



Tree morphology in seasonally dry montane forest in Argentina: Relationships with shade tolerance and nutrient shortage

Authors: Easdale, Tomás A., Gurvich, Diego E., Sersic, Alicia N., and Healey, John R.

Source: Journal of Vegetation Science, 18(3) : 313-326

Published By: International Association of Vegetation Science

URL: [https://doi.org/10.1658/1100-9233\(2007\)18\[313:TMISDM\]2.0.CO;2](https://doi.org/10.1658/1100-9233(2007)18[313:TMISDM]2.0.CO;2)

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Tree morphology in seasonally dry montane forest in Argentina: Relationships with shade tolerance and nutrient shortage

Easdale, Tomás A.^{1,5*}; Gurvich, Diego E.^{2,3}; Sersic, Alicia N.^{2,4} & Healey, John R.^{5,6}

¹Laboratorio de Investigaciones Ecológicas de las Yungas, Universidad Nacional de Tucumán, C.C. 34, 4107 Yerba Buena, Argentina; ²Instituto Multidisciplinario de Biología Vegetal, FCEFyN, Universidad Nacional de Córdoba - CONICET, C.C. 495, 5000 Córdoba, Argentina; ³E-mail dgurvich@com.uncor.edu; ⁴E-mail asersic@com.uncor.edu; ⁵School of the Environment and Natural Resources, University of Wales, Bangor, Gwynedd, LL57 2UW, UK; ⁶E-mail j.healey@bangor.ac.uk; *Corresponding author; E-mail tom.easdale@univ.bangor.ac.uk

Abstract

Question: How does form (leaf and trunk morphology) relate to function (tolerance of shade and nutrient storage) in trees?

Location: Los Toldos montane valley in NW Argentina.

Methods: We analysed the relationships amongst (1) ten vegetative and four reproductive traits across 40 tree species, (2) a distribution based measure of recruitment under shade and (3) a distribution based measure of recruitment over a soil fertility gradient.

Results: Ordinations revealed three main axes of species' morphological differentiation: (1) evergreen species had leaves with a lower specific leaf area, greater tensile resistance and slower decomposition rate, denser wood and thinner bark than deciduous species; (2) tall tree species that lack spines and are anemochorous were separated from short, spinescent and zoochorous species and (3) species were distinguished according to clonal growth, seed mass and pollination syndromes. Notably, species' recruitment under shade and over a soil fertility gradient were independent of each other, but both were correlated with species' scores along the first axis of morphological variation (tolerant species have attributes that favour resource conservation). Different sets of traits were correlated with recruitment under shade and over a soil fertility gradient when traits were assessed individually. Amongst shade tolerant species, recruitment under shade was negatively correlated with species' maximum height, suggesting differential responses to vertical gradients of light.

Conclusions: These results provide new evidence of integration between leaf and stem morphology which is consistent with an evolutionary compromise between high rate of resource acquisition and resource conservation. Generalizations about the functional value of individual morphological characteristics and of 'strategies' vary with the resolution of analyses.

Keywords: Allocation; Comparative ecology; Functional significance; Neotropical cloud forest; Plant functional trait.

Abbreviations: PCoA = Principal coordinates analysis; SLA = Specific leaf area.

Nomenclature: Zuloaga & Morrone (1999) for species; Anon. (2003) for families and orders.

Introduction

There has been a marked historical assumption in biological research that organisms have an optimum fit with both their associated physical and biotic environments. However, several evolutionary forces other than natural selection can cause traits to persist (Antonovics 1976; Gould & Lewontin 1979; Harper 1982), including continuous production of less fit traits/individuals through mutation or immigration; genetic drift and genetic, biochemical or architectural constraints in the evolution of traits. In addition to evolutionary forces, historical and random processes can also bring noise into trait-environment relationships and eventually be more important than ecophysiology in determining species distributions (Herrera 1992; Hubbell 2005). All this should make us question whether every single trait is necessarily relevant to the success of an organism in a particular environment.

The functional significance of plant traits can be evaluated by testing the connection between the structure/physiology of plants and their performance under particular conditions or levels of resource availability by means of comparative studies (Keddy 1992; Poff 1997; Press 1999; Wilson 1999). Understanding these connections is essential for a better interpretation of plant community dynamics and a critical step before attempting to achieve any functional classifications for predicting the response of species to the environment. Here we want to draw attention to two issues that should be considered when conducting such studies. First, traits are not independent of each other but rather are conditioned by trade-offs, genetic linkages and other mechanisms (Chapin et al. 1993; Begon et al. 1996). The possession of one life history attribute may limit the possible range of some other attribute, and the general morphology of an organism may limit the possible range of all its life history attributes. This indicates the need to explore not only the connection between individual

traits and environment but also the connection between groups of correlated traits, or axes of morphological differentiation, and the environment. Second, organisms face a combination of limitations of resources simultaneously so it is important to explore their responses to a combination of resources and conditions (e.g. Smith & Huston 1989; Latham 1992; Grubb et al. 1996).

Studies of different floras and plant life forms have provided support for a main axis of functional differentiation which distinguishes species that maximize resource acquisition and are superior competitors in resource rich environments from those that maximize resource conservation and are able to persist in resource limited environments (e.g. Coley et al. 1985; Lambers & Poorter 1992; Grime et al. 1997; Reich et al. 2003; Díaz et al. 2004; Wright et al. 2004). At one end of the spectrum, species with high growth potential and typical of resource rich habitats are characterized by fast tissue turnover, high metabolic rates and attributes that enhance resource acquisition such as high specific leaf area (SLA), high leaf nutrient concentrations and high photosynthetic rates. At the other end of the spectrum, species that tolerate limitation of resources tend to have opposite attributes such as slow tissue turnover and traits that enhance resource conservation. Most of these observations have arisen from studies of leaf ecophysiology, but some preliminary observations on root and stem traits seem consistent with the trends observed in leaves (Eissenstat 2000; Reich et al. 2003). Two critical questions derive from these trends. Do species which tolerate limitation of a given resource tolerate scarcity of other resources? Provided that this takes place, does the potential of a species to tolerate limitation of different resources arise from possession of the same traits? The empirical evidence related to the first question seems very varied (e.g. Sack & Grubb 2002). The opposite sets of attributes associated respectively with each side of the resource availability spectrum seem to share similarities when considered in the context of the three basic resources limiting plant growth: nutrients, water and light (Reich et al. 2003). This contrasts with Grubb's (1998) emphasis that different suites of traits are advantageous according to the most limiting resource in question.

Here, we examine the regeneration patterns of 40 broad-leaved tree species in a South American montane forest in relation to soil fertility and shade and assess the morphological features (individual traits and sets of associated traits) related to species' response. Specifically, we ask (1) what are the main dimensions of morphological differentiation across the sampled tree species and what is the functional characteristic underlying each of these dimensions? For this, we analyse various vegetative and reproductive morphological

traits and identify the interrelationships between different organs and functions of the tree. Secondly, we estimate species' affinity for light and soil resources and ask, (2) is there a correlation amongst species in their recruitment under shade and their recruitment in soils of low fertility? To the extent that they differ we then ask, (3) is there a clear differentiation in the traits associated with each measure of performance? and (4) is there any distinction when traits are considered individually or as axes of 'specialization'?

Study site

The study was conducted in Los Toldos valley (22°14' to 22°21' S and 64°39' to 64°45' W), an upper montane valley 20 km south of the border between Argentina and Bolivia. The bottom of the valley is ca. 1550 m a.s.l. and we sampled forest sites up to 1950 m a.s.l. These are classified as upper montane forests within the Yungas phytogeographic region, which comprises montane cloud forests in Bolivia and NW Argentina (Cabrera & Willink 1973). There are ca. 64 tree species within the valley, and a large proportion of them also occur, or have near relatives, in the equatorial Andes (Hueck 1978). The forests are mainly semi-deciduous, partly due to a markedly seasonal climate with wet summers and dry winters. The mean annual precipitation recorded between 1981 and 1992 on the valley floor was 1308 mm, and the mean precipitation between May and September, the dry season, was 53 mm. However, in the dry season, water input by fog interception can equal that of direct rainfall (Hunzinger 1997). Mean temperatures were 11.7 °C for the whole year, 5.2 °C for the coldest month (July) and 16.4 °C for the warmest month (January). Local soils vary from haplic phaeozems to eutric regosols (Nadir & Chafatinos 1990) and the study was carried out over most of this range. The phaeozems are young dark soils rich in organic matter, with a high base saturation developed on unconsolidated residual deposits and characterized by A, Ac and C profiles. Parts of the valley have been affected by intense soil erosion due to forest conversion to pastures and frequent burning combined with high rainfall and steep slopes. This has resulted in denuded or highly eroded regosols with a single ochric or umbric superficial horizon and the underlying unconsolidated materials approaching the surface. These are being recolonized in some areas by secondary forest with a distinct species composition (Gurvich et al. 2003).

Methods

We analysed ten vegetative traits and four reproductive traits (Table 1) for 40 broad-leaved tree species (Table 2, App. 1). The species selected were the most common in a 3.45-ha forest census described below. Although *Podocarpus parlatorei* is a dominant conifer in these forests we did not include it in our analysis because, as a phylogenetically distant species, its ecophysiology and mode of resource use seems very different from those of broad-leaved trees (cf. Grubb 1998). We selected traits related to different functional roles in the life of a tree, which were likely to have functional importance according to the literature, and which could be measured with simple methods. Although morphological characteristics are generally considered to be of secondary importance to more fundamental physiological traits such as those of the photosynthetic and respiratory systems (e.g. Grubb

& Metcalfe 1996) some morphological traits (mainly those related to relative size, costs of construction and maintenance and longevity of plant organs) are known to play a critical role in plant ecological performance (Korner 1991). Eleven traits were measured in the field and three were based on simple observations and the flora of Digilio and Legname (1966). Leaf decomposition rates were taken from Gurvich et al. (2003).

The procedures for trait measurement are listed in Table 1, and any discrepancies with standardized protocols (Hendry & Grime 1993; Cornelissen et al. 2003) are specified where appropriate. Leaves were not uniformly collected from full sun conditions as suggested by the protocols but, instead, were gathered from the outer crown of trees > 10 cm DBH in the most common illumination conditions where each species was found. We selected undamaged mature, but not senescent, leaves.

Table 1. List of character traits with general description of measurement method; cont = continuous; ord = ordinal; nom = nominal.

Trait (type of scale)	No. of replicates (ind/species)	Measurement unit / categories	Description / mode of measurement
Leaf lamina area (cont)	6	Measured on scanned leaves, average size of folioles was computed in compound leaves, area was completed for damaged leaves	cm ²
Specific leaf area (SLA) (cont)	6	Leaf area allocation per unit leaf dry weight with petioles removed	mm ² .g ⁻¹
Leaf dry matter content (cont)	6	Leaf dry weight per unit leaf fresh weight with petioles removed	g.g ⁻¹
Leaf tensile strength (cont)	6	Measured with leaf tensiometer as in Hendry & Grime (1993)	N.mm ⁻¹
Leaf decomposition rate (cont)	6	Proportion of dry weight loss from 1-2 g leaf litter samples in 0.3 mm mesh bags after 15 weeks burial. See Gurvich et al. (2003) for more detail	proportion of dry weight loss
Leaf phenology (ord)	10	July-August (winter leaf-fall peak) visual observations of the proportion of potential leaf canopy fullness for trees > 10 cm DBH	deciduous, semideciduous, evergreen
Wood density (cont)	6 to 7	Oven dry weight / fresh volume of first order branches between 8 and 12 cm diameter. Measures were made on sticks of 2-3 cm width and 7-11 cm length which were cut across the diameter of branch disks. Bark was removed	g.cm ⁻³
Bark thickness (cont)	6	Depth between outer bark and cambium at ca. 1 m height on stems between 7 and 10 cm DBH	mm
Spinescence (nom)		Any sharp pointed structure on stems or branches was considered as a spine regardless of density within the tree	presence / absence
Pollination syndrome (nom)		Pollination syndromes were assessed on the basis of: (a) morphological features of flowers that precluded or facilitated utilization of floral rewards by a particular class of visitor, (b) colour of the flowers, (c) previous observations and published work	wind, butterfly, bee, moth, generalist pollination
Dispersal mode (nom)		Based on observations of fruit morphology	autochorous, anemochorous, endozoochorous
Seed mass (cont)	6	Mean air dry weight of ten seeds, wings removed	g
Maximum height (cont)	Variable	Average of: (a) maximum size reported by Digilio & Legname (1966), (b) maximum height measured with clinometer within 1 ha of old-growth forest, (c) height of the largest tree in each of 41 secondary forest plots (0.075-ha). (b) and (c) were available only for some species	m
Clonal growth (nom)	10	Roots of stems < 1 m height were tracked. Only stems growing beneath the forest canopy were uprooted. Although stems were close to potential parent trees in most cases, no restriction was made with respect to distance to them. A stem was recorded as clonal either when its roots were connected to a large tree or when a horizontal root, stolon or rhizome extended horizontally by more than three heights from the uprooted stem	yes (at least one clonal stem), no (none clonal of ten uprooted stems)

Table 2. List of species common to Los Toldos valley, NW Argentina, included in this study. We base the geographic distribution of the genera on Prado (2000) and tentatively categorize the upper montane forests as part of a separate biogeographic unit (Andes) with links to both north and south cold-temperate forests. TrS = Tropical seasonal.

Order	Family	Species list	Codes	Distribution of the genera within South America
Sapindales	Sapindaceae	<i>Allophylus edulis</i>	Aed	Chaco, TrS, Andes
Fagales	Betulaceae	<i>Alnus acuminata</i>	Aac	Andes
Myrtales	Myrtaceae	<i>Amomyrtella güili</i>	Agu	Chaco, Andes
Asterales	Asteraceae	<i>Baccharis latifolia</i>	Bla	Chaco, Andes
Ranunculales	Berberidaceae	<i>Berberis jobii</i>	Bjo	Chaco, Andes
Myrtales	Myrtaceae	<i>Blepharocalyx salicifolius</i>	Bsa	Amazonia, Andes
Sapindales	Meliaceae	<i>Cedrela lilloi</i>	Cli	TrS, Andes
Laurales	Lauraceae	<i>Cinnamomum porphyrium</i>	Cpo	Amazonia, TrS, Andes
Unplaced in Euasterids II	Icacinaceae	<i>Citronella apogon</i>	Cap	TrS, Andes
Ericales	Clethraceae	<i>Clethra scabra</i>	Csc	Amazonia, Andes
Oxalidales	Elaeocarpaceae	<i>Crinodendron tucumanum</i>	Ctu	Andes
Lamiales	Verbenaceae	<i>Duranta serratifolia</i>	Dse	Andes
Unplaced in Euasterids II	Escalloniaceae	<i>Escallonia millegrana</i>	Emi	Andes
Myrtales	Myrtaceae	<i>Eugenia hyemalis</i>	Ehy	Amazonia, TrS, Andes
Asterales	Asteraceae	<i>Eupatorium saltense</i>	Esa	Chaco, TrS, Andes
Sapindales	Rutaceae	<i>Fagara coco</i>	Fco	Chaco, Amazonia, TrS, Andes
Aquifoliales	Aquifoliaceae	<i>Ilex argentina</i>	Iar	Amazonia, TrS, Andes
Fagales	Juglandaceae	<i>Juglans australis</i>	Jau	Andes;
Celastrales	Celastraceae	<i>Maytenus cuezzoi</i>	Mcu	Chaco, TrS, Andes
Myrtales	Myrtaceae	<i>Myrcianthes mato</i>	Mma	Chaco, TrS, Andes
Myrtales	Myrtaceae	<i>Myrcianthes pseudo-mato</i>	Mps	Chaco, TrS, Andes
Fagales	Myricaceae	<i>Myrica pubescens</i> var. <i>glabra</i>	Mpu	Andes
Ericales	Myrsinaceae	<i>Myrsine coriacea</i>	Mco	Amazonia, TrS, Andes
Fabales	Fabaceae	<i>Parapiptadenia excelsa</i>	Pex	TrS, Andes
Rosales	Rosaceae	<i>Prunus tucumanensis</i>	Ptu	Amazonia, Andes
Gentianales	Rubiaceae	<i>Randia armata</i>	Rar	TrS, Andes
Rosales	Rhamnaceae	<i>Rhamnus sphaerosperma</i>	Rsp	Andes
Proteales	Proteaceae	<i>Roupala meisneri</i>	Rme	Amazonia, TrS, Andes
Dipsacales	Caprifoliaceae	<i>Sambucus nigra</i> ssp. <i>peruviana</i>	Sni	TrS, Andes
Sapindales	Anacardiaceae	<i>Schinus meyeri</i>	Sme	Chaco, TrS, Andes
Rosales	Rhamnaceae	<i>Scutia buxifolia</i>	Sbu	Chaco, TrS, Andes
Malpighiales	Euphorbiaceae	<i>Sebastiania brasiliensis</i>	Sbr	Chaco, TrS, Andes
Solanales	Solanaceae	<i>Solanum symmetricum</i>	Ssy	Chaco, Amazonia, TrS, Andes
Lamiales	Bignoniaceae	<i>Tabebuia lapacho</i>	Tla	Chaco, Amazonia, TrS, Andes
Myrtales	Combretaceae	<i>Terminalia triflora</i>	Ttr	Amazonia, TrS, Andes
Ericales	Pentaphragaceae	<i>Ternstroemia congestiflora</i>	Tco	Andes
Solanales	Solanaceae	<i>Vassobia breviflora</i>	Vbr	Chaco, TrS, Andes
Dipsacales	Caprifoliaceae	<i>Viburnum seemenii</i>	Vse	Andes
Malpighiales	Salicaceae	<i>Xylosma longipetiolata</i>	Xlo	TrS, Andes
Malpighiales	Salicaceae	<i>Xylosma pubescens</i>	Xpu	TrS, Andes

Data analysis

Correlations amongst character traits

To explore the main trends of morphological differentiation across species, we ordinated the matrix of mean values of 14 traits for 40 species (App. 1). Because the dataset consisted of nominal, ordinal and continuous variables, we first computed a species similarity matrix using the Gower coefficient (Gower 1971), a general measure of proximity that can combine different types of variable. We then performed a principal coordinate analysis (PCoA) on this similarity matrix using GenStat 8. PCoA is a general form of principal component analysis (PCA) that allows the use of a wide array of distance measures (Legendre & Legendre 1998). The results of

this analysis were (a) equivalent to those of a PCA restricted to continuous variables previously transformed to correct for skewed distributions and (b) identical to those of a non-metric multidimensional scaling analysis of the same similarity matrix. The significance of the extracted axes was tested using a broken-stick model distribution which predicts the partition of the total variance amongst the axes if it is made at random; observed ordination axes are considered interpretable when they explain more variation than expected from this model distribution (Legendre & Legendre 1998). To explore in detail the correlations between pairs of traits and between traits and ordination axes (not provided in PCoA) we used Kendall rank correlations because many of the variables did not fit normal distributions and some of them had natural outliers.

Although our data matrix and replicates were almost complete, in a few cases we could not collect any samples and had to estimate values in order to run the ordination. For six species we estimated seed mass from seed sizes reported by Diglio & Legname (1966) through a seed size - seed mass regression ($R^2 = 0.69$, $n = 32$, $p < 0.001$), for *Xylosma longipetiolata* we replaced leaf decomposition rate with the all-species mean and for *Eugenia hyemalis* we used visual estimations of maximum height. Any error introduced by these estimations was probably minimal compared with the benefit gained by including all species in the ordination analyses. Nominal multistate variables (dispersal and pollination syndromes) were split into dummy variables for analysis.

Measures of performance

To assess the functional significance of traits in terms of use of light or soil resources, we analysed the correlation of traits and groups of correlated traits with distribution-based measures of recruitment under shade and of recruitment over a gradient of soil fertility (App. 1). Both measures were based on a census of trees (> 5 cm DBH) in 46 plots (0.075 ha) (5 in old growth and 41 in secondary closed canopy forest) which were distributed across a wide range of soil types (pH 3.97 – 6.30) and land use histories (Easdale unpubl.) within Los Toldos valley. All plots were in closed canopy forest stands but they differed widely in structure and shade cast; maximum tree stature ranged from 9.5 m to 35.1 m amongst the stands and the density of stems > 5 cm DBH ranged from 747 stems/ha to 5480 stems/ha. Because both measures of performance were based on patterns of recruitment in the field and under competition with other species, they are estimates of the species' realized, rather than fundamental, responses.

Recruitment under shade was estimated from the capacity of each species to support a population of saplings/sprouts under closed canopy cover. It was computed as the quotient between each species' frequency of saplings/sprouts (> 0.3 m height and < 1 cm DBH) amongst the 46 plots and its frequency of trees > 5 cm DBH in the same plots. The measure assumes that if trees > 5 cm DBH of a certain species are present in a forest plot, the species is able to reach the site, grow and possibly produce progeny in that site. Therefore, the more shade tolerant the species the more likely that its saplings/sprouts would be found under the canopy of that stand. We report results for all 40 species but analyses in which we discarded the six resprouting species that could be falsely recorded as functionally shade tolerant (if 'saplings' recorded were actually sprouts that were physiologically sustained by their 'parent'

trees) exhibited similar results in all cases except for a marked increase in the statistical significance of the relationship with pollination syndromes.

Recruitment was assessed over a gradient of soil fertility with the purpose of estimating the capacity of each species to establish in infertile soils. For this, we computed weighted averages (ter Braak & Looman 1986) from the depth of the upper organic soil layer (ca. A horizon), standard chemical analysis and species' abundance for each of the 46 plots. The soil analyses were done on upper soil (5 cm to 15 cm depth) composite samples (three sub-samples per plot) and included pH (potentiometric, 1:2.5 (v/v) soil to water suspension), total N (micro-Kjeldahl), available P (modified Bray-Kurtz), total C (loss on ignition), available K (flame photometry) and available Ca and Mg (EDTA complexometric titration). Exchangeable cations were extracted with 1 N ammonium acetate at pH 7. For each of the 40 species, mean values of each of the nine soil variables were calculated over the plots in which the species occurs, and these were weighted by the species' abundance on those same sites. Two species that were surveyed in only one site were excluded from this analysis. To give an approximation of the conditions where each species established (because current soil conditions in old growth forest could differ substantially from those prevalent at the time of establishment of old trees) we only used counts of trees in old growth forest plots that were smaller or equal in DBH to the largest trees found in secondary forest for that species.

We thus created a matrix of weighted averages for each of nine soil variables and each of 40 species. We subjected the matrix to a PCA to summarize these results and took the loadings on the first principal component of the ordination as the measure of recruitment over a soil fertility gradient. This first principal component explained 36.7% of the total variation and summarized species' differential affinities (weighted averages) for pH, K, Mg, depth of organic soil layer and available P (factor loadings 0.83, 0.74, -0.65, 0.63 and 0.61 respectively). Ca, total N and total C had loadings with absolute values lower than 0.41 on the first principal component, indicating that species' affinities for these variables were largely independent from their affinities for the other variables and that they had no weight in this index.

Table 3. Signs and probabilities of Kendall rank correlations: (a) amongst morphological traits, (b) between PCoA axes and both morphological traits and measures of performance and (c) between measures of performance and morphological traits, and amongst measures of performance. Cases with a grey background have significant correlations. Bold numbers indicate correlations significant at $p \leq 0.01$. Frames that expand from the upper left corner distinguish traits grouped by each of the three PCoA axes.

p values for Kendalls tau	Morphological traits										Performance													
	Specific leaf area	Leaf tensile strength	Leaf phenology	Leaf dry matter content	Leaf area	Wood density	Leaf decomposition	Bark thickness	Anemochory	Endozochory	Autochory	Spines	Maximum height	Generalist pollination	Clonal growth	Moist pollination	Bee pollination	Wind pollination	Seed weight	Butterfly pollination	Recruitment under shade	Recruitment on infertile soil		
(a)																								
	Correlations																							
	Leaf tensile strength	(+) 0.000																						
	Leaf phenology	(-) 0.003 (+) 0.001																						
	Leaf dry matter content	(+) 0.000 (+) 0.000 (+) 0.027																						
	Leaf area	(+) 0.004 (+) 0.001 (-) 0.015 (-) 0.007																						
	Wood density	(-) 0.017 (+) 0.004 (+) 0.021 (+) 0.014 (-) 0.032																						
	Leaf decomposition	(+) 0.003 (-) 0.038 (-) 0.015 (+) 0.008 (+) 0.012 (-) 0.545																						
	Bark thickness	(+) 0.133 (-) 0.249 (-) 0.031 (-) 0.037 (+) 0.075 (+) 0.008 (+) 0.180																						
	Morphological traits																							
	Anemochory	(-) 0.662 (-) 0.466 (-) 0.074 (-) 0.961 (+) 0.593 (-) 0.293 (-) 0.833 (+) 0.466																						
	Endozochory	(+) 0.705 (+) 0.458 (+) 0.012 (+) 0.596 (-) 0.705 (+) 0.705 (+) 0.797 (-) 0.660 (+) 0.000																						
	Autochory	(+) 0.951 (-) 0.901 (-) 0.087 (-) 0.321 (-) 0.804 (+) 0.215 (-) 0.901 (-) 0.620 (-) 0.440 (-) 0.020																						
	Spines	(+) 0.486 (+) 0.833 (-) 0.371 (+) 0.639 (+) 0.961 (+) 0.686 (+) 0.225 (-) 0.593 (-) 0.070 (+) 0.038 (-) 0.440																						
	Maximum height	(-) 0.161 (+) 0.161 (+) 0.960 (+) 0.042 (-) 0.076 (+) 0.870 (-) 0.375 (+) 0.935 (+) 0.626 (-) 0.564 (+) 0.804 (-) 0.516																						
	Generalist pollination	(+) 0.622 (+) 0.495 (+) 0.296 (-) 0.649 (+) 0.762 (+) 0.570 (+) 0.150 (-) 0.289 (-) 0.157 (+) 0.524 (+) 0.160 (+) 0.496 (-) 0.204																						
	Clonal growth	(-) 0.179 (+) 0.409 (+) 0.371 (+) 0.169 (-) 0.373 (+) 0.169 (-) 0.021 (-) 0.237 (-) 0.982 (+) 0.691 (-) 0.440 (+) 0.383 (-) 0.236 (-) 0.714																						
	Moist pollination	(+) 0.367 (-) 0.443 (-) 0.062 (-) 0.279 (+) 0.718 (-) 0.443 (+) 0.279 (+) 0.685 (+) 0.009 (-) 0.027 (-) 0.633 (+) 0.901 (-) 0.498 (-) 0.382 (+) 0.901																						
	Bee pollination	(-) 0.174 (+) 0.277 (+) 0.708 (-) 0.370 (-) 0.302 (+) 0.370 (-) 0.724 (+) 0.765 (-) 0.475 (+) 0.461 (-) 0.886 (-) 0.143 (+) 0.141 (-) 0.004 (-) 0.475 (-) 0.021																						
	Wind pollination	(-) 0.762 (-) 0.225																						
	Seed weight	(+) 0.944 (+) 0.780 (+) 0.157 (+) 0.402 (-) 0.235 (+) 0.142 (+) 0.944 (-) 0.159 (-) 0.000 (+) 0.002 (+) 0.576 (-) 0.833 (+) 0.065 (+) 0.363 (-) 0.293 (-) 0.115 (+) 0.532 (-) 0.910																						
	Butterfly pollination	(+) 0.121 (-) 0.576																						
	PCoA 1	(+) 0.000 (-) 0.000 (+) 0.000 (+) 0.000 (+) 0.000 (+) 0.011 (+) 0.031 (-) 0.011 (+) 0.291 (+) 0.734 (+) 0.233 (+) 0.880 (+) 0.089 (+) 0.027 (-) 0.103 (-) 0.970 (-) 0.108 (+) 0.321 (-) 0.024 (-) 0.012																						
	PCoA 2	(-) 0.045 (+) 0.658 (-) 0.551 (+) 0.339 (-) 0.328 (-) 0.816 (-) 0.177 (+) 0.408 (+) 0.000 (+) 0.000 (+) 0.456 (+) 0.000 (+) 0.002 (-) 0.007 (-) 0.089 (+) 0.417 (+) 0.007 (-) 0.198 (-) 0.415 (-) 0.420 (-) 0.014 (+) 0.589																						
	PCoA 3	(-) 0.113 (-) 0.798 (+) 0.691 (+) 0.108 (+) 0.576 (-) 0.244 (+) 0.032 (+) 0.311 (+) 0.002 (+) 0.003 (-) 0.756 (-) 0.486 (+) 0.797 (-) 0.762 (-) 0.000 (+) 0.047 (+) 0.000 (+) 0.004 (+) 0.021 (-) 0.620 (+) 0.294 (-) 0.910																						
	Performance																							
	Recruitment under shade	(-) 0.675 (+) 0.053 (+) 0.045 (+) 0.305 (+) 0.514 (+) 0.009 (+) 0.675 (-) 0.110 (+) 0.003 (+) 0.010 (+) 0.619 (+) 0.132 (-) 0.332 (+) 0.248 (+) 0.783 (-) 0.289 (+) 0.568 (-) 0.705 (+) 0.072 (-) 0.264																						
	Recruitment on infertile soil	(-) 0.048 (+) 0.016 (+) 0.019 (+) 0.285 (-) 0.372 (+) 0.204 (-) 0.010 (-) 0.028 (-) 0.571 (+) 0.791 (+) 0.438 (-) 0.092 (-) 0.357 (+) 0.746 (+) 0.595 (-) 0.051 (+) 0.261 (-) 0.746 (-) 0.831 (+) 0.845 (+) 0.372																						

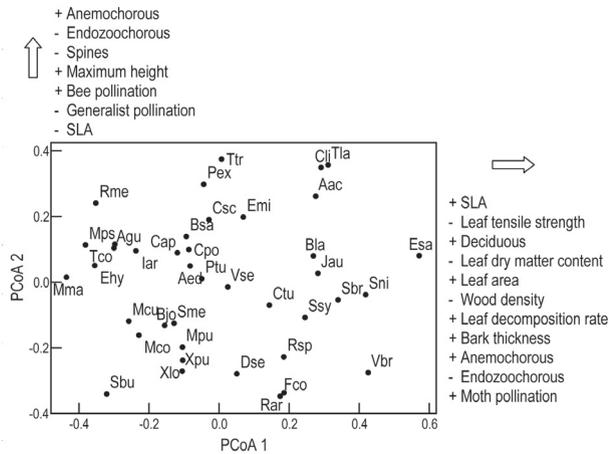


Fig 1. Arrangement of species along the first two axes of a 40 species by 14 trait PCoA of sympatric montane tree species in NW Argentina. The traits listed are those integrated by each of these axes; they are enumerated in sequence from strongest to weakest strength of association with each axis; signs indicate the direction of association. Table 2 gives the full names of the species shown here as three letter abbreviations.

Results

The first seven axes of a PCoA of species by traits explained more variation than expected for a random (broken-stick) partitioning of variance. No eigenvalue was negative (cf. Legendre & Legendre 1998). We interpret only the first three axes (which explain 18.8, 11.8 and 9.8 % of the variation respectively) because they are sufficient to integrate all the morphological descriptors (axes four to seven represent new combinations of the same variables integrated by previous axes). Six of the 20 variables (dummy states counted separately) were significantly related to more than one ordination axis (Table 3b); those most strongly related to the first axis were leaf traits, wood density and bark thickness. In decreasing order of importance, this first axis separates species with high specific leaf area, low leaf tensile strength, deciduous leaf phenology, low leaf dry matter content, large leaf area, low wood density, fast leaf decomposition rate, thick bark and dispersal by wind from species with opposite attributes (Fig. 1, Table 3b).

The second axis separates tree species dispersed by wind, free of spines and reaching tall stature from those dispersed by animals, bearing spines, restricted to a short stature and with a generalist pollination syndrome (Fig. 1, Table 3b). The third axis separates species with clonal growth, moth and wind pollination and light seeds from those without clonal growth, with bee pollination and with heavier seeds.

A detailed examination of all trait correlations (Table 3a) revealed a clear and consistent array of associations

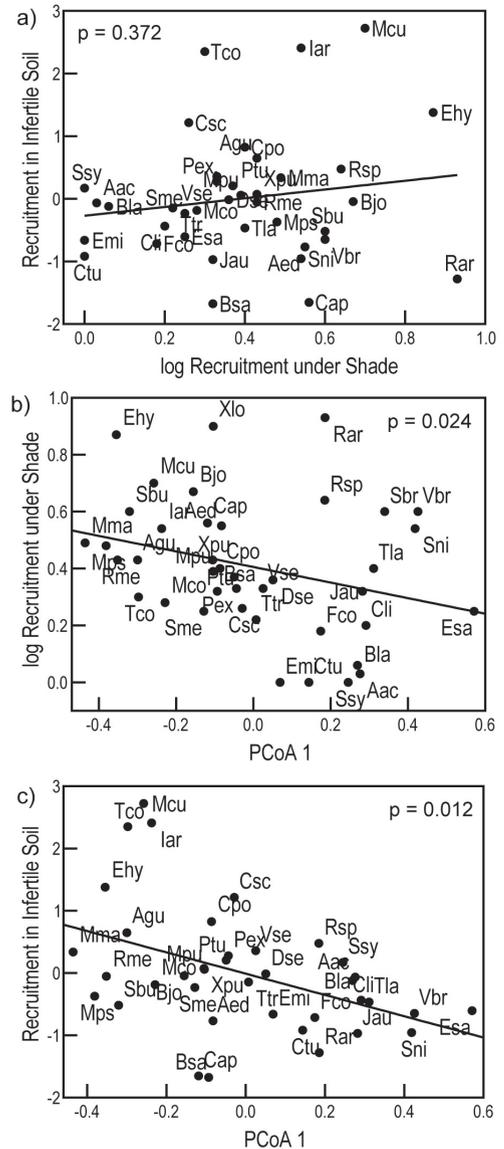


Fig. 2. Relationships between recruitment under shade, recruitment in a soil fertility gradient, and the first axis of the species by trait PCoA (which condenses leaf traits, wood density and bark thickness correlations) of 40 sympatric montane tree species from NW Argentina. *p* values correspond to Kendall rank correlations. Recruitment under shade is log transformed for graphical purposes and regression lines are drawn only for reference. Table 2 gives the full species names.

amongst all the leaf traits, wood density and bark thickness (first eight traits in the correlation matrix, Table 3a). However, we did not find any clear and consistent association of these eight traits with: (a) maximum height, (b) clonal growth or (c) the reproductive traits. Leaf phenology, spinescence and clonal growth are the only vegetative traits that exhibit significant correlations

with reproductive traits. Three interesting associations emerged: a tendency for evergreen species to have animal seed dispersal (and deciduous species to have wind dispersal), for spiny trees to be zoochorous and for clonal tree species to have slow leaf decomposition (Table 3a).

There is little evidence of associations amongst the reproductive variables, particularly if we consider that several of the significant correlations between them are trivial because they are associations between dummy states of the same trait (e.g. bee vs. wind pollination). The only meaningful associations were that plants pollinated by moths tend to have wind dispersed seeds, trees with seeds dispersed by wind tend to have lighter seeds (and species with animal dispersed seeds to have heavy seeds) and clonal species tend to be wind pollinated (Table 3a).

When we examined the species' distributions in natural conditions in relation to light and soil resources, we found no significant association (Kendall $p = 0.95$) between their capacity to recruit under canopy shade and their capacity to recruit in infertile soils (Fig. 2a): although species such as *Eugenia hyemalis* (Ehy) and *Maytenus cuezoi* (McU) were able to tolerate both shade and nutrient shortage, species such as *Ternstroemia congestiflora* (Tco) tolerate nutrient shortage but not shade and species such as *Citronella apogon* (Cap) tolerate shade but not infertile soil. Despite this result, the position of species along the first PCoA axis, which simplifies the connection between leaf traits, wood density and bark thickness, showed a significant association with the capacity of the species to recruit under canopy shade (Kendall $P = 0.02$) and also with the capacity of the species to recruit in infertile soils (Kendall $P = 0.02$) (Fig. 2 b, c). As Figures 2b and c indicate, the association has the same sign in both cases, and species towards the negative side of the ordination tend to recruit in infertile soils and/or under shade. This implies that species which, generally, have some or most of the following traits: low SLA, high leaf tensile strength, evergreen leaf phenology, high leaf dry matter content, small leaf area, high wood density, slow leaf decomposition, thin bark and dispersal by animals, tend (with lots of scatter) to be more tolerant of infertile soils and/or more tolerant of shade.

This correlation indicates that species which recruit more commonly in infertile soils and/or shade will tend to have the characteristics listed but not necessarily all of them. When we examine separately the individual traits associated with each type of response, we find that only leaf tensile strength and leaf phenology are correlated both with recruitment under shade and in soils of low fertility; otherwise each of the two environmental responses is associated with a different set of traits. Species that recruit more commonly under shade tend, in decreasing order

of importance, to have seed dispersal by animals, higher wood density, an evergreen habit and high leaf tensile strength. They also show a statistically marginal trend to produce heavy seeds. On the other hand, species which recruit more commonly in infertile soils tend, in decreasing order of importance, to have slower leaf decomposition, tensile-resistant leaves, an evergreen habit, thin bark, thick leaves and not to be pollinated by moths.

The species' scores along the second PCoA axis also show a significant negative association with their potential to establish under canopy shade (Table 3c). This is linked to the tendency of zoochorous species (a trait best represented by the second PCoA axis) to recruit significantly more under shade than species that are anemochorous.

Because both short and tall stature pioneer trees are associated with well lit conditions throughout their ontogeny, and there is no reason to expect physiological or morphological changes with height amongst them in the context of response to vertical gradients of light, we re-evaluated the relationship between maximum height and the remaining variables only for the shade tolerant species. Of all possible relationships, shade tolerant species that reached tall stature tended to lack spines (Kendall's $\tau = -0.323$, $p = 0.046$, $n = 28$), had a marginal trend to low SLA (Kendall's $\tau = -0.244$, $p = 0.071$, $n = 28$) and recruited less commonly under closed canopy shade (Kendall's $\tau = -0.347$, $p = 0.01$, $n = 28$) than shorter shade tolerant species.

Discussion

Relationships amongst vegetative traits

The broad-leaved tree species analysed in this study can be discriminated in their morphology according to at least three independent sets of traits. The first axis exhibits close and consistent associations amongst leaf traits: deciduous species tend to have leaves with high specific area, low tensile strength, low dry matter content, large laminae and fast decomposition, whereas opposite attributes tend to be associated with evergreen species. If we consider leaf phenology as a coarse indicator of leaf longevity, and leaf decomposition rate as an indicator of high leaf nutrient content and/or low leaf defence, then the set of leaf attributes associated with deciduous species indicate increased capacity for resource acquisition and those associated with evergreen species indicate resource conservation. In consequence, the observed associations are consistent with the major axis of plant evolutionary differentiation which reflects a fundamental trade-off between rapid acquisition of resources and conservation of resources.

The close association amongst the measured leaf traits reflects an expected integration of form and function within the leaf. However, the correlation of leaf morphological traits with wood density and bark thickness, which *a priori* had a less obvious linkage, suggests a functional integration within the whole plant. Indications of a link between leaf and stem traits were originally derived from rather indirect and qualitative observations that fast growing pioneer tree species had high photosynthetic rates and low wood density (Bazzaz & Pickett 1980; Swaine & Whitmore 1988) but there is now growing empirical evidence of an integration between leaf and stem ecophysiology. An association between hydraulic conductivity and photosynthetic capacity has recently been found for 16 angiosperm tree species in tropical New Caledonia and sub-alpine Tasmania (Brodribb & Feild 2000) as well as for 12 deciduous and evergreen tree species in tropical dry forests of Costa Rica (Brodribb et al. 2002). Additionally, Santiago et al. (2004) found that branch wood density is negatively correlated with hydraulic conductivity, and with net CO₂ assimilation rate per unit leaf area and per unit leaf mass, for 20 tree species of wet seasonal tropical forests in Panama. Parallel support can be drawn from the positive association between wood density and cavitation resistance (e.g. Hacke et al. 2001) and the correlation found between phenology and cavitation resistance. As initially hypothesized by Orians & Solbrig (1977), Sobrado (1993) found that drought deciduous species from the seasonal tropics had higher hydraulic conductivity in the short term at the risk of embolisms in the xylem, while evergreen species had lower water transport capacity but maintained relatively constant hydraulic conductivity during the wet and dry seasons. This body of evidence suggests that high hydraulic conductivity, imparted by low density woods, is necessary to sustain leaves with high assimilation potential while cavitation resistance, a property of dense woods, is necessary to support water transport in the dry season in evergreen species. Although we did not measure wood densities of the functional xylem (which are relevant to water transport) and wood densities are known to vary from pith to bark, our measures can be assumed to be proportional to those of the functional xylem because we sampled branches (presumably with a low fraction of heart-wood) of similar sizes and because most species (16 out of 20 in a study of tropical woods, Wiemann & Williamson (1989)) exhibit positive gradients in stem wood density from pith to bark. The high wood density of evergreen species is also consistent with high resource conservation since it increases mechanical resistance to decay, wind and fallen debris and is likely to contribute to longer individual lifespans (Loehle 1988). A thicker bark can result from faster growth and increased accumulation of necromass on the outer side

of the bark and/or from thicker phloem on its inner side which may provide an increased transport rate of soluble carbohydrates and peptides/amino acids within the plant. Therefore, our evidence of the association of thick bark with lower wood density, as well as with traits indicative of productive leaves, is consistent with the more general interspecific trade-off between high resource acquisition and resource conservation.

Not all stem traits are associated with leaf traits however; spines and maximum tree height are grouped by the second independent axis rather than the first. The observed lack of association between spinescence and leaf traits does not support the hypothesis of Coley (1983) and Coley et al. (1985) that plants which grow in resource poor sites invest more heavily in immobile defences but seems to follow Grubb's (1992) observation that both fast and slow growing species (i.e. the extreme syndromes represented by the first morphological axis) can commonly be found to bear spines.

In Malaysian tropical rain forests Thomas (1996) and Thomas and Bazzaz (1999) showed an association between leaf traits and maximum tree height, a probable result of evolutionary responses in shade tolerant species to the selective forces of vertical light gradients (analogous to the differentiation between pioneer and shade tolerant tree species in their response to horizontal gradients of light). Saplings of small stature species growing under similar light conditions were found to have an inherently lower area-based photosynthetic capacity (A_{max}) than species of the same genus that achieved greater heights (Thomas & Bazzaz 1999). The associations seemed more evident for physiological than for morphological traits but amongst shade tolerant trees they also detected inverse associations between the SLA of adult tree leaves and maximum height (Thomas & Bazzaz 1999) and between wood density and maximum height (Thomas 1996). Interestingly, the links mediated by maximum height are opposite to those exhibited by the fundamental trade-off of plant differentiation described above, where high A_{max} and low wood densities are associated with high SLA rather than with low SLA. When all species in our dataset were compared, there was only a positive association between maximum height and leaf dry matter content but when the comparison was restricted to shade tolerant species, taller species showed a significant tendency to lack spines and a marginal tendency to have lower SLA, as previously shown by Thomas & Bazzaz (1999).

Reproductive traits

Our results did not show strong associations amongst the reproductive traits measured: seed mass, pollination and seed dispersal syndromes and clonal growth.

They also indicate a lack of association between (1) reproductive traits and (2) leaf traits, wood density and bark thickness. This concurs with predictions by Loehle (2000) and results from several studies carried out with herbaceous or shrubby floras that found only weak or no evidence of coupling between 'regeneration' and vegetative traits (Montalvo et al. 1991; Leishman & Westoby 1992; McIntyre et al. 1995; Grime et al. 1997; Díaz & Cabido 1997). The few exceptions to this are indications of associations between maximum height and some reproductive traits in forest communities. Momose et al. (1998) found that large trees in Malaysian tropical rain forest can produce large floral displays that attract more generalist pollinators and increase pollination success while small understorey plants have limited displays and therefore 'employ' specialist pollinators. This is in agreement with observations of Bawa et al. (1985) at La Selva, Costa Rica, that canopy trees were pollinated by bees and small diverse insects, while hummingbird, sphingid moth and beetle pollination were mainly restricted to sub-canopy trees. This non-random distribution of plant-pollinator interactions is expected on the basis of vertical stratification of animal communities (Smith 1973). However, in the present study we found no significant evidence of an association between pollination syndrome and species' maximum height. A comparable relationship that has been detected by most surveys of seed dispersal type among tropical tree species (as reviewed by Turner (2001)) is the preponderance of anemochory amongst taller trees, and our results do support this association.

Tolerance of shade versus tolerance of low soil fertility

Species' realized potential to recruit under conditions of low soil fertility was orthogonal to their potential to recruit under shade. This is in agreement with experiments on temperate woody species (Latham 1992; Grubb et al. 1996) that indicate an important range of niche differentiation among species which permits each species to be favoured in a different combination of light and soil nutrient conditions in natural forests. Under a patchy distribution of resources, this would provide a basis for species' coexistence. This contrasts, however, with evidence from montane tropical forests in Jamaica, where the results of Goodland et al. (1998) and McDonald et al. (2003) indicate that species which had their highest tree density in the least fertile soils (the Mor ridge forest type) had a significantly greater tendency to be light demanding than those species with highest tree density in the more fertile Mull ridge and Col forest types. The results from Jamaica could be attributed to soil infertility being correlated with a more open canopy (even in mature forest) in these conditions of very low soil pH (Bellingham et al. 1996).

Functional significance of leaf traits, wood density and bark thickness

The finding that species with characteristics indicative of high resource conservation (evergreen leaves, low SLA, high leaf tensile strength, low leaf decomposition rate and dense wood), as summarized by the first PCoA axis, are better able to recruit where light or soil resources are in short supply, and that species with opposite traits recruit less commonly under such conditions, is consistent with our functional interpretation of this first PCoA axis. We conclude that it indicates an evolutionary trade-off between high resource acquisition and resource conservation, and that species that recruit under shade and in infertile soils tend to have similar morphology. However, there is still considerable scatter in the relationships between species' traits and their capacity to recruit where there is a shortage of these two resources (Fig. 2b, c), and it is precisely this dispersion that accommodates the observed independence of species' recruitment in shade and over the soil fertility gradient. The first PCoA axis scores are a coarse simplification of species morphology and the results indicate that, although species which score close to one extreme of this axis tend to be tolerant of shortage of light and/or soil resources, they are not necessarily tolerant of shortage of both resources simultaneously. Similar interpretations are applicable to species at the other extreme of the axis.

The morphological variables condensed by the first PCoA axis also show some noise in their pairwise associations and it is this 'play', combined with the independence of the response variables, that results in different sets of individual traits being associated with the species' recruitment under shade from those associated with the potential to colonize infertile soils, when the traits are analysed individually. Therefore, our results agree, to some extent, with both sides of the debate on whether the same suites of traits confer tolerance of shortages of different resources (Grime 1977; Grime et al. 1989; Chapin et al. 1993) or whether different suites of traits are advantageous according to the most limiting resource under consideration (Grubb 1985, 1998; Tilman 1987) and show that results and interpretations can vary considerably depending on the resolution of the analysis or the degree of generalization allowed.

The connections observed between species' above-ground traits and their recruitment under shade or in infertile soils are consistent with previous studies on broad-leaved woody species. Our finding that evergreen species are common colonizers of infertile soils and shaded conditions match the recurrent observations that evergreen woody plants are associated with nutrient poor soils (Goldberg 1982; Grubb 1985; Givnish 1987; Aerts 1995), and that shade tolerant tree species have a longer

leaf lifespan than sympatric intolerants in tropical moist (Coley 1988) and rain forests (Williams et al. 1989; Reich et al. 2004). Other leaf traits have also been found in association with shade tolerance. In a study of six to seven sympatric *Piper* shrubs, the more shade tolerant species had lower leaf N concentration, SLA and A_{\max} than the shade intolerant species (Chazdon & Field 1987; Williams et al. 1989), which indicates that related taxa varying in shade tolerance are arranged along the trade-off surface of leaf resource conservation and high resource exploitation (however, it should again be noted that there is usually a wide variation in these associations for individual traits, e.g. some tropical species that are shade tolerant have high SLA, Grubb (1998)). Our finding that wood density also forms part of this trade-off is consistent with the positive association between wood density and shade tolerance initially described by Wells (1976), and later confirmed quantitatively by Augsburger (1984). Large seeds have often been associated with regeneration under low resource conditions, but the many field studies that have examined this relationship seem to find little empirical support (e.g. Westoby et al. 1992). We found weak evidence of a positive association between seed size and recruitment under shade and no evidence of an association between seed size and recruitment on infertile soils.

Other axes of morphological variation and their meaning

The tree species of this montane forest can be differentiated according to no less than three main axes based on shoot form. However, only the first axis has a consistent internal structure (i.e. it links variables that are significantly correlated amongst each other through consistent signs), whereas the remaining axes group variables that are not significantly related to each other and their grouping by the ordination most likely results from articulated signs (trends) in the relationships among them. This implies that there is even more morphological diversification than that condensed by the three axes and suggests that there is much room for functional differentiation across species if different axes or traits do really imply different ecological functions (cf. Loehle 2000). For instance, the second axis of morphological differentiation, which integrates maximum height, dispersal mode and spinescence, is also markedly associated with recruitment under shade and, at least partly, seems to represent the differential responses to vertical gradients of light availability amongst shade tolerant species, as judged from the negative association between maximum height and recruitment in shade observed in this group of species. Reproductive traits, which are mainly integrated in the third axis of morphological variation, could also

be associated with response to disturbance as suggested by several other studies (e.g. Noble & Slatyer 1980).

We find some resemblance between these dimensions and observations from studies encompassing different plant life forms in that SLA (a surrogate for our first axis), height at maturity (second axis) and seed mass (third axis) vary widely amongst species at any given level of the other two (Westoby 1998). In several temperate floras, 70%-83% of the variation in log seed mass is independent of variation in log height (Leishman et al. 1995); similarly SLA varies widely amongst species and is only weakly correlated with the other two variables (unpubl. in Westoby 1998). The ecological meaning of these traits and their independence across species led Westoby (1998) to propose a leaf-height-seed plant ecology 'strategy' scheme (based on the CSR strategies of Grime (1977) and Grime et al. (1989)) as a framework for classifying plant 'strategies' in comparative research. Our results also support Loehle's (2000) suggestion that vegetative reproduction is largely independent of shade tolerance and maximum height, which led him to propose it as another main dimension of tree 'strategy space'.

Limitations of the study and future challenges

An association between species' traits and realized distribution in the field does not necessarily mean that those traits are functionally responsible for the observed distribution. Although the recent literature in plant ecology, physiology and evolutionary ecology is providing possible explanations for the causes and consequences of some trait associations, many of the mechanisms behind these links remain unclear. In this respect, it is still uncertain to what degree observed interspecific trait correlations result from cost-benefit compromises or from other processes such as simple 'trait co-ordination' or the stochastic effect of genetic drift to which the evolutionary process is exposed (Reich et al. 2003). 'Trait co-ordination' could arise because particular trait values function more successfully in combination (driven by reciprocal relationships or due to common causation from a third variable) rather than because some traits drive others mechanically or physiologically (Shipley & Lechowicz 2000; Reich et al. 2003).

The functional value of other traits should also be tested. For instance, root properties (especially of mycorrhiza) are expected to be very important for tolerance of nutrient shortage. It would also be interesting to examine whether our findings on trait associations are similar in other habitats and woody floras. Borchert (1994) showed that tropical dry forests in Costa Rica contain both evergreen trees with light wood (that 'avoid' drought by storing water in their stems) and deciduous species with dense wood. This suggests that the associations we found

between wood density and leaf traits may not hold in drier forests.

Our measures of species' regeneration in natural field conditions provide just one coarse estimator of their response to light and to soil fertility. Our measure of recruitment under shade gives an approximation of species' capacity to tolerate shade but does not consider (a) their potential for net carbon fixation and growth under shade or (b) ontogenetic changes in their light response such as those known for non-pioneer light demanding trees. There might also be sources of error in the computation of recruitment over the soil fertility gradient: (1) soil analyses were done on upper layer soil samples (5-15 cm depth) and although this seems appropriate for assessing tree establishment, it may not be representative of the soil volume that large trees exploit; (2) soil samples were taken from established forest stands between 12 and 80 years old, and although soil properties change at slower rates than vegetation, physico-chemical properties may be different from those prevalent when the trees established; (3) species recorded in only a few sites are vulnerable to biased estimations of their tolerance ranges and (4) the effect of differential dispersal was controlled for in the computation of recruitment under shade, but not for recruitment over the soil fertility gradient where performance is directly assessed on the basis of tree distribution patterns. Field experiments that evaluate species' growth/survival under conditions of controlled resource availability with competition should be conducted to test our findings. Finally, phylogenetic linkages amongst species could bring a problem of pseudo-replication, especially for traits with low levels of convergence (Ackerly 1999).

Irrespective of its limitations, this study does provide solid evidence that wood density and bark thickness integrate the 'construction costs' axis commonly reported for broad-leaved plants. This is also the first quantitative attempt to test the correlations (and functional value) of various morphological characteristics with species' realized tolerances of (a) shade and (b) nutrient shortage. The results indicate that the functional value of morphological traits differs with the resolution of analysis: when traits are considered as part of sets of correlated traits or 'strategies', species that recruit under shade and on infertile soils tend to have similar morphology but when traits are considered individually they show different correlations with each ecological response.

Acknowledgements. We gratefully acknowledge funding from CONICET (Argentina) and Fundación PROYUNGAS. T.A.E. also thanks WWF-US (FA96), ORSAS (UK), the British Council and Fundación Antorchas (Argentina) for financial support through different stages of this research. We thank C. Martini, S. Quinzio, G. Quero, M. Paolorosi, A. Cosacov and L. Heil for valuable help with trait measurements. The study benefited from discussions with J. Lichstein, S. Díaz and C.K. Kelly and from comments by P.J. Grubb.

References

- Anon. 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Bot. J. Linn. Soc.* 141: 399-436.
- Ackerly, D.D. 1999. Comparative plant ecology and the role of phylogenetic information. In: Press, M., Scholes, J.D. & Barrer, M.G. (eds.) *Physiological plant ecology*, pp. 391-413. Blackwell Scientific, Oxford, UK.
- Aerts, R. 1995. The advantages of being evergreen. *Trends Ecol. Evol.* 10: 402-407.
- Antonovics, J. 1976. The nature of limits to natural selection. *Ann. Mo. Bot. Gard.* 63: 224-247.
- Augsburger, C.K. 1984. Light requirements of neotropical tree seedlings: a comparative study of growth and survival. *J. Ecol.* 72: 777-795.
- Bawa, K.S., Bullock, S.H., Perry, D.R., Coville, R.E. & Grayum, M.H. 1985. Reproductive-biology of tropical lowland rain-forest trees. 2. Pollination systems. *Am. J. Bot.* 72: 346-356.
- Bazzaz, F.A. & Pickett, S.T.A. 1980. Physiological ecology of tropical succession: a comparative review. *Annu. Rev. Ecol. Syst.* 11: 287-310.
- Begon, M., Harper, J.L. & Townsend, C.R. 1996. *Ecology: individuals, populations, and communities*. 3rd ed. Blackwell Scientific, Oxford, UK.
- Bellingham, P.J., Tanner, E.V.J., Rich, P.M. & Goodland, T.C.R. 1996. Changes in light below the canopy of a Jamaican montane rainforest after a hurricane. *J. Trop. Ecol.* 12: 699-722.
- Borchert, R. 1994. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology* 75: 1437-1449.
- Brodribb, T.J. & Field, T.S. 2000. Stem hydraulic supply is linked to leaf photosynthetic capacity: evidence from New Caledonian and Tasmanian rainforests. *Plant Cell Environ.* 23: 1381-1388.
- Brodribb, T.J., Holbrook, N.M. & Gutierrez, M.V. 2002. Hydraulic and photosynthetic co-ordination in seasonally dry tropical forest trees. *Plant Cell Environ.* 25: 1435-1444.
- Cabrera, A. & Willink, A. 1973. *Biogeografía de América Latina*. OEA, Washington DC, US.
- Chapin, F.S., III, Autumn, K. & Pugnaire, F. 1993. Evolution of suites of traits in response to environmental stress. *Am. Nat.* 142: S78-S92.
- Chazdon, R.L. & Field, C.B. 1987. Determinants of photosynthetic capacity in six rain-forest *Piper* species. *Oecologia* 73: 222-230.

- Coley, P.D. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecol. Monogr.* 53: 209-233.
- Coley, P.D. 1988. Effects of plant growth rate and leaf lifetime on the amount and type of anti-herbivore defense. *Oecologia* 74: 531-536.
- Coley, P.D., Bryant, J.P. & Chapin, F.S., III. 1985. Resource availability and plant anti-herbivore defense. *Science* 230: 895-899.
- Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., ter Steege, H., Morgan, H.D., van der Heijden, M.G.A., Pausas, J.G. & Poorter, H. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Aust. J. Bot.* 51: 335-380.
- Díaz, S. & Cabido, M. 1997. Plant functional types and ecosystem function in relation to global change. *J. Veg. Sci.* 8: 463-474.
- Díaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C. et al. 2004. The plant traits that drive ecosystems: evidence from three continents. *J. Veg. Sci.* 15: 295-304.
- Digilio, A.P. & Legname, P. 1966. *Los árboles indígenas de la Provincia de Tucumán*. Opera Lilloana XV, Instituto Miguel Lillo, S.M. de Tucumán, AR.
- Eissenstat, D. 2000. Root structure and function in an ecological context. *New Phytol.* 148: 353-354.
- Givnish, T.J. 1987. Comparative-studies of leaf form – assessing the relative roles of selective pressures and phylogenetic constraints. *New Phytol.* 106 (Suppl.): 131-160.
- Goldberg, D.E. 1982. The distribution of evergreen and deciduous trees relative to soil type: an example from the Sierra Madre, Mexico and a general model. *Ecology* 63: 942-951.
- Goodland, T.C.R., Bellingham, P.J., Healey, J.R. & Tanner, E.V.J. 1998. *The woody plant species of the Blue Mountains of Jamaica*. School of Agricultural and Forest Sciences, University of Wales, Bangor, UK.
- Gould, S.J. & Lewontin, R.C. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* 205: 581-598.
- Gower, J.C. 1971. A general coefficient of similarity and some of its properties. *Biometrics* 27: 857-874.
- Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am Nat.* 111: 1169-1194.
- Grime, J.P., Hodgson, J.G. & Hunt, R. 1989. *Comparative plant ecology: a functional approach to common British species*. Unwin-Hyman, London, UK.
- Grime, J.P., Thompson, K., Hunt, R., Hodgson, J.G., Cornelissen, J.H.C. et al. 1997. Integrated screening validates primary axes of specialisation in plants. *Oikos* 79: 259-281.
- Grubb, P.J. 1985. Plant populations and vegetation in relation to habitat, disturbance and competition: problem of generalisation. In: White, J. (ed.) *The population structure of vegetation*, pp. 595-622. Junk, Dordrecht, NL.
- Grubb, P.J. 1998. Strategies of plants which cope with shortages of resources. *Persp. Plant Ecol. Evol. Syst.* 1: 3-31.
- Grubb, P.J. 1992. A positive distrust in simplicity – lessons from plant defences and from competition among plants and among animals. *J. Ecol.* 80: 585-610.
- Grubb, P.J. & Metcalfe, D.J. 1996. Adaptation and inertia in the Australian tropical lowland rain-forest flora: contradictory trends in intergeneric and intrageneric comparisons of seed size in relation to light demand. *Funct. Ecol.* 10: 512-520.
- Grubb, P.J., Lee, W.G., Kollmann, J. & Wilson, J.B. 1996. Interaction of irradiance and soil nutrient supply on growth of seedlings of ten European tall-shrub species and *Fagus sylvatica*. *J. Ecol.* 84: 827-840.
- Gurvich, D.E., Easdale, T.A. & Perez-Harguindeguy, N. 2003. Subtropical montane tree litter decomposition: links with secondary forest types and species' shade tolerance. *Aust. Ecol.* 28: 666-673.
- Hacke, U.G., Sperry, J.S., Pockman, W.T., Davis, S.D. & McCulloch, K.A. 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* 126: 457-461.
- Harper, J.L. 1982. After description. In: Newman, E.I. (ed.) *The plant community as a working mechanism*, pp. 11-25. Blackwell Scientific, Oxford, UK.
- Hendry, G.A.F. & Grime, J.P. 1993. *Methods in comparative plant ecology: a laboratory manual*. Chapman & Hall, London, UK.
- Herrera, C.M. 1992. Historical effects and sorting processes as explanations for contemporary ecological patterns: character syndromes in Mediterranean woody plants. *Am. Nat.* 140: 421-446.
- Hubbell, S.P. 2005. Neutral theory in community ecology and the hypothesis of functional equivalence. *Funct. Ecol.* 19: 166-172.
- Hueck, K. 1978. *Los bosques de Sudamerica*. GTZ, Berlin, DE.
- Hunzinger, H. 1997. Hydrology of montane forests in the Sierra de San Javier, Tucumán, Argentina. *Mt. Res. Dev.* 17: 299-308.
- Keddy, P.A. 1992. A pragmatic approach to functional ecology. *Funct. Ecol.* 6: 621-626.
- Körner, Ch. 1991. Some often overlooked plant characteristics as determinants of plant growth: a reconsideration. *Funct. Ecol.* 5: 162-173.
- Lambers, H. & Poorter, H. 1992. Inherent variation in growth rate between plants: a search for physiological causes and ecological consequences. *Adv. Ecol. Res.* 23: 187-261.
- Latham, R.E. 1992. Co-occurring tree species change rank in seedling performance with resources varied experimentally. *Ecology* 73: 2129-2144.
- Legendre, P. & Legendre, L. 1998. *Numerical ecology*. 2nd ed. Elsevier, Amsterdam, NL.
- Leishman, M.R. & Westoby, M. 1992. Classifying plants into groups on the basis of associations of individual traits – evidence from Australian semiarid woodlands. *J. Ecol.* 80: 417-424.
- Leishman, M.R., Westoby, M. & Jurado, E. 1995. Correlates of seed size variation: a comparison of five temperate floras. *J. Ecol.* 83: 517-530.

- Loehle, C. 1988. Tree life history strategies: the role of defenses. *Can. J. For. Res.* 18: 209-222.
- Loehle, C. 2000. Strategy space and the disturbance spectrum: a life-history model for tree species coexistence. *Am. Nat.* 156: 14-33.
- McDonald, M.A., Hofney-Collins, A., Healey, J.R. & Goodland, T.C.R. 2003. Evaluation of trees indigenous to the montane forest of the Blue Mountains, Jamaica for reforestation and agroforestry. *For. Ecol. Manage.* 175: 379-401.
- McIntyre, S., Lavorel, S. & Tremont, R.M. 1995. Plant life-history attributes: their relationship to disturbance response in herbaceous vegetation. *J. Ecol.* 83: 31-44.
- Momose, K., Yumoto, T., Nagamitsu, T., Kato, M., Nagamasu, H., Sakai, S., Harrison, R.D., Itioka, T., Hamid, A.A. & Inoue, T. 1998. Pollination biology in a lowland dipterocarp forest in Sarawak, Malaysia. I. Characteristics of the plant-pollinator community in a lowland dipterocarp forest. *Am. J. Bot.* 85: 1477-1501.
- Montalvo, J., Casado, M.A., Levassor, C. & Pineda, F.D. 1991. Adaptation of ecological systems: compositional patterns of species and morphological and functional traits. *J. Veg. Sci.* 2: 655-666.
- Nadir, A. & Chafatinos, T. 1990. *Los suelos del NOA (Salta y Jujuy)*. Universidad Nacional de Salta, Salta, AR.
- Noble, I.R. & Slatyer, R.O. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio* 43: 5-21.
- Orians, G.H. & Solbrig, O.T. 1977. A cost-income model of leaves and roots with special reference to arid and semi-arid areas. *Am. Nat.* 111: 677-690.
- Poff, N.L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *J. N. Am. Benthol. Soc.* 16: 391-409.
- Prado, D.E. 2000. Seasonally dry forests of tropical South America: from forgotten ecosystems to a new phyto-geographic unit. *Edin. J. Bot.* 57: 437-461.
- Press, M.C. 1999. The functional significance of leaf structure: a search for generalizations. *New Phytol.* 143: 213-219.
- Reich, P.B., Wright, I.J., Cavender-Bares, J., Craine, J.M., Oleksyn, J., Westoby, M. & Walters, M.B. 2003. The evolution of plant functional variation: traits, spectra, and strategies. *Int. J. Plant Sci.* 164: S143-S164.
- Reich, P.B., Uhl, C., Walters, M.B., Prugh, L. & Ellsworth, D.S. 2004. Leaf demography and phenology in Amazonian rain forest: a census of 40 000 leaves of 23 tree species. *Ecol. Monogr.* 74: 3-23.
- Sack, L. & Grubb, P.J. 2002. The combined impacts of deep shade and drought on the growth and biomass allocation of shade-tolerant woody seedlings. *Oecologia* 131: 175-185.
- Santiago, L.S., Goldstein, G., Meinzer, F.C., Fisher, J.B., Machado, K., Woodruff, D. & Jones, T. 2004. Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees. *Oecologia* 140: 543-550.
- Shiple, B. & Lechowicz, M.J. 2000. The functional co-ordination of leaf morphology, nitrogen concentration, and gas exchange in 40 wetland species. *Ecoscience* 7: 183-194.
- Smith, A.P. 1973. Stratification of temperate and tropical forests. *Am. Nat.* 107: 671-683.
- Smith, T. & Huston, M. 1989. A theory of the spatial and temporal dynamics of plant-communities. *Vegetatio* 83: 49-69.
- Sobrado, M.A. 1993. Trade-off between water transport efficiency and leaf life-span in a tropical dry forest. *Oecologia* 96: 19-23.
- Swaine, M.D. & Whitmore, T.C. 1988. On the definition of ecological species groups in tropical rain forests. *Vegetatio* 75: 81-86.
- ter Braak, C.J.F. & Looman, C.W.N. 1986. Weighted averaging, logistic regression and the Gaussian response model. *Vegetatio* 65: 3-11.
- Thomas, S.C. 1996. Asymptotic height as a predictor of growth and allometric characteristics in Malaysian rain forest trees. *Am. J. Bot.* 83: 556-566.
- Thomas, S.C. & Bazzaz, F.A. 1999. Asymptotic height as a predictor of photosynthetic characteristics in Malaysian rain forest trees. *Ecology* 80: 1607-1622.
- Tilman, D. 1987. On the meaning of competition and the mechanisms of competitive superiority. *Funct. Ecol.* 1: 304-315.
- Turner, I.M. 2001. *The ecology of trees in the tropical rain forest*. Cambridge University Press, Cambridge, UK.
- Wells, P.V. 1976. A climax index for broadleaf forest: an *n*-dimensional ecomorphological model of succession. In: Fralish, J.S., Weaver, G.J. & Schlesinger, R.C. (eds.) *Central hardwood conference*, pp. 131-176. Department of Forestry, Southern Illinois University, Carbondale, IL, US.
- Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant Soil* 199: 213-227.
- Westoby, M., Jurado, E. & Leishman, M. 1992. Comparative evolutionary ecology of seed size. *Trends Ecol. Evol.* 7: 368-372.
- Wiemann, M.C. & Williamson, G.B. 1989. Radial gradients in the specific gravity of wood in some tropical and temperate trees. *For. Sci.* 35: 197-210.
- Williams, K., Field, C.B. & Mooney, H.A. 1989. Relationships among leaf construction cost, leaf longevity, and light environment in rain-forest plants of the genus *Piper*. *Am. Nat.* 133: 198-211.
- Wilson, J.B. 1999. Guilds, functional types and ecological groups. *Oikos* 86: 507-522.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z. et al. 2004. The worldwide leaf economics spectrum. *Nature* 428: 821-827.
- Zuloaga, F. & Morrone, O. 1999. *Catálogo de las plantas vasculares de la República Argentina II*. Missouri Botanical Garden, Saint Louis, MS, US.

Received 17 February 2006;

Accepted 3 December 2006;

Co-ordinating Editor: P.S. White.

For App. 1, see also JVS/AVS Electronic Archives;
www.opuluspress.se/