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Original article

Variation of functional traits in trees from a biogeographically complex Mexican cloud forest

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ABSTRACT

Several studies have proposed a group of morpho-functional traits as determinants of the ecological strategy of species. Among these, four morpho-functional traits are considered to be relevant in determining a plant's ecological strategy: specific leaf area (SLA), height at maturity (Hmax), wood density (WD), and seed mass (SM). We examined the variation of these traits and attempted to identify functional groups among 33 tree species with different biogeographical affinities from a montane cloud forest. Covariation among the four traits was examined using Principal Component Analysis (PCA) and species clustering. Bivariate trait relationships were evaluated through two methods: cross-species correlations, and evolutionary divergence correlations using phylogenetically independent contrasts (PICs). Correlations between attributes were overall weak, the most obvious ones being between Hmax and SM, and between Hmax and WD; this latter trait pair was also correlated in PICs. In both analyses SLA was unrelated to all other traits. In the PCA ordination the first two axes explained 66.9% of the between-species variation. Despite a largely continuous between-species variation, species clustering allowed differentiation of two main groups. Observed trait correlations were consistent with those reported for other floras, with the important exception of the independent behaviour of SLA. This study indicates a variety of comparable successful life history strategies among the studied species. The effect of phylogeny in trait covariation was unimportant, in fact, a mixture of clades was represented in several groups among the species they contained, suggesting among-lineage convergence.

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1. Introduction

The quantitative study of plant traits has revealed the existence of an extremely large across-species variation, some of which seems to reflect the occurrence of trade-offs in plant life histories (Wright et al., 2004); therefore plant traits provide a useful base for the classification of plants in functional groups (Díaz and Cabido, 1997). Functional groups have been defined as sets of species sharing biological traits and playing similar roles in ecosystem processes (Gitay and Noble, 1997; Lavorel et al., 1998). The benefits of classifying plants in functional groups have been recognized by many authors (Lavorel et al., 1997; Díaz et al., 1999); for example, such groups may be viewed as plant life strategies, inasmuch as they represent different ways in which plants secure carbon profit during vegetative growth, and acquire, use, and conserve resources (Westoby et al., 2002). A fruitful approach in developing functional classifications of plants is represented by ecological strategies schemes, which consists in grouping species in categories, according to a varying number of ecological traits (Raunkiaer, 1934; Drury and Nisbet, 1973; Grime, 1977; Noble and Slatyer, 1980).

Several studies have proposed a group of morpho-functional traits that have proven to be appropriate, independent predictors of a species ecological behaviour (Westoby, 1998; Westoby et al., 2002; Wright et al., 2006b). Among these, four have received much attention because of their ease of measurement and interpretation: (a) specific leaf area (SLA); (b) maximum height (Hmax); (c) wood density (WD); and (d) seed mass (SM). SLA is an important determinant of growth rate because the larger SLA, the larger the area for capturing light per unit of previously captured mass (Lambers and Poorter, 1992).

There is empirical evidence that SLA is weakly related with plant height and seed size, and that it often shows no relationship with WD and leaf size across many species and community types (Díaz et al., 2004; Wright et al., 2006b). However, site-specific studies based on controlled protocols and on an ample knowledge of the system's ecology have succeeded in finding relationships of SLA with other traits, e.g. with WD and leaf size (Wright et al., 2006b). These contrasting results imply a lack of a strong basis to support the existence of significant correlations between SLA and other traits. In turn, Hmax is linked to strategies that ensure carbon gain through light interception, e.g. slow growth in low light levels vs. fast growth in gap conditions (a trade-off between height gain and shade tolerance) (Falster and Westoby, 2005b). Apparently due to mechanical reasons, Hmax is tightly associated to WD (Lawton, 1984; Muller-Landau, 2004; King et al., 2005); a higher WD provides more resistance against xylem cavitation (Cavender-Bares and Holbrook, 2001; Maherali et al., 2004) and pathogens (Coley, 1988). WD is positively correlated with tree height along successional gradients, with the opposite being true along light-availability gradients (Falster and Westoby, 2005a), and in general, negatively correlated with leaf size across different vegetation types (Cavender-Bares et al., 2004; Wright et al., 2006a). Also, a trend has been reported for bigger plants to bear bigger seeds (Moles et al., 2004).

Finally, SM is a regenerative trait playing a central role for reproduction and the seedling establishment phase because it determines the amount of resources available for seedlings' early growth (Paz and Martínez-Ramos, 2003; Moles and Westoby, 2004b; Paz et al., 2005). SM has been shown to be positively correlated with dispersal mode, leaf size, seedling functional type and plant height (Leishman et al., 1995; Kitajima, 1996; Falster and Westoby, 2005b).

The occurrence of multiple trade-offs involving these attributes allows visualization of a gradient of ecological strategies, ranging from fast-growing, short-lived pioneer species on one extreme, to slow-growing, long-lived, late successional species, associated with increased shade tolerance, on the other (Muller-Landau, 2004). According to existing theory and available empirical information, often contradictory as shown above, it is difficult to propose specific hypotheses establishing a definite directionality for the relationships between the four attributes. However, based on the results of the majority of studies analysing between-trait correlations, it is reasonable to state that most small-seeded trees are fast growing species, while the opposite will be true for large seeded trees. Because growth rate of a tree is usually positively associated to a larger light interception area per leaf and negatively to WD, we predict here that species with small seeds should tend to have high SLA, relatively low WD and a wide variation in total height, whereas species bearing large seeds should tend to have medium to high WD, low SLA, and a large Hmax.

It has been demonstrated that patterns of species distribution and functional covariation in an ecological community can reflect both species' inherited traits from a common ancestor (phylogenetic effect) and adaptive convergences among distantly related species (Webb et al., 2002; Ackerly, 2003; Chazdon et al., 2003). The evolutionary comparative methods that incorporate a phylogenetic approach have proven useful in solving questions about ecological significance of functional variation among plant species (Ackerly, 1999). For example, the question whether the trend toward a shorter leaf life-span and a high SLA in more recent cloud forest taxa reflects ecological variation, or if it is rather related with the phylogenetic relationships among species (Williams-Linera, 2000). In general, more related taxa tend to be more similar, which implies a lower level of evolutionary divergence between related taxa (Ackerly, 2000).

An underlying assumption of the general relationships discussed above is that they derive from the evolution of many species in common communities, and that strategies have emerged through the appearance of different trade-offs (Westoby et al., 2002; Wright et al., 2006a). However, the possibility of generalizing trait correlations may be limited; for example, the significant correlation between SLA and WD observed in tropical rain forests may not be valid for other forest types (Wright et al., 2006b). This uncertainty is particularly relevant for cloud forests (CF) of the mountains of southern/central Mexico, which is a highly complex community from a biogeographical point of view, as it is composed of a mixture of both tropical and temperate Laurasian elements, together with tropical and temperate taxa of Gondwanic origin (Wendt, 1998). In addition to this particular concoction, these are not post-glacial communities, since they have existed since at least 20 Ma ago (Miranda and Sharp, 1950; Axelrod, 1975; Rzedowski, 1991), so that the appearance of the different lineages may not be synchronic. Therefore, these forests may be regarded as an excellent system for investigating the role of the phylogenetic loading and the ecological constraints in the determination of functional properties of trees.

In Mexican CF, studies on patterns of forest regeneration have shown that the pioneer species of *Pinus* form almost pure stands shortly after disturbances, subsequently facilitating the establishment of a second wave of non-pioneer, typical CF tree species; with time, the latter replace the pines, forming mature cloud forests (González-Espinosa et al., 1991; Sánchez-Velásquez and García-Moya, 1993; Saldaña-Acosta, 2001). Although the establishment of the second group appears to be relatively homogeneous at first sight, field observations including density variation and microsite selection suggest that each of these species may actually be finely adapted to particular environmental conditions, especially but not only to light environment (Ortíz-Arrona, 1999). This suggests that life-history traits are important in species regeneration strategies in Mexican CF, as they are in tropical forests in general. Management of forests for biodiversity, conservation or economic activities such as carbon offset trading requires understanding of trait-environment relationships. For this purpose we sought to determine functional groups for regeneration.

In this study we constructed a phylogenetic tree as a working hypothesis for examining the effects of phylogeny on the correlations between morphological attributes in a Mexican CF. Specifically, we addressed the following questions: are there patterns of functional covariation in the cloud forest, and if so, are they similar to those described in other forest types? Based on this variation, is it possible to recognize natural groups of cloud forest species based on morpho-functional traits? Finally, are groups made up primarily of single clades or do members of the same clade present different combinations of traits belonging to several different groups?

2. Materials and methods

2.1. *Study area and stand selection*

Fieldwork was conducted at Las Joyas Scientific Station located in the Sierra de Manantlán Biosphere Reserve (hereafter referred to as Manantlán), Jalisco State, Mexico (19° 35′ N; 104° 17′ W). Vegetation cover comprises pine, pine-oak, and cloud forests, as well as scrub and secondary grasslands (Sánchez-Velásquez et al., 1996). Cloud forests (CF; known in Mexico as bosque mesófilo de montaña), grow along ravines and protected slopes, or in the higher parts of the mountains of tropical and subtropical regions, where fog is frequent (Rzedowski, 1978).

Four CF stands were established for the selection of individuals using the belt transect method (five by stand, 50 m × 1 m each) located at random distances from each other. The four stands were located in an altitudinal range between 1800 and 2100 m. At random intervals, points were determined for measurements and/or sample collections; at each one, we selected individuals falling on the transect for the sampling of leaves, seeds, and wood core, and for the measurement of height.

2.2. *Species and traits*

Thirty-three of the most common canopy tree species of the regional CF (Vázquez et al., 1995) were selected for the study. SLA was determined in fully expanded, healthy leaves collected from the highest parts of the crowns. Any petiole or rachis in the case of compound leaves, and all veins were considered (Westoby, 1998). We took five leaves from 15 individuals per species (75 leaves in total). To determine leaf area we scanned leaves to create digital images and measured their area by using the SigmaScan PRO 5, SPSS Inc. Finally, leaves were oven dried at 80 °C for at least 48 h and their dry mass was determined.

For determination of SM we collected five seeds from each of 25 mature and healthy trees, giving a total of 125 seeds, for each of the 33 species that had been selected. Trees were chosen at random along the transects. Seeds were dried at 80 °C for 48 h and weighed.

Tree height and WD were measured on the same randomly chosen 25 individuals per species with a Haga clinometer. The closest tree height value to the 95th percentile was defined as Hmax. For WD (oven dry mass/fresh wood volume) 15–50 cm long cores that included heartwood were taken from these trees with a Pressler increment borer. Volume of fresh wood was determined with the volume replacement method, after which samples were oven-dried at 70 °C and weighed and expressed in mg mm^{-3}.

2.3. *Data analysis*

Two of the four traits were $\log_{10}$ transformed before analysis because they showed right skewed distributions (SLA and SM). In order to explore patterns of multiple covariation among SLA, Hmax, SM and WD, we used Principal Component Analysis (PCA). We then constructed a dendrogram by using Ward's grouping linkage method and Euclidian distances, in PC-ORD Ver. 4.10 (McCune and Mefford, 1999). This clustering method, based on an analysis of variance approach to measure distance between clusters, is considered to be very robust and to yield readily interpretable results (Cao et al., 1997).

We used two methods to evaluate bivariate trait relationships: (1) cross-species correlation (among attribute Pearson product-moment correlations); and (2) evolutionary divergence correlations analysis using phylogenetically independent contrasts (PICs) to test for correlations among evolutionary trait-divergences. Phylogenetic relationships between the 33 studied species were constructed by using the Phylomatic database V.3.22 (Webb and Donoghue, 2002). This software uses a backbone family-level tree of angiosperms, based on recent family level phylogenies from published molecular studies (e.g. Soltis et al., 2000). An online program (http://www.phylodiversity.net/phylomatic) translates the input list of taxa into a phylogeny for those taxa, and the genera are attached as polytomies within families, and species as polytomies within genera. Generic polytomies could be resolved for those groups for which more detailed phylogenies were available (Fig. 1). More detailed information is given in the figure legend.

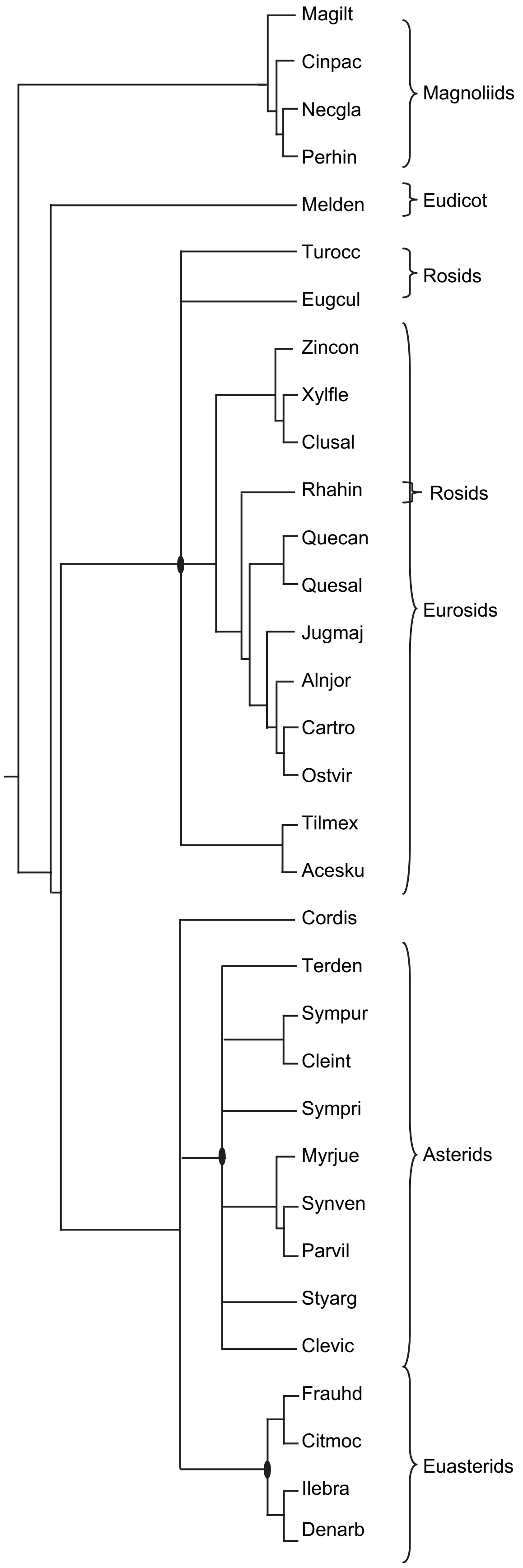

Fig. 1 – Phylogenetic relationships among 33 cloud forest species from Manantlán, Jalisco, Mexico. Circles indicate those divergences that were the most important contributors to PICs correlations (see text for further explanation). The phylogeny for the 33 cloud forest species is dominated by the Eurosids and Asterid clades (both with 14 species), although the minor clade of Magnoliid (four species) is also present. Phylomatic produced a large number of polytomies which were resolved in the following manner: the polytomy of *Cleyera*, *Ternstroemia* and *Symplococarpon* was resolved by using the phylogenetic relationships of Theaceae of Prince and Parks (2001). For the Betulaceae (*Alnus*, *Carpinus* and *Ostrya*), we used the study of Chen et al. (1999), and the study of Chanderbali et al. (2001) for the Lauraceae (*Persea*, *Cinnamomun* and *Nectandra*). For the Myrsinaceae (*Myrsine*, *Parathesis* and *Synardisia*), Ricketson and Pipoly (1997) and Stevens et al. (2001) locate *Parathesis* as a section of *Ardisia* sect. *Parathesis* A. DC, as well as *Synardisia* but as a subgenus (Ardisia subg. Synardisia Mez); *Myrsine* was considered as a synonym of *Rapanea* (*R. juergensenii* Mez).

The regressions based on PICs *sensu* Felsenstein (1985) are a very powerful statistical tool which is used to assess correlated evolutionary changes between variables; therefore they have been amply used to incorporate phylogenetic information in studies based on continuous attributes (Ackerly, 1999). This method permits statistically controlling for potential non-independence of species due to common ancestry. Contrasts are constructed from differences between the values of attributes in pairs of sister taxa along the phylogenetic tree, allowing contrasts at deep nodes. Each contrast represents an evolutionary divergent and independent event in the history of a particular trait. Standardized independent contrasts were obtained for all traits using CAIC Ver. 2.0 (Purvis and Rambault, 1995). Regression through zero was used to test for the hypothesis of evolutionary correlation between each pair of traits.

3. Results

3.1. *Character correlations*

Two correlations were significant based on cross-species analyses (Table 1). The strongest correlation was observed between Hmax and SM, followed by a less strong correlation among between Hmax and WD. Interestingly, the latter pair of characters was also correlated when phylogeny was taken into account; PICs of the former pair were not significantly correlated but showed a clear trend (Table 1; Fig. 2a,b). For PICs analyses, the most important contributors to the relationship between Hmax and WD were old divergences located specifically in the clade of the Eurosids I (which includes the orders Celastrales, Fagales, Malpighiales and Rosales), and the clade of the Eurosids II (comprising the orders Malvales and Sapindales), more recent ones in the clade of the Asterids (which encompasses the order Ericales), and very recent ones in the clades of the Euasterids I (with the Lamiales), and Euasterids II (Aquifoliales and Apiales) (Fig. 1; Table 2).

Table 1 – Between-trait correlations for species-based analysis (lower left triangle) and PICs analysis (upper right triangle) for cloud forest species from Manantlán, Jalisco, Mexico. SLA and SM were $\log_{10}$ transformed before analysis. Bivariate fit of SLA by SM is an artefact due to two points representing *Juglans major* and *Nectandra glabrescens*. Figures in bold indicate the strongest correlations

		Plant height	Wood density	Seed mass	SLA
Plant height	*r*		**0.18**	**0.12**	0.034
	n		25	25	25
	P		<0.05	0.082	0.366
Wood density	*r*	**0.29**		0.37	0.012
	n	33		25	25
	P	<0.05		0.762	0.587
Seed mass	*r*	**0.36**	0.11		0.09
	n	33	33		25
	P	<0.05	<0.05		0.116
SLA	*r*	0.11	−0.05	0.20	
	n	33	33	33	
	P	0.522	0.859	<0.05	

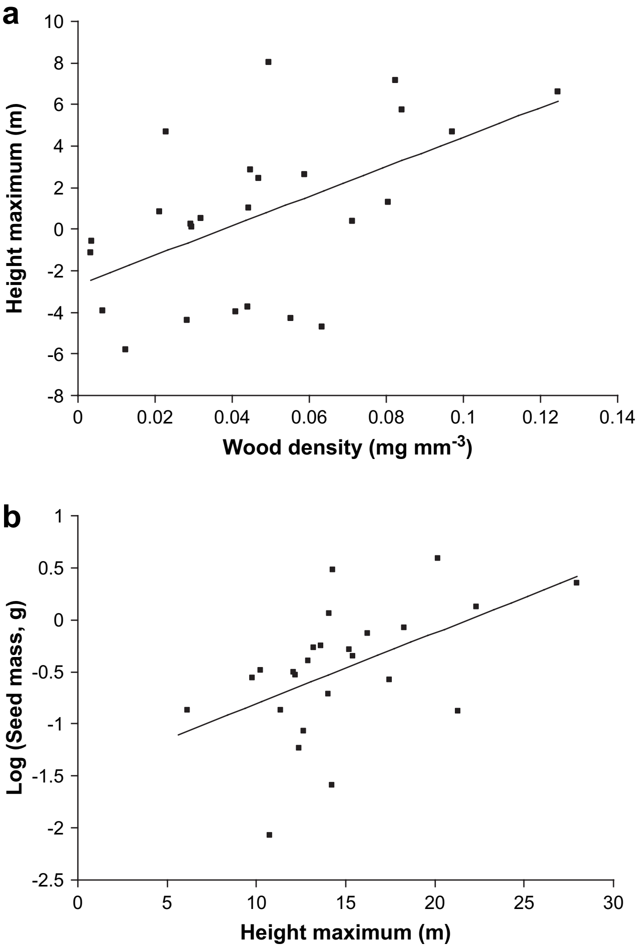

Fig. 2 – Correlations between (a) maximum height (Hmax, m) and wood density (WD, mg mm^{-3}), and (b) maximum height and seed mass (log SM, g), using phylogenetically independent contrasts as data points (PICs analysis). Correlation and *P* values as follows: Hmax and WD, *r* = 0.18; *P* = 0.030; log SM and Hmax (*r* = 0.12; *P* = 0.0821).

3.2. *Multivariate trait relationships*

In the PCA ordination the first two axes explained together 66.9% of the between-species variation (36.1% and 30.8%, respectively) (Fig. 3). Three traits were most strongly associated with axis 1, WD ($r = 0.712$), SM ($r = 0.790$) and Hmax ($r = 0.507$). In contrast, the second axis was more strongly correlated (albeit negatively) with SLA ($r = -0.855$). The loadings of each trait for axis 1, as assessed through the eigenvalues, showed that the ordination dimensions are related to three attributes. Only in the case of SLA a strong asymmetry was observed, as its eigenvalue for axis 2 (negative) was almost four-fold that of its corresponding value for axis 1 (also negative) (Table 3).

The distribution of the species in ordination space revealed continuous variation, with the majority of species (26) being concentrated in the upper central sector of the PCA plot. Seven species had positions relatively distant from this central species cloud (Fig. 3). On the far right end of the plot are located *Quercus salicifolia*, *Nectandra glabrescens* and *Juglans major*, characterized by intermediate to high SLA (183.43–284.67 cm^2 g^{-1}), very high SM (2.63–12.06 g), and high Hmax (19.7–35.15 m). In turn, in the left far end of the graph *Xylosma flexuosum* stands out as a quite distinct species, with an intermediate Hmax (16.6 m), but low SM (0.03 g) and the lowest SLA (22.75 cm^2 g^{-1}). Finally, *Rhamnus hintonii*, *Eugenia culminicola* and *Cinnamomum pachypodum* formed a loose cluster located towards the bottom of the ordination plot; these are short species (3.4–10.3 m), with high SLA (119.66–153.25 cm^2 g^{-1}) and intermediate SM (0.15–2.53 g).

The dendrogram obtained from the cluster analysis did not lead to a clear division into several groups. In fact, only two major groups could be distinguished at a cut-off distance of 18. One group was small and well defined, and comprised the nine species mentioned previously in the PCA (Group 1). The other one, named Group 2, encompassed all remaining 24 species and was very heterogeneous, and it could be divided into two subgroups at a cut-off Euclidean distance of 12. Subgroup 2a included five species and Subgroup 2b had 19 species (Fig. 4; Table 2). The nine species of Group 1 showed the largest mean values for all studied traits. The species of Subgroup 2a had smaller mean SM, SLA and Hmax, but a mean WD that was indistinguishable from that observed in the other group. Subgroup 2b comprised the smallest mean values for most traits except for SM, which was intermediate (Fig. 5). Some family level taxa were restricted to one group, as was the case of Betulaceae, all of the members formed part of Subgroup 2a, of Fagaceae, with its two species belonging to Group 1, and of Myrsinaceae, with three species in Subgroup 2b. Likewise, other species not belonging to the same family but that emerged as sister species in the phylogenetic reconstruction of the study species were grouped together (e.g. *Tilia americana* and *Acer skutchii* in Subgroup 2b). Such taxonomic homogeneity was not perfect, however, as illustrated by Lauraceae, with two species in Group 1, and a third one in Subgroup 2b. Also, it is noticeable that the

Table 2 – Species names with their family, order, biogeographical origin and abbreviation, for cloud forest tree species of Manantlán, Jalisco, Mexico. Specific leaf area (SLA, $cm^2\ g^{-1}$), seed mass (SM, g), wood density (WD, $mg\ mm^{-3}$), and maximum height (Hmax, m) organised by groups produced by hierarchical classification using Ward's method and Euclidean distances

Species	Family	Order	Origin	Abbreviation	SLA	SM	WD	Hmax
Group 1								
Cinnamomun pachypodum (Nees) Kosterm.	Lauraceae	Laurales	Boreotropical	Cinpac	153.25	2.539	0.5447	10.33
Cleyera integrifolia (Benth.) Choisy	Theaceae	Ericales	Boreotropical	Cleint	256.21	1.623	0.4665	12.8
Cornus disciflora Moc. et Sessé ex DC.	Cornaceae	Cornales	Holarctic	Cordis	183.77	0.892	0.5352	13.71
Ilex brandegeana Loes.	Aquifoliaceae	Aquifoliales	?	Ilebra	142.75	2.23	0.5831	20.07
Juglans major (Torr.) Heller	Juglandaceae	Fagales	Neotropical	Jugmaj	284.67	12.06	0.4818	19.7
Nectandra glabrescens Benth.	Lauraceae	Laurales	Holarctic	Necgla	183.43	8.45	0.4691	25.97
Quercus candicans Née	Fagaceae	Fagales	Holarctic	Quecan	79.39	1.948	0.4621	20.79
Q. salicifolia Née	Fagaceae	Fagales	Holarctic	Quesal	190.52	2.639	0.627	40.15
Ternstroemia dentisepala B.M. Barthol.	Ternstroemiaceae	Ericales	Pantropical	Terden	186.47	0.771	0.5201	11.5
Group 2								
Subgroup 2a								
Alnus jorullensis Kunth	Betulaceae	Fagales	Holarctic	Alnjor	228.65	0.004	0.4436	8.4
Carpinus tropicalis (Donn. Sm.) Lundell	Betulaceae	Fagales	Holarctic	Cartro	246.96	0.028	0.5459	14.0
Fraxinus uhdei (Wenz.) Lingelsh.	Oleaceae	Lamiales	Holarctic	Frauhd	103.77	0.037	0.5306	13.67
Ostrya virginiana (Mill.) K. Koch	Betulaceae	Fagales	Holarctic	Ostvir	49.04	0.024	0.6046	14.48
Zinowiewia concinna Lundell	Celastraceae	Celastrales	Neotropical	Zincon	172.68	0.033	0.4394	16.6
Subgroup 2b								
Acer skutchii Rehder	Sapindaceae	Sapindales	Boreotropical	Acesku	47.65	0.135	0.564	27.93
Citharexylum mocinnii D. Don	Verbenaceae	Lamiales	Neotropical	Citmoc	38.38	0.194	0.4495	11.6
Clethra vicentina Standl.	Clethraceae	Ericales	Neotropical	Cletvic	48.3	0.227	0.4126	17.34
Clusia salvinii Donn. Sm.	Clusiaceae	Malpighiales	Neotropical	Clusal	95.48	0.127	0.5401	10.1
Dendropanax arboreus (L.) Decne. et Planch.	Araliaceae	Apiales	Neotropical	Denarb	35.52	0.09	0.3887	10.72
Eugenia culminicola McVaugh	Myrtaceae	Myrtales	Neotropical	Eugcul	119.66	0.565	0.5306	3.89
Magnolia iltisiana A. Vázquez	Magnoliaceae	Magnoliales	Boreotropical	Magilt	129.68	0.38	0.6213	20.82
Meliosma dentate (Liebm.) Urb.	Sabiaceae	Ranunculales	Boreotropical	Melden	204.15	0.27	0.4355	11.65
Myrsine juergensenii (Mez) Lundell	Myrsinaceae	Ericales	Neotropical	Myrjue	43.21	0.254	0.6089	22.56
Parathesis villosa Lundell	Myrsinaceae	Ericales	Neotropical	Parvil	218.21	0.214	0.4651	6.0
Persea hintonii C.K. Allen	Lauraceae	Laurales	Boreotropical	Perhin	32.0	1.811	0.4938	14.33
Rhamnus hintonii M.C. Johnst. et L.A. Johnst.	Rhamnaceae	Rosales	Holarctic	Rhahin	142.87	0.148	0.4001	3.45
Styrax argenteus C. Presl	Styracaceae	Ericales	Neotropical	Styarg	60.99	0.68	0.4646	10.79
Symplococarpon purpusii (Brandegee) Kobuski	Theaceae	Ericales	Neotropical	Sympur	28.12	0.834	0.6276	15.35
Symplocos prionophylla Hemsl.	Symplocaceae	Ericales	Neotropical	Sympri	49.23	0.601	0.3536	10.59
Synardisia venosa (Mast.) Lundell	Myrsinaceae	Ericales	Neotropical	Synven	146.71	0.355	0.3769	13.52
Tilia mexicana Schldtl.	Malvaceae	Malvales	Holarctic	Tilmex	69.28	0.131	0.3151	14.71
Turpinia occidentalis (Sw.) G. Don	Staphylaceae	Crossosomatales	Boreotropical	Turocc	146.83	0.452	0.5846	13.7
Xylosma flexuosum (Kunth) Hemsl.	Salicaceae	Malpighiales	Pantropical	Xylfle	22.75	0.033	0.6221	16.6

groups and subgroups identified in the cluster analysis were not segregated on the PCA ordination plot.

4. Discussion

4.1. *Between-trait correlations*

The studied CF encompasses a biogeographical mixture of tree species that have evolved not only in different geographic regions, but also in quite different habitat types (i.e. tropical vs. temperate). At least three major sets are included in the studied flora: in addition to the typical temperate Laurasian (e.g. *Cornus disciflora*) and tropical Gondwanan (e.g. *Myrsine juergensenii*) elements (see Table 2), there also are tropical Laurasian taxa (e.g. *Magnolia iltisiana*), and at least one species without a clear biogeographical affinity (*Ilex brandegeana*). Despite this mixture of biogeographical histories, it must be stressed that the effect of phylogeny in the covariation of the functional attributes was rather unimportant. In fact, in several groups a mixture of clades was represented among the species they contained, suggesting the convergence of many lineages. Overall, our results showed that the relationships between the four traits studied are weak in Manantlán's cloud forest. The most obvious relationship was that between Hmax and SM, a pair of characters that were significantly correlated when using cross-species analyses, and nearly so in PICs. A loose relationship between Hmax and SM has been reported for several floras (r^2 ranging from 0.12 to 0.35; Rees, 1997; Westoby et al., 1997; Moles et al., 2004; Falster and Westoby, 2005a). The link between Hmax and SM has been proposed to reflect the association between two life

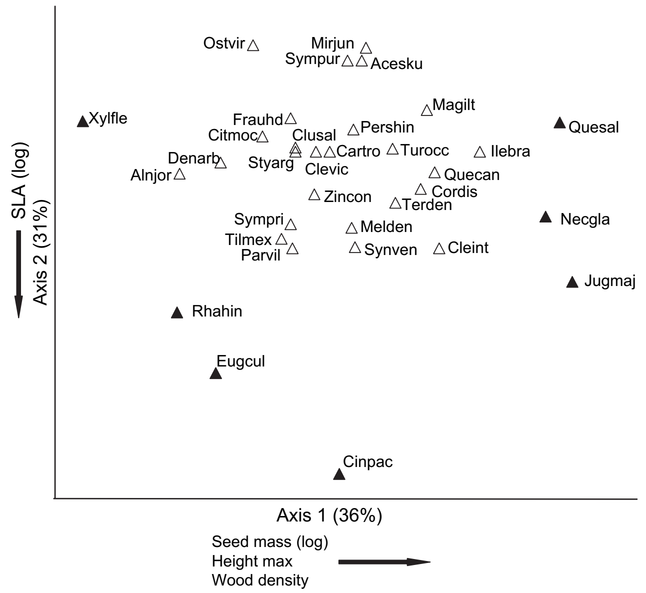

Fig. 3 – Ordination plot along two first principal components of 33 cloud forest species from Manantlán, Jalisco, W Mexico, based on the following traits: specific leaf area (SLA), seed mass (SM), wood density (WD) and maximum height (Hmax). Total variation explained by the first axis was 36.1%, and by the second was 30.8%. Black triangles distributed in the periphery of the ordination plot represent seven species and white triangles distributed in the central sector represent 26 species. Species abbreviations as in Table 2.

history components; big plants require longer periods before attaining adult size and reproductive maturity, and juvenile survivorship, an essential step in this process, is positively associated with seed size, especially in forests with a dense canopy and shaded understories (Moles and Westoby, 2004a; Wright et al., 2006b).

We expected that species with larger seeds would tend to have a large Hmax. In the case of Manantlán's cloud forest, taller trees tended to have larger SM, e.g. those species belonging to Group 1. This was well exemplified by *Juglans major* and *Quercus salicifolia*; however, there were important exceptions of taller trees having smaller SM, as illustrated by *Acer skutchii* and *Magnolia iltisiana*, both of which belong to groups with boreotropical affinities (see Table 2).

Table 3 – Loadings of traits that better explain between-species variation in the PCA ordination of 33 cloud forest tree species from Manantlán, Jalisco, Mexico

	Axis 1	Axis 2	Axis 3	Axis 4
Plant height	0.42 (+)	0.46 (−)	0.76 (+)	0.14 (−)
Seed mass	0.65 (+)	0.32 (+)	0.03 (−)	0.67 (+)
Wood density	0.59 (+)	0.28 (−)	0.58 (−)	0.46 (−)
SLA	0.19 (−)	0.77 (−)	0.26 (−)	0.54 (+)
Eigenvalue	1.44	1.23	0.79	0.52

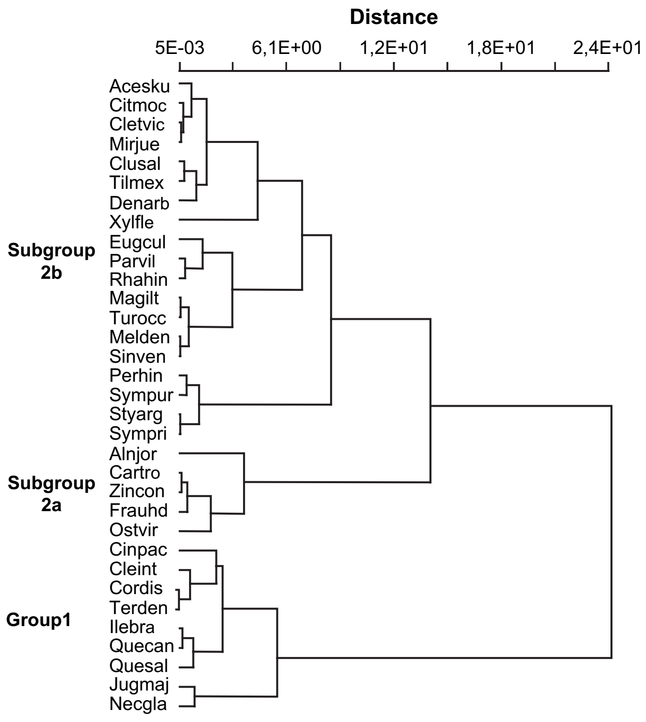

Fig. 4 – Species clustering for the cloud forest of Manantlán, Jalisco, W Mexico, based on Ward's grouping linkage method and Euclidian distances. Species abbreviations as in Table 2.

Hmax and WD also showed a significant positive correlation in the cross-species analysis, and this relationship was also significant in PICs. This frequently reported association has been interpreted as a pure mechanical relationship, as taller trees need more substantial investments in supporting structures to maintain a safety factor (Niklas, 1994; Sterck et al., 2006a). In this case, we expected a tight correlation between Hmax and WD; however, this relationship was very loose, suggesting that other factors may account for the positive relationship between Hmax and WD. Alternatively, Falster and Westoby (2005b) found that a positive Hmax vs. WD relationship can be expressed through a correlation with successional status; early successional plants have lower stature and softer wood than late successional ones. This possibility may apply to the species studied, but our field observations suggest that the range of successional status is rather narrow, with only a few species like *Nectandra glabrescens* and *Quercus salicifolia* being relatively more shade-tolerant. One must recall that pines, the true pioneers in this community (early fast colonizers with high growth rates and a short time to reproduction; Saldaña-Acosta, 2001) were not included in the study. Moreover, the relatively open canopy of this forest could prevent the existence of extremely shade tolerant species, as those described for lowland forests. In fact, all studied species may be clearly classified as mature forest components in Manantlán.

We hypothesized that species with medium to high WD would have a large Hmax, but that total height would be unrelated to a relatively low WD. In Manantlán, the variation

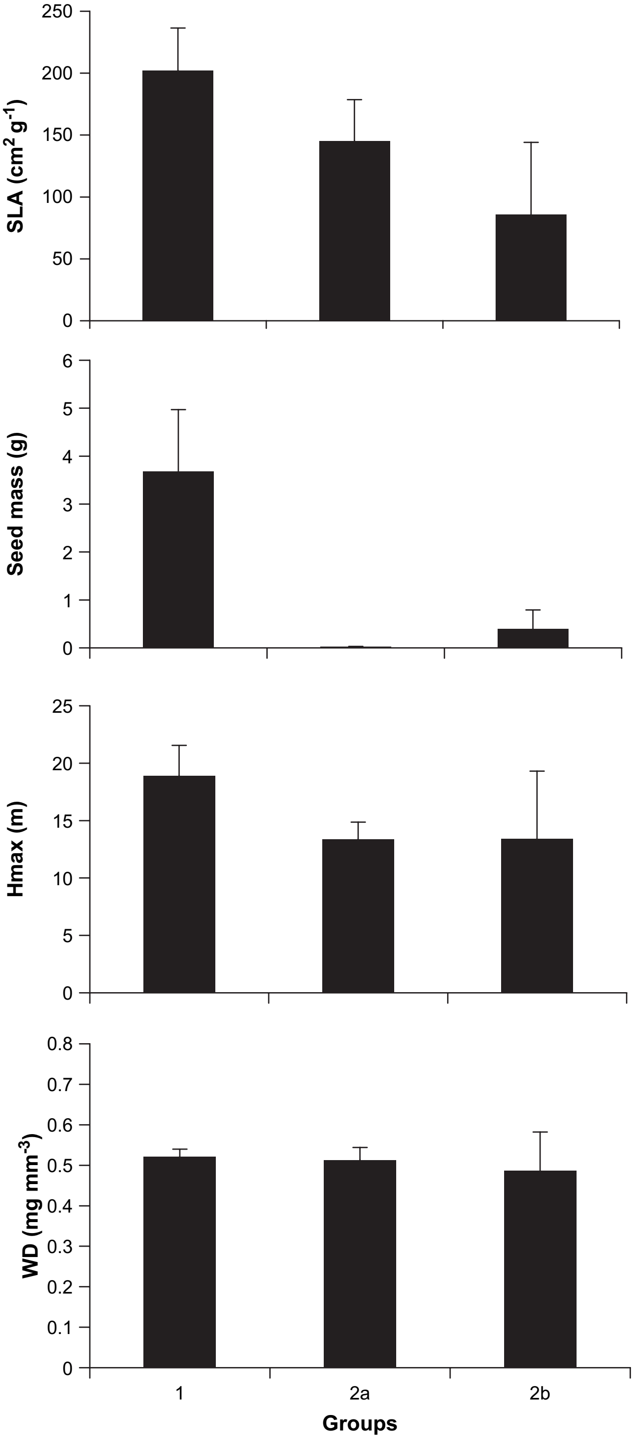

Fig. 5 – Mean values and ± SE of specific leaf area (SLA, cm^2 g^{-1}), seed mass (SM, g), wood density (WD, mg mm^{-3}) and maximum height (Hmax, m) for species forming the two different groups: Group 1 (1), and Group 2 (the latter with two Subgroups, 2a and 2b).

in WD observed across species was relatively small (range: 0.3–0.6 mg mm^{-3}), and there were no large differences in WD between short and tall plants, leading to the conclusion that this trait makes a very minor contribution to the multivariate between-species variation. Contrastingly, plant height in our cloud forest did vary across one order of magnitude (4–35 m). Consequently, there are both shorter species (e.g. *Ternstroemia dentisepala* and *Ostrya virginiana*), and tall species (e.g. *Quercus salicifolia* and *Magnolia iltisiana*) with similar WD. In fact, of the entire range of WD values reported in the literature, our set of cloud forest species is quite homogeneous (Lawton, 1984; King et al., 2005). In the case of lowland tropical trees, WD ranges from ca. 0.12 mg mm^{-3} for light-wooded species to ca. 1.15 mg mm^{-3} for the densest woods (Baker et al., 2004; Muller-Landau, 2004; King et al., 2006; Wright et al., 2006b). For temperate trees of higher latitudes this trait varies from 0.24 mg mm^{-3} for the light wooded species, to 0.77–0.98 mg mm^{-3} for the very heavy wood species (US Department of Agriculture, 1999; Woodcock and Shier, 2003). Finally, among tropical montane rain forest trees in sites other than Manantlán, WD ranges from 0.27 to 0.48 mg mm^{-3} for shade intolerant species, and from 0.39 to 0.58 for the shade tolerant ones (Lawton, 1984).

Unlike other forests, particularly lowland tropical ones, where vegetation structure is denser and the canopy is more closed (Sterck et al., 2006b), in Manantlán specialisation through WD differentiation for specific light environments appears to be less important. In this community, species differentiation along the vertical light gradient may derive from a trade-off between shade tolerance and growth in height, mediated by other traits such as the light capture architecture (see Poorter et al., 2005).

SLA showed the most independent behaviour among all traits, as it was unrelated to either Hmax, SM and WD in the cross-species and PICs analyses. This result is in partial disagreement with other studies that reported this trait to be related at times to other plant attributes such as SM, WD, Hmax and leaf size (Wright et al., 2006a,b; Falster and Westoby, 2005b; Poorter and Bongers, 2006), and to show phylogenetic correlations (Ackerly and Reich, 1999). The inconsistent correlations of SLA and Hmax, WD or SM found in the literature can be due to a variety of reasons related to the use of different protocols (collecting sun or shade leaves), to the particular community or site as they differ in nutrients or water or canopy openness, and even to the ontogenetic stage of sampled individuals (see Niinemets, 2006 for a discussion). Yet when comparing forests where sun leaves of adult trees were sampled, the direction of the SLA vs. Hmax correlation exhibited opposite directions between forests; positive for La Chonta, Bolivia, and negative for Los Tuxtlas, Mexico (Wright et al., 2006b). This result suggests that vertical variation in SLA is reflecting multiple correlations with life history as well as direct responses to environmental gradients, which need to be understood for each community. Perhaps the least generalised correlation of SLA is its proposed negative relationship with WD, which should reflect a trade-off between fast growth (high leaf return per mass invested) and survival in the shade (high resistance to losses of plant parts due to pathogens or physical damage). Again, in our study, the reduced variation in WD is likely to preclude the detection of such a functional relationship between SLA and WD.

In Manantlán we found a large among-species variation in SLA, ranging across one order of magnitude (22.3 cm^2 g^{-1} in *Xylosma flexuosum* to 284.6 cm^2 g^{-1} in *Juglans major*). Similar levels of variation have been found in other studies for lowland tropical and temperate forests, as well as for montane cloud forest communities (e.g. Reich et al., 1999; Williams-Linera, 2000; Wright et al., 2004; Pickup et al., 2005). We also found differences in SLA within taller and shorter species, i.e. there are both shorter and taller species with low and high SLA (Table 2). This kind of variation has been interpreted as an indication of a large plasticity of SLA, allowing plants to adjust continuously to the changing light environment experienced by trees during their ontogenetic development (Popma et al., 1992; Rozendaal et al., 2006). This is particularly relevant if one considers that there is a significant SLA reduction with tree age, suggesting ontogenetic changes in leaf traits (Niinemets, 2006). More studies are needed that analyze the variations of the four traits in response to changing conditions in different light levels and during ontogeny, as well as their relations with growth and mortality.

The lack of functional correlations in Manantlán may provide valuable insights as to which are the main axes of phenotypic variation in cloud forest trees. For instance, the fact that SLA represents an independent axis of niche differentiation and of evolutionary change (Ackerly, 2003) may be extremely useful in defining major functional strategies. Therefore, we may expect SLA to make a significant contribution to specialisation (through net carbon gain) to the heterogeneous light environments in CF, as previously demonstrated for tropical tree communities (Sterck et al., 2006a).

A particularly important goal of this study was to examine the possibility that correlations defining groups would still be present within particular clades, or whether they would reflect mainly between-clades differences. In our study we found a general concordance of functional correlations (Hmax vs. SM, and Hmax vs. WD) when evaluated based on cross-correlations or phylogenetic contrasts. This overall agreement suggests that a given functional relationship found among extant species has resulted from repeated divergence of the traits in different clades along the evolutionary history (Ackerly, 1999), and thus that common ancestry does not account fully for all potential variables affecting a given relationship (Paz et al., 2005). For example, for the relationship between Hmax and WD we detected several significant evolutionary divergences: the one corresponding to Eurosid trees took place at a very early stage of divergence. Thus it appears that these two attributes were acquired long ago and have been maintained since. Finally, the changes observed in the Asterid and Euasterid trees indicate that these attributes emerged as an adaptation in recent evolutionary stages of these two large groups.

4.2. *Species grouping*

Regarding our initial question about the possibility of morpho-functional traits indicating natural groups of cloud forest species, our results point out to a largely continuous among-species variation, as seen in the PCA plot (see Fig. 3). However, the trait-based classification allowed differentiating two main groups, whose distinction assisted in the effort to recognise a natural grouping among the studied species. The consistency of this distinction along a large range of linkage distance axis indicates that it is not completely artificial. Yet species classification in these groups is better justified from a practical perspective, i.e. for management purposes, than because of the existence of significant discontinuities between groups. In fact, the range of variation within groups, e.g. for SM and SLA, shows the large heterogeneity existing within the defined groups. According to dendrogram topology, Group 1 was better defined. Interestingly, the two main groups represented a combination of phylogenetic lineages, highlighting the role of ecological rather than phylogenetic constraints.

Cloud forest tree species of Manantlán do not form permanent seed banks so that a persistent seedling bank is the commonest regeneration strategy (Saldaña-Acosta, 2001). The diametric structures of some taxa (e.g. *Nectandra glabrescens*, *Magnolia iltisiana*, and *Myrsine juergensenii*) are characteristic of populations having advanced regeneration and probably a good response capacity when gaps open in the canopy. In contrast, other species like *Fraxinus uhdei* are large canopy trees, with their seedlings and saplings being scarce or absent in the understorey. This study suggests the existence of a variety of comparable, but by no means identical, successful life history strategies for Manantlán's cloud forest species, and reflects the coexistence of species with varying functional traits but living under similar conditions. As it happens in other montane forests, cloud forest tree species possess a set of traits that are linked to key aspects of the establishment phase of their life cycles.

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