea contorta S.Vidal	Sc	Dipterocarpaceae	Cienda	Native	Timber	10.0 ± 0.8 ^{abc}	9.6 ± 0.8 ^{cd}
Shorea polsyperma Merr.	Sp	Dipterocarpaceae	Patag	Native	Timber	8.5 ± 0.4 ^{bc}	10.6 ± 1.5 ^{bcd}
Lansium domesticum Corr.	Ld	Meliaceae	Marcos	Native	Fruit	8.4 ± 0.2 ^{bc}	10.7 ± 1.4 ^{bcd}
Sandoricum koetjape Merr.	Sk	Meliaceae	Marcos	Native	Fruit	11.5 ± 1.0 ^{ab}	24.8 ± 2.1 ^{a}
Swietenia macrophylla King	Sm	Meliaceae	Patag	Exotic	Furniture	8.5 ± 0.7 ^{bc}	11.2 ± 1.0 ^{bcd}
Artocarpus blancoi Merr.	Ab	Moraceae	Patag	Native	Timber	9.2 ± 1.7 ^{abc}	17.0 ± 4.2 ^{abcd}
Artocarpus odoratissimus Blanco	Ao	Moraceae	Marcos	Exotic	Fruit	10.9 ± 0.8 ^{abc}	20.5 ± 2.3 ^{abc}
Gmelina arborea Roxb.	Ga	Verbenaceae	Marcos	Exotic	Furniture	10.6 ± 1.4 ^{abc}	25.1 ± 5.1 ^{a}
Vitex parviflora A. Juss.	Vp	Verbenaceae	Marcos	Native	Timber	11.1 ± 0.4 ^{abc}	21.7 ± 1.7 ^{ab}
Durio zibethinus L.	Dz	Bombacaceae	Marcos	Exotic	Fruit	10.9 ± 0.5 ^{abc}	18.4 ± 3.8 ^{abcd}
Terminalia microcarpa Decne.	Tm	Combretaceae	Cienda	Native	Timber	10.2 ± 0.8 ^{abc}	12.7 ± 1.9 ^{bcd}
Calophyllum blancoi Pl. and Tr.	Cb	Guttiferae	Cienda	Native	Timber	9.5 ± 0.5 ^{abc}	11.3 ± 0.7 ^{bcd}
Nephelium lappaceum L.	Nl	Sapindaceae	Marcos	Exotic	Fruit	10.2 ± 0.8 ^{abc}	17.8 ± 2.1 ^{abcd}
Melia dubia Cav.	Md	Meliaceae	Marcos	Native	Timber	13.1 ± 0.7 ^{a}	19.2 ± 2.1 ^{abc}
Myrica javanica Blume	Mj	Myricaceae	Marcos	Native	Timber	8.8 ± 0.8 ^{c}	15.9 ± 5.3 ^{abcd}
Mean						**9.8 ± 0.3 A**	**15.2 ± 1.3 A**
Min						**7.1**	**7.0**
Max						**11.5**	**25.1**

Table 1. Characteristics of the twenty six species studied in mixed reforestation stands. Tree height and diameter at breast height (dbh) of sample individuals, n = 5. Means are reported ± standard error. Significant differences are indicated by small letters (analysis of variance, $p < 0.05$) and capital letters for the differences between crown-exposed and shaded crown species (unpaired t-test, $p < 0.05$).

Species	Species code	Family	Study sites	Native or Exotic	Main uses	Tree height (m)	dbh (cm)
Shaded-crown species							
Dipterocarpus kerrii King	Dk	Dipterocarpaceae	Marcos	Native	Timber	8.3 ± 0.3 ^{ab}	11.4 ± 0.3 ^{ab}
Dracontomelon dao Merr.& Rolfe	Dd	Anacardiaceae	Marcos	Native	Timber	8.0 ± 0.5 ^{ab}	11.5 ± 1.7 ^{ab}
Annona muricata L.	Am	Annonaceae	Marcos	Exotic	Fruit	6.4 ± 0.1 ^{bc}	8.0 ± 0.1 ^{b}
Pterocarpus indicus Willd.	Pi	Fabaceae	Marcos	Native	Timber	7.6 ± 0.3 ^{abc}	10.1 ± 0.3 ^{ab}
Garcinia mangostana L.	Gm	Guttiferae	Marcos	Native	Fruit	*	*
Artocarpus heterophylla Lmk.	Ah	Moraceae	Marcos	Exotic	Fruit	8.7 ± 0.8 ^{a}	14.1 ± 0.8 ^{a}
Theobroma cacao L.	Tc	Sterculiaceae	Marcos	Exotic	Fruit	6.0 ± 0.4 ^{c}	7.4 ± 0.7 ^{b}
Vitex turczaninowii Merr.	Vt	Verbenaceae	Marcos	Native	Timber	7.2 ± 0.3 ^{abc}	9.1 ± 0.9 ^{b}
Mean						**7.0 ± 0.5 B**	**9.6 ± 1.0 B**
Min						**< 5**	**< 4**
Max						**8.7**	**14.1**

*sample individuals have < 5cm dbh, < 4m height

Table 2. Leaf morphology and chemistry of the sunlit and shade leaves of the twenty six species studied with five tree individuals per species. Full names of species are listed in Table 1. Means ± standard error are given per species. Significant differences among species are indicated by small letters (analysis of variance, $p < 0.05$) and differences between crown exposed and shaded crown species by capital letters (unpaired t-test, $p < 0.05$).

Species code	Leaf size (cm^2)	Leaf length (cm)	Leaf width (cm)	WLR ($cm\ cm^{-1}$)	SLA ($m^2\ kg^{-1}$)	N_{area} ($g\ m^{-2}$)	N_{mass} ($g\ kg^{-1}$)	C (%)	$\delta^{13}C$ (‰)
Crown exposed									
Hm	16.5 ± 2.3^{gh}	7.8 ± 0.5^{j}	3.6 ± 0.3^{g}	0.44 ± 0.02^{cdef}	14.8 ± 0.7^{abc}	1.9 ± 0.1^{cdef}	18.6 ± 0.7^{cdef}	50.0 ± 0.3^{ab}	-31.4 ± 0.6^{bcd}
Hp	49.2 ± 4.0^{ef}	12.2 ± 0.4^{hi}	6.3 ± 0.3^{def}	0.50 ± 0.01^{bcd}	10.8 ± 0.4^{def}	1.6 ± 0.0^{ef}	15.6 ± 0.5^{ef}	50.0 ± 0.3^{ab}	-33.2 ± 0.2^{d}
Pm	76.9 ± 8.1^{de}	15.6 ± 0.8^{efg}	7.7 ± 0.5^{d}	0.50 ± 0.03^{bcd}	12.0 ± 0.6^{cdef}	2.0 ± 0.1^{cde}	20.4 ± 0.8^{cde}	46.6 ± 0.5^{cd}	-31.2 ± 0.2^{bcd}
Sc	59.7 ± 2.2^{def}	17.4 ± 0.4^{efgh}	7.6 ± 1.1^{def}	0.44 ± 0.01^{cdef}	14.4 ± 0.8^{abcd}	1.8 ± 0.0^{def}	18.4 ± 0.3^{def}	45.7 ± 0.5^{de}	-31.3 ± 0.3^{bcd}
Sp	66.7 ± 2.8^{def}	16.2 ± 0.3^{def}	6.5 ± 0.2^{def}	0.40 ± 0.01^{ef}	10.4 ± 0.4^{ef}	1.8 ± 0.0^{def}	17.8 ± 0.4^{def}	50.7 ± 0.1^{a}	-31.8 ± 0.4^{cd}
Ld	94.8 ± 9.0^{cd}	17.7 ± 1.1^{def}	7.7 ± 0.3^{d}	0.44 ± 0.03^{cdef}	9.2 ± 0.6^{f}	2.3 ± 0.1^{bc}	23.4 ± 1.0^{bc}	45.7 ± 0.3^{de}	-31.4 ± 0.2^{bcd}
Sk	159.1 ± 8.2^{c}	23.8 ± 0.5^{c}	12.3 ± 0.4^{c}	0.52 ± 0.01^{bc}	13.9 ± 0.4^{abcde}	1.9 ± 0.1^{cde}	19.4 ± 1.0^{cde}	45.7 ± 0.5^{de}	-30.7 ± 1.1^{abc}
Sm	77.2 ± 6.1^{de}	17.9 ± 0.7^{de}	6.4 ± 0.3^{def}	0.36 ± 0.00^{fg}	16.3 ± 1.4^{ab}	1.9 ± 0.2^{cdef}	19.0 ± 1.7^{cdef}	47.1 ± 0.5^{cd}	-30.4 ± 0.2^{abc}
Ab	762.9 ± 221.1^{a}	36.0 ± 3.3^{ab}	27.1 ± 3.6^{a}	0.74 ± 0.04^{a}	10.1 ± 0.4^{ef}	2.0 ± 0.1^{cde}	20.4 ± 0.7^{cde}	42.9 ± 0.6^{fg}	-28.7 ± 0.3^{a}
Ao	601.0 ± 70.1^{a}	34.6 ± 1.0^{b}	23.7 ± 0.9^{ab}	0.67 ± 0.04^{a}	10.1 ± 0.5^{ef}	1.8 ± 0.1^{def}	18.2 ± 0.9^{def}	41.7 ± 1.0^{g}	-30.8 ± 0.5^{abc}
Ga	291.3 ± 21.6^{b}	24.0 ± 1.5^{b}	13.2 ± 0.7^{b}	0.55 ± 0.03^{b}	17.5 ± 0.8^{a}	2.6 ± 0.2^{b}	26.4 ± 1.9^{b}	45.8 ± 0.6^{d}	-28.7 ± 0.4^{a}
Vp	51.2 ± 5.7^{ef}	13.9 ± 0.6^{fgh}	5.7 ± 0.4^{ef}	0.41 ± 0.01^{def}	11.0 ± 0.6^{cdef}	1.8 ± 0.1^{def}	18.2 ± 0.9^{def}	46.3 ± 0.7^{cd}	-30.9 ± 0.6^{abcd}
Dz	83.7 ± 12.3^{de}	19.9 ± 1.1^{cd}	6.2 ± 0.5^{def}	0.30 ± 0.01^{g}	12.1 ± 1.4^{cdef}	1.9 ± 0.1^{cde}	19.4 ± 1.2^{cde}	43.2 ± 0.3^{efg}	-32.5 ± 0.6^{cd}
Tm	39.3 ± 1.7^{f}	13.3 ± 0.2^{gh}	5.0 ± 0.1^{f}	0.38 ± 0.00^{fg}	14.6 ± 1.3^{abcd}	2.2 ± 0.1^{bcd}	22.0 ± 0.7^{bcd}	45.2 ± 0.3^{def}	-30.6 ± 0.4^{abc}
Cb	17.7 ± 0.7^{g}	10.0 ± 0.2^{i}	3.0 ± 0.0^{gh}	0.30 ± 0.00^{g}	12.3 ± 0.8^{bcdef}	1.4 ± 0.0^{f}	14.4 ± 0.3^{f}	48.5 ± 0.3^{abc}	-31.6 ± 0.3^{cd}
Nl	69.1 ± 3.0^{def}	14.2 ± 0.4^{efgh}	6.9 ± 0.1^{de}	0.49 ± 0.01^{bcde}	10.0 ± 0.6^{ef}	1.9 ± 0.1^{cdef}	19.0 ± 0.7^{cdef}	47.6 ± 0.6^{bcd}	-31.6 ± 0.3^{cd}
Md	9.9 ± 1.6^{h}	7.0 ± 0.6^{j}	2.6 ± 0.2^{h}	0.37 ± 0.01^{fg}	17.4 ± 0.8^{a}	3.4 ± 0.1^{a}	33.9 ± 0.6^{a}	47.7 ± 0.1^{bcd}	-29.1 ± 0.2^{ab}
Mj	372.2 ± 32.1^{ab}	44.5 ± 1.7^{a}	13.0 ± 0.5^{c}	0.29 ± 0.01^{g}	11.8 ± 0.4^{cdef}	2.5 ± 0.1^{b}	25.3 ± 0.7^{b}	47.5 ± 0.4^{bcd}	-32.1 ± 0.3^{cd}
Mean	**161.0 ± 50.3 A**	**19.2 ± 2.4 A**	**9.1 ± 1.6 A**	**0.5 ± 0.03 A**	**12.7 ± 0.6 A**	**2.0 ± 0.1 A**	**20.5 ± 1.1 A**	**46.6 ± 0.6 A**	**-31.1 ± 0.3 A**
Min	**17.7**	**7.8**	**2.6**	**0.29**	**9.2**	**1.4**	**14.4**	**41.7**	**-33.2**
Max	**762.9**	**44.5**	**27.1**	**0.74**	**17.4**	**3.4**	**33.9**	**50.7**	**-28.7**

Table 2 (continuation). Leaf morphology and chemistry of the sunlit and shade leaves of the twenty six species studied with five tree individuals per species. Full names of species are listed in Table 1. Means ± standard error are given per species. Significant differences among species are indicated by small letters (analysis of variance, $p < 0.05$) and differences between crown exposed and shaded crown species by capital letters (unpaired t-test, $p < 0.05$).

Species code	Leaf size (cm^2)	Leaf length (cm)	Leaf width (cm)	WLR ($cm\ cm^{-1}$)	SLA ($m^2\ kg^{-1}$)	N_{area} ($g\ m^{-2}$)	N_{mass} ($g\ kg^{-1}$)	C (%)	$\delta^{13}C$ (‰)
Shaded crown									
Dk	111.2 ± 6.6 ^{b}	21.5 ± 0.6 ^{b}	8.3 ± 0.4 ^{b}	0.39 ± 0.0 ^{bcd}	7.3 ± 0.1 ^{b}	1.6 ± 0.1 ^{cd}	15.9 ± 0.8 ^{cd}	43.1 ± 0.9 ^{c}	-32.0 ± 0.4^{a}
Dd	33.4 ± 1.1 ^{d}	12.5 ± 0.3 ^{d}	4.1 ± 0.1 ^{d}	0.33 ± 0.01 ^{d}	16.3 ± 0.5 ^{a}	1.8 ± 0.1 ^{bcd}	18.1 ±1.0 ^{bcd}	40.5 ± 0.3 ^{c}	-31.1 ± 0.2 ^{a}
Am	53.8 ± 2.5 ^{c}	14.6 ± 0.3 ^{cd}	5.7 ± 0.4 ^{c}	0.39 ± 0.0 ^{bcd}	19.1 ± 0.6 ^{a}	2.1 ± 0.1 ^{b}	21.2 ±0.9 ^{b}	43.5 ± 0.3 ^{bc}	-32.1 ± 0.8 ^{a}
Pi	43.9 ± 4.5 ^{cd}	12.2 ± 0.7 ^{d}	5.5 ± 0.3 ^{c}	0.46 ± 0.03 ^{ab}	21.4 ± 2.3 ^{a}	3.6 ± 0.2 ^{a}	36.2 ±1.9 ^{a}	46.9 ± 0.3 ^{b}	-30.4 ± 0.5 ^{a}
Gm	175.0 ± 11.0 ^{a}	25.9 ± 1.2 ^{b}	10.5 ± 0.3 ^{a}	0.41 ± 0.01 ^{bc}	7.3 ± 0.1 ^{b}	1.4 ± 0.0 ^{d}	14.4 ±0.4 ^{d}	51.6 ± 0.3 ^{a}	-31.5 ± 0.4 ^{a}
Ah	60.5 ± 8.8 ^{c}	13.1 ± 1.0 ^{cd}	6.9 ± 0.6 ^{bc}	0.53 ± 0.0 ^{a}	18.8 ± 1.3 ^{a}	2.3 ± 0.1 ^{b}	22.5 ±0.8 ^{b}	43.2 ± 0.9 ^{bc}	-31.9 ± 0.6 ^{a}
Tc	239.5 ± 26.9 ^{a}	33.8 ± 1.7 ^{a}	11.3 ± 0.7 ^{a}	0.34 ± 0.02 ^{d}	19.6 ± 1.2 ^{a}	1.9 ± 0.1 ^{bc}	19.4 ±0.6 ^{bc}	43.3 ± 0.3 ^{bc}	-32.3 ± 0.4 ^{a}
Vt	49.3 ± 4.2 ^{cd}	15.9 ± 0.9 ^{c}	5.7 ± 0.3 ^{c}	0.36 ± 0.02 ^{cd}	16.7 ± 1.5 ^{a}	1.9 ± 0.1 ^{bcd}	19.2 ±1.2 ^{bcd}	42.6 ± 1.7 ^{c}	-32.1 ± 0.2 ^{a}
Mean	**95.8 ± 24.6 A**	**18.7 ± 2.6 A**	**7.3 ± 0.8 A**	**0.40 ± 0.03 A**	**15.8 ± 1.8 A**	**2.0 ± 0.2 A**	**20.4 ± 1.9 A**	**44.3 ± 1.0 A**	**-31.7 ± 0.2 A**
Min	**33.4**	**12.2**	**4.1**	**0.33**	**7.3**	**1.4**	**14.4**	**40.5**	**-32.3**
Max	**239.5**	**33.8**	**11.3**	**0.53**	**21.4**	**3.6**	**36.2**	**51.6**	**-30.4**

Data shown in abbreviations are width to lenght ratio (WLR), specific leaf area (SLA), leaf nitrogen content per unit leaf mass (N_{mass}), leaf nitrogen content per unit leaf area (N_{area}), leaf carbon content (C) stable carbon isotope ratio ($\delta^{13}C$).

A few species, such as *G. arborea, S. koetjape* and *T. microcarpa,* possess pubescent leaves, and most have glabrous to shiny. Leaves of *A. odoratissimus* have distinct sandy-like texture on top and are hairy at the underside, with hairs extending up to the petioles.

Leaf sampling and leaf stable isotopes analysis

Ten mature fully exposed sunlit leaves were taken from the upper canopy of crown exposed species with the use of a bamboo tower. Leaf sampling however from trees with extreme heights was made possible with the help of a tree climber and with the use of a tree pruner. Shade leaves from species, mostly from fruit trees were randomly collected from opposing sides of the canopy from north, south, west and east direction. Individuals were described as over-shadowed by other height dominant species in the sites.

Leaf morphological traits of sunlit and shaded leaves from various species were collected and measured. Fresh leaves were scanned and their sizes and width to length ratio (WLR, cm cm^{-1}) were analyzed using Winfolia software (Winfolia, 2004a). For species with compound leaves i.e. with trifoliate, palmate and pinnate, leaflets were collected in similar position for example the middle leaflet in trifoliate. .*M. dubia* is a species with tripinnate compound leaves and with small pinnules. Samples were consistently taken from the upper left pinnae of the leaves and the middle pinnule. Collected leaves were oven-dried at 70˚C for 48 hours and specific leaf area (SLA, m^2 kg^{-1}) was calculated as the leaf size divided by the leaf dry mass. Dried leaves were ground into a fine powder using a plant sample mill. A sub-sample of 1 to 2 mg of powdered leaves was combusted and analyzed in five replicates per species for stable carbon isotope signature ($\delta^{13}C$) using a gas isotope mass spectrometer (Delta Plus, Finnigan MAT, Bremen, Germany) via a ConFlo III interface. Results were reported in parts per thousands (‰) referring them to the international standard (Pee Dee Belemnite). Leaf nitrogen and carbon content was determined with an elementar analyser (NA 2500, CE-Instruments, Rodano, Milano, Italy). All chemical analyses were done at the Centre for Stable Isotope Research, University of Göttingen. The $\delta^{13}C$ composition was calculated as:

$$\delta^{13}C = \left(R_{sample}/R_{standard}\right) * 1000$$

where R_{sample} and $R_{standard}$ refer to the $^{13}C/^{12}C$ ratio based on Pee Dee Belemnite standard.

Data analysis

Descriptive statistics including the mean and standard error of measured tree variables were computed from five individual trees per species. Leaf morphological and chemical variables were tested for normal distribution using the Shapiro-Wilk test. Data not normally distributed were log-transformed prior to statistical analysis. The relationship between leaf morphological and chemical traits was analyzed using Pearson's correlation. Comparison of measured variables between crown exposed and shaded crown species was performed using unpaired t-test. One-way analysis of variance (ANOVA) was applied to test for significant differences among the 26 species and a post-hoc Honest Significant Differences (HSD) Tukey´s test was used to assign species to statistically different groups. The significance level was set at $p < 0.05$. Multivariate association of leaf morphological and chemical traits (leaf size, width to length ratio, specific leaf area, leaf nitrogen per area basis, carbon content and stable carbon isotope) was analyzed with a principal component analysis (PCA) based on a correlation matrix. Leaf traits used for PCA were standardized prior to analysis. Most calculations were performed with the R Programming Software version 2.7.1 (2008) while for the multivariate analysis PC-ORD version 5.12 (2006) was used.

Results

Leaf morphology and chemistry

Sample leaves were taken from eighteen crown exposed individuals and eight shaded crown species in three rainforestation plots. Significant differences in tree height (unpaired t-test, $t = 4.37$, $df = 12.9$, $p = 0.001$) and diameter at breast height (dbh) (unpaired t-test, t = 3.42, df = 23.32, p = 0.01) among the species studied was observed (Table 1).

A great significant variation, 77-fold among the leaf sizes of eighteen studied species with sun-exposed crowns was observed (range, 10 to 763 cm^2). On the other hand, leaf sizes among the canopy shade species have sevenfold difference (range, 33 to 240 cm^2). The highest WLR was observed on the two crown exposed species of *Artocarpus* (*A.blancoi* and *A. odoratissimus*) and lowest in *C. blancoi, D. zibethinus* and *M. javanica* (Table 2). Among the shaded crown species, another Artocarpus (*A. heterophylla*) obtained the highest WLR with 0.53 cm cm^{-1} while *Dipterocarpus kerrii* has the lowest value, 0.33 cm cm^{-1}. Significant differences on SLA were observed among the crown exposed species (twofold). High SLA was observed from sunlit leaves of *G. arborea* and *M.dubia* with 17.5 and 17.4 m^2 kg^{-1}, respectively. Lowest SLA however was obtained from *L.domesticum* fruit tree (9.2 m^2 kg^{-1}). On the other hand, the SLA among shaded crown species revealed that six out of eight have no significant differences in SLA while two species have low values namely: *D. kerrii* and *G.mangostana,* both with 7.3 m^2 kg^{-1}. Comparison between leaf morphology (leaf sizes, WLR, leaf length, leaf width, SLA) and chemistry (N_{area}, N_{mass}, C content and $\delta^{13}C$) of crown exposed versus shaded crown species were invariant (Table 2).

Three crown exposed dipterocarps species namely: *S. polysperma* (50.7 %), *H.malibato* and *H. plagata* (50.0 %) have the highest C content while both Artocarpus species have low C content in their leaves, *A. blancoi* (42.9 %) and *A. odoratissimus* (41.7 %). Among the shaded crown individuals, *G. mangostana* fruit tree has the highest C content with 51.6 % and *D. dao* has the lowest value observed value with 40.5 %. The mean leaf nitrogen content per mass (N_{mass}, g kg^{-1}) and per area (N_{area}, g m^{-2}) basis among the crown exposed species was 20.5 g kg^{-1} and 2.0 g m^{-2}, respectively. Similar mean values were obtained among shaded crown individuals. We found a significant variation in N_{mass} (twofold) among the studied crown exposed species ($p < 0.05$, n = 18). *M. dubia* has the highest N_{mass}, 33.9 g kg^{-1} and N_{area}, 3.4 g m^{-2} followed by *G. arborea* (26.4 g kg^{-1} and 2.6 g m^{-2}) and *M.javanica* (25.3 g kg^{-1} and 2.5 g m^{-2}). The lowest leaf nitrogen content values however were obtained from a native species *C.blancoi* and two dipterocarps namely: *H.plagata* and *S.polysperma*. High variation in the leaf nitrogen content among the shaded crown species was observed ($p < 0.05$, n = 8). The highest

N_{mass} was obtained from *P. indicus*, a native species and known to be a nitrogen fixing tree with 36.2 g kg^{-1} while the lowest values were observed from *G. mangostana* and *D. kerrii* with 14.4 and 15.9 g kg^{-1}, respectively.

A highly significant variation was found on the species-specific $\delta^{13}C$ of leaves taken from sun exposed canopy of eighteen co-occurring species in rainforestation plots (range, -28.7 to -33.2‰). In contrast, no significant difference on leaf $\delta^{13}C$ was observed among the eight shaded crown species (Table 2). *A. blancoi* and *G. arborea* species were both found to be more enriched in $\delta^{13}C$ (-28.7‰) and *Melia dubia* (-29.1‰), an early successional species, compared to *H. plagata*, (-33.2‰) which was more depleted in $\delta^{13}C$. The mean $\delta^{13}C$ of the canopy exposed species was -31.1 ‰, and -31.7‰ for canopy shaded species. Unpaired t-test analysis revealed that there was no significant difference in $\delta^{13}C$ between crown exposed and shaded crown species ($p = 0.14$, $n = 26$).

Values of leaf $\delta^{13}C$ obtained from this study were found to be in the range from various studies presented in Table 4 (range, -26.7 to -32.1 ‰). We found limited investigations on $\delta^{13}C$ signature of shade leaves from the understorey or lower strata in the tropical forests field condition. Some studies were done in the greenhouse setting (Huc et al. 1994, Sternberg et al. 1989) and in the temperate forest (Hölscher 2003, Chevillat et al. 2005), hence values were not included in the table.

Correlation between tree variables and leaf traits

A positive correlation was observed between $\delta^{13}C$ and tree height and dbh of all the species studied ($r > 0.40$, $p < 0.05$, $n = 26$, Table 3). Leaf $\delta^{13}C$ was also significantly correlated with other leaf traits i.e. WLR ($r = 0.47$, $p < 0.05$) and leaf nitrogen content ($r > 0.50$, $p < 0.05$ $n = 26$). Moreover, a highly significant relationship was found in SLA and nitrogen content in the leaves of species studied ($r = 0.58$, $p < 0.01$, $n = 26$). No relationship was found between tree variables such as height and dbh and other leaf traits.

Table 3. Pearsons correlation between tree variables of co-existing tree species in studied reforestation stands. Tree variables included the total tree height, diameter at breast height (dbh), leaf size, width to length ratio (WLR), specific leaf area (SLA), leaf nitrogen content per area (N_{area}) and per mass(N_{mass}) basis, carbon content (C) and stable carbon isotope signature ($\delta^{13}C$).

	height	dbh	Lsize	WLR	SLA	N_{area}	N_{mass}	C
dbh	**_0.86*_**							
Lsize	-0.10	0.21						
WLR	0.21	0.31	0.36					
SLA	-0.04	-0.02	-0.30	-0.09				
N_{area}	0.32	0.33	-0.10	0.17	**_0.58*_**			
N_{mass}	0.32	0.34	-0.07	0.16	**_0.58*_**	**_1.0*_**		
C	-0.14	-0.28	-0.29	-0.01	-0.27	-0.09	-0.10	
$\delta^{13}C$	**0.42**	**0.46**	0.17	**0.47**	0.18	***0.50***	***0.51***	-0.09

Note: Correlations in bold are significant at $p < 0.05$, bold and italics are significant at $p < 0.01$, bold and italics with asterisk are significant at $p < 0.001$.

Table 4. Range of leaf δ¹³C (in parts per mill, ‰) values from various tropical tree species obtained from different study.

Location	δ¹³C values (‰)	Type of forest	Study
Rondônia, Brazil	-36.0 to -28.0	tropical moist forest (*Terra firme*)	Martinelli et al. 1998
S.C. Rio Negro, Venezuela	-30.2 to -26.4	*Terra firme*	Medina & Minchin 1980
French Guiana	-30.5 to -26.8	tropical rain forest	Huc et al. 1994
Guanacaste, Costa Rica	-31.5 to -27.7	tropical dry forest	Leffler & Enquist 2002
Luquillo, Puerto Rico	-31.1 to 27.6	sub-tropical wet forest	Medina et al. 1991
French Guiana	-31.4 to -26.7	ten year old plantation	Guehl et al. 1998
French Guiana	-34.8 to -27.5	lowland tropical rainforest	Bonal et al. 2000
Andulau, Brunei	-33.4 to -30.3	heath forest	Turner et al. 2000
Badas, Brunei	-32.6 to -29.3	mixed dipterocarp forest	Turner et al. 2000
Sulawesi, Indonesia	-33.8 to -26.0	natural forest forest garden	Bohman, 2004
Sulawesi, Indonesia	-28.4 to -27.5	second growth forest	Juhrbandt et al. 2004
Leyte, Philippines	-31.1 to-28.7	mixed-species stands	This study

Multivariate analysis of leaf variables

Multivariate approach using principal component analysis showed that the two axes, principal component axes 1 and 2 (PCA 1 and PCA 2) explained 65 % variation in leaf traits of 26 co-occurring species in rainforestation. PCA 1 explained 36% of variation while PCA 2 has 29 % variation (Figure 1a). Some species were grouped together in PCA 1 (e.g., *M. Dubia*, *P. indicus*, *G. arborea*, *A. odoratissimus* and *A. blancoi*) with high loading scores obtained from the two leaf traits i.e. more enriched in $\delta^{13}C$ (heavy isotopes) and more round leaf shapes (high WLR). Most species studied however were grouped on the left side of the first axis showing the opposite leaf traits i.e. more depleted in $\delta^{13}C$ and species with more elongated or narrow leaf shapes. On the other hand, species studied were closely associated with high scores on PCA 2 having high SLA and high N_{mass} for example *M. Dubia* and *P. indicus.* Species which belonged to this group with similar traits but have lesser scores are *G. arborea*, *T. microcarpa*, *S. macrophylla* and shaded crown species namely: *A. muricata, A. heterophylla, T. cacao, D.dao* and *V. turczaninowii* (Figure 2b). All dipterocarps species are grouped together in the lower side of the second axis with distinct leaf traits of having low SLA and low N_{mass}. Two native species (*C. blancoi* and *V. parviflora*), two Artocarpus (*A. odoratissimus* and *A. blancoi*) and five fruit trees (*D. zibethinus, L. domesticum, N. Lappaceum*, *S. koetjape* and *G. mangostana*) were also found in this group. Carbon content variable has a high score in the leaf traits loading shown in the third axis however, the explained variation in this axis was low (18 percent) while leaf size has lower score in the first axis (Figure 2a) but more reflected in the fifth axis with low variance (6 percent).

Discussion

Species-specific variability in leaf stable carbon isotope ($\delta^{13}C$) observed from the sunlit leaves (-28.7 to -33.2 ‰) and shaded leaves (-30.4 to -32.3 ‰) in the studied reforestation overlapped with the range of values obtained in tropical tree species from various studies (range, -26.7 to -32.1 ‰). Atmospheric CO_2 and light penetration within the canopy are the two driving forces that affect the variability in tree leaf $\delta^{13}C$ within the forest (Martinelli et al. 1998). Significant variation in $\delta^{13}C$ among the crown exposed individuals could be explained by the high number of species found in rainforestation,

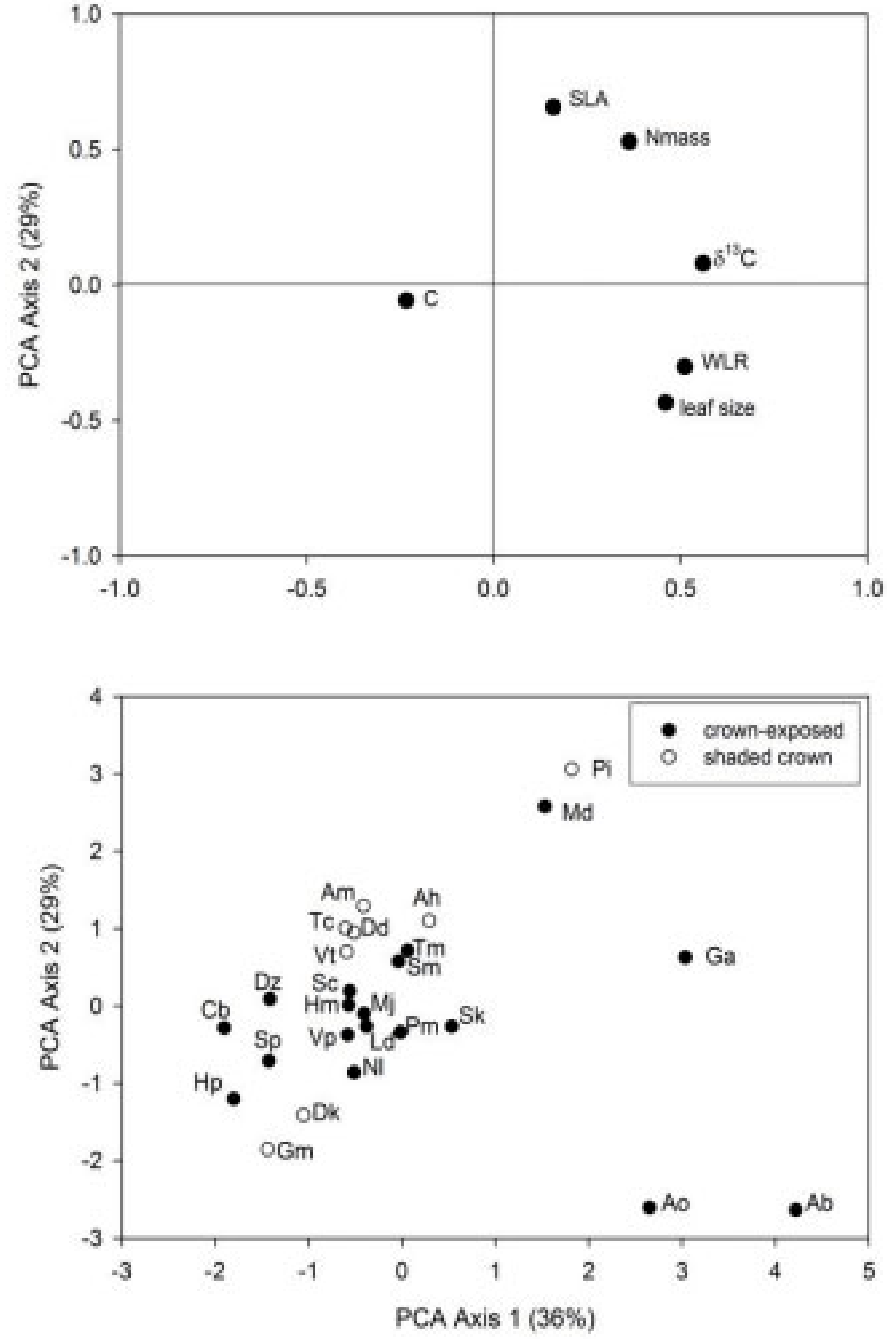

Figure 1. Principal component analysis of leaf chemical and morphological traits of 26 tree species co-occurring in rainforestation stands. (a) Loading plots for the first axis (explained variation is 36%) and second axis (explained variation is 29%). (b) Species loadings. Crown exposed species are indicated by filled symbols and shaded crown species with open symbols. Leaf traits and species abbreviations are given in Tables 1 and 2.

more than 40. This heterogeneity in species could promote a highly variable environment in terms of photosynthesis which will affect the $\delta^{13}C$ values of the vegetation (Farquhar et al. 1989, Martinelli et al. 1998). Moreover, species with more depleted $\delta^{13}C$ could be explained by the high ratios of stomatal conductance and photosynthesis, thus high leaf internal carbon and atmospheric carbon ratio resulting to high fractionation in relation to carbon dioxide (CO_2) in the atmosphere (Martinelli et al. 1998). High variation was observed in the leaf maximal stomatal conductance (g_{smax}) of co-existing species in rainforestation stands (Chapter 3). This physiological trait is closely linked to CO_2 assimilation rate of trees (Farquhar et al. 1982). In addition, leaf $\delta^{13}C$ was found to be a good predictor for foliar gas exchange rate i.e. g_{smax} (see results in Chapter 3) and photosynthesis especially in mixed species stands (Bohman 2004).
No significant difference observed in the leaf $\delta^{13}C$ of the shaded crown species could be explained by the less light availability that limits the photosynthetic activity of these species. Another possible reason is that well mixed air decreases in a closed canopy forest and influences leaf $\delta^{13}C$ of shaded crown species compare to crown exposed canopy (Martinelli et al. 1998). Although in this study, a clear separation between leaf $\delta^{13}C$ from 18 species studied with exposed crown and 8 shaded crown species was not observed in contrast to some studies that revealed a decrease in leaf $\delta^{13}C$ of plants towards the forest floor (Kapos et al. 1993, Hölscher 2003). This result suggests that rainforestation stands are not limited in light and water supply, the two important environmental factors affecting the CO_2 concentration in the leaf intercellular space that affects $\delta^{13}C$ (Farquhar et al. 1982). Compare to a natural forest with a closed canopy, sunlight is almost impenetrable making it more difficult for species at the lower structure to use direct radiation for photosynthesis. This observation was confirmed when sunlit and shade leaves of similar species, *S. contorta* and *P. malaanonan* showed no significant difference in $\delta^{13}C$ although samples were taken from different canopy exposure in rainforestation stands (data not shown). Results suggest that similar species belonging to different canopy strata (as assumed based on the height and crown exposure) could still exhibit the same trait.

In our study, we took leaf samples for stable isotopes analysis once, only during the period of sunny days. Integration of time scale in the analysis could give a better picture on how species vary in leaf δ^{13}C as suggested in other studies (Guehl et al. 1998, Chevillat et al. 2005).

A significant relationship found between leaf δ^{13}C and tree height and dbh was comparable with the high correlation obtained on the leaf δ^{13}C ratio and tree heights of various tropical forest species in Brazil (Martinelli et al. 1998). The result could be explained by the carbon fixation in the biomass of bigger trees than relatively smaller or slow-growing shade tolerant species observed in the study sites.

Significant relationship found between leaf δ^{13}C and width to length ratio between the 26 species studied could be explained by the efficient CO_2 supply because of the less boundary layer conductance in small and elongated leaves. In contrast, species with round and bigger leaves have lesser discrimination rates against ^{13}C Rubisco, hence with more enriched δ^{13}C (Bohman, 2004).

High nitrogen concentration found in the leaves of both crown exposed and shaded crown species in rainforestation suggests that stands that we investigated were not limited in nitrogen. Presence of nitrogen fixing trees i.e. *Pterocaprus indicus* and *Myrica javanica*, and various species from family Caesalpiniaceae and Fabaceae found in the understorey and intermediate canopy in the stands could have enhanced the nitrogen content in the soil (Chapter 2, Site characterization).A strong positive correlation between δ^{13}C and leaf nitrogen content among all the species studied could be explained by the high C/N ratio found in the soil of rainforestation (Marohn, 2007). On the other hand, higher C content found in the sunlit than shaded leaves could be due to the amount on the lipid content of the species studied (Turner et al. 2000, 2001). The highest C content (51.6%) was obtained from *G. mangostana*, a fruit tree with very thick and shiny leaves and found in the lower canopy layer.

High leaf δ^{13}C signature observed in most pioneers can be linked to high water use efficiency of this group of species compared to shade tolerant. Pioneer species growing in lowland tropical forest in French Guiana exhibited a lower leaf δ^{13}C signature (-30.5‰) than the intermediate species (in between pioneer and shade tolerant) with -

29.3‰ and -31.4‰ among shade tolerant species (Bonal et al. 2000). Their findings are similar to the values obtained in co-occurring species in rainforestation.

Coordination of species according to measured leaf variables showed a grouping of species according to most distinct traits i.e. $\delta^{13}C$ and WLR in PCA 1 and SLA and leaf N_{mass} in PCA 2. The first axis presented a clear separation of species according to their leaf $\delta^{13}C$. Most species studied had depleted leaf $\delta^{13}C$. Among the species studied with more enriched $\delta^{13}C$ are identified as light demanding species (*P.indicus, M. dubia*), intermediate species (*A.blancoi*), fast growing exotic (*G. arborea*) and an exotic fruit tree (*A. odoratissimus*). According to Bonal et al. 2007, species belonging to different successional groups have distinct leaf functional and morphological traits, which we have also observed in our study. For example, all dipterocarps species are grouped together according to low SLA and low N_{mass}, which characterizes shade tolerant species. This strategy has been observed in many late successional species with long leaf life span and producing tougher leaves (Reich et al., 1991). In addition, low leaf N content of this group minimizes damage caused by leaf herbivores (Coley et al., 1985). Late successional species like dipterocarps used up minimal resources (i.e. light, water) (Wright et al., 2004; Poorter and Bongers, 2006) and utilise high irradiances and are more tolerant of water and nutrient deficiency exhibiting slow and long time leaf investment to produce longer leaf life span for their higher chance of survival under shade (Reich et al., 1991; 1999; Poorter and Bongers, 2006).

Conclusion

In general, leaf stable carbon isotopes trait of co-occurring species in mixed reforestation stands showed significant correlation to other measured tree variables. A distinct separation in terms of leaf traits of tree species occupying two different canopy strata was not apparent in this study. However, this separation could be more expressed as the stand matures, attaining a well-structured canopy nearly comparable to natural stands. Results obtained from the young stands already suggest a high functional diversity and ecophysiological differences among the co-occurring species. Species grouping according to their leaf traits may imply differences in plant performance especially when planted in mixture.

CHAPTER 5

Leaf traits of seedlings for mixed-species reforestation

Introduction

In the Philippines, revegetation of most degraded areas for many years has relied on the use of a limited number of species with established methods of regeneration. Most of them are exotics from the genera *Eucalyptus, Gmelina* and *Acacia*. In contrast, many native tree species have a high potential for timber production and for other uses, but requirements for successful regeneration are not known (Sawyer, 1993). In many cases, a poor choice of species could be blamed for the failure of reforestations in the country (Carandang and Cardenas, 1991) as well as combined with a poor quality of planting stocks. Hence, the attainment of quality stands entails careful planning and assessment of species to be used at the early years of establishment. Species-specific requirements are essential in the management of these stands for a specified purpose (Kitajima, 1996).

Deviating from the traditional approach to reforestation, a multi-species scheme, the so called rainforestation, was developed and implemented in Leyte, Philippines. This scheme emphasizes the use of native species and combines early and late successional species planted in mixed stands with fruit trees (Margraf and Milan, 1996). Production of seedlings to attain diversified tree species stands however faces a big challenge requiring species-specific regeneration and determination of their ecological requirements.

Seedling stage is the most vulnerable phase in the whole plant development. Mortality is very high at this stage due to many factors such as water, light and nutrients which may limit seedling growth and survival. Early determination of the ability of specific species to access soil water resources (Gazal et al. 2004) and how to tolerate drought conditions (Poorter and Markesteijn, 2008) is vital. Natural selection of individuals due to mortality occurs at seedling stage, and could have an influence on the diversity of the forest (Swaine, 1996). In contrast to natural regenerations, the diversity of trees in planted forest relies on the selection of appropriate species that will comprise the stand.

Assessment of seedlings in the nursery on the basis of leaf traits and stomatal conductance (g_s, mmol $m^{-2}s^{-1}$) prior to outplanting may be an important step in the characterization of tree species. Leaf traits have been shown to differ in early and late successional species (Strauss-Debenedetti and Bazzaz, 1996, Juhrbandt et al. 2004). Thus, may share common successional position (Reich et al. 1999). However, as in many other regions of the tropics, species-specific information on life history and other ecological characteristics of many of the native species is presently not available. This difficulty has been exacerbated by the fact that many tree species are threatened due to habitat loss.

One important physiological trait of trees is the leaf water conductance to water vapour (g_s, mmol $m^{-2}s^{-1}$). It plays an important role in the exchange of water vapour with the atmosphere through leaves and stomates. Therefore, g_s is important in the modeling of the global water and carbon cycle (Schultze et al. 1994). Moreover, g_s has been used to estimate stand transpirational water loss and to delineate differences among species (Khamzina et al. 2009). Another significant trait is the specific leaf area, leaf size per leaf dry weight (SLA, m^2 kg^{-1}) which has been used to assess plant adaptation to environment (Wilson et al. 1999) and plant function (Castro-Díez et al. 2000) as expressed in their leaves. For seedlings of species used in mixed reforestation, data on leaf traits, g_s in particular, are still lacking. Species leaf traits, g_s in particular, are easy to measure in seedlings compared to adults. Plant performance, e.g. growth and survival, may be predicted based on leaf traits. Species may possess traits at an early stage that determine their capability to cope with environmental limitations (such as drought). This was apparent from a study on seedlings of 38 tropical tree species using a dry-down experiment (Poorter and Markesteijn, 2008). They observed functional grouping of species based on seedling traits. For example, species that evade drought conditions are deciduous and have a developed taproot, thus suggesting that seedling traits can be used to predict plant performance.

Knowledge on the growth responses as reflected in traits of seedlings in nurseries at early stages in their life cycle may be indicative of their performance as adult trees in the field. In the study conducted by Popma and Bongers (1988) comparing ten species growing in different environment revealed a range of growth responses of seedlings.

Some species for example prefer to grow in full sunlight rather than under the shade. Therefore it is important to identify species-specific preferences and on how they utilize resources in a heterogeneous environment (Popma and Bongers, 1988). Hence, species-specific differences could be more pronounced during seedling than in adult stage.

Seedling leaf traits may be useful to predict important leaf functional characteristic in adult stage of species. Thus, seedling traits could be decisive on the determination of tree species performance at the later stage of development.

In this chapter, 25 species of potted seedlings from four nurseries located near the rainforestation sites were investigated. Measurements on seedling morphology, g_s and leaf morphological traits were taken. The objectives of the study were (1) to assess the species-specific variation of leaf traits and in particular of maximal leaf stomatal conductance (g_{smax}, mmol $m^{-2}s^{-1}$) of seedlings grown in nurseries (2) to search for relationships between g_{smax} and seedling and leaf morphology (3) to find out whether seedling leaf traits group the species studied and (4) to compare leaf traits of seedlings and adult trees of the same species. Recommendations for rainforestation nursery management were also included in this chapter.

Methods

Study site

The study was conducted from May to June 2007 in four nurseries located in the lowlands adjacent to the Leyte Cordillera, and near the campus of the Visayas State University (VSU) in Baybay, Leyte. Three nurseries are all being under the management of the staff of VSU namely: College of Forestry and Natural Resources nursery (CFNR), Institute of Tropical Ecology-Deutsche Gesselschaft für Technische Zusammenarbeit (ITE-GTZ) and Department of Horticulture (DOH) (10°45'55''N, 124°47'25''E). Another nursery is located in the nearby village Patag (10°44'10''N, 124°48'16''E) and is operated by an organized farmers association (Patag Rainforest Association). Data on adult trees were taken from rainforestation stands (see Chapter 3).

Sources of planting stocks and nursery operations

Planting materials for rainforestation were obtained from seeds and wildlings of dipterocarps from the identified parent trees inside the secondary forest at Mt. Pangasugan. Another source was the lowland forest in Silago, located in the southern part of Leyte (Solano, E. and Sabando, E., pers. comm., 2007). Seeds of fruit tree species were collected from the established fruit tree orchard in VSU (Alcober, E., pers.comm., 2007). Seedlings raised in the nursery at the time of study (range, five to ten months) were found to vary in age, wildlings of dipterocarps were of unknown age. According to the nursery operators, no fertilizer was applied in any of the species studied. Watering of seedlings was done once in the early morning and repeated again in the late afternoon. All dipterocarps species were at the hardening stage, or ready for outplanting. The medium used for the pots was a mixture of forest top soil and sand. Patag nursery used rice hulls instead of sand as it is more available.

During the initial stage of establishment of rainforestation stands in 1996, planting materials of dipterocarp species were from the mother trees in natural forests of provinces i.e. Samar, Palawan and Bohol aside from Mt. Pangasugan (Margraf and Milan, 1996).

Study species

We studied 25 tree species belonging to 17 families (Table 1). Two species represented Anacardiaceae (*Dracontomelon dao* Merr. & Rolfe, *Mangifera altissima* Blanco) one Bombacaceae (*Durio zibethinus* L.), one Combretaceae (*Terminalia microcarpa* Decne.), four Dipterocarpaceae, (*Dipterocapus grandiflorus* Blanco, *Hopea plagata* S. Vidal, *Parashorea malaanonan* Merr*.*, *Shorea contorta* S.Vidal*)*, one Ebenaceae (*Diospyrus philippinensis* A. DC.), two Fabaceae (*Pterocarpus indicus* Willd. and *Samanea saman* Merr.), one Fagaceae (*Lithocarpus luzoniensis* Rehder.), one Guttiferae (*Calophyllum blancoi* Pl. and Tr.), three Meliaceae (*Lansium domesticum* Corr. *, Sandoricum koetjape* Merr*., Swietenia macrophylla* King), three Moraceae (*Artocarpus blancoi* Merr., *Artocarpus odoratissimus* Blanco, *A. heterophylla* Blanco), one Myricaceae (*Myrica javanica* Blume), one Sapindaceae (*Nephelium lappaceum* L.*)*, one Sapotaceae

Table1. Characteristics of the 25 species commonly used for mixed reforestation stands in Leyte.

Species	Species code	Studied as adult (Yes/No)	Common Name	Family Name	Site	Main uses	Successional stage	Native/ Exotic
Dracontomelon dao Merr. & Rolfe	Dd	No	Dao	Anacardiaceae	Patag	All purpose	Light demanding	Native
Mangifera altissima Blanco	Ma	No	Pahotan	Anacardiaceae	ITE-GTZ	Fruit	Shade tolerant	Native
Durio zibethinus L.	Dz	Yes	Durian	Bombacaceae	CFNR	Fruit	Shade tolerant	Exotic
Terminalia microcarpa Decne.	Tm	Yes	Kalumpit	Combretaceae	CFNR	All purpose	Light demanding	Native
Dipterocarpus grandiflorus Blanco	Dg	No	Apitong	Dipterocarpaceae	Patag	All purpose*	Shade tolerant	Native
Hopea plagata S. Vidal	Hp	Yes	Yakal saplungan	Dipterocarpaceae	Patag	All purpose*	Shade tolerant	Native
Parashorea malaanonan Merr.	Pm	No	Bagtikan	Dipterocarpaceae	Patag	All purpose*	Shade tolerant	Native
Shorea contorta S. Vidal	Sc	Yes	White lauan	Dipterocarpaceae	Patag	All purpose*	Shade tolerant	Native
Diospyrus philippinensis A.DC.	Dph	No	Kamagong	Ebenaceae	Patag	All purpose	Shade tolerant	Native
Pterocarpus indicus Willd.	Pi	No	Narra	Fabaceae	Patag	All purpose*	Light demanding	Native
Lithocarpus luzoniense Rehder.	Ll	No	Kilog	Fagaceae	ITE-GTZ	-	-	Native
Calophyllum blancoi Pl. and Tr.	Cb	Yes	Bitanghol	Guttiferae	CFNR	All purpose	Light demanding	Native
Lansium domesticum Corr.	Ld	Yes	Lansones	Meliaceae	ITE-GTZ	Fruit	Shade tolerant	Native
Sandoricum koetjape Merr.	Sk	Yes	Santol	Meliaceae	DOH	Fruit	Shade tolerant	Native
Swietenia macrophylla King	Sm	Yes	Mahogany	Meliaceae	Patag	All purpose	Light demanding	Exotic
Samanea saman Merr.	Ss	No	Rain tree	Fabaceae	CFNR	Fodder/Medicine	Light demanding	Exotic
Artocarpus blancoi Merr.	Ab	Yes	Antipolo	Moraceae	ITE-GTZ	All purpose r	Intermediate	Native
Artocarpus heterophylla Lam.	Ah	No	Nangka	Moraceae	DOH	Fruit	Shade tolerant	Exotic
Artocarpus odoratissimus Blanco	Ao	Yes	Marang	Moraceae	ITE-GTZ	Fruit	Shade tolerant	Exotic
Myrica javanica Blume	Mj	No	Hindang laparan	Myricaceae	ITE-GTZ	All purpose r	Pioneer	Native
Nephelium lappaceum L.	Nl	Yes	Rambutan	Sapindaceae	DOH	Fruit	Shade tolerant	Exotic
Palaquium luzoniense Vidal	Pl	No	Red nato	Sapotaceae	ITE-GTZ	All purpose	Light demanding	Native
Samadera indica Gaertn.	Si	No	Manungal	Simaroubaceae	ITE-GTZ	Latex/Medicine	Shade-tolerant	Exotic
Diplodiscus paniculatus Turcz.	Dpa	No	Balobo	Tiliaceae	Patag	All purpose	Shade tolerant	Native
Vitex parviflora A. Juss.	Vp	Yes	Molave	Verbenaceae	Patag	All purpose	Pioneer	Native

*preferred as construction material

(*Palaquium luzoniense*), one Simaroubaceae (*Simadera indica* Gaertn.), one Tiliaceae (*Diplodiscus paniculatus* Turcz.) and one Verbenaceae (*Vitex parviflora* A. Juss.). Sixteen species were considered native to the region, while seven were exotic. The major uses of these species are listed in Table 1, most of them have high value timber for construction (14 species), fruit trees (7 species) and for other purposes including latex, fodder for animals and medicinal (4 species).

Species selection was guided by the requirement to have ten seedlings per species available in the nurseries of nearly identical age. It was however difficult to obtain similar ages for all the seedlings studied, due to different nurseries where the samples were obtained. Dipterocarps wildlings were initially grown in a plastic chamber prior to transplanting in polyethylene bags with 10 cm x 15 cm size for acclimatization from forest to nursery. Older samples (ten months) were available for fruit trees grown in 25 cm x 30 cm size polybags i.e. *L. domesticum*, *D. zibethinus* and *S. koetjape* except for *N. lappaceum* (six months). We further wanted to represent species from the different categories mentioned in the guidelines of rainforestation which are based on biogeographic origin, main use and successional status (Margraf and Milan, 1996). Most species, particularly dipterocarps, were listed as late successional or shade-tolerant species, all fruit trees were considered as shade tolerant at least in their seedling stage (Margraf and Milan, 1996) while *D. dao, T. microcarpa, P. indicus, C. blancoi, S. macrophylla, S. saman, M. javanica* and *V. parviflora* were classified as early successional or pioneer species (Margraf and Milan,2006). *A. blancoi* was considered as intermediate, in between early and late successional (E. Fernando, pers.comm. 2009). All the dipterocarp species, *A. blancoi, M. altissima* and *P. luzoniense* are classified as critically endangered, threatened or vulnerable due to habitat loss (IUCN, 2009).

Most of the species studied have simple leaves, while *L. domesticum*, *N. lappaceum* and *S. macrophylla*, *V. parviflora, S. koetjape* and *S. saman* have compound leaves. Leaf shapes vary from oblong, elliptic, obtuse, lanceolate to acuminate. While a few species, such as *S. koetjape* and *T. microcarpa,* possess pubescent leaves, most have glabrous to shiny leaves. Seedlings possess different leaf morphological features when compared to leaves taken from the adult trees of some species. For example *A. blancoi* has an entire leaf shape when still young and heavily lobed leaves when mature. *A. heterophylla* has lobed leaf shape when young, forming a deeply indented margin but with entire shape when old. On the other hand, young leaves of *A. odoratissimus* have fine hairs but coarser as it matures and extending up to the petioles.

Of thirteen species studied in the nursery, sufficient adult trees were found in rainforestation stands and sampled on stands were taken as samples (Table 2). For species characterization of adult trees see Chapter 3, Table 2.

Stomatal conductance of leaves

Ten seedlings per species and two partially shaded leaves per individual seedling were investigated (n = 20 leaves). Stomatal conductance (g_s) was measured on the abaxial surface of the leaf using a Delta-T Porometer type AP4 (Delta-T Devices Ltd., Cambridge, England, UK). Prior to g_s measurement, the porometer was calibrated with a calibration plate wetted with distilled water (AP4 Porometer manual, 2004). Diurnal courses of g_s were measured on sunny days. Measurements were taken at hourly intervals, starting in the morning at around 9:00 am when the dew on the leaves had completely evaporated and continued until 3:00 pm before the onset of afternoon rains. A similar method was applied for measuring g_s in ten mature leaves of five adult trees,a larger number of leaves sampled per species (n = 50) (see Methodology, Chapter 2). The average leaf temperature of seedlings in the nursery was 30°C and average photosynthetically active photon flux density during the study was 227 µmol m^{-2} s^{-1}. Seedlings were partially shaded by surrounding nurse trees in the sites (Figure 1).

Seedling morphology and leaf traits

The root collar diameter was measured 0.5 cm from the stem base (rcd, mm) was taken using a vernier caliper. Seedling total height (ht, cm) was measured from the root collar to the tip of the terminal leaf bud. Another height measurement was taken from the lowest leaf observed to the terminal leaf per seedling (ht_{low}, cm), using a standard measuring ruler. Total number of leaflets per individual seedling was also recorded; counting included the newly developed shoots (Table 2).

Two leaves per seedling from 10 individuals per species were collected (n = 20). Fresh leaves were scanned and leaf size and width to length ratio (WLR) of sample leaves were analyzed from the images using Winfolia software (Winfolia, 2004a). Leaves were oven-dried at 70°C for 48 hours for dry weight determination. The specific leaf area (SLA, m^2 kg^{-1}) was calculated as the leaf size divided by the leaf dry mass.

Figure 1. ITE-GTZ nursery showing polybag-grown seedlings of various species intended to be used as planting materials to establish rainforestation stands.

Table 2. Seedling morphology of 25 species grown in nurseries near rainforestation. Morphology included total height, height at the lowest leaf from the top soil, root collar diameter (rcd) and number of leaflets. Full names of species are listed in Table 1. Data shown in abbreviations are width to length ratio (WLR) and specific leaf area (SLA).Means with standard errors are per species. Significant different means are indicated by different letters (analysis of variance, $p < 0.05$, n = 10).

Specie code	height (cm)	height at the lowest leaf (cm)	rcd (mm)	Leaf number (count)	Leaf size (cm^2)	Leaf length (cm)	Leaf width (cm)	WLR (cm cm^{-1})	SLA (m^2 kg^{-1})
Dd	41.1 ± 3.0^{defgh}	32.1 ± 2.8^{abc}	3.6 ± 0.3^{defg}	8 ± 0.6^{ijk}	11.2 ± 1.7^{kl}	7.0 ± 0.6^{kl}	2.4 ± 0.2^{kl}	0.36 ± 0.01^{ghi}	5.0 ± 0.6^{l}
Ma	25.4 ± 1.2^{klmn}	19.0 ± 0.9^{ghij}	2.3 ± 0.2^{ghij}	8 ± 0.3^{ijkl}	25.1 ± 1.1^{efgh}	13.6 ± 0.5^{defg}	3.4 ± 0.1^{ijk}	0.25 ± 0.01^{kl}	18.1 ± 0.7^{efg}
Dz	38.1 ± 1.3^{fghi}	21.1 ± 1.9^{efghi}	8.1 ± 0.4^{a}	12 ± 1.2^{efgh}	41.0 ± 2.7^{cd}	14.6 ± 0.6^{cdefg}	4.5 ± 0.2^{defghi}	0.31 ± 0.00^{ijk}	21.5 ± 0.5^{cde}
Tm	24.4 ± 0.8^{lmn}	11.1 ± 0.5^{jklm}	1.5 ± 0.1^{jk}	23 ± 0.9^{bc}	9.9 ± 0.5^{kl}	8.8 ± 0.3^{ijk}	2.0 ± 0.1^{l}	0.23 ± 0.01^{l}	20.7 ± 0.5^{def}
Dg	42.2 ± 3.6^{defgh}	29.9 ± 3.2^{bcde}	3.9 ± 0.3^{cdef}	7 ± 0.4^{jkl}	66.9 ± 5.0^{ab}	21.0 ± 0.7a	5.7 ± 0.2^{bcd}	0.27 ± 0.01^{kl}	24.6 ± 0.6^{bcd}
Hp	35.8 ± 2.3^{ghijk}	11.1 ± 0.5^{jklm}	2.3 ± 0.2^{ghij}	26 ± 2.0^{b}	25.9 ± 1.6^{defgh}	8.6 ± 0.3^{jk}	4.4 ± 0.1 ^{defghi}	0.51 ± 0.01^{c}	14.6 ± 0.6^{ghi}
Pm	60.0 ± 2.8^{ab}	23.0 ± 2.0^{defgh}	3.6 ± 0.3^{defg}	10 ± 0.6^{fghij}	52.3 ± 5.7^{bc}	15.3 ± 0.8^{bcde}	6.0 ± 0.4^{bc}	0.39 ± 0.01^{efgh}	20.9 ± 0.5^{cde}
Sc	59.4 ± 2.2^{abc}	23.9 ± 2.1^{cdefg}	4.1 ± 0.2^{bcde}	11 ± 0.6^{fgh}	73.7 ± 5.3^{ab}	17.3 ± 0.8^{bc}	7.7 ± 0.3^{a}	0.44 ± 0.01^{de}	15.9 ± 0.5^{fgh}
Dph	26.6 ± 1.2^{jklmn}	14.8 ± 0.5^{hijkl}	3.4 ± 0.3^{defg}	18 ± 1.5^{cd}	27.1 ± 1.8^{defgh}	12.7 ± 0.5^{efgh}	3.5 ± 0.1^{ghijk}	0.27 ± 0.01^{kl}	11.2 ± 0.2^{hijk}
Pi	36.3 ± 2.1^{ghij}	28.1 ± 2.3^{cdef}	2.0 ± 0.2^{hijk}	6 ± 0.6^{kl}	22.2 ± 1.4^{ghi}	7.6 ± 0.3^{k}	4.7 ± 0.2^{cdefg}	0.63 ± 0.01^{b}	11.7 ± 0.9^{hij}
Ll	18.8 ± 1.3^{n}	9.3 ± 1.2^{lm}	2.4 ± 0.2^{ghij}	14 ± 1.0^{defg}	22.9 ± 1.8^{fghi}	11.8 ± 0.4^{fghij}	3.4 ± 0.1^{hijk}	0.29 ± 0.01^{jkl}	27.6 ± 1.1^{b}
Cb	34.7 ± 2.0^{ghijkl}	3.9 ± 0.5^{m}	2.6 ± 0.2^{fghi}	56 ± 5.7^{a}	14.3 ± 0.8^{ijk}	9.8 ± 0.2^{hijk}	2.2 ± 0.1^{kl}	0.23 ± 0.00^{l}	13.0 ± 0.4^{hi}
Ld	49.9 ± 3.0^{bcd}	37.2 ± 3.0^{ab}	6.0 ± 0.4^{abc}	14 ± 0.8^{def}	59.8 ± 10.8^{abc}	14.6 ± 1.2^{cdefg}	6.3 ± 0.5^{b}	0.43 ± 0.02^{def}	10.8 ± 1.8^{ijk}
Sk	69.6 ± 2.1^{a}	18.9 ± 1.3^{ghij}	6.3 ± 0.2^{ab}	9 ± 0.6^{hij}	77.6 ± 5.0^{ab}	18.4 ± 0.8^{ab}	7.6 ± 0.2^{a}	0.42 ± 0.02^{ef}	6.3 ± 0.3^{kl}
Sm	31.7 ± 1.6^{hijklm}	20.4 ± 1.4^{fghi}	2.5 ± 0.2^{fghi}	10 ± 0.5^{ghij}	52.3 ± 5.7^{bc}	16.3 ± 1.0^{bcd}	5.6 ± 0.3^{bcd}	0.34 ± 0.01^{hij}	24.8 ± 0.8^{bcd}
Ss	47.2 ± 1.7^{def}	40.9 ± 0.8^{a}	2.8 ± 0.1^{efgh}	6 ± 0.3^{l}	8.4 ± 0.7^{l}	4.1 ± 0.2^{l}	2.9 ± 0.1^{jkl}	0.70 ± 0.02^{a}	4.9 ± 0.5^{l}
Ab	30.3 ± 1.4^{ijklm}	26.5 ± 1.4^{cdefg}	1.7 ± 0.2^{ijk}	6 ± 0.3^{kl}	28.4 ± 3.3^{defgh}	11.9 ± 0.8^{fghi}	5.1 ± 0.6^{bcde}	0.42 ± 0.02^{efg}	25.2 ± 2.0^{bcd}
Ah	49.0 ± 2.2^{cde}	19.8 ± 2.0^{fghij}	6.3 ± 0.3^{ab}	14 ± 0.7^{defg}	84.2 ± 4.2^{a}	15.3 ± 0.4^{bcde}	8.2 ± 0.2^{a}	0.54 ± 0.02^{c}	18.1 ± 0.3^{efg}
Ao	17.2 ± 0.8^{n}	9.0 ± 0.2^{lm}	0.8 ± 0.1^{l}	6 ± 0.3^{kl}	28.5 ± 2.3^{defg}	9.7 ± 0.5^{hijk}	4.7 ± 0.2^{cdefgh}	0.49 ± 0.01^{cd}	25.7 ± 0.4^{bc}
Mj	37.1 ± 2.0^{fghij}	19.0 ± 1.9^{ghij}	5.0 ± 0.3^{bcd}	12 ± 0.6^{fgh}	13.7 ± 1.3^{jkl}	7.7 ± 0.4^{k}	2.9 ± 0.2^{jkl}	0.37 ± 0.01^{fghi}	15.0 ± 0.4^{ghi}
Nl	22.1 ± 1.2^{mn}	12.4 ± 1.5^{ijklm}	2.5 ± 0.1^{fghi}	7 ± 0.4^{jkl}	35.3 ± 1.7^{cdef}	11.6 ± 0.5^{ghij}	4.8 ± 0.2^{cdef}	0.42 ± 0.01^{efg}	7.6 ± 0.5^{jkl}

Table 2 (continuation). Seedling morphology of 25 species grown in nurseries near rainforestation. Morphology included total height, height at the lowest leaf from the top soil, root collar diameter (rcd) and number of leaflets. Full names of species are listed in Table 1. Data shown in abbreviations are width to length ratio (WLR) and specific leaf area (SLA).Means with standard errors are per species. Significant different means are indicated by different letters (analysis of variance, $p < 0.05$, n = 10).

Species	height	height at the lowest leaf	rcd	Leaf number	Leaf size	Leaf length	Leaf width	WLR	SLA
code	(cm)	(cm)	(mm)	(count)	(cm^2)	(cm)	(cm)	($cm\ cm^{-1}$)	($m^2\ kg^{-1}$)
Pl	25.0 ± 1.2^{lmn}	9.5 ± 0.5^{klm}	2.4 ± 0.2^{ghij}	11 ± 0.6^{fghi}	17.1 ± 1.1^{hij}	8.1 ± 0.3^{k}	3.5 ± 0.1^{fghijk}	0.44 ± 0.01^{def}	32.5 ± 1.2^{a}
Si	23.8 ± 0.9^{mn}	15.0 ± 1.1^{hijkl}	1.3 ± 0.1^{kl}	$6 \pm 0\ 7^{kl}$	84.2 ± 4.2^{defg}	15.3 ± 0.4^{bcde}	8.2 ± 0.2^{a}	0.54 ± 0.02^{c}	21.7 ± 2.5^{cde}
Dpa	43.8 ± 2.9^{defg}	18.1 ± 1.2^{ghijk}	3.6 ± 0.5^{defg}	17 ± 0.9^{cde}	38.3 ± 4.2^{cde}	14.9 ± 0.9^{cdef}	$3.9 \pm 0.2\ ^{efghij}$	$0.26 \pm .0.01^{kl}$	21.0 ± 0.7^{cde}
Vp	38.4 ± 2.2^{efghi}	30.8 ± 1.7^{bcd}	1.4 ± 0.2^{k}	8 ± 0.3^{ijk}	11.8 ± 1.8^{jkl}	7.1 ± 0.5^{kl}	2.6 ± 0.2^{jkl}	0.37 ± 0.01^{fghi}	10.4 ± 0.4^{ijk}
Mean	**37.1**	**20.2**	**3.3**	**13**	**37.3**	**12.1**	**4.6**	**0.40**	**17.2**
Min	**17.2**	**3.9**	**0.8**	**5**	**8.4**	**4.1**	**2.0**	**0.23**	**4.9**
Max	**69.6**	**40.9**	**8.1**	**56**	**84.2**	**21.0**	**8.2**	**0.70**	**32.5**

Data analysis

Descriptive statistics including the mean and standard deviation of measured seedling variables were computed from ten individuals per species. To determine the species-specific maximal stomatal conductance (g_{smax}, mmol $m^{-2}s^{-1}$), we selected the daily maxima of g_s for the two leaves per seedling individual per species and calculated the average. Seedling variables were tested for normal distribution using the Shapiro-Wilk test. Not normally distributed data were log-transformed prior to statistical analysis. The relationship between g_{smax}, seedling morphology and leaf traits was analyzed using simple and multiple linear regressions. One-way analysis of variance (ANOVA) was applied to test for significant differences among the 25 species and a post-hoc Honest Significant Differences (HSD) Tukey´s test was used to assign species to statistically different groups. Spearman´s rank correlation was used to find leaf traits relationship between adult trees and seedlings of the same species. The significance level was set at $p < 0.05$. A combination of multivariate analysis using principal component analysis (PCA) and cluster analysis (CA) was used to determine the association or grouping of seedling species using leaf traits (g_{smax}, leaf size, WLR and SLA). Species-specific leaf trait values used for PCA were standardized prior to PCA, and values were adjusted to maximum prior to CA analysis. Cluster analysis was done to search for patterns in the dataset using leaf traits. Most calculations were performed with the R Programming Software version 2.7.1 (2008), while for the multivariate analysis PC-ORD version 5.12 (2006) was used.

Results

Seedlings leaf traits of 25 species

Species-specific g_{smax} of polybag-grown seedlings of 25 species in the nurseries differed nine-fold (72 to 643 mmol m^{-2} s^{-1}) (Figure 2). Among the species studied, *A. heterophylla* had the highest value followed by *D. zibethinus* and *S. saman* with values over 400 mmol m^{-2} s^{-1}.The lowest g_{smax} was observed in *M. altissima*, a fruit tree species with 72 mmol m^{-2} s^{-1}.

Correlations between seedling g_{smax} and leaf morphology of 25 species

For leaf morphological traits, only leaf WLR showed a simple linear correlation with g_{smax} ($r^2 = 0.20$, $p = 0.03$, $n = 25$, Figure 3). Stepwise regression of leaf variables showed that rcd and WLR explained 28 percent of the variation in g_{smax} ($r^2 = 0.28$, $p = 0.03$, $n = 25$).

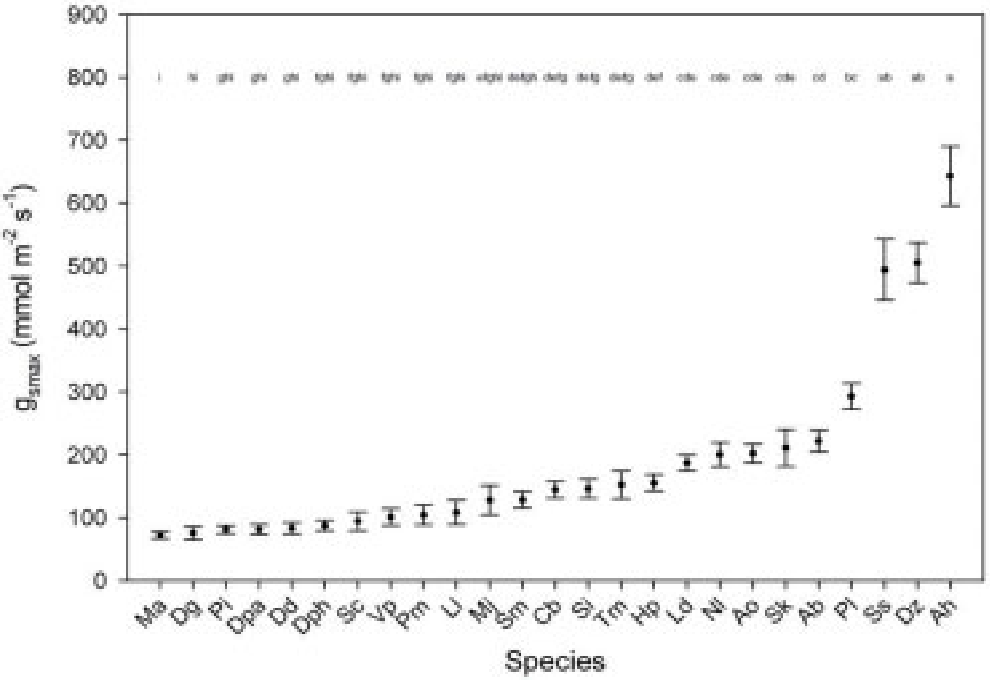

Figure 2. Maximal stomatal conductance (g_{smax}) of 25 species studied. Means are shown with standard error in vertical bars. Significantly different means are indicated by different letters (analysis of variance, $p < 0.05$, $n = 10$). Species abbreviations are found in Table 1.

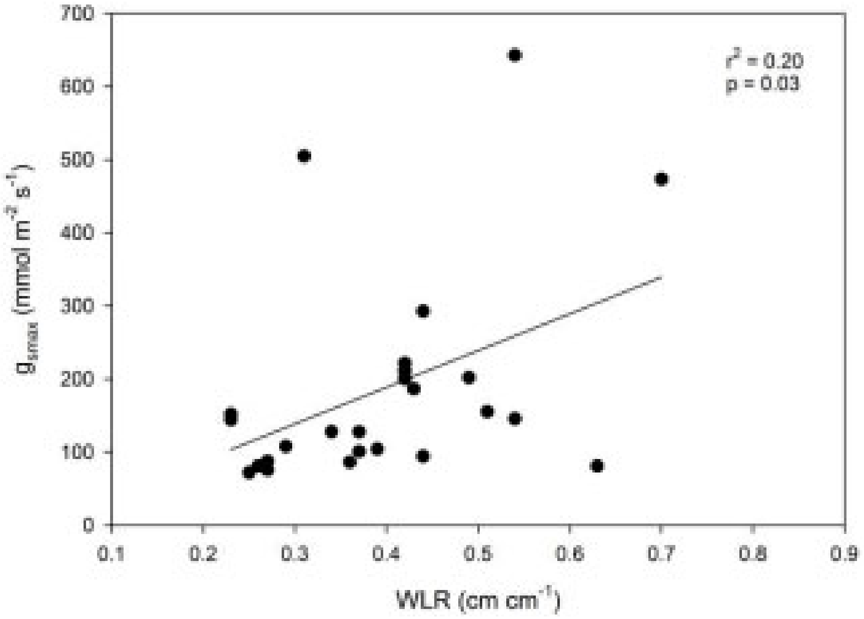

Figure 3. Linear regression analysis of of g_{smax} and leaf width to length ratio of studied species in the nursery (n = 25).

Coordination of seedlings leaf traits of 25 species

Results of the principal component analysis (PCA) showed that two axes still explain 68 percent the first and second principal component axes (PCA 1 and PCA 2) explained 39 and 29 percent of the total variance of leaf traits, respectively (Figure 6a). Higher loadings along PCA 1 indicated species with high g_{smax} and high leaf width to length ratio (WLR) or rounded leaves species, while higher loadings on PCA 2 indicated species with low specific leaf area (SLA). A number of species e.g., *A. heterophylla, S. koetjape, S. indica* and *S. saman* were closely associated with high scores on PCA 1 indicating high g_{smax} and high WLR (Figure 6b). Others however, (e.g., *C. blancoi, T. microcarpa, D. paniculatus, D. philippinensis, L. luzoniense* and *M. altissima*) showed low scores on PCA 1 and thus reflect that they have low g_{smax} values and have low WLR (oblong or elliptic shape). More than half of the species (15) were grouped together in between the measured leaf traits, g_{smax} and WLR.

High scores on PCA 2 for *N. lappaceum, V. parviflora, D. dao, P. indicus, and S. saman* reflected high SLA of these species. *D. zibethinus, S. macrophylla, A. heterophylla, D. grandiflorus, P. luzoniense* and *S. indica* species however were all separated by their distinct characteristics of having high SLA. Leaf size of the seedlings as one of the variables used was more reflected on the third axis of the PCA with less variance (20%). Most species exhibited an intermediate group in terms of the SLA trait.

As a further multivariate approach, hierarchical cluster analysis (CA) was used to look for patterns in the leaf traits data of the 25 species. Euclidean distances approximated the distances between the species and Wards linkage method was used to determine the distances between clusters and to minimize distortion of the data. (McCune and Grace, 2002).

Analysis results suggest that six distinct clusters of species can be distinguished in which more than 70 % information remains (Figure 6).

Cluster 1 was composed of two Artocarpus species (*A. blancoi* and *A. odoratissimus*) and *P. luzoniense*. Both Artocarpus species were very similar to each other with respect to their leaf traits as can be seen from the fact that these species can be grouped without significant loss of information (100% remaining). Cluster 2 consisted of *D. paniculatus, M. altissima, L. luzoniensis, T. microcarpa, D. grandiflorus, P. malaanonan* and *S. macrophylla*. Cluster 3 consisted of *C. blancoi, D. philippinensis, D. dao, M. javanica, V. parviflora, N. lappaceum, H. plagata* and *P. indicus*. Most of these species were native to the country except for exotic fruit tree, *N. lappaceum.* Another cluster (Cluster 4) is composed of fruit tree species, *L. domesticum* and *S. koetjape*, and native species *S. indica* and *S. contorta*. On the other hand, *A. heterophylla* and *D. zibethinus* were in the fifth cluster. However, *S. saman* species was separated from the clustering of species with only 55% remaining information in the leaf traits of this species. Groupings of species suggested by cluster analysis correspond approximately with the groupings of species produced in the PCA. Interestingly, dipterocarp species were found in different clusters i.e. *P. malaanonan* and *D. grandis* were found in cluster 2, *H. plagata* in cluster 3 and *S. contorta* in cluster 4.

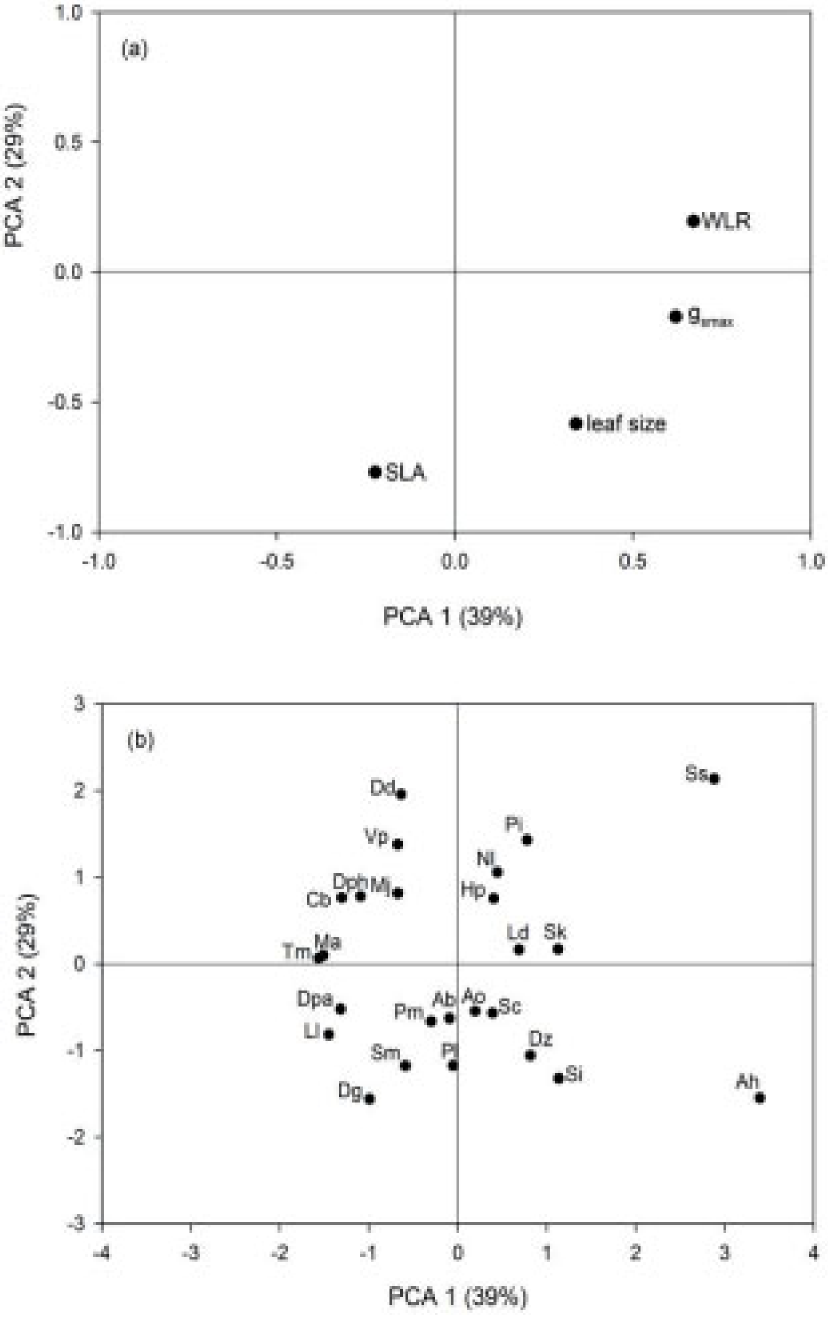

Figure 4. Principal component analysis of seedling g_{smax} and leaf morphological traits of 25 species studied. (a) Loading plots for the PCA 1 (explained variation is 39 percent) and PCA 2 (explained variation is 29 percent). (b) Species loadings on the first and second axes with species abbreviations found in Table 1.

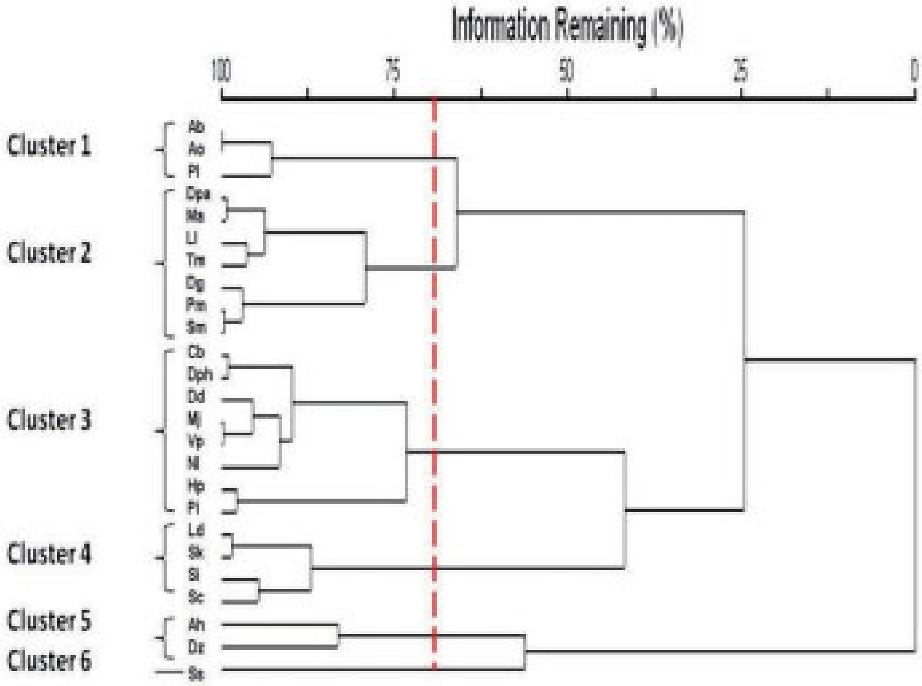

Figure 5. Hierarchical cluster analysis of 25 species according to similarity in their leaf traits. Distances among species was approximated using Euclidean distances and Wards linkage was used to specify the linkage between two clusters. Six clusters of species were found with more than 70 percent information remained after the analysis.

Leaf traits of adults and seedlings

Leaf traits including g_{smax}, leaf size, WLR and SLA of adult trees were significantly different than the seedlings. Species-specific differences are shown in Table 3. Among the thirteen species studied, only *D. zibethinus* does not show a significant difference in terms of g_{smax} of adult versus seedling (unpaired t-test, $t = 0.85$, $df = 5.28$, $p = 0.43$). High differences in g_{smax} were observed in the species *S. macrophylla* and *V. parviflora* (6-fold). Leaf size differences between adult and seedlings were highly significant in two Artocarpus species namely: *A. blancoi* and *A. odoratissimus* with 27-fold and 21-fold differences, respectively. In the comparison between the WLR of adult trees and seedlings, highly significant differences were observed in *A. blancoi, T. microcarpa, C. blancoi* and *N. lappaceum* showing round leaves in adults versus specify shape in seedling ($p < 0.001$). On the other hand, species such as *H. plagata, S. contorta*, *L. domesticum* and *S. macrophylla* showed no significant differences in WLR. Another leaf trait, SLA which is a measure of the thinness of the leaves was used in the comparison. Results showed low SLA values in adult trees compared to seedlings, Table 3. The SLA of leaves of adult *A. odoratissimus* was found to be three-fold lower than of seedlings depicting thicker leaves in adult trees. However, the reverse was found for mature leaves of *S. koetjape,* which were two-fold higher in SLA than in seedlings showing thinner leaves when mature. No significant differences were observed in the species *S. contorta, L. domesticum, V. parviflora* and *C. blancoi* (unpaired t- test, $p > 0.18$).

Correlation among adult and seedling species in terms of their leaf traits was analyzed using Spearmans rank. Results showed no correlation in g_{smax}, leaf size and SLA (Figures 4a, 4c and 4d). However, a highly significant correlation was observed in the WLR of adults versus seedlings ($r_s = 0.74$, $p < 0.001$, $n = 13$, Figure 4b).

Table 3. Species-specific difference in leaf traits between adult trees and seedlings. Leaf variables included maximal stomatal conductance, g_{smax} (in mmol m^{-2} s^{-1}), leaf size, width to length ratio (WLR), and specific leaf area (SLA) (unpaired t-test, $p < 0.05$, $n = 13$).

Species	g_{smax}		leaf size		WLR		SLA	
	p-value	Factor	p-value	Factor	p-value	Factor	p-value	Factor
Hp	0.001	2	<0.001	2	0.39	1	<0.001	0.7
Pm	0.001	4	0.03	1	0.02	1	<0.001	0.6
Sc	0.03	2	0.04	0.8	0.86	1	0.18	0.9
Ld	0.001	2	0.01	2	0.91	1	0.38	0.8
Sk	0.01	2	<0.001	2	0.001	1	<0.001	2.0
Sm	<0.001	6	0.01	1	0.21	1	0.001	0.7
Ab	<0.001	4	<0.001	27	<0.001	2	0.001	0.4
Ao	0.03	2	<0.001	21	0.01	1	<0.001	0.4
Vp	<0.001	6	<0.001	4	0.03	1	0.41	1.0
Dz	0.43	1	<0.001	2	0.04	1	0.001	0.6
Tm	<0.001	5	<0.001	4	<0.001	2	0.01	0.7
Cb	0.03	2	0.01	1	<0.001	1	0.49	0.9
Nl	<0.001	3	<0.001	2	<0.001	1	0.01	1.0

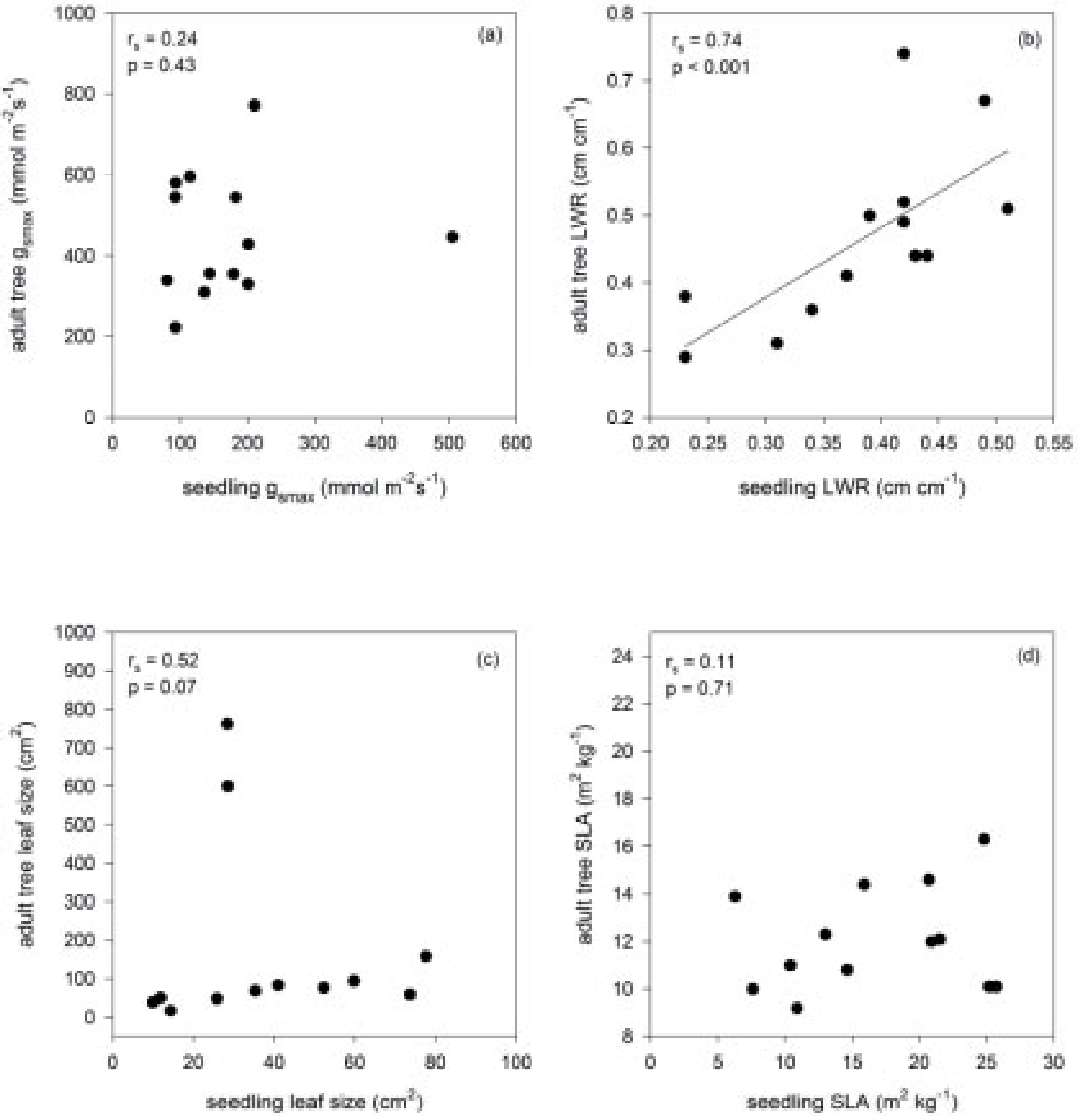

Figure 6. Spearmans rank correlation of seedlings and adult trees of the same species. Leaf traits included (a) maximal stomatal conductance (g_{smax}) (b) leaf width to length ratio (c) leaf size and (d) specific leaf area, ($p < 0.05$, n = 13).

Discussion

g_{smax} of seedlings

Species-specific maximal stomatal conductance among 25 species ranged between 72 and 643 mmol m^{-2} s^{-1}. These results were considerably more variable (ninefold range) than the g_{smax} of adult trees in the first Chapter (fivefold). In particular seedlings of three species namely: *A. heterophylla*, *D. zibethinus* and *S. saman* have high g_{smax} which was unexpected as they grow partly shaded. The highest value was observed in *A. heterophylla*, one of the most important exotic fruit trees in the Philippines (Elevitch and Manner, 2006). It also possesses the largest mean leaf size (84 cm^2) among the seedlings studied. We also observed high leaf conductance in *D. zibethinus* and *S. saman* promoting high CO_2 assimilation rates. These species utilize captured light efficiently, hence encouraging fast growth (Poorter and Bongers, 2006). Seedlings in the nursery grow in pots near the forest floor. They are surrounded by shade trees with canopies serving as natural light filters to direct sunlight. This set up has less canopy cover compared to the natural site condition thus, more light is penetrating the ground floor (R. Sales-Come, pers. obs.). This increases conductance in some species so that greater carbon gain can be attained. Excessive sunlight could damage seedlings as observed in the young dipterocarps seedlings in a gap created forest in Sabah (Brown and Whitmore, 1992). Stomatal conductance and photosynthetic rate (mass and area basis) was found to decrease with increasing leaf life span (Reich et al. 1991). Strong stomatal control to reduce water loss as observed in most species showed seedling adjustment to the shaded conditions in the nursery and for leaf longevity.

Relationship between g_{smax} and leaf morphological traits

Among all leaf traits of 25 species, only leaf width to length ratio (WLR) showed a significant simple linear correlation with g_{smax} although the explained variance was low. Higher WLR represents species with round leaves, which characterizes most pioneers (Ackerly, 1996). Round or expanded leaves can capture more light thus, promoting high photosynthetic capacity which explains the high g_{smax} (Körner, 1994). The possibility to predict g_{smax} of studied species from combined data on WLR and SLA emphasizes the importance of these traits. However, this trait cannot be used independently as a single predictor based on the results of this study. In addition, SLA has a direct link to foliar nitrogen content of species (Reich et al. 1991, 1999). *Samanea saman* and *Pterocarpus indicus* are both nitrogen fixing species but low SLA was observed. Mature leaves of *P. indicus* have high amounts of foliar nitrogen per mass basis (36 g kg^{-1}, Chapter 4, Table 2). This value exceeds the optimum of 30 g kg^{-1} in temperate (van den Burg, 1990) and in some tropical species (Hölscher et al. 2006). Furthermore, leaves of this species contained high amounts of carbon (47%). A possible explanation could be the few and small root nodules in potted seedlings which are responsible for the nitrogen fixation. Limitations to root growth and expansion are common in potted seedlings and may mean that fixation could only start at the later stage of development.

Grouping of species

In our multivariate analysis using PCA, the 25 species were ordinated according to four leaf traits (g_{smax}, leaf size, WLR and SLA). The main leaf traits determine the species scores were high g_{smax} and round leaves or high WLR. Distinct grouping of species was observed with *A. heterophylla, S. koetjape, S. indica* and *S. saman* having similar leaf traits that were mentioned above. These traits characterize typical early successional species (Juhrbandt et al. 2004; Ackerly, 1996, Bazzaz, 1991). The opposite side of the axis showed grouping of species such as *C. blancoi, T. microcarpa, D. paniculatus, D. philippinensis, L. luzoniense* and *M. altissima* with low g_{smax} and low WLR. In comparison, grouping of dipterocarps in the first chapter i.e. low g_{smax} and low WLR was not observed among the species atseedling stage (*P. malaanonan, S. contorta, H.plagata* and *D. grandiflorus*) and were found in the middle of the axis or with intermediate values of g_{smax} and WLR. These may be a strategy of dipterocarps at seedling stage for their growth and survival that changesas they mature.

The main contributors to high values in PCA 2 axis were decreasing SLA values. *N. lappaceum, V. parviflora, D. dao, P. indicus* and *S. saman* seem to form a group with low SLA values. These species may characterize slow leaf investmentand a longer leaf life span which in general results in tougher leaves (Reich et al. 1991). Interestingly, this finding is contradictory to the characteristic of pioneers. Mature leaves of *V. parviflora, D. dao* and *P. indicus,* have high SLA values (Chapter 4). This particular trait differs as species mature particularly for the species mentioned. Thus, it could be difficult to assess the successional position using this trait alone especially at seedling stage. *S. saman* species showed a distinctive trait with high g_{smax} but with low SLA. Based on observation, seedling leaflets of this pinnate-leaved species are thin compare to mature leaves of trees planted around VSU campus. Unfortunately, only one *S. saman* tree was found in Patag rainforestation, hence not enough samples were available to be included in the study. The opposite side of axis 2 grouped the species *D. zibethinus, S. macrophylla, A. heterophylla, P. luzoniense S. indica* and *D. grandiflorus* with increasing SLA. These species share the same leaf traits and were described as physiologically active species with fast leaf growth rates but with short leaf lifespan (Reich et al., 1991, 1992, 1999). High leaf conductance observed in seedlings of *D. zibethinus, S. indica* and *A. heterophylla* facilitate high assimilation rates that enable them to capture and utilize more light thus encouraging increase in growth and good seedling performance (Poorter and Bongers, 2006). Grouping of dipterocarps species according to SLA traits was not found. *P. malaanonan* and *S. contorta* were located in the middle of the axis which means that they have intermediate SLA values. However, contrasting SLA values in *H. plagata* (low SLA, intermediate g_{smax}) and *D. grandiflorus* (high SLA, low g_{smax}) wereobserved. This follows the strong inverse relationship found in mature leaves in Chapter 3. A study on successional classification of tropical rainforest species in French Guiana suggests a classification of late successional species into fast-growing and slow-growing (Bonal et al., 2007). Our data implies that *H. plagata* possess leaf traits that characterize slow-growing species while *D. grandiflorus* may be grouped under fast-growing late succesional species with low g_{smax} and high SLA.

Among the studied dipterocarps, *S. contorta* showed no significant difference in SLA and WLR between leaves in seedlings and adult trees. This may imply that this species can already establish leaf structural traits known to fast-growing species. A study conducted by Utsugi et al. (2009) on growth and photosynthesis performance of *S. contorta* and *D. grandiflorus* revealed a fast-growing characteristic of these species when planted in open bare ground. Our results suggest that dipterocarp species indeed posses special leaf traits as also observed by the strong inverse correlation in g_{smax} and SLA of adult trees in Chapter 3. Further investigation however is necessary as limited number of species were used in this study.

Using CA, six clusters or grouping of species were found according to their association using the above mentioned leaf traits. In the first cluster, two Artocarpus species were both associated with their g_{smax}, SLA and WLR. High association in adult trees of the same species was also observed (low SLA, high WLR and moderate to high g_{smax}) which may suggest that these species are exhibiting similar traits at seedling stage. *P. luzoniensis* which also belong in this cluster has intermediate g_{smax} but with the highest SLA among all seedlings studied. This species is deciduous and has leathery leaves when adult and is known to produce latex.

The association of species in the second cluster was explained by their low g_{smax}, and low WLR. Most native species are found in this cluster together with the exotic species *S. macrophylla*. Leaf morphological traits however in seedling stage were found to vary from adult leaves of this species, referring to the values observed in Chapter 3. Cluster three species on the other hand were grouped according to low SLA of species. This trait is known to species that invest a lot in their leaf structure and is characteristic for late successional species. These are known to have longer leaf life span (Reich et al. 1991, 1999). This group of species needs to have this certain trait in order to minimize damage from herbivores especially in the understorey (Coley et al. 1995) and to increase their chance of survival under shade (Reich et al., 1991; 1999; Poorter and Bongers, 2006). Interestingly, in potted seedlings this trait is not well express in known shade tolerant species for example the dipterocarps. Only *H. plagata* showed a low SLA. Pioneers like *P. indicus, D. dao* and *V. parviflora* were also found in this group, which is in contrast to their normal traits when mature with high SLA. These traits may however change as these species mature. One explanation could be the condition in the nursery which is different from the real situation in the field.

Cluster four is composed of species with high g_{smax} and with greater leaf size and round leaves. *L. domesticum*, *S. koetjape, S. indica* and *S. contorta* are all native species. Seedling leaf traits from these species characterize fast-growing with high leaf turn-over (Reich et al. 1991; Poorter and Bongers, 2006). *S. contorta*, known to be a shade-tolerant dipterocarp species was interestingly found in this group. Previous studies revealed that this species performs well when planted in open areas (Utsugi et al.2009). Cluster five formed by these fruit trees (*A. heterophylla* and *D. durian*) showed physiologically active leaves which have high growth but may have low survival rates in the field (Poorter and Bongers, 2006). *S. saman* forms a separate cluster as its traits deviate from the usual continuum of leaf traits i.e. high g_{smax}, high SLA of pioneer species. Seedlings of this species haveless number of leaves when young (mean of 6 leaflets in 10 seedlings, Table 2).Extremely low SLA may imply a strategy of this species to avoid further damage from herbivory to ensure survival (Coley et al. 1985). The separation of species in our study according to their life history (early or late successional) was not clear as most of them, especially fruit trees were domesticated and some are exotics. Leaf traits observed also do not agree with the successional position of the species studied.

Leaf morphological traits comparison between seedlings and adult trees

Significant differences in g_{smax} between seedlings and adult trees were found. This is similar to the finding of Thomas and Winner (2002) that gas exchange rates in seedlings are greater than in adult trees. Moreover, various studies compiled by Körner in 1994 showed that young leaves grown under protected condition, for example in the nurseries, exhibit lower stomatal responses than leaves from the upper part of the vegetation in the field. Among the 13 species of seedlings with similar adult species, only *D. zibethinus* showed no significant difference in the g_{smax} values. Although no measurement on the leaf anatomical features was done e.g. cell size, stomatal size and density, this species (*D. zibethinus*) might have already traits like leaves of adults. Moreover, this species grows fast during early years of development with its main shoot axis and main root grow in a balance wayor in radial symmetry (PROSEA, 1982) which suggest good provision of water from the roots to the leaves resulting to its high g_{smax}. *D. durian* has leaf investment strategies i.e. high SLA, high g_{smax} that cater its fast-growing characteristic. Margraf and Milan (1996) classified most fleshy fruit trees under late successional species. However, based on the result of this study, *A. heterophylla* and *D. durian* showed g_{smax} and other leaf traits similar to pioneer species e.g. high g_{smax}, high SLA (Juhrbandt et al., 2004). In addition, pioneers have large cells and less densely packed stomata which makes it difficult to control water loss by these species (Ackerly, 1996).

In the comparison of leaf morphological traits, *S. contorta* exhibited an exceptional characteristic with seedlings being similar to adult. This may entail traits that should cater to its demand for light as a fast growing dipterocarp species (Weidelt and Banaag, 1982, Utsugi et al. 2009). In contrast, low g_{smax} observed in seedling and adult stage may imply a special trait, i.e. tolerance to water and nutrient deficient sites like open bare grounds as already suggested in the study of Utsugi et al. 2009. *L. domesticum* is a native fruit tree showing similar traits observed in *S. contorta* and may also be a potential species for open sites.

S.macrophylla and *H.plagata* seedlings possess traits similar to adults, however with lower WLR in the former. On the other hand, *V. parviflora* and *C. blancoi* have the same SLA values observed (intermediate) in seedlings and adult leaves. Results suggest leaf structural traits of these species which are already evident at seedling stage and may be decisive to their performance in the field.

Summary and Conclusion

Species leaf characterization and leaf water conductance at seedlings stage appear to provide important information on the requirements of species prior to outplanting. Overall, associations of seedling species with distinct leaf traits including g_{smax} as variables indicate species leaf investment strategies, which may be critical to whole plant performance. Grouping of species according to known successional position was not apparent in some species. Hence, leaf traits of most species at seedling stage characterized an intermediate status (in between late and early succession). This suggests an acclimation of species to limited light condition in the nursery. Findings from this study showed that seedling characteristics in some species change as they mature and may not clearly reflect the successional status. In addition, an assessment of leaf traits and performance at mature states may not necessarily be indicative for leaf traits and performance at the seedling stage, which may be of great importance for reforestation success.

Recommendations for rainforestation nursery management

Seedling production for the purpose of establishing rainforestation stands should be given enough attention in order to attain quality planting materials. Care must be taken starting from the collection of the seeds to be raised in the nursery up to the time when the seedlings are ready for outplanting. A limited number of mother trees are available as seed sources in Leyte. Thus, this could promote inbreeding of planting materials which may reduce the quality of the future stands. In this case, collection of seeds from certified seed production areas or from natural vegetation with identified plus trees are highly recommended. Furthermore, investigations on the species-specific light requirement of native species are deemed vital. Optimal light conditions in the nursery could prepare seedling better prior to outplanting. Hence may increase the chance of survival and the attainment of quality growth performance in the field. Identification of the most suitable approach to seedling production for some species is also important. This could be done through an artificial way aside from growing them in polybags (e.g. bareroot, direct seedling). High survival can be attained through direct seeding in *S. macrophylla* which could reduce high cost polybags. Last point is the grading of seedlings prior to distribution for outplanting. This should be strictly implemented in order to ensure quality planting materials that could adapt and survive well in the field.

CONCLUSIONS

Species-specific characterization in schemes to reforestation in terms of functional diversity is important. For this study, a pioneering work to assess reforestation in terms of leaf traits founded a basis on the functional diversity in co-occurring species. Leaf water conductance of the species, as an important physiological trait that predicts the growth performance of tropical trees was significantly different between species studied. Although, minor correlations between leaf traits and g_{smax} were found in some species, an important dipterocarp family showed high correlations. Along the successional gradient, this family may show slightly different characteristics from the other species in the reforestation sites. In the seedling study, a conclusion can be drawn that an assessment of leaf traits and performance at mature states may not necessarily be indicative for leaf traits and performance at the seedling stage, which may be of great importance for reforestation success.

Overall, association of species with distinct leaf traits in rainforestation may indicate leaf investment strategies, which may be critical to whole plant performance such as growth and mortality. Leaf traits information may help to adjust the species combination in further developments of the reforestation scheme to specific goals. The relatively high variability in leaf traits among co-occurring tree species suggests that the multi-species reforestation is already quite successful in – at least partly - restoring the functional variability of the former natural forest.

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Appendix table 1. Most frequent tree families found in Cienda rainforestation stand in Baybay, Leyte. Inventory was conducted in April, 2007. The total number of family was 24. Total area is 1.0 hectare. Only trees with diameter at breast height of more than 7 cm were considered in the inventory.

Family name	No. of occurrence (count)	Frequency (%)	No. of trees per hectare
Moraceae	6	25	6
Dipterocarpaceae	4	17	4
Fabaceae	3	13	3
Guttiferae	2	8	2
Meliaceae	2	8	2
Podocarpaceae	2	8	2
Verbenaceae	2	8	2
Anacardiaceae	1	4	1
Araucariaceae	1	4	1
Bignoniaceae	1	4	1
Bombacaceae	1	4	1
Caesalpiniaceae	1	4	1
Casuarinaceae	1	4	1
Combretaceae	1	4	1
Euphorbiaceae	1	4	1
Leguminosae	1	4	1
Lythraceae	1	4	1
Malvaceae	1	4	1
Mimosaceae	1	4	1
Myrtaceae	1	4	1
Olocaceae	1	4	1
Rubiaceae	1	4	1
Sinaroubaceae	1	4	1
Sterculiaceae	1	4	1

Appendix table 2. Most frequent tree families found in Marcos rainforestation stand in Baybay, Leyte. Inventory was conducted in April, 2007. The total number of family was 28. Total area is 0.4 hectare. Only trees with diameter at breast height of more than 7 cm were considered in the inventory.

Family name	No. of occurrence (count)	Frequency (%)	No. of trees per hectare
Moraceae	7	25	18
Dipterocarpaceae	4	14	10
Meliaceae	4	14	10
Verbenaceae	4	14	10
Anacardiaceae	3	11	8
Fabaceae	3	11	8
Burseraceae	2	7	5
Mimosaceae	2	7	5
Sterculiaceae	2	7	5
Annonaceae	1	4	3
Araliaceae	1	4	3
Bombacaceae	1	4	3
Combretaceae	1	4	3
Euphorbiaceae	1	4	3
Flacourtiaceae	1	4	3
Guttiferae	1	4	3
Lauraceae	1	4	3
Lecythidaceae	1	4	3
Linaceae	1	4	3
Lythraceae	1	4	3
Myricaceae	1	4	3
Myrtaceae	1	4	3
Pandanaceae	1	4	3
Sapindaceae	1	4	3
Sapotaceae	1	4	3
Tiliaceae	1	4	3
Urticaceae	1	4	3
Unidentified	1	4	3

Appendix table 3. Most frequent tree families found in Patag rainforestation stand in Baybay, Leyte. Inventory was conducted in April, 2007. The total number of family was 17. Total area is 0.3 hectare. Only trees with diameter at breast height of more than 7 cm were considered in the inventory.

Family name	No. of occurrence (count)	Frequency (%)	No. of trees per hectare
Dipterocarpaceae	5	31	17
Moraceae	4	25	13
Guttiferae	3	19	10
Meliaceae	3	19	10
Fabaceae	2	13	7
Verbenaceae	2	13	7
Euphorbiaceae	1	6	3
Lauraceae	1	6	3
Mimosaceae	1	6	3
Myricaceae	1	6	3
Oxalidaceae	1	6	3
Sapindaceae	1	6	3
Sapotaceae	1	6	3
Sterculiaceae	1	6	3
Tiliaceae	1	6	3
Urticaceae	1	6	3
Unidentified	1	6	3

Appendix table 4. Most frequent tree species found in Cienda rainforestation stand.

Common name	Scientific name	Family name	No. of occurrence (count)	Freq (%)	No. of trees per hectare
Kalumpit	*Terminalia microcarpa*	Combretaceae	183	17.8	183
White lauan	*Shorea contorta*	Dipterocarpaceae	118	11.5	118
Molave	*Vitex parviflora*	Verbenaceae	117	11.4	117
Bitanghol	*Calophyllum blancoi*	Guttiferae	114	11.1	114
Bagtikan	*Parashorea malaanonan*	Dipterocarpaceae	100	9.7	100
Thailand acacia	*Acacia siamea*	Caesalpiniaceae	58	5.6	58
Antipolo	*Artocarpus blancoi*	Moraceae	54	5.3	54
Agoho	*Casuarina equisetifolia*	Casuarinaceae	49	4.8	49
Suyapao	*Commersonia bartramia*	Sterculiaceae	35	3.4	35
Narra	*Pterocarpus indicus*	Fabaceae	29	2.8	29
Malakauayan	*Podocarpus rumphiana*	Podocarpaceae	26	2.5	26
Yakal kaliot	*Hopea malibato*	Dipterocarpaceae	19	1.9	19
Teak	*Tectona grandis*	Verbenaceae	15	1.5	15
Anubing	*Artocarpus ovatus*	Moraceae	13	1.3	13
Paguringon	*Cratoxylum sumatranum*	Guttiferae	12	1.2	12
Dao	*Dracontomelon dao*	Anacardiaceae	10	1.0	10
Marang	*Artocarpus odoratisimus*	Moraceae	10	1.0	10
Tibig	*Ficus nota*	Moraceae	9	0.9	9
Bagalunga	*Melia dubia*	Meliaceae	7	0.7	7
Malubago	*Hibiscus tiliaceus*	Malvaceae	7	0.7	7
Unidentifed			6	0.6	6
Nangka	*Artocarpus heterophylla*	Moraceae	5	0.5	5
African tulip	*Spathodea campanulata*	Bignoniaceae	3	0.3	3
Almaciga	*Agathis philippinensis*	Araucariaceae	3	0.3	3
Ipil	*Intsia bijuga*	Liguminosae	3	0.3	3
Kariskis	*Albizia lebbekoides*	Mimosaceae	3	0.3	3
Bahai	*Ormosia calavensis*	Fabaceae	2	0.2	2
Hindang laparan	*Myrica javanica*	Moraceae	2	0.2	2
Tamayuan	*Strombosia philippinensis*	Olacaceae	2	0.2	2
Yakal saplungan	*Hopea plagata*	Dipterocarpaceae	2	0.2	2
Banaba	*Lagerstroemia speciosa*	Lythraceae	1	0.1	1
Bayabas	*Psidium guajava*	Myrtaceae	1	0.1	1
Binunga	*Macaranga tanarius*	Euphorbiaceae	1	0.1	1
Bitaog	*Calophyllum inophyllum*	Guttiferae	1	0.1	1
Coffee	*Coffea arabica*	Rubiaceae	1	0.1	1
Durian	*Durio zibethinus*	Bombacaceae	1	0.1	1
Langil	*Albizia lebbek*	Fabaceae	1	0.1	1
Mahogany	*Swietenia macrophylla*	Meliaceae	1	0.1	1
Malaalmaciga	*Podocarpus blumei*	Podocarpaceae	1	0.1	1
Malasapsap	*Ailanthus integrifolia*	Simaroubaceae	1	0.1	1
Santol	*Sandoricum koetjape*	Meliaceae	1	0.1	1

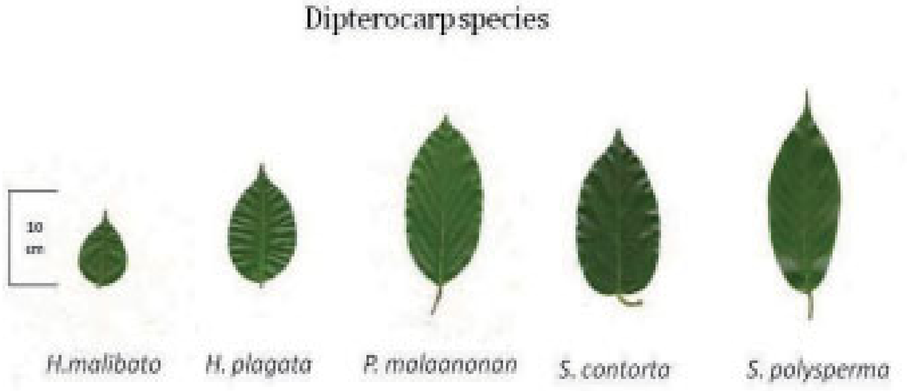
Appendix table 5. Most frequent tree species found in Marcos rainforestation stand.

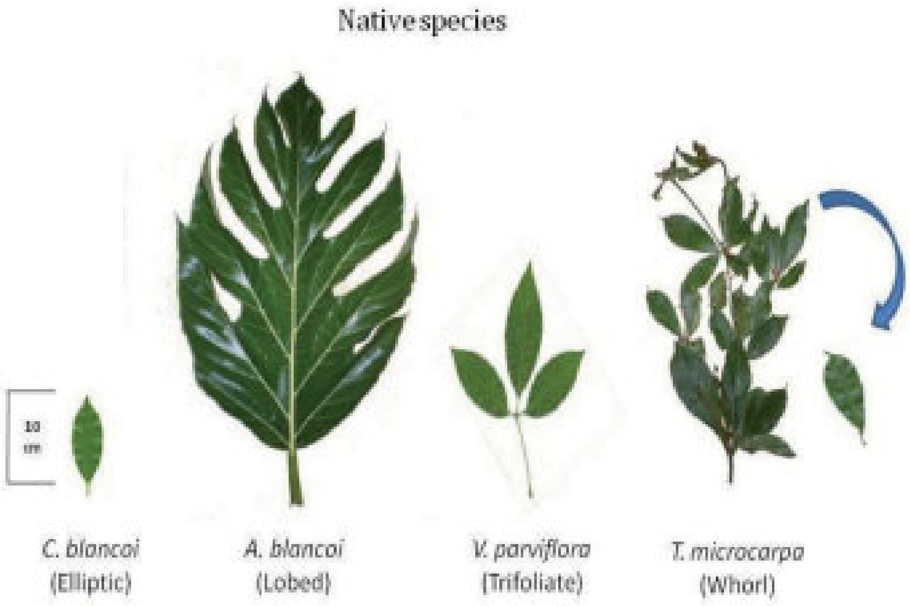
Common name	Scientific name	Family name	No. of occur. (count)	Freq (%)	No. of trees per hectare
Rambutan	*Nephelium lappaceum*	Sapindaceae	34	8.6	85
Molave	*Vitex parviflora*	Verbenaceae	29	7.3	73
Dao	*Dracontomelon dao*	Anacardiaceae	27	6.8	68
Antipolo	*Artocarpus blancoi*	Moraceae	24	6.1	60
White lauan	*Shorea contorta*	Dipterocarpaceae	22	5.6	55
Bagalunga	*Melia dubia*	Meliaceae	21	5.3	53
Hindang Laparan	*Myrica javanica*	Myricaceae	21	5.3	53
Santol	*Sandoricum koetjape*	Meliaceae	17	4.3	43
Durian	*Durio zibethinus*	Bombacaceae	16	4.0	40
Narra	*Pterocarpus indicus*	Fabaceae	16	4.0	40
Lingo-lingo	*Vitex turczaninowii*	Verbenaceae	14	3.5	35
Lansones	*Lansium domesticum*	Meliaceae	13	3.3	33
Bahai	*Ormosia calavensis*	Fabaceae	12	3.0	30
Yakal saplungan	*Hopea plagata*	Dipterocarpaceae	12	3.0	30
Marang Banguhan	*Artocarpus odoratissima*	Moraceae	11	2.8	28
Anubing	*Artocarpus ovatus*	Moraceae	10	2.5	25
Alagasi	*Leucosyke capitellata*	Urticaceae	7	1.8	18
Cacao	*Theobroma cacao*	Sterculiaceae	7	1.8	18
Malapanau	*Dipterocarpus kerrii*	Dipterocarpaceae	7	1.8	18
Nangka	*Artocarpus heterophylla*	Moraceae	7	1.8	18
Kalumpit	*Terminalia microcarpa*	Combretaceae	6	1.5	15
Alagau	*Premna odorata*	Verbenaceae	5	1.3	13
Anilau	*Colona serratefolia*	Tiliaceae	5	1.3	13
Gmelina	*Gmelina arborea*	Verbenaceae	5	1.3	13
Guyabano	*Annona muricata*	Annonaceae	5	1.3	13
Bitanghol	*Calophyllum blancoi*	Guttiferae	4	1.0	10
Toog	*Petersianthus quadrialatus*	Lecythidaceae	4	1.0	10
Dapdap	*Erythrina orientalis*	Fabaceae	3	0.8	8
Milipili	*Canarium hersutum*	Burseraceae	3	0.8	8
Amugis	*Koordersiodendron pinnatum*	Anacardiaceae	2	0.5	5
Ipil-Ipil	*Leucaena leucocephala*	Mimosaceae	2	0.5	5
Layugan	*Pandanus exaltus*	Pandanaceae	2	0.5	5
Mahogany	*Sweitenia macrophylla*	Meliaceae	2	0.5	5
Mangga	*Mangifera indica*	Anacardiaceae	2	0.5	5
Nato	*Palaquium luzoniense*	Sapotaceae	2	0.5	5
Sinaligan	*Sterculia feruginea*	Sterculiaceae	2	0.5	5
Tibig	*Ficus nota*	Moraceae	2	0.5	5
Avocado	*Lagerstromia speciosa*	Lauraceae	1	0.3	3
Banaba	*Lagerstroemia speciosa*	Lythraceae	1	0.3	3
Binunga	*Macaranga tanarius*	Euphorbiceae	1	0.3	3
Governor´s plum	*Flacourtia jangomas*	Flacourtiaceae	1	0.3	3
Hagakhak	*Dipterocarpus validus*	Dipterocarpaceae	1	0.3	3
Kubi	*Artocarpus nitidus*	Moraceae	1	0.3	3
Malapapaya	*Polysias nodosa*	Araliaceae	1	0.3	3
Mangium	*Acacia mangium*	Mimosaceae	1	0.3	3
Piling liitan	*Canarium luzonicum*	Burseraceae	1	0.3	3
Sudiang	*Ctenolophan parvifolius*	Linaceae	1	0.3	3
Tambis	*Syzygium aqueum*	Myrtaceae	1	0.3	3
Tangisang bayawak	*Ficus varigata*	Moraceae	1	0.3	3
Unidentified 6	-	-	1	0.3	3

Appendix table 6. Most frequent tree species found in Patag rainforestation stand.

Common name	Scientific name	Family name	No. of occur. (count)	Freq. (%)	No. of trees per hectare
White lauan	*Shorea contorta*	Dipterocarpaceae	169	37.5	563
Bagtikan	*Parashorea malaanonan*	Dipterocarpaceae	59	13.1	197
Yemane	*Gmelina arborea*	Verbenaceae	43	9.5	143
Tanguile	*Shorea polysperma*	Dipterocarpaceae	41	9.1	137
Mahogany	*Swietenia macrophylla*	Meliaceae	34	7.5	113
Yakal kaliot	*Hopea malibato*	Dipterocarpaceae	21	4.7	70
Antipolo	*Artocarpus blancoi*	Moraceae	17	3.8	57
Cacao	*Theobroma cacao*	Sterculiaceae	10	2.2	33
Unidentified	-	-	9	2.0	30
Molave	*Vitex parviflora*	Verbenaceae	5	1.1	17
Alagasi	*Leukosyke capitellata*	Urticaceae	5	1.1	17
Caimito	*Chrysophyllum caimito*	Sapotaceae	4	0.9	13
Santol	*Sandoricum koetjape*	Meliaceae	4	0.9	13
Bitanghol	*Calophyllum blancoi*	Guttiferae	4	0.9	13
Yakal saplungan	*Hopea malibato*	Dipterocarpaceae	4	0.9	13
Alahan	*Guiea koelreuteria*	Sapindaceae	3	0.7	10
Tibig	*Ficus nota*	Moraceae	3	0.7	10
Anubing	*Artocarpus ovatus*	Moraceae	2	0.4	7
Nangka	*Artocarpus heterophylla*	Moraceae	2	0.4	7
Avocado	*Persia gratissima*	Lauraceae	2	0.4	7
Balobo	*Diplodiscus paniculatus*	Tiliaceae	1	0.2	3
Balimbing	*Averrhoa carambola*	Oxalidaceae	1	0.2	3
Hindang laparan	*Myrica javanica*	Myricaceae	1	0.2	3
Rain tree	*Samanea saman*	Mimosaceae	1	0.2	3
Lansones	*Lansium domesticum*	Meliaceae	1	0.2	3
Bitaog	*Calophyllum inophyllum*	Guttiferae	1	0.2	3
Anii	*Erythrina fusca*	Fabaceae	1	0.2	3
Narra	*Pterocarpus indicus*	Fabaceae	1	0.2	3
Anislag	*Securinega flexousa*	Euphorbiaceae	1	0.2	3
Salingogon	*Cratoxyllum formosum*	Clusiaceae	1	0.2	3

Appendix figures. Photos of the leaves of the species studied in rainforestation.

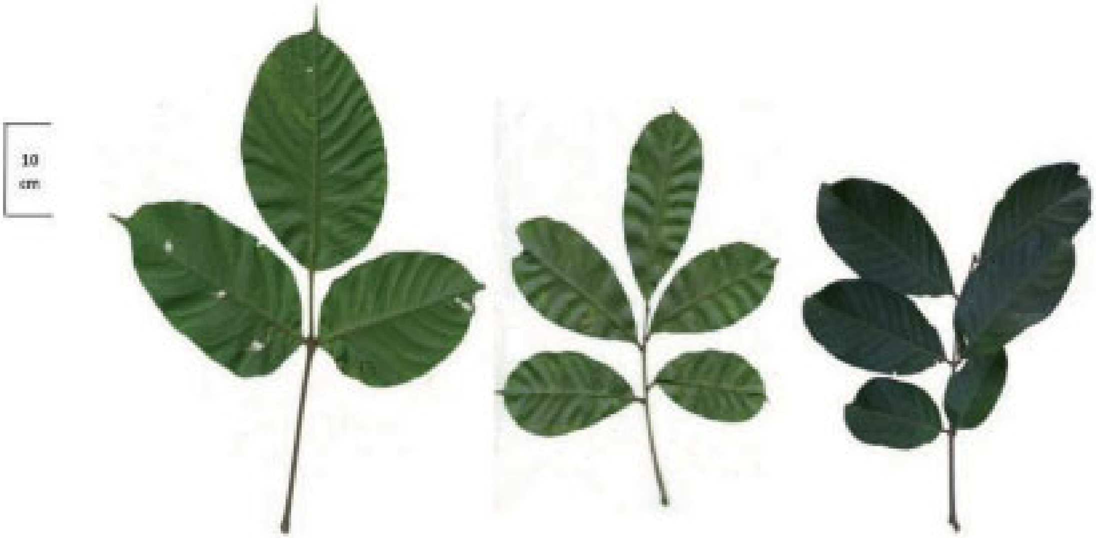




Exotic species

D. zibethinus *A. odoratissimus* *G. arborea* *S. macrophylla*

Fruit tree species with compound leaves



S. koetjape *L. domesticum* *N. lappaceum*

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DECLARATION OF HONOR

I hereby declare that I am the sole author of this dissertation entitled "Variability and grouping of tree leaf traits in multi-species reforestation (Leyte, Philippines)" and that all references and data sources used have been acknowledged as such. I further declare that this work has never been submitted in any form as part of other dissertation procedures.

Göttingen, February 2010 ____________________________

(Renezita Sales-Come)