Forest Ecology and Management 260 (2010) 846–855

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Variability and grouping of leaf traits in multi-species reforestation (Leyte, Philippines)

Renezita Sales-Come[a,b,*], Dirk Hölscher[a]

[a] Tropical Silviculture and Forest Ecology, Burckhardt Institute, Georg August University of Göttingen, Büsgenweg 1, 37077 Göttingen, Germany
[b] College of Forestry and Natural Resources, Visayas State University, Visca 6521-A, Baybay, Leyte, Philippines

ARTICLE INFO

Article history:
Received 20 November 2009
Received in revised form 29 April 2010
Accepted 3 June 2010

Keywords:
Dipterocarps
Exotic species
Functional diversity
Maximal stomatal conductance
Rainforestation
Species groups

ABSTRACT

Conventional reforestation in the tropics often results in stands with low tree species and functional diversities. A different approach to reforestation, the so-called rainforestation, has been developed in the Philippines. It emphasizes mixed stands and the preferential use of native species supplemented by fruit trees. In such stands, we studied several functional leaf traits (stomatal conductance for water vapour, leaf morphology and chemistry) with the objectives (1) of assessing the species-specific variation of leaf traits and in particular that of maximal leaf stomatal conductance (g_{smax}), (2) of determining relationships between g_{smax} and other tree variables, and (3) of assessing whether leaf traits group the species studied. Sixteen broad-leaved species were studied, using five individual trees per species and ten fully expanded sunlit leaves per individual tree. Species-specific g_{smax} differed fivefold (165–772 mmol m^{-2} s^{-1}). Among studied leaf traits, only the carbon isotope ratio δ^{13}C exhibited a simple linear correlation with g_{smax}. A separate analysis for dipterocarp species indicated a strong negative relationship between g_{smax} and specific leaf area (SLA) ($r^2 = 0.96$, $P < 0.001$, $n = 5$). For all 16 species, a multiple linear regression with the combinations leaf size/tree height and leaf size/canopy projection area also resulted in significant relationships, which partly explained the variability in g_{smax}. A multivariate approach (principal component analysis) combining the leaf traits provided an explanation of 75% of the variability along the first two axes. All native dipterocarps species, a native Guttiferae and the durian tree (*Durio zibethinus*) were associated with more depleted δ^{13}C, small leaves and a low leaf width to length ratio. Two exotic species frequently used for reforestation (*Gmelina arborea* and *Swietenia macrophylla*) and the native early successional *Terminalia microcarpa* were differentiated by their high SLA and high leaf nitrogen content per leaf area (N_{area}). Both species of *Artocarpus* (*A. blancoi* and *A. odoratissima*) were also differentiated 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 imply that there are differences in whole plant performance. We conclude that rainforestation creates substantial variation in leaf traits, which is based on the combination of species with different leaf trait groupings. This can be seen as an important step towards – partly – restoring the functional diversity which characterizes many natural tropical rainforests.

1. Introduction

Natural rainforests in the tropics are typically highly diverse in tree species and exhibit a substantial functional variability. After conversion to other land use systems, much of this variability is lost. Thus-far, reforestation in the tropics often relies on a few species, which are often planted in monospecific stands. Such stands contribute little to conservation (Lamb et al., 2005), and studies addressing more appropriate tree species selection and species mixtures are currently being conducted (Wishnie et al., 2007; Potvin and Dutilleul, 2009). In particular when restoration of a near-natural forest is among the goals of reforestation, functional diversity may be a criterion for species selection and composition.

Forests and their trees play an important role in the exchange of water vapour with the atmosphere via 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). The maximal leaf stomatal conductances (g_{smax}) of the sun leaves of tropical tree species vary 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

---

[*] Corresponding author at: Visayas State University, College of Forestry and Natural Resources, Visca, Baybay, Leyte 6521-A, Philippines. Tel.: +49 551 399556; fax: +49 551 394019.
E-mail addresses: rcome@gwdg.de, rfs_lsu@yahoo.com (R. Sales-Come).

0378-1127/$ – see front matter © 2010 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2010.06.002

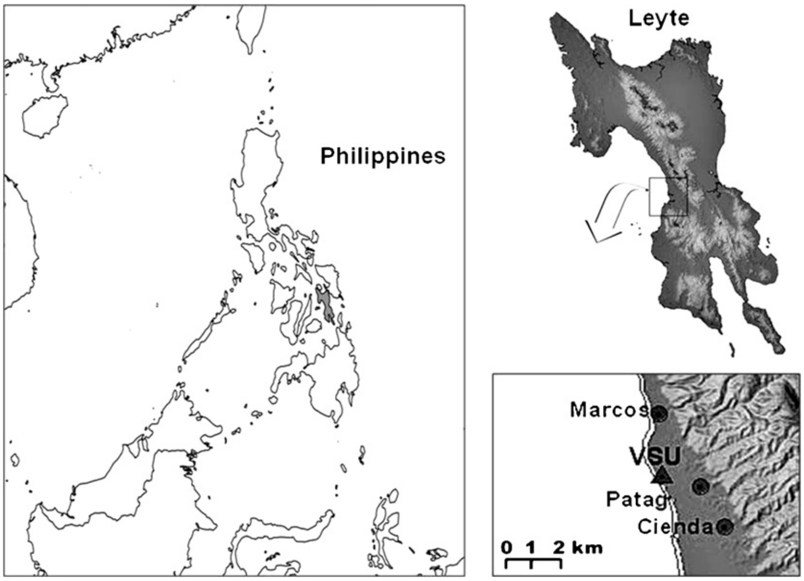

Fig. 1. Location of the rainforestation plots in three villages, namely: Marcos, Patag and Cienda on Leyte, Philippines. Map shows the proximity of the study sites to Visayas State University (VSU).

trait data, Wright et al. (2004) described a universal spectrum of leaf traits that extends from rapid to slow return of invested resources and functions independently of plant functional types. Thus, leaf traits that are relatively easy to assess, such as specific leaf area, leaf area per leaf dry weight (SLA, m^2 kg^{-1}), may be used to predict other functional leaf traits such as stomatal conductance. Additionally, plant performance, for example, growth and survival, may be predicted on the basis of leaf traits. A high variability in leaf traits was found between 53 co-existing rainforest species in Bolivia (Poorter and Bongers, 2006). Their study demonstrated that species with short-lived, physiologically active leaves have high growth rates but low survival rates and vice versa, thus demonstrating that leaf traits can be used to predict plant performance.

Our study was conducted in the Philippines, which has only 3% primary forest cover countrywide (ESSC, 1999; Myers et al., 2000). The Philippines are a very important world biodiversity hotspot with a large number 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, which are planted in mixed stands with fruit trees (Margraf and Milan, 1996). 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 not currently available. From the existing data from various biomes, Reich et al. (1999) found that leaf traits suggest the successional position which 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 exhibit rapid growth rate. This could be used as a guide to assess species with unknown successional classification.

In three 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.

2. Methods

2.1. Study site

This study was conducted in Leyte in the Eastern Visayas, Philippines. The three study 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) (Fig. 1). Criteria for site selection were the comparability of the climate, the volcanic origin of the soil, the richness in tree species and similarity in altitudinal setting. The proximity from one study site to another was small. The area covered by study stands ranged from 0.3 to 1 ha, and comprises between 30 and 50 tree species (Table 1). At the time of the study, the three stands were 11–12 years old. The climate affecting the study sites is characterized by more or less evenly distributed rainfall throughout the year although less rain is received in the period from March to May (below 150 mm, Fig. 2). The island is frequently hit by typhoons, on average 19 times per year. The average rainfall amounts to 2753 mm year^{-1} as measured at the nearby climate station at the Visayas State University approximately 2 km

Table 1
Description of the study sites.

Site	Age (year)	Area (ha)	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

Trees with dbh > 7 were included for the stand characterization.

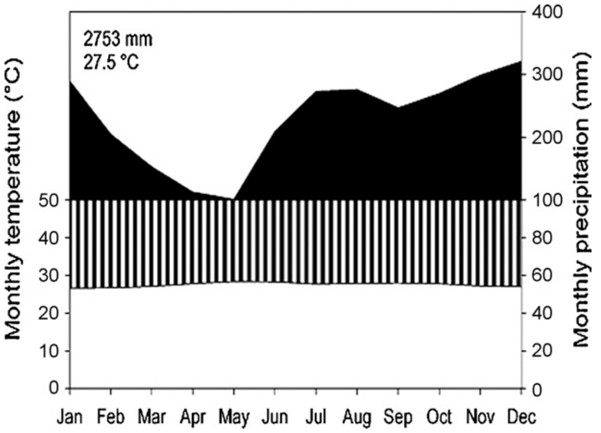

Fig. 2. Climatic diagram showing the average annual precipitation and temperature in Leyte from 1969 to 2007. Data were taken from the nearest weather station within the Visayas State University (PAGASA, 2007).

from the study rainforestation plots (PAGASA, 2007). The average annual air temperature is 27.5 °C.

The soils are derived from volcanic parent material and were slightly acidic with a pH (KCl) of 4.9 in Cienda, 4.1 in Patag and 4.3 in Marcos at 0–10 cm depth (C. Fischer, pers. comm., 2008). Nutrient availability in the soil ranged from moderate to high and C/N ratio ranged from 10.2 to 10.9 (Marohn, 2007).

The natural vegetation in the region is species-rich, lowland, dipterocarp forest, but natural forest only remains on the less accessible slopes of the Leyte Cordillera (Langenberger, 2006). After deforestation and intermittent cultivation of annual crops, coconut plantations were established. Since they were in a degraded state, the study sites were reforested in accordance with the rainforestation approach while maintaining the coconut present at the site.

The rainforestation approach was introduced in 1992 by the Visayas State University, formerly called Visayas State College of Agriculture, and the Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) (Margraf and Milan, 1996). It aims to restore degraded areas and farms planted with old coconut stands by means of planting native trees and supplemented by fruit trees thus, creating highly diverse sites. The proposed planting scheme for rainforestation was to initially plant native pioneers with a close separation of 2 m × 2 m and then to plant shade-tolerant species and fruit trees between them in the second year. Shade-tolerant species are mainly composed of high-value timber tree species of the Dipterocarpaceae family. This approach to reforestation is considered promising in the Philippines, and future extensions of the approach are discussed at http://www.haribon.org.ph/Road/About-Road-2020.

We selected sixteen tree species belonging to nine families for our experiments. Species selection was guided by the requirement for five tree individuals per species with well-exposed crowns for sun leaf measurement. We additionally wanted to represent trees from the three categories used in the rainforestation based on their biogeographic origin, main use, and successional status (Margraf and Milan, 1996). Although successional classification of the species according to the latter category is uncertain due to limited ecological studies of native species. 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, whereas five were exotic, three thereof are domesticated fruit trees. The main uses of these species are listed in Table 2. Most of them have all purpose use timber that is utilized for construction (nine species); some are fruit trees (five species); and others are used for light construction (two species). Most species, particularly the dipterocarps, were listed as late successional species, whereas *C. blancoi*, *T. microcarpa* and *V. parviflora* were classified as early successional ones (Margraf and Milan, 1996). *S. macrophylla* also occupies the latter successional position (Whitmore, 1996), and *G. arborea* is known for its light-demanding characteristic. The five fruit tree species were classified as shade-tolerant at least in their early developmental stages (Margraf and Milan, 1996). However, *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 by habitat loss (IUCN, 2009). Most species studied, dipterocarps in particular, were classified as evergreens according to their leaf phenology. On the contrary, some species (e.g. *S. macrophylla*, *G. arborea*, *S. koetjape*, *V. parviflora* and *T. microcarpa*) are semi-deciduous (Table 2).

Dipterocarps species, *C. blancoi*, *D. zibethinus*, *G. arborea*, and the two Artocarpus species have simple leaves, whereas *L. domesticum*, *N. Lappaceum*, *S. macrophylla*, *S. koetjape*, *V. parviflora* and *T. microcarpa* have compound leaves. Leaf shapes of the species vary from oblong to elliptical to obtuse to lanceolate to acuminate. A few species, such as *G. arborea*, *S. koetjape* and *T. microcarpa*, possess pubescent leaves, and most have glabrous to shiny ones. *A. odoratissimus* has a distinct sandy-like texture on the leaves' upper surface, whereas the lower surfaces are hairy up to the petioles.

2.2. *Stomatal conductance of leaves*

Five individual trees per species and ten fully expanded sunlit leaves per individual tree were studied. Leaflets were considered as leaves in samples for species with compound leaves, i.e. *L. domesticum*, *N. Lappaceum*, *S. macrophylla*, *S. koetjape*, *V. parviflora* and *T. microcarpa*. 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 User 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, just before the usual afternoon rain began. The average leaf temperature during the study days was 31 °C, and the average photosynthetically active photon flux density was 878 μmol m^{-2} s^{-1}.

2.3. *Tree architecture*

Diameter at breast height (1.3 m, dbh) was measured using a diameter tape. Tree heights (total height, height of the maximum canopy extension, and height of the lowest branch of the canopy) were assessed using an Abney-hand level or a stick with 3 m 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 of the four quadrants using a standard equation for a quarter ellipse ($\mathrm{Pi} \times x \times y/4$) centred at the origin. The above-ground biomass of the 16 species was computed using an equation provided by Chave et al. (2005): $\mathrm{AGB} = \exp\,(-2.977 + \ln(\rho \mathrm{dbh}^2 H))$ where AGB is the above-ground biomass (kg); ρ is wood density (g cm^{-3}); dbh is diameter at breast height (cm); H is the tree height (m).

Table 2

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/exotic	Main uses	Successional position[a]	Leaf phenology	Height (m)	dbh (cm)	CPA (m^2)
Hopea malibato Foxw.	Hm	Dipterocarpaceae	Patag	Native	All purpose[b]	Shade-tolerant	Evergreen	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	Shade-tolerant	Evergreen	7.1 (1.0) b	7.0 (0.5) d	7.4 (1.4) d
Parashorea malaanonan Merr.	Pm	Dipterocarpaceae	Cienda	Native	All purpose	Shade-tolerant	Evergreen	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	Shade-tolerant	Evergreen	10.0 (1.7) ab	9.6 (1.7) cd	6.6 (2.5) d
Shorea polysperma Merr.	Sp	Dipterocarpaceae	Patag	Native	All purpose	Shade-tolerant	Evergreen	8.5 (1.0) ab	10.6 (3.4) bcd	11.6 (4.3) bcd
Lansium domesticum Corr.	Ld	Meliaceae	Marcos	Native	Fruit	Shade-tolerant	Evergreen	8.4 (0.5) ab	10.7 (3.0) bcd	12.0 (7.2) bcd
Sandoricum koetjape Merr.	Sk	Meliaceae	Marcos	Native	Fruit	Shade-tolerant	Semi-deciduous	11.5 (2.2) a	24.8 (4.6) a	29.5 (7.6) abc
Swietenia macrophylla King	Sm	Meliaceae	Patag	Exotic	All purpose	Light demanding	Semi-deciduous	8.5 (1.5) ab	11.2 (2.2) bcd	10.5 (4.6) cd
Artocarpus blancoi Merr.	Ab	Moraceae	Patag	Native	All purpose	Intermediate	Evergreen	9.2 (3.7) ab	17.0 (9.4) abcd	20.9 (16.7) abcd
Artocarpus odoratissimus Blanco	Ao	Moraceae	Marcos	Exotic	Fruit	Shade-tolerant	Evergreen	10.9 (1.7) ab	20.5 (5.1) abc	36.8 (12.1) a
Gmelina arborea Roxb.	Ga	Verbenaceae	Marcos	Exotic	Light construction	Light demanding	Semi-deciduous	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	Light demanding	Semi-deciduous	11.1 (0.9) ab	21.7 (3.8) ab	37.4 (18.2) a
Durio zibethinus L.	Dz	Bombacaceae	Marcos	Exotic	Fruit	Shade-tolerant	Evergreen	10.9 (1.2) ab	18.4 (8.5) abcd	36.7 (28.6) ab
Terminalia microcarpa Decne.	Tm	Combretaceae	Cienda	Native	Light construction	Light demanding	Semi-deciduous	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	Light demanding	Evergreen	9.5 (1.1) ab	11.3 (1.5) bcd	10.8 (2.6) bcd
Nephelium lappaceum L.	Nl	Sapindaceae	Marcos	Exotic	Fruit	Shade-tolerant	Evergreen	10.2 (1.8) ab	17.8 (4.6) abcd	43.0 (19.1) a
Mean								9.7 (1.3)	14.9 (5.8)	(12.5)

[a] Classification according to Margraf and Milan (1996).

[b] Use as general construction material.

2.4. *Leaf morphological and chemical traits*

Ten sun leaves per tree were taken from five individuals per species. Fresh leaves were scanned and the leaf area (cm^2) and leaf width to length ratio (WLR, $cm\,cm^{-1}$) of sample leaves were analyzed from the images using Winfolia software (Winfolia, 2004a). Petioles were not included in any of the measurements. The leaves were then oven-dried at 70 °C for 48 h for dry weight determination. The specific leaf area (SLA, $m^2\,kg^{-1}$) was calculated as the leaf area divided by the leaf dry mass. Prior to laboratory analysis, all the leaves were combined and composite sampling was done and took five samples per species. The dried leaves were ground into a fine powder using a plant sample mill and analyzed in five replicates per species for their 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 elemental analyser (NA 2500, CE-Instruments, Rodano, Milano, Italy). All chemical analyses were done at the Centre for Stable Isotope Research at the University of Göttingen.

2.5. *Soil moisture content*

Soil moisture was measured at 0–30 cm of 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% (range: 43–68%).

2.6. *Statistical analysis*

Descriptive statistics including the mean and standard deviation of measured tree variables were computed for five individual trees per species. To determine the species-specific g_{smax}, we selected the daily maxima of g_s for the 10 leaves measured per tree and calculated the species average of g_{smax} for the five tree individuals per species. Tree species variables were tested for normal distribution using the Shapiro–Wilk test. Data that was 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 regression analyses. One-way analysis of variance (ANOVA) was applied to test for significant differences among the 16 species and a Tukey's test for post hoc Honest Significant Differences (HSD) 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 area, WLR, SLA, $\delta^{13}C$ and leaf nitrogen content) was analyzed using 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), whereas PC-ORD version 5.12 (2006) was used for the multivariate analysis.

3. Results

3.1. *Leaf traits*

The g_{smax} varied significantly among the species by a factor of five (165–772 $mmol\,m^{-2}\,s^{-1}$, Fig. 3A). The highest g_{smax} was found in *A. blancoi*, whereas low values were observed for the dipterocarp species *S. contorta* and *H. malibato* in particular. The mean g_s was found to have strong correlation with g_{smax} ($r^2 = 0.93$, $P < 0.001$,

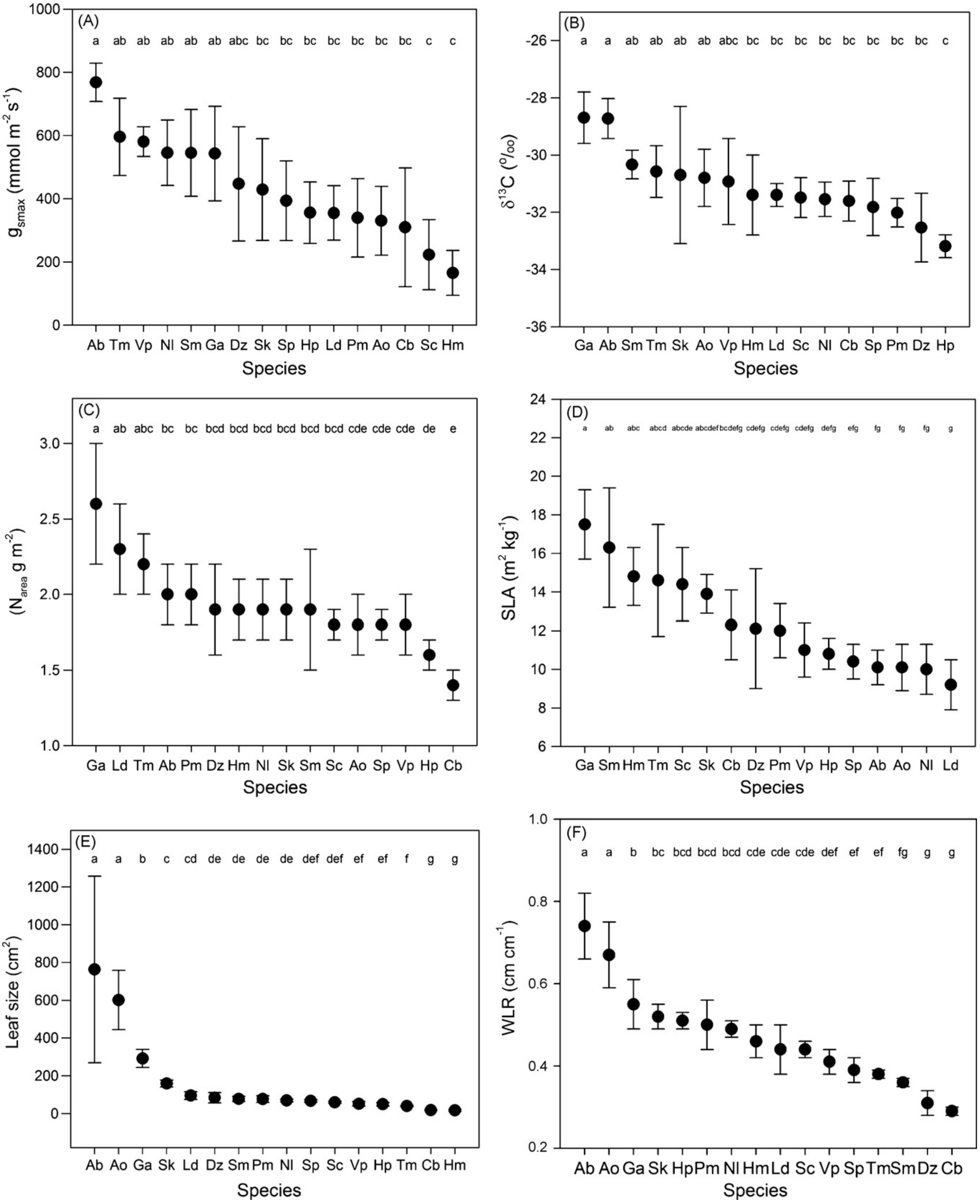

Fig. 3. (A) Maximal stomatal conductance (g_{smax}, mmol m^{-2} s^{-1}) of sixteen species studied, (B) leaf stable carbon isotope (δ^{13}C, ‰), (C) leaf nitrogen content in area basis (N_{area}, g m^{-2}), (D) specific leaf area, leaf area per leaf dry weight (SLA, m^2 kg^{-1}), (E) leaf size of species (cm^2), and (F) leaf width to length ratio (cm cm^{-1}). 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 2.

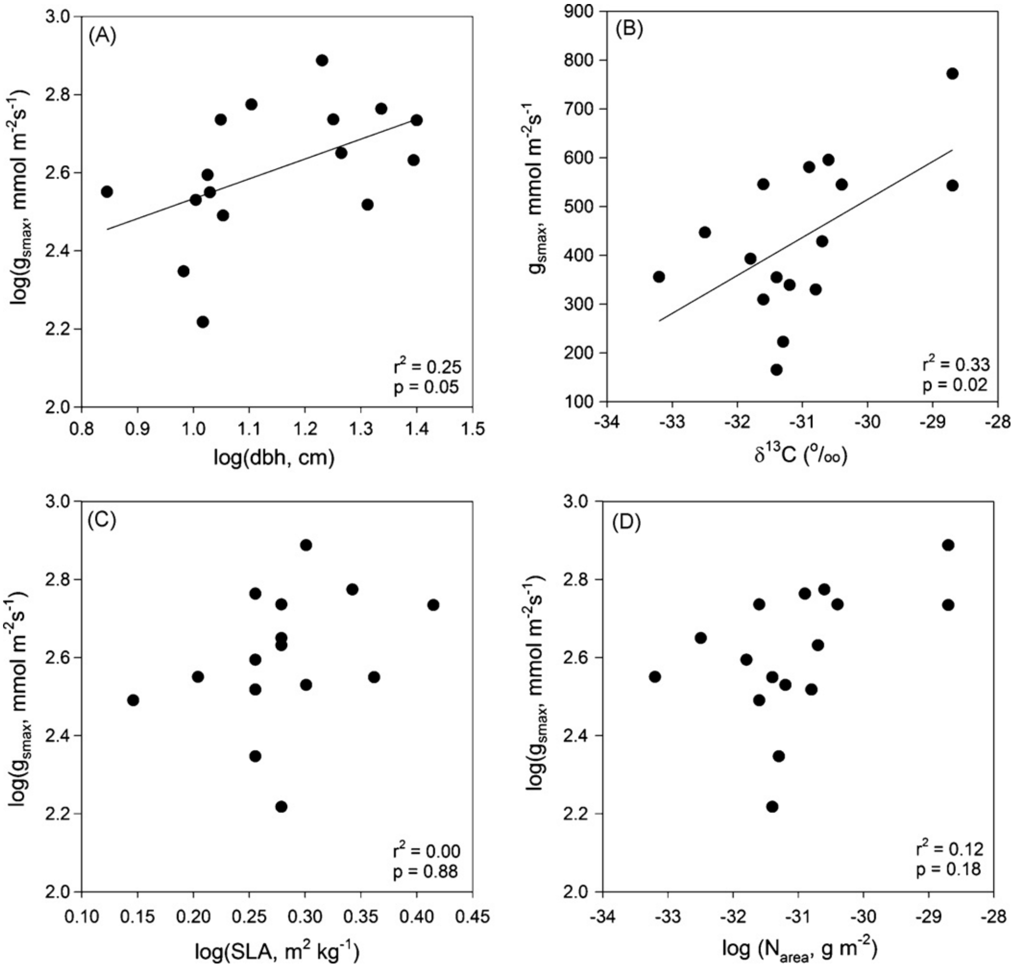

Fig. 4. Relationship between g_{smax} and (A) dbh (cm), (B) leaf stable carbon isotope (δ^{13}C, ‰), (C) specific leaf area (SLA, m^{-2} kg) and (D) leaf nitrogen content per leaf area basis (N_{area}, g m^{-2}) of sun-exposed leaves in sixteen species studied in rainforestation stands. Regression lines, coefficient of determination and significant levels are given. Note the log-log scale.

$n = 16$); thus, similar result in terms of g_s variation was found among the species studied.

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 δ^{13}C species belonging to the Dipterocarpaceae was found, i.e. they were more depleted in δ^{13}C (range: −33.2 to −31.2‰) than *A. blancoi* and *G. arborea*—species with less negative values (more enriched in δ^{13}C) (−28.7‰) (Fig. 3B). Leaf nitrogen content per unit area (N_{area}, g m^{-2}) among the species studied varied twofold (Fig. 3C). 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 A1).

3.2. *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 ($r^2 = 0.25$, $P = 0.05$, $n = 16$, Fig. 4A). 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. When all species were considered, no significant relationship was found between SLA and leaf nitrogen concentration and g_{smax}. However, a separate analysis of the g_{smax} and SLA for dipterocarp species revealed a highly significant inverse relationship ($r^2 = 0.96$, $P < 0.001$, $n = 5$).

Linear regression analysis using log-transformed values of AGB predicts 33% of the g_{smax} of all species studied ($r^2 = 0.33$, $P = 0.02$, $n = 16$, Table 3).

A multiple linear regression analysis using leaf size and tree height as independent variables explained 57% 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; it explained 55% of the variation of g_{smax} ($P = 0.02$, $n = 16$).

Table 3
Linear regression analysis between maximum stomatal conductance (g_{smax}, mmol m^{-2} s^{-1}) and tree variables (tree height in m, diameter at breast height (dbh, cm), crown projection area (CPA, m^2) above-ground biomass (AGB, kg), leaf traits (leaf size in cm^2, width to length ratio (WLR, cm cm^{-1}), specific leaf area (SLA, m^2 kg^{-1}), leaf nitrogen content per area (N_{area}, g m^{-2}) and stable carbon isotope signature (δ^{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**
AGB	kg	**0.33**	**0.02**
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
δ^{13}C	‰	**0.33**	**0.02**

[*] Log-transformed leaf size and g_{smax} was found to be significant when *A. odoratissimus* was excluded from the analysis due to its hairy leaf characteristic ($r^2 = 0.40$, $P = 0.01$, $n = 15$).

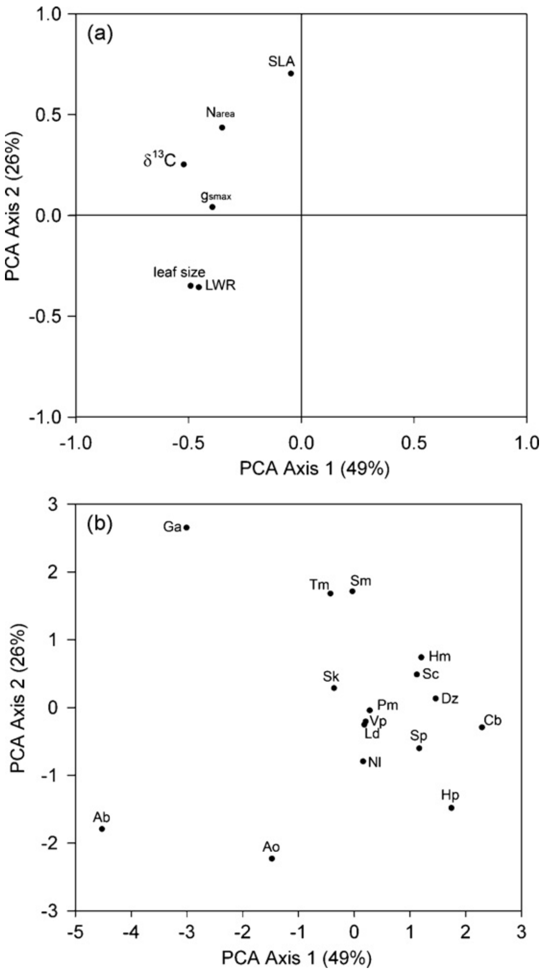

Fig. 5. Principal component analysis of six leaf traits of sixteen species studied. (A) Loading plots for the PC 1 (explained variation is 49%) and PC 2 (explained variation is 26%). (B) Species loadings on the first and second axes. Leaf traits and species abbreviations are found in Tables 2 and A1.

3.3. *Coordination of leaf traits*

The results of the principal component analysis (PCA) showed a high percentage of explained variance (75%) among the tested variables for all the species studied. The first and second principal component (PC 1 and PC 2) explained 49 and 26% of the total variance of leaf traits, respectively (Fig. 5A). Positive loadings along PC 1 indicated species which are more depleted in $\delta^{13}C$, with low leaf size and low leaf width to length ratio (WLR), whereas positive loadings on PC 2 indicated species with higher specific leaf area (SLA) and higher leaf nitrogen content per area (N_{area}). Most species were closely associated with high scores on PC 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*) (Fig. 5B). However, *A. blancoi*, *A. odoratissimus* and *G. arborea* exhibited low scores on PC 1 which reflects the fact that they are more enriched in $\delta^{13}C$, with large 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. However, the two *Artocarpus* species (*A. blancoi* and *A. odoratissimus*) were differentiated by their distinct characteristics of having low SLA and low N_{area} (PC 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.

4. Discussion

The species-specific variability of maximal stomatal conductance in the studied reforestation stands (165–772 mmol m^{-2} s^{-1}) was rather high, but the highest and the lowest measured values were less than the values in the literature review covering trees from very different locations and life histories (Juhrbandt et al., 2004). At a given site in Indonesia, g_{smax} values between 393 and 734 mmol m^{-2} s^{-1} were found in co-occurring early successional species in secondary forests; in nearby natural old-growth forests variability was more pronounced and additionally very low values were reported (68–583 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 to be an intermediate species (i.e. a species in between early and late succession, E. Fernando, pers. comm., 2008). This species has a lobed leaf shape formed by a deeply indented margin that probably prevents formation of a thick continuous boundary layer, which is common to large leaves (Stokes et al., 2006; Grace, 1983). Such an interrupted boundary layer may allow the leaf to absorb more CO_2 or release more water from the stomata; this 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).

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 diametrically opposed to the findings on eight early successional tree species in Indonesia, where leaf sizes were negatively correlated with g_{smax} (Juhrbandt et al., 2004). The relationship of 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 the two species were excluded. We therefore suggest that, although the relationship leaf size to boundary layer conductance is quite clear, there was no general relationship because other leaf traits such as leaf shape and hairiness also exert a strong influence.

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 reduced CO_2 assimilation and a relatively low growth rate compared to large diameter and fast-growing species (e.g. *G. arborea* and *A. blancoi*).

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

No significant correlation was found between g_{smax} and SLA when all species were included in the analysis. However, a strong inverse relationship was found when dipertocarp species were analysed as a sub-set, with SLA as predictor variable. 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 ones (Bonal et al., 2007). Our data implies that *H. plagata* and *S. polysperma* have leaf traits that characterize slow-growing species, whereas *H. malibato* and *S. contorta* may be grouped as fast-growing, late successional species with low

g_s and high SLA, with *P. malaanonan* intermediate. The close relationship found between SLA and g_{smax} suggests that this group of species could possess special physiological leaf traits that differentiate them from other species studied in the rainforestation. However, further investigation is necessary because the inverse relationship between g_{smax} and SLA does not conform with the reported general trend 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 in sun-exposed leaf $\delta^{13}C$ values among the co-occurring species in rainforestation stands (range: −33.2‰ to −28.7 ± 1.2). The mean species $\delta^{13}C$ signature varied by 4.5‰ 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 7.6‰ (range: −35.9 to −28.0‰) (Martinelli et al., 1998). However, our data is similar to the $\delta^{13}C$ values obtained by Guehl et al. (1998) from a study site in French Guiana but including only 18 species. The 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 compared 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 phylogenetically close relationship of the genera *Hopea*, *Shorea* and *Parashorea* (Zhang and Cao, 2009), which were all represented in our study.

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 a 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 the remarkable variation in $\delta^{13}C$ could be attributed to species-specific physiological diversity (Leffler and Enquist, 2002). However, a precise ecophysiological explanation for the variation of $\delta^{13}C$ among species will require 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 (N_{area})). The main contributors to high values of PC 1 (explained variance 49%) were the species which are more depleted in $\delta^{13}C$ (more negative values), and exhibit low leaf size and low WLR. Thus, in the PCA run all dipterocarps species, *D. zibethinus* and *C. blancoi* appear to form a group having similar leaf traits as mentioned above. The two *Artocarpus* species in our study reflect a unique strategy compared to the majority of the studied species; they show 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 because most of them, especially the fruit trees, were domesticated and some were exotics. Based on their close relatives and origin, all of them can be considered to be late successional species with the exception of *A. blancoi*, which falls in between early and late successional stage (E. Fernando, pers. comm., 2008).

The high scores of the two exotic species (*G. arborea* and *S. macrophylla*) and a fast-growing native (*T. microcarpa*) along the PC 2 was influenced by their high SLA and high N_{area}. The first two species are known to be fast-growing exotics that perform very well in the tropics. These species share the same leaf traits and were described as physiologically active species with fast leaf growth rates and are semi-deciduous. These traits could indicate the same successional position similar to early successional species (Reich et al., 1991, 1992, 1999). We also observed high leaf conductance, which facilitates high assimilation rates and thus enables them to capture and utilize more light thus encouraging rapid growth (Poorter and Bongers, 2006). This characterizes *G. arborea*, *S. macrophylla* and *T. microcarpa*, which are semi-deciduous species.

In contrast, dipterocarp species have low SLA, which in general produces tougher leaves (Reich et al., 1991) and low leaf N content, as their strategy is to minimize damage caused by leaf herbivores (Coley et al., 1985). Late successional species, such as dipterocarps, require minimal resources (i.e. light, water) (Wright et al., 2004; Poorter and Bongers, 2006), utilize high irradiances, and are more tolerant of water and nutrient deficiency. Consequently, they exhibit 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).

5. Conclusions

Overall, there were only minor correlations between leaf traits and g_{smax}, which may have to do with the planting of native tree species mixed with fruit tree species, which had been domesticated for a long time, and exotic species. However, in the important Dipterocarpaceae family, a high correlation was indicated; thus, along a successional gradient, dipterocarps may exhibit slightly different characteristics. Moreover, some of the species were grouped according to their leaf traits, which may indicate differences in overall plant performance such as growth and mortality. The information on leaf traits may contribute to further developments in the reforestation scheme and to the successful attainment of specific objectives. Furthermore, the relatively high variability found in leaf traits among 16 study tree species suggests that the multi-species reforestation ‘rainforestation’ is already quite successful in – at least partly – restoring the functional variability of the former natural forest.

Acknowledgements

We are grateful to the German Academic Exchange Service (DAAD) for funding this research through the scholarship granted to R. Sales-Come. Many thanks to the staff of the Visayas State University, in particular the College of Forestry and Natural Resources and Institute of Tropical Ecology, for supporting the work and also to the people of barangay Marcos, barangay Patag and barangay Cienda for allowing us to conduct our study and for their assistance during the field work. Special thanks to Diego Dierick and Luitgard Schwendenmann for their valuable comments on the earlier versions of this manuscript. We also thank the two reviewers. We would also like to acknowledge the Department of Environment and Natural Resources, Tacloban for facilitating sample collection in the framework of this study.

Appendix A.

See Table A1.

Table A1
Maximum stomatal conductance (g_{smax}, mmol m^{-2} s^{-1}) and leaf morphological and chemical traits of the sun leaves in the sixteen species studied. Full names of species are listed in Table 2. 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_{area} (g m^{-2})	δ^{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	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	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	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	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	1.8 (0.1) cde	−31.8 (1.0) bc
Ld	354.6 (86.2) abc	94.8 (20.2)[a] cd	17.7 (2.4) c	7.7 (0.7) cd	0.44 (0.06) cde	9.2 (1.3) g	2.3 (0.3) ab	−31.4 (0.4) bc
Sk	428.5 (160.9) abc	159.1 (18.3)[a] c	23.8 (1.2) bc	12.3 (0.9) cd	0.52 (0.03) bc	13.9 (1.0) abcdef	1.9 (0.2) bcd	−30.7 (2.4) ab
Sm	544.7 (137.4) ab	77.2 (13.6)[a] de	17.9 (1.5) c	6.4 (0.6) cd	0.36 (0.01) fg	16.3 (3.1) ab	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	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	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	2.6 (0.4) a	−28.7 (0.9) a
Vp	580.3 (46.9) ab	51.2 (12.7)[a] ef	13.9 (1.3) c	5.7 (0.8) cd	0.41 (0.03) def	11.0 (1.4) cdefg	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	1.9 (0.3) bcd	−32.5 (1.2) bc
Tm	595.4 (122.5) ab	39.3 (3.9)[a] f	13.3 (0.5) c	5.0 (0.3) cd	0.38 (0.01) ef	14.6 (2.9) abcd	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	1.4 (0.1) e	−31.6 (0.7) bc
Nl	545.1 (103.6) ab	69.1 (6.8)[a] de	14.2 (0.9) c	6.9 (0.2) cd	0.49 (0.02) bcd	10.0 (1.3) fg	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)	1.9 (0.3)	−31.1 (1.2)
Min	165.2	16.5	7.8	3.0	0.29	9.2	1.4	−33.2
Max	772.1	762.9	36.0	27.1	0.74	17.5	2.6	−28.7

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

[a] Measurements were taken from the leaflet of compound-leaved species.

References

AP4 Porometer User Manual, 2004. In: Webb, N. (Ed.). Delta-T Devices Ltd., Cambridge, England, UK, 197 pp.

Bazzaz, F.A., 1991. Habitat selection in plants. In: The American Naturalist, vol. 137, Supplement: Habitat Selection (June, 1991), pp. S116–S130.

Bohman, K., 2004. Functional and Morphological Diversity of Trees in Different Land Use Types along a Rainforest Margin in Sulawesi, Indonesia. Diss. Georg-August-Universität, Göttingen, Germany.

Bonal, D., Sabatier, D., Montpied, P., Tremeaux, D., Guehl, J.M., 2000. Interspecific variability of δ^{13}C among trees in rainforests of French Guiana: functional groups and canopy integration. Oecologia 124, 454–468.

Bonal, D., Born, C., Brechet, C., Coste, S., Marcon, E., Roggy, J.C., Guehl, J.M., 2007. The successional status of tropical rainforest tree species is associated with differences in leaf carbon isotope discrimination and functional traits. Ann. For. Sci. 64, 169–176.

Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q., Eamus, D., Fölster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J.P., Nelson, B.W., Ogawa, H., Puig, H., Riéra, B., Yamakura, T., 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. Oecologia 145, 87–99.

Coley, P.D., Bryant, J.P., Chapin III, F.S., 1985. Resource availability and plant antiherbivore defense. Science 230, 895–899.

Dierick, D., Hölscher, D., 2009. Species-specific tree water use characteristics in reforestation stands in the Philippines. Agric. For. Meteorol. 149, 1317–1326.

ESSC, 1999. Decline of the Philippine Forest. Environmental Science for Social Change, Inc., The Bookmark, Inc., Makati City, The Philippines.

Farquhar, G.D., Ehleringer, J.R., Hubick, K.T., 1989. Carbon isotope discrimination and photosynthesis. Annu. Rev. Plant Physiol. Plant Mol. Biol. 40, 503–537.

Grace, J., 1983. Plant–Atmosphere Relationships. Chapman and Hall, London, 92 pp.

Guehl, J.M., Domenach, A.M., Bereau, M., Barigah, T., Casabianca, H., Ferhi, A., Garbaye, J., 1998. Functional diversity in an Amazonian rainforest of French Guiana. A dual isotope approach (δ^{15}N and δ^{13}C). Oecologia 116, 316–330.

Haribon Foundation-Philippines. www.haribon.org.ph (last visited: 02.20.10).

Hölscher, D., Leuschner, Ch., Bohman, K., Hagemeier, M., Juhrbandt, J., Tjitrosemito, S., 2006. Leaf gas exchange of trees in old growth and young secondary forest stands in Sulawesi, Indonesia. Trees 20, 278–285.

IUCN, 2009. IUCN Red List of Threatened Species. Version 2009.1 (downloaded on 27.08.09) www.iucnredlist.org.

Juhrbandt, J., Leuschner, Ch., Hölscher, D., 2004. The relationship between maximal stomatal conductance and leaf traits in eight Southeast Asian early successional tree species. For. Ecol. Manage. 202, 245–256.

Khamzina, A., Sommer, R., Lamers, J.P.A., Vlek, P.L.G., 2009. Transpiration and early growth of tree plantations established on degraded cropland over shallow saline groundwater table in northwest Uzbekistan. Agric. For. Meteorol. 149, 1865–1874.

Lamb, D., Erskine, P.D., Parotta, J.A., 2005. Restoration of degraded tropical landscapes. Science 310, 1628–1632.

Langenberger, G., 2006. Habitat distribution of dipterocarp species in the Leyte Cordillera: an indicator for species-site suitability in local reforestation programs. Ann. For. Sci. 63, 149–156.

Leffler, A.J., Enquist, B.J., 2002. Carbon isotope composition of tree leaves from Guanacaste, Costa Rica: comparison across tropical forests and tree life history. J. Trop. Ecol. 18, 151–159.

Margraf, J., Milan, P.P., 1996. Ecology of dipterocarp forests and its relevance for island rehabilitation in Leyte, Philippines. In: Schulte, A., Schöne, D. (Eds.), Dipterocarp Forest Ecosystems: Towards Sustainable Management. World Scientific, Singapore, pp. 124–154.

Marohn, C., 2007. Rainforestation Farming on Leyte Island, Philippines-Aspects of Soil Fertility and Carbon Sequestration Potential. Diss. University of Hohenheim, Germany.

Martinelli, L.A., Almeida, S., Brown, I.F., Moreira, M.Z., Victoria, R.L., Sternberg, L.S.L., Ferreira, C.A.C., Thomas, W.W., 1998. Stable carbon isotope ratio of tree leaves, boles and fine litter in a tropical forest in Rondônia, Brazil. Oecologia 114, 170–179.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

PAGASA, 2007. Philippine Atmospheric, Geophysical and Astronomical Services Administration, Philippines. http://www.pagasa.dost.gov.ph (last visited: 01.08.08).

Poorter, L., Bongers, F., 2006. Leaf traits are good predictors of plant performance across 53 rain forest species. Ecology 87, 1733–1743.

Potvin, C., Dutilleul, P., 2009. Neighborhood effects and size-asymmetric competition in a tree plantation varying in diversity. Ecology 90, 321–327.

R Development Core Team, 2008. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN: 3-900051-07-0, http://www.R-project.org (last visited: 01.10.08).

Rana, R., Langenfeld-Heyser, R., Finkeldey, R., Polle, A., 2008. Functional anatomy of five endangered tropical timber wood species of the family Dipterocarpaceae. Trees 23, 521–529.

Reich, P.B., Uhl, C., Walters, B., Ellsworth, D., 1991. Leaf life span as a determinant of leaf structure and function among 23 tree species in Amazonian forest communities. Oecologia 86, 16–24.

Reich, P.B., Walters, M.B., Ellsworth, D.S., 1992. Leaf lifespan in relation to leaf, plant and stand characteristics among diverse ecosystems. Ecol. Monogr. 62, 365–393.

Reich, P.B., Ellsworth, D.S., Walters, M.B., Vose, J.M., Gresham, C., Volin, J.C., Bowman, W.D., 1999. Generality of leaf trait relationships: a test across six biomes. Ecology 80, 1955–1969.

Schreuder, M.D., Brewer, C.A., Heine, C., 2001. Modelled influences of non-exchanging trichomes on leaf boundary layers and gas exchange. J. Theor. Biol. 210, 23–32.

Stokes, V.J., Morecroft, M.D., Morison, J.I.L., 2006. Boundary layer conductance for contrasting leaf shapes in a deciduous broadleaved forest canopy. Agric. For. Meteorol. 139, 40–54.

Strauss-Debenedetti, S., Bazzaz, F., 1996. Photosynthetic characteristics of tropical trees along successional gradients. In: Mulkey, S.S., Chadzon, R.L., Smith, A.P. (Eds.), Tropical Forest Plant Ecophysiology. Chapman and Hall, New York, USA, pp. 162–186.

Whitmore, T.C., 1996. A review of some aspects of tropical rainforest seedling ecology with suggestions for further enquiry. In: Swaine, M.D. (Ed.), The Ecology of Tropical Forest Tree Seedlings. UNESCO/The Parthenon Publishing Group Limited/The Parthenon Publishing Group Inc., Paris/UK/USA, pp. 3–30.

Winfolia, 2004a. Manual for Leaf Analysis. Regent Instruments, Inc., Canada, 58 pp.

Wishnie, M.H., Dent, D.H., Mariscal, E., Deago, J., Cedeño, N., Ibarra, D., Condit, R., Ashton, P.M.S., 2007. Initial performance and reforestation potential of 24 tropical tree species planted across a precipitation gradient in the Republic of Panama. For. Ecol. Manage. 243, 39–49.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Guilas, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S., Tjoelker, M.G., Veneklaas, E.K., Villar, R., 2004. The worldwide leaf economics spectrum. Nature 428, 821–827.

Wuenscher, J.E., 1970. The effect of leaf hairs of *Verbascum thapsus* on leaf energy exchange. New Phytol. 69, 65–73.

Zhang, J.L., Cao, K.F., 2009. Stem hydraulics mediates leaf water status, carbon gain, nutrient use efficiencies and plant growth rates across dipterocarp species. Funct. Ecol. 23, 658–667.