New Phytol. (1999), **144**, 35–47

Research review
Components of leaf dry mass per area – thickness and density – alter leaf photosynthetic capacity in reverse directions in woody plants

ÜLO NIINEMETS

Department of Ecophysiology, Institute of Ecology, Tallinn University of Educational Sciences, Riia 181, EE 51014 Tartu, Estonia (fax: +372 7 383013; e-mail ylo@zbi.ee)

Received 11 December 1998; accepted 19 May 1999

SUMMARY

The relationships of foliage assimilation capacity per unit area ($P^{\mathrm{P}}_{\max}$) with leaf dry mass per unit area (LMA) and nitrogen content per unit area (N_{P}) differ between species and within species grown in different habitats. To gain a more mechanistic insight into the dependencies of $P^{\mathrm{P}}_{\max}$ on LMA and N_{P}, this literature study based on 597 species from a wide range of earth biomes with woody vegetation examines the relations between leaf photosynthetic capacity and the components of LMA (leaf density (D, dry mass per volume) and thickness (T)), and also the correlations of D and T with leaf nitrogen content and fractional leaf volumes in different tissues. Across all species, $P^{\mathrm{P}}_{\max}$ varied 12-fold and photosynthetic capacity per unit dry mass ($P^{\mathrm{m}}_{\max}$) 16-fold, N_{P} 12-fold, and nitrogen per unit dry mass (N_{m}) 13-fold, LMA 46-fold, D 13-fold, and T 35-fold, indicating that foliar morphology was more plastic than foliar chemistry and assimilation rates. Although there were strong positive correlations between $P^{\mathrm{P}}_{\max}$ and N_{P}, and between $P^{\mathrm{m}}_{\max}$ and N_{m}, leaf structure was a more important determinant of leaf assimilation capacities. $P^{\mathrm{P}}_{\max}$ increased with increasing LMA and T, but was independent of D. By contrast, $P^{\mathrm{m}}_{\max}$ scaled negatively with LMA because of a negative correlation between $P^{\mathrm{m}}_{\max}$ and D, and was poorly related to T. Analysis of leaf nitrogen and tissue composition data indicated that the negative relationship between D and $P^{\mathrm{m}}_{\max}$ resulted from negative correlations between D and N_{m}, D and volumetric fraction of leaf internal air space, and D and symplasmic leaf fraction. Thus, increases in leaf density bring about (1) decreases in assimilative leaf compounds, and (2) extensive modifications in leaf anatomy that may result in increases in intercellular transfer resistance to CO_2. Collectively, (1) and (2) lead to decreased $P^{\mathrm{m}}_{\max}$, and also modify $P^{\mathrm{P}}_{\max}$ versus LMA relationships.

Key words: interspecific comparisons, leaf mass per area, leaf density, leaf nitrogen, leaf thickness, photosynthesis, leaf anatomy, woody species.

INTRODUCTION

The relationships between foliage structural and functional variables reported are contradictory and not universal. Within single species, leaf dry mass per unit area (LMA) is generally positively related to leaf photosynthetic capacity per unit leaf area ($P^{\mathrm{P}}_{\max}$ see Table 1 for abbreviations and units; Sims & Pearcy, 1989; Ellsworth & Reich, 1993; Pearcy & Sims, 1994; Niinemets & Tenhunen, 1997; Niinemets *et al.*, 1998a,b), and this positive association may also hold for interspecific correlations (Reich & Walters, 1994). Yet, LMA and $P^{\mathrm{P}}_{\max}$ often correlate poorly in other multispecies data sets (Reich *et al.*, 1991, 1995, 1997; Reich & Walters, 1994). Variability of leaf nitrogen (N) content per unit leaf dry mass (N_{m}) with LMA has been highlighted as a potential source of these contrasting patterns (Reich & Walters, 1994; Reich *et al.*, 1995, 1997). However, the mechanisms underlying the scaling of N_{m} with LMA have not yet been characterized in detail. Commonly, there are negative relationships between LMA and leaf N content per unit leaf dry mass (Sobrado & Medina, 1980; Reich *et al.*, 1991, 1992, 1995; Cornelissen *et al.*,

Supplementary material: Appendices 1 and 2 can be found in the online version of this article (www.journals.cup.org).

1997), but again, these dependencies are species- and site-specific (Reich & Walters, 1994; Garnier *et al.*, 1997; Niinemets, 1997b).

Although researchers tend to attribute the variability in leaf dry mass per unit area only to changes in leaf thickness (Chabot *et al.*, 1979; Sims & Pearcy, 1992; Chazdon & Kaufmann, 1993; Enríquez *et al.*, 1996), LMA is a product of leaf density (D, dry mass per unit volume) and thickness (T) in flat broad-leaved species, and D and volume to surface area ratio (V/A) in needle-leaved species. Both D and T (or V/A) may vary many-fold, they are not necessarily interdependent, and they may be controlled by different environmental variables (Witkowski & Lamont, 1991). Garnier *et al.* (1997) hypothesized that the contrasting patterns in LMA vs N relations are the outcome of the variation of D and T in opposite directions. Given that there is a trade-off between the investments in structural and assimilative leaf compounds (Niinemets & Kull, 1998), and that the increases in density are compatible with greater apoplastic leaf fraction and greater fraction of support tissues in the leaves (Niklas, 1989; Garnier & Laurent, 1994), increases in D may lead to decreases in N_m, but T and N_m should not necessarily be correlated. However, the dependencies of N_m on T and D have not been examined before.

An extensive set of data including shrubs and trees from all major earth biomes with woody vegetation was compiled to analyse the following. What is the nature of changes in LMA; do the variations in both thickness and density play an equal role? How does the foliage partitioning between assimilative and support tissues scale with D and T, and how are D and T related to internal leaf architecture? How do the variation patterns in D and T alter LMA vs leaf N and photosynthesis relationships?

MATERIALS AND METHODS

Database compilation

A thorough literature survey was conducted to find studies where leaf thickness (T, dorsiventral leaf dimension) and leaf dry mass per unit projected area ($\mathrm{LMA_P}$) or leaf density (D) had been measured simultaneously. Studies providing sufficient information to calculate T or $\mathrm{LMA_P}$ from graphs or tabulated data were also considered. When not directly reported in the original publication, D was computed from leaf thickness (or from volume to projected leaf area ratio, V/A_P, in needle-leaved species) and $\mathrm{LMA_P}$, or $\mathrm{LMA_P}$ was calculated from T and D. For needle-leaved species, leaf dry mass per unit total surface area ($\mathrm{LMA_T} = DV/A_T$, where A_T is needle total surface area) and V/A_T were also included in the database. Contrary to broad-leaved species, where the absorption of direct light scales with projected leaf area, the light interception capacity of individual needles is a complex function of their cross-sectional geometry, and the light intercepting surface may be larger at a common projected area (A_P) in needles than in broad leaves (Jordan & Smith, 1993). Moreover, at a common A_P, the surface area for gaseous and heat exchange with the atmosphere is also generally greater in individual needles. Given the higher functional surface area in needle-leaved species, functional equivalent of $\mathrm{LMA_P}$ of broad-leaved species falls between the values of $\mathrm{LMA_P}$ and $\mathrm{LMA_T}$ of needle-leaved taxa.

Since plant age may crucially alter the relationships between foliage anatomy, morphology and environment (Steele *et al.*, 1989; Lee & Richards, 1991; Groom *et al.*, 1997; Niinemets, 1997a), preference was given to field investigations in which mature plants had been used. However, several important foliar anatomical characteristics, for example, the fraction of intercellular air spaces in the leaves, have rarely been measured for the leaves in the field. Therefore, a few glasshouse and growth chamber studies reporting estimates of such foliar variables were also included. Only species with C_3 and C_4 metabolism were considered. Although foliar morphology and anatomy of some Crassulacean acid metabolism (CAM) shrubs have been studied in detail, CAM species with succulent leaves were not included in the analysis. Overall, 690 paired values of T and D were found for 16 needle- and 290 broad-leaved shrubs and trees distributed over a wide geographical range covering all major earth communities with woody vegetation (Appendices 1, 2; www.journals.cup.org). In a search for a functional explanation of the observed variability in leaf morphological variables, information was also extracted for foliage chemical (N and P) contents, anatomical (leaf volumetric composition of different tissues, mesophyll and epidermis cell size, cell wall thickness, fractions of intercellular air spaces) and physiological (photosynthesis, stomatal conductance) response variables. Apart from the investigations reporting values for T and D, several additional studies providing data for foliar thickness and other foliar anatomical variables (Appendix 2B) were chosen to obtain a broader range of data for the analysis of anatomical relationships (Fig. 2e–h). Including the species from these other studies, the final data set consisted of 39 needle-leaved and 558 broad-leaved species.

Analysis of foliar anatomical variables

In all species, leaf fractions were separated into: cuticle, epidermis, palisade and spongy parenchyma. In addition, resin ducts and vasculature were important leaf tissues in conifers, and the hypodermis formed a large leaf proportion in three broad-leaved species. To characterize the relative contribution of various tissues, the ratios of all tissue

Table 1. *Definition, minimum (Min), maximum (Max) and mean ± SD values of foliage morphological, anatomical and physiological variables for the compiled literature data (cf. Appendices 1, 2, (www.journals.cup.org) and the Materials and Methods section)*

Definition	Min	Max	Mean ± SD
Leaf dry mass per unit projected area ($\mathrm{LMA_P}$, g $\mathrm{m^{-2}}$)	11.8	560	115 ± 90
Leaf thickness (T, µm)	55	1960	293 ± 234
Leaf density (D, g $\mathrm{cm^{-3}}$)	0.092	1.33	0.41 ± 0.15
Dry to fresh mass ratio (D_W, g $\mathrm{g^{-1}}$)	0.098	0.572	0.34 ± 0.10
Mesophyll to projected leaf surface area ratio (A_{mes}/A_P, $\mathrm{mm^2\ mm^{-2}}$)	6.0	39	17.0 ± 9.1
Fraction of leaf mesophyll as intercellular air spaces ($\mathrm{mm^3\ mm^{-3}}$)	0.10	0.36	0.24 ± 0.07
Fraction of leaf tissue (F) in palisade parenchyma ($\mathrm{mm^3\ mm^{-3}}$)	0	0.94	0.37 ± 0.11
F in spongy parenchyma ($\mathrm{mm^3\ mm^{-3}}$)	0	0.91	0.42 ± 0.13
F in cuticle ($\mathrm{mm^3\ mm^{-3}}$)	0.002	0.307	0.033 ± 0.031
F in epidermis ($\mathrm{mm^3\ mm^{-3}}$)	0.021	0.527	0.182 ± 0.094
F in hypodermis ($\mathrm{mm^3\ mm^{-3}}$)	0.079	0.275	0.19 ± 0.10
Nitrogen content per unit dry mass (N_m, %)	0.445	6.18	1.73 ± 0.92
Nitrogen content per unit projected area (N_P, g $\mathrm{m^{-2}}$)	0.462	6.23	1.79 ± 0.98
Light-saturated net photosynthesis rate (P_{max}) per unit dry mass (P^m_{max}, nmol $\mathrm{g^{-1}\ s^{-1}}$)	17.0	296	119 ± 55
P_{max} per unit projected area (P^P_{max}, µmol $\mathrm{m^{-2}\ s^{-1}}$)	1.41	18.1	6.7 ± 3.0
Maximum Rubisco* carboxylase activity (V_{cmax}) per unit dry mass (V^m_{cmax}, nmol $\mathrm{g^{-1}\ s^{-1}}$)	58.5	779	381 ± 178
V_{cmax} per unit projected area (V^P_{cmax}, µmol $\mathrm{m^{-2}\ s^{-1}}$)	4.2	56.8	19.2 ± 9.9
Fraction of leaf N in Rubisco (g $\mathrm{g^{-1}}$)	0.043	0.173	0.121 ± 0.033

*Ribulose-1,5-bisphosphate carboxylase/oxygenase.

volumes to total leaf volume (volumetric fractions) were calculated. Upper and lower cuticle thicknesses were summed to calculate the fractions of leaf tissue present in cuticle and epidermis. Since only one third of the studies distinguished between cuticle and epidermis, the sum of epidermis and cuticle was also used as the response variable in the correlation analysis. Cases where the sum of all tissue fractions was > 1.05 or < 0.95 were considered 'bad' data and excluded from the database.

Analysis of leaf photosynthesis data

Foliar photosynthesis data were only analysed for C_3 species. The leaf net assimilation capacity (P_{max}) was defined as the net assimilation rate measured at saturating irradiance, at ambient CO_2 concentrations of 310–380 µmol $\mathrm{mol^{-1}}$ (mean ± SD = 350 ± 12 µmol $\mathrm{mol^{-1}}$), and at leaf temperatures around the temperature optimum of C_3 photosynthesis (mean ± SD across all photosynthesis values was 26.6 ± 2.7°C with a range of 18–33°C). Whenever intercellular CO_2 concentration (C_i) was provided, or it was possible to calculate C_i from leaf photosynthesis and paired stomatal conductance data, the values of P_{max} were further used to calculate the maximum ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) carboxylase activity (V_{cmax}) as described in Niinemets *et al.* (1999b) and briefly outlined here. First, gross leaf assimilation rate was estimated as $P_{max} + 0.5R_d$ (see Niinemets & Tenhunen, 1997 for a discussion), where R_d is the respiration rate measured in darkened leaves at the same temperature. Assuming that the light-saturated value of assimilation rate is constrained by Rubisco activity at current ambient CO_2 concentrations (von Caemmerer & Farquhar, 1981), V_{cmax} was further calculated as:

$$V_{cmax} = \frac{(P_{max} + 0.5R_d)\,[C_i + K_c(1 + O/K_o)]}{C_i - \Gamma^*} \qquad \text{Eqn 1}$$

(where K_c and K_o are Michaelis–Menten constants for Rubisco carboxylase and oxygenase activities, respectively, O is intercellular oxygen concentration, Γ^* is the CO_2 compensation point in the absence of mitochondrial respiration (von Caemmerer & Farquhar, 1981)). Michaelis–Menten constants and Γ^* were calculated for each leaf temperature, and finally V_{cmax} was standardized to 25°C employing the temperature parameters of Rubisco given in Niinemets & Tenhunen (1997). Although V_{cmax} estimations by this procedure do not take into account the liquid and gaseous phase resistances to CO_2 transfer from intercellular air spaces to carboxylation sites in the chloroplasts, and the true values of V_{cmax} are therefore somewhat underestimated (see e.g. Epron *et al.*, 1995; Syvertsen *et al.*, 1995), the obtained values are insensitive to stomatal limitations of photosynthesis, and give a more effective assessment of leaf photosynthetic potentials than P_{max}.

The fractional investment of leaf N in Rubisco was calculated from the estimates of V_{cmax} and leaf N content according to Niinemets & Tenhunen (1997) and using the specific activity of Rubisco of 20.5 µmol CO_2 $\mathrm{g^{-1}}$ Rubisco $\mathrm{s^{-1}}$ at 25°C measured for the enzyme purified from *Spinacia oleracea* (Jordan & Ogren, 1984).

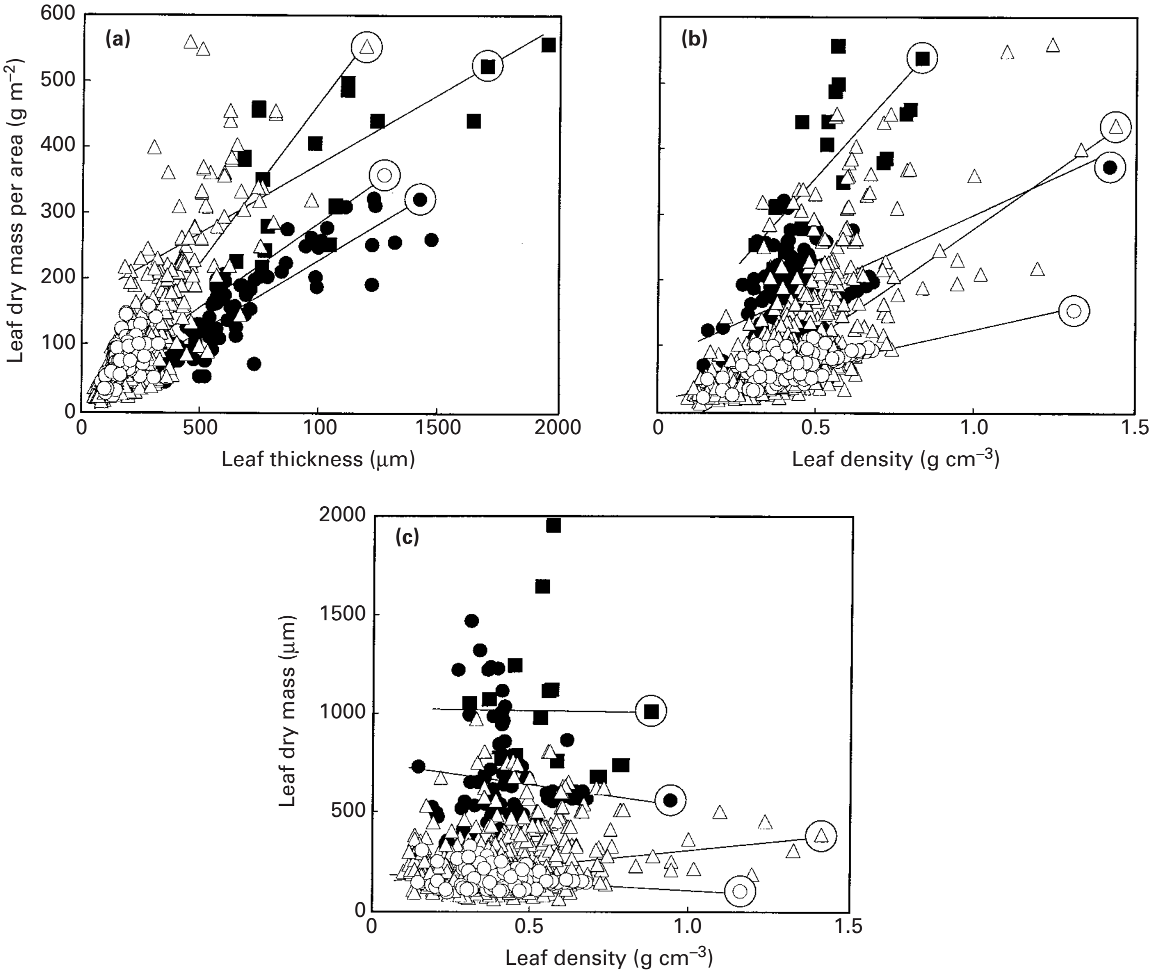

Fig. 1. Leaf dry mass per unit projected area (LMA$_P$) in relation to (a) leaf thickness (T) and (b) density (D), and (c) the correlation between foliar thickness and density for the analysed broad-leaved (open triangles), terete-leaved (filled squares) and conifer (filled circles) species (Appendices 1 and 2, see www.journals.cup.org.). For conifers, the relationships of leaf dry mass per unit total surface area (LMA$_T$) with (a) volume to total surface area ratio (V/A_T) and (b) D, and (c) the correlation between V/A_T and D (open circles) are also depicted. In broad-leaved species, LMA$_P = DT$, but in needle-leaved species, LMA$_P = DV/A_P$, where V/A_P is needle volume to projected area ratio. In a similar manner, LMA$_T = 2DT$ in broad-leaved, and LMA$_T = DV/A_T$ in needle-leaved species. The lines are fitted to the data by linear regression (see Table 2 for regression equations). The symbols within circles are not data points, but define the regression lines.

Statistical treatment of the data

Simple and multiple linear regressions were calculated where appropriate. Occasionally, Log$_{10}$ transformation was applied to the data to normalize the distributions of the values and/or regression residuals. One-way covariation analyses (species group as main effect) followed by Bonferroni test were used to separate the differences in morphological relationships between conifers, terete-leaved and broad-leaved species. All relationships were considered significant at $P < 0.01$ (Wilkinson, 1990).

RESULTS

Dependence of leaf dry mass per area on leaf thickness and density

Given that leaf dry mass per unit projected area (LMA$_P$) varied 46-fold, but leaf thickness 35-, and leaf density 13-fold across all analysed species (Table 1), both T (Fig. 1a, Table 2) and D (Fig. 1b, Table 2) were important determinants of LMA$_P$. However, because T showed greater variability, the relationships of LMA$_P$ were stronger with T than with D (cf. Fig. 1a,b, Table 2). The statistical dependencies between D and T (Fig. 1c) were significant in several cases, but the explained variance was always very low (Table 2).

At a common leaf thickness (T), LMA$_P$ tended to be greater in broad-leaved species than in conifers (Fig. 1a). Given that LMA$_P$ is the product of leaf density and leaf volume (V) to projected surface area ratio (A_P), differences in V/A_P provide one explanation for this difference. V/A_P is equal to T in broad-leaved taxa, to $\pi T/4$ in terete-leaved species with a circular cross section, and to $T/2$ in conifers with needles of triangular or rhomboidal cross

Table 2. *Statistical dependencies betweeen leaf dry mass per projected (LMA_P g m^{-2}) and total (LMA_T g m^{-2}) area, leaf thickness (μm), density (g cm^{-3}) and volume to total area ratio (V/A_T): results of linear regressions analyses*

Species group*	Dependent variable	Independent variable	Intercept	P	Slope	P	r^2	n
T	LMA_P	T	171	0.05	0.195	0.01	0.43	15
C	LMA_P	T	15.34	0.2	0.219	0.001	0.68	82
C	LMA_T	V/A_T	27.7	0.001	0.262	0.001	0.36	122
B	LMA_P	T	−17.7	0.001	0.492	0.001	0.68	593
T	LMA_P	D	91.0	0.3	548	0.01	0.42	15
C	LMA_P	D	83.5	0.001	223	0.001	0.16	122
C	LMA_T	D	24.9	0.001	110	0.001	0.32	122
B	LMA_P	D	−36.7	0.001	329	0.001	0.43	593
T	T	D	1034	0.05	−24.0	0.9	0.00	15
C	T	D	766	0.001	−235	0.3	0.01	82
C	V/A_T	D	204	0.001	−86.2	0.05	0.04	122
B	T	D	164	0.001	159	0.001	0.04	593
All	LMA_P	T	20.1	0.001	0.297	0.001	0.61	690
All	LMA_P	D	−29.5	0.001	356	0.001	0.35	736
All	T	D	194	0.001	252	0.001	0.03	690

*T, terete-leaved species; C, conifers; B, broad-leaved species.
The data are plotted in Fig. 1. Terete-leaved species have circular, and conifers rhomboidal or triangular cross sections.

section. When the data for V to total leaf area ratio (V/A_T) were plotted against leaf dry mass to A_T ratio (LMA_T) in conifers (open circles in Fig 1a), this relationship was close to LMA_P vs T dependence in broad-leaved species (triangles in Fig. 1a). However, LMA_T is equal to $2LMA_P$ in broad-leaved species, implying that the slope of LMA_T vs T is less steep in broad-leaved than in coniferous species.

At a common leaf density, conifers and terete-leaved species possessed a greater LMA_P than broad-leaved taxa ($P < 0.001$, Fig. 1b). This was related to a tendency for a greater leaf thickness at a common D in these species than in broad-leaved taxa (Fig. 1c).

Correlations of foliar anatomical variables with leaf density and thickness

Across all data, there was a negative correlation between the volumetric leaf fractions in epidermal (sum of epidermis and cuticle) and parenchymal (sum of palisade and spongy parenchyma) tissues ($r^2 = 0.89$, $P < 0.001$), implying a trade-off between leaf tissue partitioning between covering and assimilative structures. Leaf cuticle and epidermis may constitute a large proportion of the leaf (Table 1), and in a few species the hypodermis also significantly contributed to leaf covering tissues.

On average (± SD) cuticle comprised 15 ± 13% of the sum of epidermis and cuticle; there was a positive correlation between the volumetric fraction of leaf in cuticle and leaf density (Fig. 2a), but none with the leaf fraction in epidermis (Fig. 2b). Leaf density was positively correlated with the fraction of leaf in palisade parenchyma (Fig. 2c) and with palisade to spongy tissue ratio ($r^2 = 0.08$, $P < 0.001$), and negatively with the fraction of mesophyll as intercellular air spaces (Fig. 2d). Given that palisade parenchyma consists of tightly packed cells with a low fraction of intercellular air spaces, both the correlations depicted in Fig. 2c and d indicate that leaf density scales positively with the compactness of leaf mesophyll.

Despite a slight positive correlation between mean cell heights of epidermis (dorsiventral dimension of epidermal cells) and leaf thickness ($r^2 = 0.08$, $P < 0.01$), both the fraction of leaf in cuticle and epidermis decreased with increasing leaf thickness (Fig. 2e,f). Thus, thicker leaves are less expensive in terms of biomass investment in epidermal structures than thinner leaves. Although leaf thickness was weakly related to both the leaf fractions in palisade (Fig. 2g) and spongy parenchyma ($r = 0.23$, $P < 0.001$), the explained variance was very low for both relationships, indicating that the internal structure of leaves may be extremely variable at a common leaf thickness, and is not directly linked to overall leaf thickness. Despite this, the volume fraction of mesophyll as intercellular air spaces increased with increasing T (Fig. 2h).

Leaf dry to fresh (turgid) mass ratio, which is compatible with the fraction of leaf tissue in apoplast, was closely related to leaf density (Fig. 3) and was independent of leaf thickness ($r^2 = 0.00$, $P > 0.9$).

Foliar nitrogen and photosynthetic capacity in relation to leaf density and thickness

The N content per unit projected leaf area (N_P) varied 12-fold, and per unit leaf dry mass (N_m) 13-fold. N_m decreased both with increasing leaf density (Fig. 4a) and thickness (Fig. 4c). By contrast, N_P was positively related to both leaf density (Fig. 4b) and

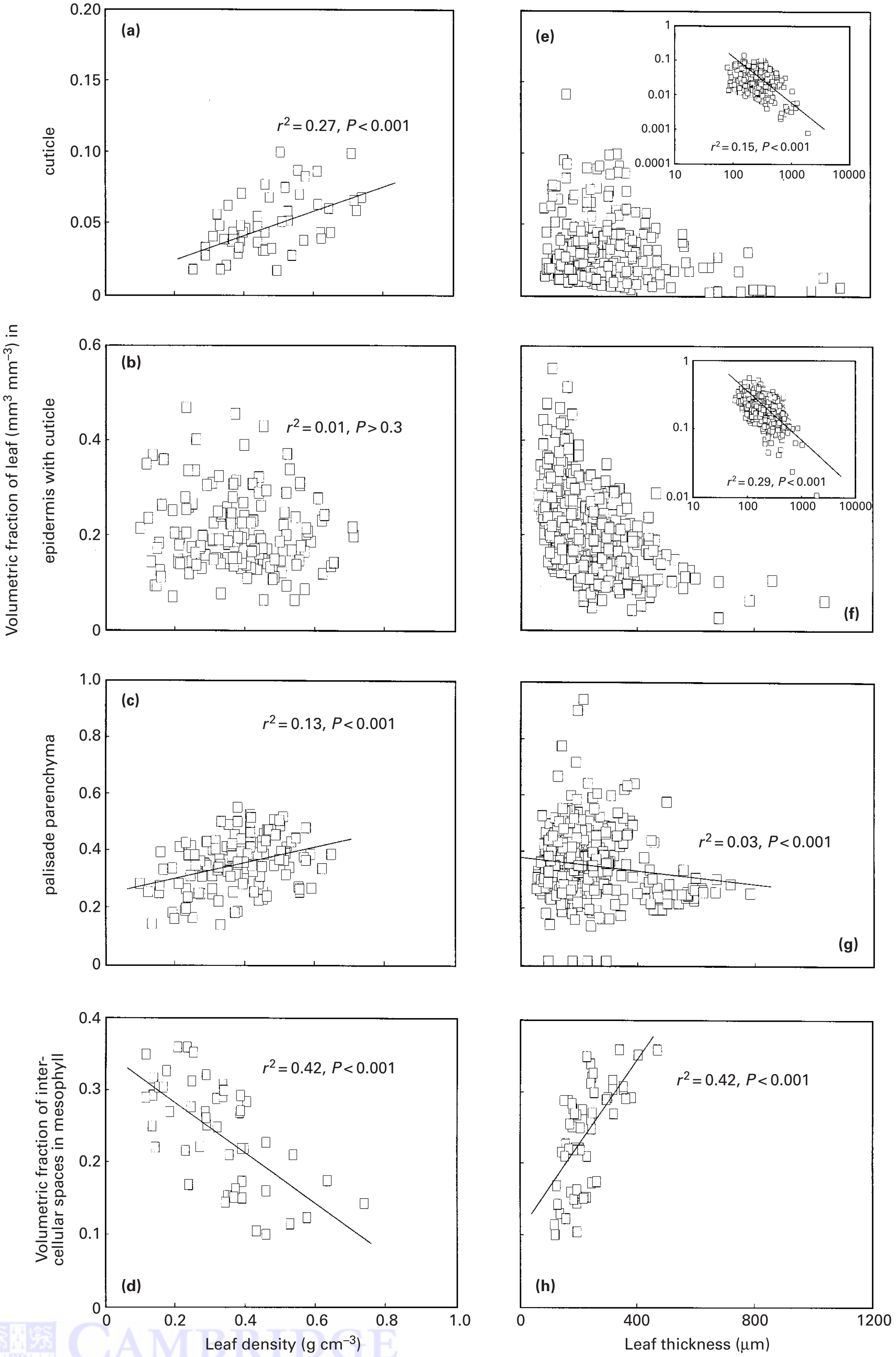

Fig. 2. For legend see opposite.

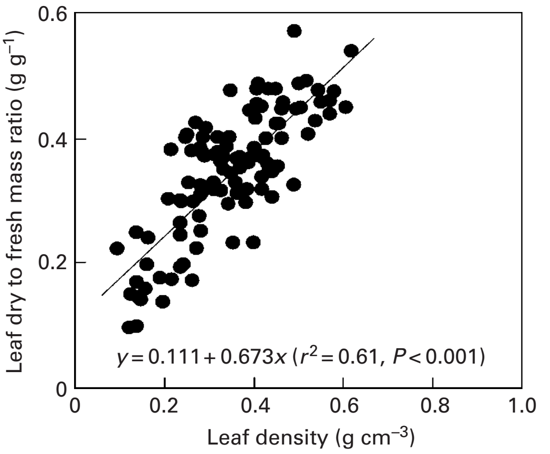

Fig. 3. Interspecific correlation (Appendices 1, 2) between leaf dry to fresh mass ratio and leaf density. All species included in Appendix 1 (www.journals.cup.org) were pooled.

thickness (Fig. 4d), whereas N_{P} was more strongly correlated with leaf thickness than with density (cf. Fig. 4b,d).

Foliar light-saturated net photosynthesis per unit dry mass ($P^{\mathrm{m}}_{\mathrm{max}}$) varied 16-fold across all data, and was positively related to N_{m} ($r^2 = 0.62$, $P < 0.001$). The photosynthetic capacity per unit projected leaf area ($P^{\mathrm{P}}_{\mathrm{max}}$) varied 12-fold, and scaled positively with N_{P} ($r^2 = 0.45$, $P < 0.001$). There was a strong negative relationship between $P^{\mathrm{m}}_{\mathrm{max}}$ and leaf density (Fig. 5a) and a poor correlation between $P^{\mathrm{m}}_{\mathrm{max}}$ and thickness (Fig. 5d). The latter relationship was dependent of photosynthesis values in two *Hakea* species of great thickness, but with very low leaf N contents (filled symbols, Fig. 5d–f). In contrast to the relationships with $P^{\mathrm{m}}_{\mathrm{max}}$, $P^{\mathrm{P}}_{\mathrm{max}}$ was independent of leaf density (Fig. 5b), but increased with increasing leaf thickness (Fig. 5e).

The relationships of foliage structural characteristics with the maximum carboxylase activity of Rubisco (V_{cmax}), which was calculated assuming that the transfer resistance from intercellular air spaces to carboxylation site is zero, were similar to the relationships with net assimilation rates (Fig. 5c,f), indicating that systematic differences in stomatal conductances to CO_2 did not drive the relationships in Fig. 5. Although N_{m} and leaf density were correlated (Fig. 4a), multiple linear regression analysis of V_{cmax} per unit dry mass ($V^{\mathrm{m}}_{\mathrm{cmax}}$) vs N_{m} and D suggested that $V^{\mathrm{m}}_{\mathrm{cmax}}$ was lower at a common N_{m} in leaves with higher density (Fig. 6a). This was further supported by the finding that the fractional investment of leaf N in Rubisco, again calculated on the assumption that intraleaf transfer conductance to CO_2 is infinite and also that the specific activity of Rubisco does not vary across C_3 species, increases with decreasing D (Fig. 6b).

DISCUSSION

Relationships between leaf dry mass per area, leaf thickness and density

High variability in foliage morphological, anatomical, chemical and physiological variables was detected in the compiled set of data (Appendices 1, 2). Across all species, LMA scaled with both density and thickness, but the correlations between D and T were very weak (Fig. 1, Table 2) indicating that the control over D and T is exerted by different mechanisms.

Between broad-leaved and needle-leaved species, LMA vs T and D relationships differed quantitatively. Given that the volume to surface area ratio at a common leaf thickness is greater in broad-leaved ($V/A_{\mathrm{P}} = T$ and $V/A_{\mathrm{T}} = T/2$) than in needle-leaved species (e.g. $V/A_{\mathrm{P}} = \pi T/4$ and $V/A_{\mathrm{T}} = T/4$ for terete-leaved species with needles of circular cross section), differences in the geometry of leaf cross section between needle- and broad-leaved species provided one explanation for this divergence in relationships. However, T was much higher in needle- than in broad-leaved species (Fig. 1c), and therefore, LMA was also larger at common D in needle-leaved taxa (Fig. 1b). In a similar manner, D was greater in broad-leaved than in terete-leaved *Hakea* species, but LMA was greater in terete-leaved species because of the greater thickness (Groom *et al.*, 1997).

Although the current study is based on woody species, the results of the analysis should also be applicable to other plant life-forms. Wilson *et al.* (1999) analysed LMA, T and D relationships for >700 herbaceous species, and found that both T and D play a role in determining LMA, and also that T and D vary independently. However, the ranges of T and D may differ between plant life forms. In the current analysis, T showed greater variability and

---

Fig. 2. Volumetric fractions of leaf tissue in cuticle (a,e), epidermis with cuticle (b,f), and in palisade parenchyma (c,g), and the fraction of mesophyll tissue in intercellular air spaces (d,h) in relation to leaf density (a–d) and thickness (e–h). All analysed species pooled (Appendix 1 (www.journals.cup.org); as explained in the Material and Methods section, additional species from studies listed in Appendix 2 (www.journals.cup.org) are included in the correlations with leaf thickness). The data for the sum of epidermis and cuticle are presented because; only a few studies provided separate values for the volumes of both epidermis and cuticle. Where it was possible to calculate the volume fraction of leaf epidermis alone, it was similarly correlated with D and T as the pooled variable (b,f). Data are fitted by linear regressions, whereas both axes were logarithmal ($\log_{10}$) to normalize the distributions of the data and regression residuals in the insets of panels e and f.

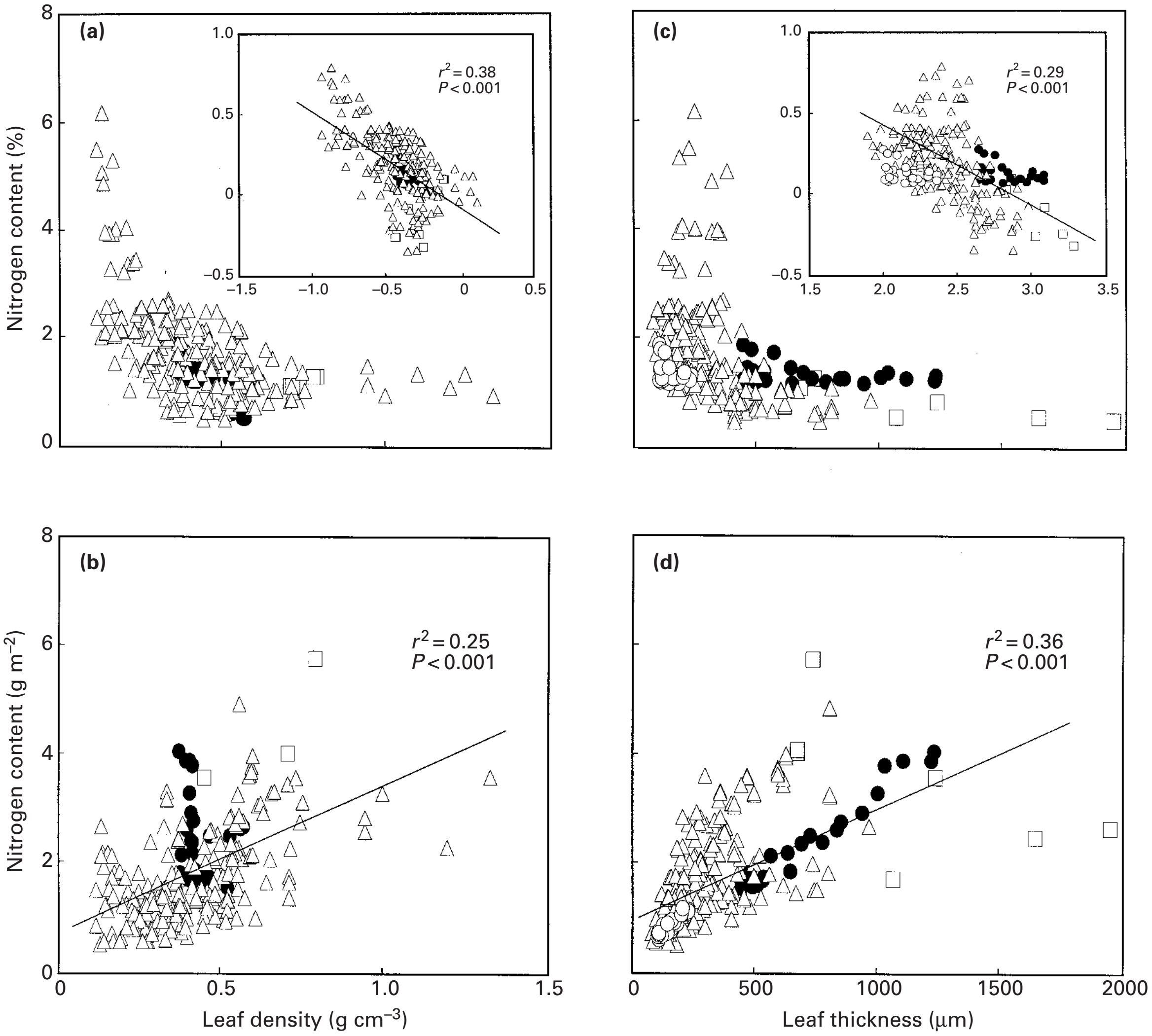

Fig. 4. Interspecific relationships (Appendices 1, 2 (www.journals.cup.org)) between leaf nitrogen content per unit leaf dry mass (N_m; a,c) and per unit projected leaf area (N_P; b,d) with leaf density (a,b) and thickness (c,d). Triangles, broad-leaved species; squares, terete-leaved species; circles, conifers. In conifers, N has been expressed both per unit total (open circles) and projected areas (filled circles). In (c) open circles represent relationships between N_m and volume to total surface are ratio (V/A_T) and in (d) the correlation between nitrogen content per unit total leaf area and V/A_T. Data were fitted by linear regressions (open circles excluded). Insets (a,c) demonstrate $\log_{10}$-transformed data.

was more strongly correlated with LMA than with *D* (cf. Fig. 1a,b). By contrast, a literature analysis across herb species indicated that leaf thickness is generally weakly correlated with specific leaf area (SLA = 1/LMA) with r^2 − s between 0.04–0.50 for four comparative studies (Garnier & Freijsen, 1994), and it appears that leaf density is a better determinant of LMA than thickness in herbs (Garnier & Laurent, 1994; Van Arendonk & Poorter, 1994). This discrepancy may relate to lower LMA and thickness in herbs than in trees and shrubs (see e.g. Eliáš, 1979).

Determinants of leaf density and thickness

The current study indicated that leaf density was greater in leaves with more densely packed mesophyll cells (Fig. 2c,d; see also Niinemets *et al.*, 1999a), and also in leaves possessing greater fractions of apoplastic tissue in the leaves (Fig. 3). The latter result is compatible with the observations of Garnier & Laurent (1994), where *D* scaled with the volume of apoplastic tissue per unit leaf area, and with van Arendonk & Poorter (1994), where *D* increased with increasing fraction of sclerenchyma and veins in the leaves.

One explanation for the positive relationship between the thickness of leaf cuticle and *D* (Fig. 2a) may lie in the positive scaling of the apoplastic leaf fraction with the fraction of leaf tissue in the cuticle. Yet, leaf cuticle rarely comprised a large fraction of the leaf (Fig. 2a), and an alternative explanation may be the correlated increases in both leaf cuticle thickness (Cooper, 1922) and *D*, for example, with increasing site aridity. Although leaf epidermis also consists of tightly packed leaf cells, no relationship between the fraction of leaf in epidermis and *D* was

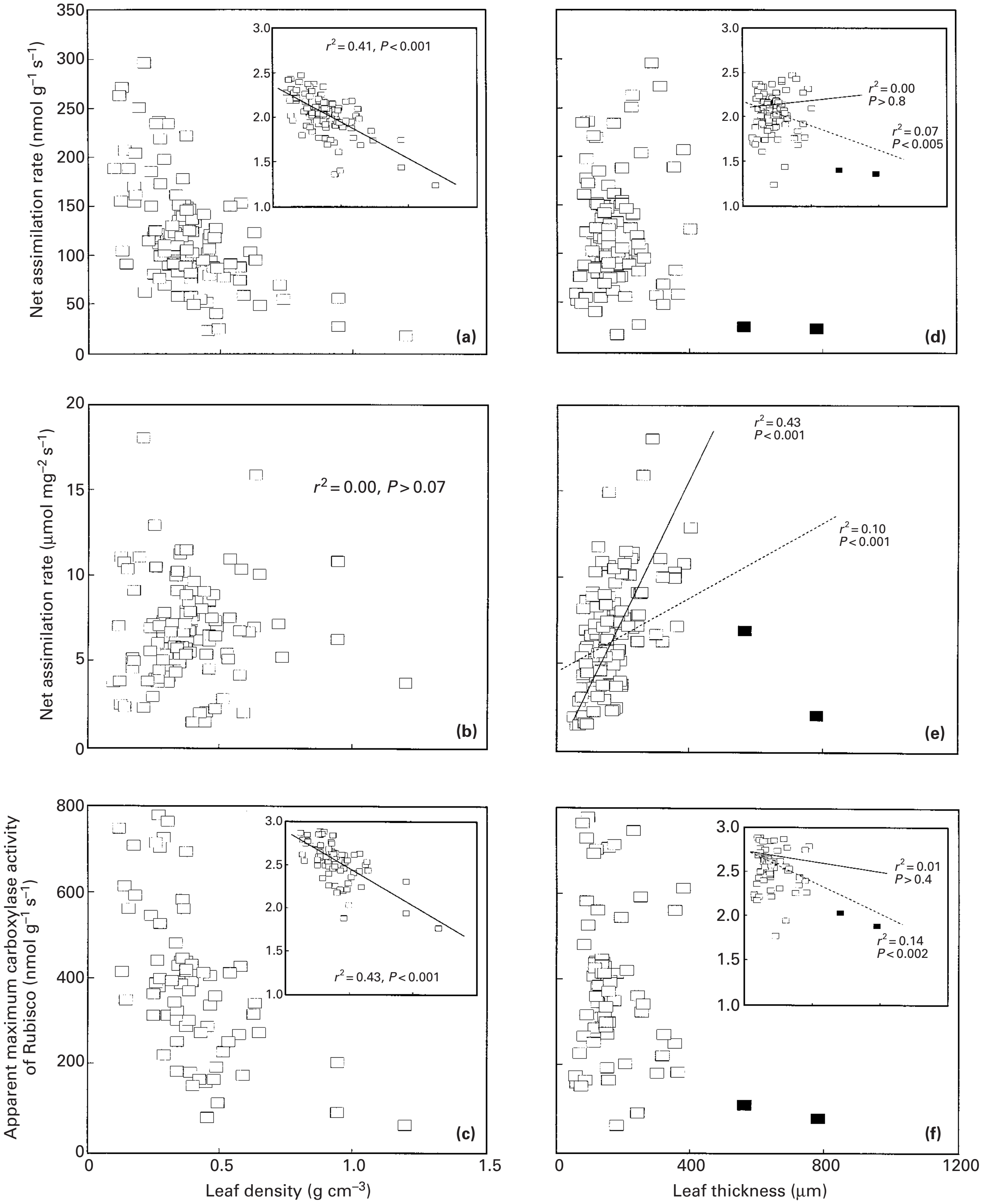

Fig. 5. Foliage light-saturated net assimilation rate at ambient CO$_2$ concentrations of 310–350 µmol mol^{-1} (P_{max}) per unit leaf dry mass ($P^{\text{m}}_{\text{max}}$; a,d) and per unit projected leaf area ($P^{\text{p}}_{\text{max}}$; b,e), and maximum carboxylase activity of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) per unit leaf dry mass ($V^{\text{m}}_{\text{cmax}}$; c,f) in relation to leaf density (a–c) and thickness (d–f). Data were fitted by linear regressions, whereas the y-axes were log$_{10}$-transformed to linearize the relationships in the insets (a,c,d,f). In statistical dependencies with leaf thickness (d–f), two *Hakea* species (filled symbols in panels d–f) fell outside the main group of the data. These points were characterized by extremely low values of leaf N and photosynthesis, and linear regressions were calculated with (dashed lines) and without (continuous lines) these data. Species and data sources are given in Appendices 1, 2 (www.journals.cup.org).

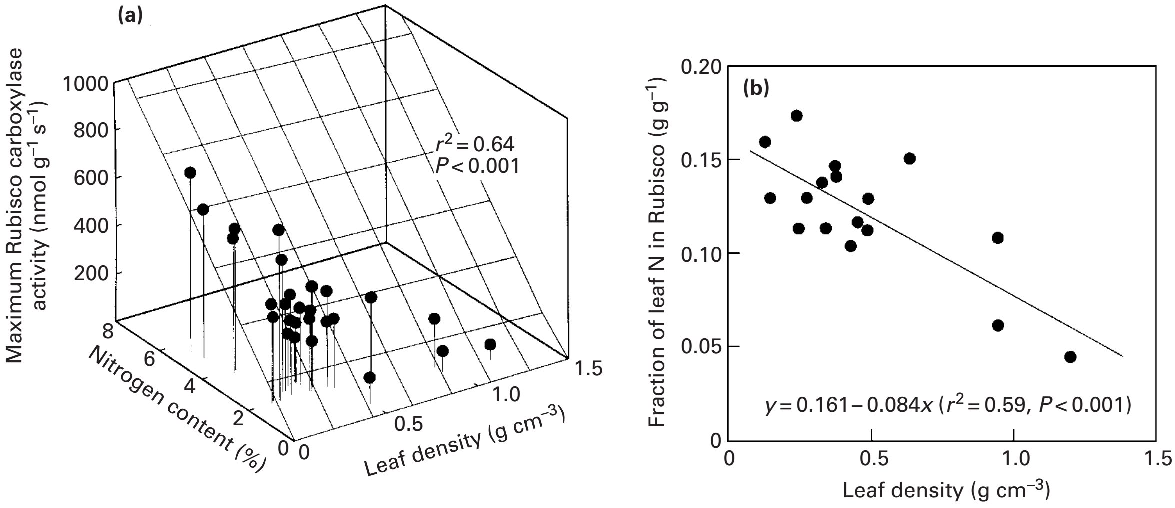

Fig. 6. Dependence of $V^{\mathrm{m}}_{\mathrm{cmax}}$ on (a) leaf nitrogen content per unit leaf dry mass (N_{m}) and leaf density, and (b) the correlation between the fractional leaf nitrogen investment in Rubisco (F_{R}) and leaf density. Regression surface for panel (a) is: $V^{\mathrm{m}}_{\mathrm{cmax}} = 253 + 83.4N_{\mathrm{m}} - 257D$. F_{R} was calculated from $V^{\mathrm{m}}_{\mathrm{cmax}}$ (Fig. 5c) and N_{m} as described in Niinemets & Tenhunen (1997). Data sources are given in Appendices 1, 2 (www.journals.cup.org).

observed in the current set of data (Fig. 2b). It is possible that traits such as epidermal cell wall thickness, which may vary greatly in different environments (Pyykkö, 1966; Schulz, 1984), are more strongly related to D than to total fractional amount of epidermis in the leaf. Epidermis is considered to play an important role in stiffening the leaves (Niklas & Paolillo, 1997), but leaf stiffness is also likely to increase with increasing density (Niklas, 1991). The fraction of mechanical tissues in leaves, such as collenhyma and sclerenchyma, increases in many species with increasing tissue density (van Arendonk & Poorter, 1994; Garnier *et al.*, 1997), but it may decrease with increasing leaf thickness (Garnier *et al.*, 1999). The lack of correlation between leaf density and thickness suggests that various mechanisms controlling leaf stiffness should not necessarily vary in a co-ordinated manner.

Both the leaf fractions in cuticle and epidermis decreased with increasing leaf thickness (Fig. 2e,f) indicating that thin leaves are expensive in terms of covering tissues, and also that thick mesophyll may fulfil an analogous function to epidermis in providing leaves with mechanical stiffness. Thus, the increase in leaf thickness enables greater fractions of leaf tissues in mesophyll at the expense of epidermis and mechanical tissues (Garnier *et al.*, 1999), thereby possibly increasing foliage photosynthetic potentials.

Foliar nitrogen content in relation to leaf thickness and density : implications for foliage photosynthetic capacity

In an earlier literature study, a negative correlation between the thickness of photosynthetic organs and tissue N and P concentrations ($r^2 = 0.39$ and $r^2 = 0.31$ for log–linear relationships with N and P, respectively; Nielsen *et al.*, 1996), and photosynthetic capacity per unit dry mass ($r^2 = 0.39$, Enríquez *et al.*, 1996) was demonstrated. Yet, in these studies foliar thickness, if not reported in the source data, was calculated from specific leaf area (SLA = 1/LMA) using an empirical relationship. Since SLA also depends on leaf density (Table 2), its use as a surrogate of leaf thickness may not necessarily be correct (see also Fig. 1). Nevertheless, in the current data compilation, there were negative relationships of N_{m} with both leaf density and thickness (Fig. 4a,c), suggesting that the fraction of support tissues in leaves may scale with both components of LMA. However, leaf photosynthetic capacity as well as the maximum Rubisco carboxylase activity per unit dry mass scaled negatively with D (Fig. 5a,c), but they were poorly related to T (Fig. 5d,f), indicating that the variability in D is primarily responsible for the negative relationship between LMA and leaf photosynthetic capacity per unit dry mass (cf. the Introduction section).

The strong positive correlation between leaf N content and photosynthetic capacity (Field & Mooney, 1986; Evans, 1989) in combination with declining N concentrations with increasing D (Fig. 4a) and LMA (Reich *et al.*, 1995, 1997) may provide one explanation for the decreasing leaf photosynthetic capacity per unit dry mass with increasing D and LMA. However, the study of Reich *et al.* (1997) demonstrated that the leaves with greater LMA possess a lower photosynthetic capacity per unit dry mass at a common N concentration. Apart from leaf biomass distribution between assimilative and support tissues, changes in leaf structure also play an important role in gas diffusion within the leaves (Evans *et al.*, 1994; Parkhurst, 1994). The diffusive resistance between the leaf intercellular air spaces and carboxylation sites tends to increase with increasing tissue density and leaf thickness and to decrease with increasing fraction of intercellular air spaces in the mesophyll (Syvertsen *et al.*, 1995). In particular, differences in leaf thickness are likely to alter diffusive resistance in the gaseous phase, and changes in leaf density and $A_{\mathrm{mes}}/A_{\mathrm{P}}$ ratio the diffusive resistance in the liquid phase, because the latter variables alter chloroplast surface area exposed to intercellular air spaces (Parkhurst, 1994; Syvertsen *et al.*, 1995; Evans & von Caemmerer, 1996). Given that the molecular diffusion coefficient for CO_2 is about three orders of magnitude smaller in the liquid than in the gaseous phase, changes in density and $A_{\mathrm{mes}}/A_{\mathrm{P}}$ ratio may play a more important role in constraining intraleaf CO_2 diffusion to the carboxylation sites than alterations in leaf thickness. Increasing diffusive resistances with *D* may be one reason for the decrease of the fraction of leaf N in Rubisco, calculated from leaf gas-exchange measurements, with increasing *D* (Fig. 6). Thus, leaves with greater *D* may need higher N concentrations and greater fractions of N in Rubisco for the same rate of photosynthesis as leaves with lower *D*. The diffusive resistances should not necessarily increase considerably with increasing leaf thickness, because of the strong positive relationships of leaf thickness with mesophyll to total leaf surface area ratio (Nobel, 1977; Öquist *et al.*, 1982), and with the fraction of intercellular air space in the leaves (Fig. 2h). The poor correlation of photosynthetic capacity per unit dry mass with thickness (Fig. 5d) also indirectly supports the idea that the diffusive resistances must not scale with *T*. Nevertheless, studies with CAM plants with extremely thick succulent leaves (up to $1.5 \cdot 10^4$ μm), indicate that increases in leaf thickness may bring about lowered intercellular transfer resistances to CO_2 (Maxwell *et al.*, 1997). Moreover, in CAM plants, there is a negative relationship between leaf thickness and discrimination of stable carbon isotopes, further indicating that CO_2 transfer resistance may increase with increasing thickness (Teeri *et al.*, 1981). Yet, the intraleaf pathway of CO_2 to the carboxylation sites is mainly through the liquid phase in the succulent leaves of CAM plants.

Leaf N content per unit area (N_{P}) scaled positively with both *D* and *T* (Fig. 4b,d), but photosynthesis per unit area was positively related only to *T* (Fig. 5b,e), and photosynthesis per dry mass was negatively related to *D* (Fig. 5a). Thus, the positive relationships between foliar photosynthetic capacity per unit area and LMA often observed within and across the wide range of species (cf. the Introduction section) are primarily attributable to the positive scaling of photosynthetic capacity per unit area with leaf thickness (Fig. 5b,e; see also Starzecki, 1975; Garnier *et al.*, 1999; Niinemets *et al.*, 1999a). Since the fraction of leaf epidermis (Fig. 2e) and the fraction of mechanical tissues, such as sclerenchyma (Garnier *et al.*, 1999), decreases with increasing leaf thickness, the thickness of leaf mesophyll tissues increases more than proportionately with increasing *T*. Consequently, the accumulation of photosynthetically competent tissues per unit area is likely to provide the explanation for the increases in leaf photosynthetic capacity with increasing *T*. The content of photosynthetic tissues may also slightly increase with *D*, since there is evidence of greater packing of leaf mesophyll (Fig. 2c,d), and this may be the reason for the positive scaling of N_{P} with *D* (Fig. 4b; see also Niinemets *et al.*, 1999a). However, the constancy of leaf photosynthetic rates per unit area with varying *D* suggests that negative effects of the increases in intercellular transfer resistance with increasing *D* are likely to more than offset the positive effects of increasing N.

CONCLUSIONS

A broad range of variation in foliage structural and functional parameters was observed in the shrubs and trees sampled across all major earth biomes with woody vegetation. The current analysis corroborates the already-known findings that foliage photosynthesis rates and N contents per unit area scale positively with foliage thickness and leaf dry mass per unit area (LMA), but it also indicates that these relationships may be critically altered by the variability in leaf density, since leaf density and thickness are not interdependent, and both play an important role in determining LMA in woody species. Increases in both *T* and *D* resulted in greater LMA and an accumulation of photosynthetic compounds per unit leaf area, but photosynthetic compounds were less effectively used in leaves with higher *D*, possibly because of higher diffusive resistances in these leaves.

Although leaf dry mass per area itself may be the target of selection in many cases, for example, leaves generally acclimate to environments with low irradiance by increasing leaf area per unit biomass investment in leaves (Givnish, 1988), the results demonstrated here also suggest that the components of LMA – density and thickness – may adjust independently to environmental and evolutionary constraints. Thus, more work along environmental gradients is necessary to gain conclusive insight into the variation patterns of leaf thickness and density.

ACKNOWLEDGEMENTS

I thank the *New Phytologist* Trust for inviting and providing means to present this work at the Fourth *New Phytologist* Symposium (5–6 Oct. 1998, Montpellier, France). Constructive comments of Eric Garnier (Centre d'Ecologie Fonctionnelle et Evolutive, C.N.R.S.–U.P.R., Montpellier, France) and Peter B. Reich (Department of Forest Resources, University of Minnesota, St. Paul, MN, USA), and technical assistance of Maarika Mäesalu (Institute of Ecology, Tallinn University of Educational

Sciences, Estonia) in data compilation and analysis are gratefully appreciated. The study was partly supported by the Estonian Science Foundation (Grant 3235).

REFERENCES

Chabot BF, Jurik TW, Chabot JF. 1979. Influence of instantaneous and integrated light-flux density on leaf anatomy and photosynthesis. *American Journal of Botany* **66**: 940–945.

Chazdon RL, Kaufmann S. 1993. Plasticity of leaf anatomy of two rain forest shrubs in relation to photosynthetic light acclimation. *Functional Ecology* **7**: 385–394.

Cooper WS. 1922. The broad-sclerophyll vegetation in California. An ecological study of the chaparral and its related communities. *Carnegie Institution of Washington Publications* **319**: 1–127.

Cornelissen JHC, Werger MJA, Castro-Díez P, van Rheenen JWA, Rowland AP. 1997. Foliar nutrients in relation to growth, allocation and leaf traits in seedlings of a wide range of woody plant species and types. *Oecologia* **111**: 460–469.

Eliáš P. 1979. Some ecophysiological features in leaves of plants in an oak–hornbeam forest. *Folia Geobotanica et Phytotaxonomica* **14**: 29–42.

Ellsworth DS, Reich PB. 1993. Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. *Oecologia* **96**: 169–178.

Enríquez S, Duarte CM, Sand-Jensen K, Nielsen SL. 1996. Broad-scale comparison of photosynthetic rates across phototrophic organisms. *Oecologia* **108**: 197–206.

Epron D, Godard D, Cornic G, Genty B. 1995. Limitation of net CO_2 assimilation rate by internal resistances to CO_2 transfer in the leaves of two tree species (*Fagus sylvatica* L. and *Castanea sativa* Mill.). *Plant, Cell and Environment* **18**: 43–51.

Evans JR. 1989. Photosynthesis and nitrogen relationships in leaves of C_3 plants. *Oecologia* **78**: 9–19.

Evans JR, von Caemmerer S. 1996. Carbon dioxide diffusion inside leaves. *Plant Physiology* **110**: 339–346.

Evans JR, von Caemmerer S, Setchell BA, Hudson GS. 1994. The relationship between CO_2 transfer conductance and leaf anatomy in transgenic tobacco with a reduced content of Rubisco. *Australian Journal of Plant Physiology* **21**: 475–495.

Field C, Mooney HA. 1986. The photosynthesis–nitrogen relationship in wild plants. In: Givnish TJ, ed. *On the economy of plant form and function. Proceedings of the Sixth Maria Moors Cabot Symposium, 'Evolutionary constraints on primary productivity: adaptive patterns of energy capture in plants', Harvard Forest, August 1983*. Cambridge, UK: Cambridge University Press, 25–55.

Garnier E, Cordonnier P, Guillerm J-L, Sonié L. 1997. Specific leaf area and leaf nitrogen concentration in annual and perennial grass species growing in Mediterranean old-fields. *Oecologia* **111**: 490–498.

Garnier E, Freijsen AHJ. 1994. On ecological inference from laboratory experiments conducted under optimum conditions. In: Roy J, Garnier E, eds. *A whole plant perspective on carbon–nitrogen interactions*. The Hague, The Netherlands: SPB Academic Publishing, 267–292.

Garnier E, Laurent G. 1994. Leaf anatomy, specific mass and water content in congeneric annual and perennial grass species. *New Phytologist* **128**: 725–736.

Garnier E, Salager J-L, Laurent G, Sonié L. 1999. Relationships between photosynthesis, nitrogen and leaf structure in 14 grass species, and their dependence on the basis of expression. *New Phytologist* **143**: 119–130.

Givnish TJ. 1988. Adaptation to sun and shade: a whole-plant perspective. *Australian Journal of Plant Physiology* **15**: 63–92.

Groom PK, Lamont BB, Markey AS. 1997. Influence of leaf type and plant age on leaf structure and sclerophylly in *Hakea* (Proteaceae). *Australian Journal of Botany* **45**: 827–838.

Jordan DB, Ogren WL. 1984. The CO_2/O_2 specificity of ribulose 1,5-bisphosphate carboxylase/oxygenase. Dependence on ribulosebisphosphate concentration, pH and temperature. *Planta* **161**: 308–313.

Jordan DN, Smith WK. 1993. Simulated influence of leaf geometry on sunlight interception and photosynthesis in conifer needles. *Tree Physiology* **13**: 29–39.

Lee DW, Richards JH. 1991. Heteroblastic development in vines. In: Mooney HA, Putz FH, eds. *The biology of vines*. New York, USA: Cambridge University Press, 205–243.

Maxwell K, von Caemmerer S, Evans JR. 1997. Is a low internal conductance to CO_2 diffusion a consequence of succulence in plants with crassulacean acid metabolism? *Australian Journal of Plant Physiology* **24**: 777–786.

Nielsen SL, Enríquez S, Duarte CM, Sand-Jensen K. 1996. Scaling maximum growth rates across photosynthetic organisms. *Functional Ecology* **10**: 167–175.

Niinemets Ü. 1997a. Distribution patterns of foliar carbon and nitrogen as affected by tree dimensions and relative light conditions in the canopy of *Picea abies*. *Trees: Structure and Function* **11**: 144–154.

Niinemets Ü. 1997b. Role of foliar nitrogen in light harvesting and shade tolerance of four temperate deciduous woody species. *Functional Ecology* **11**: 518–531.

Niinemets Ü, Bilger W, Kull O, Tenhunen J. 1998b. Acclimation to high irradiance in temperate deciduous trees in the field: changes in violaxanthin cycle pool size and in photosynthetic capacity along a canopy light gradient. *Plant, Cell and Environment* **21**: 1205–1218.

Niinemets Ü, Kull O. 1998. Stoichiometry of foliar carbon constituents varies along light gradients in temperate woody canopies: implications for foliage morphological plasticity. *Tree Physiology* **18**: 467–479.

Niinemets Ü, Kull O, Tenhunen JD. 1998a. An analysis of light effects on foliar morphology, physiology, and light interception in temperate deciduous woody species of contrasting shade-tolerance. *Tree Physiology* **18**: 681–696.

Niinemets Ü, Kull O, Tenhunen JD. 1999a. Variability in leaf morphology and chemical composition as a function of canopy light environment in co-existing trees. *International Journal of Plant Sciences* **60**. (In press.)

Niinemets Ü, Tenhunen JD. 1997. A model separating leaf structural and physiological effects on carbon gain along light gradients for the shade-tolerant species *Acer saccharum*. *Plant, Cell and Environment* **20**: 845–866.

Niinemets Ü, Tenhunen JD, Canta NR, Chaves M, Faria T, Pereira JS, Reynolds JF. 1999b. Interactive effects of nitrogen and phosphorus on the acclimation potential of foliage photosynthetic properties of cork oak, *Quercus suber*, to elevated atmospheric CO_2 concentrations. *Global Change Biology* **5**: 455–470.

Niklas KJ. 1989. Mechanical behavior of plant tissues as inferred from the theory of pressurized cellular solids. *American Journal of Botany* **76**: 929–937.

Niklas KJ. 1991. Biomechanical attributes of the leaves of pine species. *Annals of Botany* **68**: 253–262.

Niklas KJ, Paolillo DJ Jr. 1997. The role of the epidermis as a stiffening agent in *Tulipa* (Liliaceae) stems. *American Journal of Botany* **84**: 735–744.

Nobel PS. 1977. Internal leaf area and cellular CO_2 resistance: photosynthetic implications of variations with growth conditions and plant species. *Physiologia Plantarum* **40**: 137–144.

Öquist G, Brunes L, Hällgren J-E. 1982. Photosynthetic efficiency of *Betula pendula* acclimated to different quantum flux densities. *Plant, Cell and Environment* **5**: 9–15.

Parkhurst DF. 1994. Tansley review no. 65. Diffusion of CO_2 and other gases inside leaves. *New Phytologist* **126**: 449–479.

Pearcy RW, Sims DA. 1994. Photosynthetic acclimation to changing light environments: scaling from the leaf to the whole plant. In: Caldwell MM, Pearcy RW, eds. *Exploitation of environmental heterogeneity by plants. Ecophysiological processes above- and belowground. Physiological ecology. A series of monographs, texts, and treatises*. San Diego, CA, USA: Academic Press, 145–174.

Pyykkö M. 1966. The leaf anatomy of East Patagonian xeromorphic plants. *Annales Botanici Fennici* **3**: 453–622.

Reich PB, Kloeppel BD, Ellsworth DS, Walters MB. 1995. Different photosynthesis–nitrogen relations in deciduous hardwood and evergreen coniferous tree species. *Oecologia* **104**: 24–30.

Reich PB, Uhl C, Walters MB, Ellsworth DS. 1991. Leaf lifespan as a determinant of leaf structure and function among 23 Amazonian tree species. *Oecologia* **86**: 16–24.

Reich PB, Walters MB. 1994. Photosynthesis–nitrogen relations in Amazonian tree species. II. Variation in nitrogen vis-à-vis specific leaf area influences mass- and area-based expressions. *Oecologia* **97**: 73–81.

Reich PB, Walters MB, Ellsworth DS. 1992. Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecological Monographs* **62**: 365–392.

Reich PB, Walters MB, Ellsworth DS. 1997. From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences, USA* **94**: 13730–13734.

Schulz S. 1984. *Anatomisch-morphologische Untersuchungen an Blättern immergrüner Arten der Mediterranean Hartlaubformation.* Diplom Dissertation, Universität Würzburg, Germany.

Sims DA, Pearcy RW. 1989. Photosynthetic characteristics of a tropical forest understory herb, *Alocasia macrorrhiza*, and a related crop species, *Colocasia esculenta*, grown in contrasting light environments. *Oecologia* **79**: 53–59.

Sims DA, Pearcy RW. 1992. Response of leaf anatomy and photosynthetic capacity in *Alocasia macrorrhiza* (Araceae) to a transfer from low to high light. *American Journal of Botany* **79**: 449–455.

Sobrado MA, Medina E. 1980. General morphology, anatomical structure, and nutrient content of sclerophyllous leaves of the 'Bana' vegetation of Amazonas. *Oecologia* **45**: 341–345.

Starzecki W. 1975. Ecophysiological investigation on photosynthetic productivity of leaves of chosen tree species. *Polish Ecological Studies* **1**: 51–63.

Steele MJ, Coutts MP, Yeoman MM. 1989. Developmental changes in Sitka spruce as indices of physiological age. I. Changes in needle morphology. *New Phytologist* **113**: 367–375.

Syvertsen JP, Lloyd J, McConchie C, Kriedemann PE, Farquhar GD. 1995. On the relationship between leaf anatomy and CO_2 diffusion through the mesophyll of hypostomatous leaves. *Plant, Cell and Environment* **18**: 149–157.

Teeri JA, Tonsor SJ, Turner M. 1981. Leaf thickness and carbon isotope composition in the Crassulaceae. *Oecologia* **50**: 367–369.

van Arendonk JJCM, Poorter H. 1994. The chemical composition and anatomical structure of leaves of grass species differing in relative growth rate. *Plant, Cell and Environment* **17**: 963–970.

von Caemmerer S, Farquhar GD. 1981. Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. *Planta* **153**: 376–387.

Wilkinson L. 1990. *SYSTAT: The system for statistics*, Evanston, IL, USA: SYSTAT, Inc.

Wilson PJ, Thompson K, Hodgson JG. 1999. Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. *New Phytologist* **143**: 155–162.

Witkowski ETF, Lamont BB. 1991. Leaf specific mass confounds leaf density and thickness. *Oecologia* **88**: 486–493.

Appendix 1. Species studied with appropriate literature citations, species sampling locations, foliar variables included in the analysis, and number of cases averaged for the analysis (*n*)

1A. Needle-leaved species

Citation (Appendix 2A)	Species	Life form	Shape of leaf cross-section[1]	Sample location	Variables analysed[2]	*n*
14	*Abies fraseri* (Pursh) Poir.	Tree	R	35°37′N, 79°4′W	T, V/A_{T}, D	18
66, 71	*Allocasuarina pusilla* (Macklin) L. Johnson	Shrub	C	36°06′S, 140°31′E	T, V/A_{T}, D, N	1
66	*Hakea gibbosa* (Smith) Cav.	Shrub	C	26°21′S, 153°00′E	T, V/A_{T}, D, N, A, P	1
66, 71	*Hakea muelleriana* J. Black	Shrub	C	36°06′S, 140°31′E	T, V/A_{T}, D, N, A, P	1
27	*Hakea psilorrhyncha* R. M. Barker[3,5,6]	Shrub	C	37°27′N, 122°16′W	T, V/A_{T}, D, A, P	4
28	*Hakea trifurcata* (Smith) R. Br.	Shrub	C	31°59′S, 116°04′E	T, V/A_{T}, D, A, P	1
29	32 terete-leaved *Hakea* species[4]	Shrub	C	31°59′S, 115°53′E	T, V/A_{T}, D, A, P	4
54	*Juniperus communis* L.	Shrub	T	58°31′N, 25°38′E	T, V/A_{T}, D	3
66, 71	*Melaleuca uncinata* F. v. Muell.	Shrub	C	36°06′S, 140°31′E	T, V/A_{T}, D, N	1
57	*Picea abies* (L.) Karst.	Tree	R	58°44′N, 26°45′E	T, V/A_{T}, D	17
55, 56	*Picea abies* (L.) Karst.	Tree	R	49°59′N, 11°47′E	T, V/A_{T}, D, N	24
72	*Picea sitchensis* (Bong.) Carr.[4]	Tree	R	55°46′N, 2°42′W	T, V/A_{T}, D	6
85	*Pinus sylvestris* L.[3]	Tree	S	52°13′N, 20°59′E	T, V/A_{T}, D	3
64	*Pinus sylvestris* L.	Tree	S	47°17′N, 11°27′E	T, V/A_{T}, D	1
32	*Pinus taeda* L.[4]	Tree	K	37°10′N, 80°29′W	V/A_{T}, D	8
69	*Pinus taeda* L.	Tree	K	32°35′N, 88°48′W	V/A_{T}, D	28
78	*Tsuga heterophylla* (Raf.) Sarg.	Tree	R	44°6′N, 121°51′W	T, V/A_{T}, D	8
66, 71	*Xanthorrhoea australis* R. Br.	Tree	T	36°06′S, 140°31′E	T, D, N	1
66	*Xanthorrhoea resinosa* Person	Shrub	T	26°21′S, 153°00′E	T, D, N	1

1B. Broad-leaved species

Citation	Species	Life form	Sample location	Variables analysed	*n*
42, 44	*Abrus precatorius* L.[3]	Woody vine	10°28′N, 84°02′W	T, D, A	3
12	*Acalypha skutchii* I. M. Johnst.	Tree	18°35′N, 95°07′W	T, D, N, A	1
40	*Acer mono* Maxim.	Tree	42°58′N, 141°23′E	T, D, A, P	1
4	*Acer negundo* L.	Tree	43°33′N, 89°27′W	T, D	1
6	*Acer negundo* L.	Tree	40°48′N, 77°51′W	T, D	1
40	*Acer palmatum* Thunb.	Tree	42°58′N, 141°23′E	T, D, A, P	1
45	*Acer pennsylvanicum* L.[3]	Tree	45°33′N, 73°09′W	T, D	1
25	*Acer platanoides* L.	Tree	50°30′N, 37°56′E	T, D, A	3
36	*Acer platanoides* L.[3,5]	Tree	40°48′N, 77°50′W	T, D, N, P	1
5	*Acer rubrum* L.	Tree	40°48′N, 77°52′W	T, D, P	4
4	*Acer rubrum* L.	Tree	43°33′N, 89°27′W	T, D	2
8	*Acer rubrum* L.	Tree	40°49′N, 77°56′W	T, D, N, P	2
37, 38	*Acer rubrum* L.	Tree	40°49′N, 77°56′W	T, D, P	2
4	*Acer saccharinum* L.	Tree	43°33′N, 89°27′W	T, D	2
6	*Acer saccharinum* L.	Tree	40°48′N, 77°51′W	T, D	1
45	*Acer saccharum* Marsh.[3]	Tree	45°33′N, 73°09′W	T, D	1
4	*Acer saccharum* Marsh.	Tree	43°33′N, 89°27′W	T, D	2
36	*Acer saccharum* Marsh.	Tree	40°47′N, 77°53′W	T, D, N, P	2
45	*Acer spicatum* Lam.[3]	Tree	45°33′N, 73°09′W	T, D	1
12	*Aegiphila costaricensis* Mold.	Tree	18°35′N, 95°07′W	T, D, N, A	1
80	*Agonis flexuosa* (Willd.) Lindl.	Shrub	33°57′S, 120°07′E	T, D	1
24	*Alchornea triplinervia* (Spren.) M. Arg [3]	Tree	8°39′N, 71°24′W	T, D, N, P	2
65	*Aldina heterophylla* Spr. ex Benth.	Tree	2°43′S, 60°0′W	T, D	6
12	*Allophylus compostachis* Radlk.	Tree	18°35′N, 95°07′W	T, D, N, A	1
40	*Alnus hirsuta* Turcz.	Tree	42°58′N, 141°23′E	T, D, A, P	1
40	*Alnus japonica* Steud.	Tree	42°58′N, 141°23′E	T, D, A, P	1
68	*Andromeda catesbaei* Walt.	Shrub	39°18′N, 76°38′W	T, D	1
68	*Andromeda floribunda* Pursh.	Shrub	39°18′N, 76°38′W	T, D	1
68	*Andromeda japonica* Thunb.	Shrub	39°18′N, 76°38′W	T, D	1
68	*Andromeda racemosa* L.	Shrub	39°18′N, 76°38′W	T, D	1
87	*Annona glabra* L.	Tree	9°10′N, 79°51′W	T, D	1
20	*Arbutus andrachne* L.	Shrub	38°14′N, 23°48′E	T, D, A	1

1B. Broad-leaved species (*cont.*)

Citation	Species	Life form	Sample location	Variables analysed	*n*
80	*Arbutus menziesii* Pursh.	Tree	37°24′N, 122°13′W	*T*, *D*	6
20	*Arbutus unedo* L.	Tree	38°14′N, 23°48′E	*T*, *D*, A	1
84	*Asimina triloba* (L.) Dunal	Tree	37°22′N, 77°32′W	*T*, *D*, N	2
70	*Aspidosperma album* (Vahl) Pichon	Tree	1°54′N, 67°03′W	*T*, *D*, N, A	1
88	*Baccharis pedunculata* (Mill.) Cabr.	Shrub	8°43′N, 82°14′W	*T*, *D*	1
66	*Banksia aemula* R. Br.	Tree	26°21′S, 153°00′E	*T*, *D*, N	2
81	*Banksia baueri* R. Br.	Shrub	33°40′S, 120°40′E	*T*, *D*, N, P	1
80	*Banksia lemanniana* Meissner	Shrub	33°57′S, 120°07′E	*T*, *D*	1
66, 71	*Banksia marginata* Cav.	Shrub	34°59′S, 138°40′E	*T*, *D*, N	2
66, 71	*Banksia marginata* Cav.	Shrub	36°06′S, 140°31′E	*T*, *D*, N	2
66	*Banksia oblongifolia* Cav.	Shrub	26°21′S, 153°00′E	*T*, *D*, N	3
66, 71	*Banksia ornata* F. v. Muell	Shrub	36°06′S, 140°31′E	*T*, *D*, N	2
66	*Banksia robur* Cav.	Shrub	26°21′S, 153°00′E	*T*, *D*, N	1
50	*Banksia serratifolia* Salisb.	Shrub	33°57′S, 120°07′E	*T*, *D*, N, A	1
80	*Banksia speciosa* R. Br.	Shrub	33°57′S, 120°07′E	*T*, *D*	1
4	*Betula alleghaniensis* Britton	Tree	43°33′N, 89°27′W	*T*, *D*	2
40	*Betula davurica* Pall.	Tree	42°58′N, 141°23′E	*T*, *D*, A, P	1
40	*Betula ermanii* Cham.	Tree	42°58′N, 141°23′E	*T*, *D*, A, P	1
6	*Betula lenta* L.	Tree	40°48′N, 77°51′W	*T*, *D*	1
40	*Betula maximowicziana* Regel	Tree	42°58′N, 141°23′E	*T*, *D*, A, P	1
4	*Betula papyrifera* Marsh.	Tree	43°33′N, 89°27′W	*T*, *D*	2
58	*Betula pendula* Roth.[3]	Tree	61°55′N, 24°34′E	*T*, *D*, P	6
62	*Betula pendula* Roth.[3]	Tree	62°13′N, 27°13′E	*T*, *D*, N, A	5
40	*Betula platyphylla* Sukatch.	Tree	42°58′N, 141°23′E	*T*, *D*, A, P	1
34	*Bischofia javanica* Blume[3,7,8]	Tree	24°12′N, 90°9′E	*T*, *D*, A, P	3
88	*Blakea foliacea* Gleason	Hemiepiphyte	8°43′N, 82°14′W	*T*, *D*	1
12	*Brosimum alicastrum* Sw.	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
12	*Bursera simaruba* (L.) Sarg.	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
12	*Capparis baduca* L.	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
4	*Carpinus caroliniana* Walder	Tree	43°33′N, 89°27′W	*T*, *D*	2
40	*Carpinus cordata* Blume	Tree	42°58′N, 141°23′E	*T*, *D*, A, P	1
4	*Carya cordiformis* (Wangenh.) K. Koch	Tree	43°33′N, 89°27′W	*T*, *D*	2
6	*Carya cordiformis* (Wangenh.) K. Koch	Tree	40°48′N, 77°51′W	*T*, *D*	1
8	*Carya tomentosa* Nutt.	Tree	40°49′N, 77°56′W	*T*, *D*, N, P	2
12	*Casearea nitida* Jacq.	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
66	*Cassinia laevis* R. Br.	Shrub	33°55′S, 147°12′E	*T*, *D*, N	1
6	*Castanea dentata* (Marsh.) Borkh.	Tree	40°48′N, 77°51′W	*T*, *D*	1
50	*Ceanothus cuneatus* (Hook.) Nutt.	Shrub	37°27′N, 122°16′W	*T*, *D*, N, A	1
12	*Cecropia obtusifolia* Bertol.	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
6	*Celtis tenuifolia* Nutt.	Shrub	40°48′N, 77°51′W	*T*, *D*	1
20	*Ceratonia siliqua* L.	Shrub	37°58′N, 23°45′E	*T*, *D*, A	1
40	*Cercidiphyllum japonicum* Sieb. et Zucc.	Tree	42°58′N, 141°23′E	*T*, *D*, A, P	1
1, 2	*Cercis canadensis* L.[3,5]	Tree	38°57′N, 95°24′W	*T*, *D*	3
1, 2	*Cercis canadensis* L.[3,5]	Tree	40°22′N, 85°58′W	*T*, *D*	1
9	*Cissus rhombifolia* Planch[3,5,16]	Shrub	41°30′N, 2°6′E	*T*, *D*, A, P	1
88	*Citharexylum macradenium* Greenm.	Tree	8°43′N, 82°14′W	*T*, *D*	1
20	*Citrus limon* (L.) Burm. f.	Tree	38°14′N, 23°48′E	*T*, *D*	1
73, 74	*Citrus paradisi* Macf.[3]	Tree	28°6′N, 81°43′W	*T*, *D*, N, A, P	6
73, 74	*Citrus sinensis* (L.) Osb.[3]	Tree	28°6′N, 81°43′W	*T*, *D*, N, A, P	6
12	*Clarisa bifolia* R. & P.	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
68	*Clethra alnifolia* L.	Shrub	39°18′N, 76°38′W	*T*, *D*	1
12	*Coccoloba barbadensis* Jacq.	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
12	*Cordia megalantha* Blake	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
13	*Cordia megalantha* Blake[3,5]	Tree	18°35′N, 95°07′W	*T*, *D*	3
6	*Cornus alternifolia* L. f.	Shrub	40°48′N, 77°51′W	*T*, *D*	1
40	*Cornus contraversa* Hemsl.	Tree	42°58′N, 141°23′E	*T*, *D*, A, P	1
8	*Cornus florida* L.	Tree	40°49′N, 77°56′W	*T*, *D*, N	2
26	*Corylus avellana* L.	Shrub	54°19′N, 9°59′E	*T*, *D*	4
86	*Cosmibuena macrocarpa* (Benth.) Walp.	Hemiepiphyte	9°10′N, 79°51′W	*T*, *D*, N	1
86	*Coussapoa magnifolia* Trec.	Hemiepiphyte	9°10′N, 79°51′W	*T*, *D*, N	1
86	*Coussapoa panamensis* Pitt.	Hemiepiphyte	9°10′N, 79°51′W	*T*, *D*, N	1
31	*Coussapoa villosa* P. & E.	Hemiepiphyte	8°37′N, 70°12′W	*T*, *D*, A	2
4	*Crataegus pedicellata* Sarg.	Tree	43°33′N, 89°27′W	*T*, *D*	2
88	*Croton draco* Schlecht.	Tree	8°43′N, 82°14′W	*T*, *D*	1
12	*Croton schiedeanus* Schlecht.	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1

1B. Broad-leaved species (*cont.*)

Citation	Species	Life form	Sample location	Variables analysed	*n*
12	*Cupania dentata* DC.	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
12	*Cymbopetalum baillonii* R. E. Fr.	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
12	*Cynometra retusa* B. & R.	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
88	*Dendropanax arboreus* (L.) Dec. & Planch.	Hemiepiphyte	8°43′N, 82°14′W	*T*, *D*	1
12	*Dendropanax arboreus* (L.) Decne. & Planch.	Hemiepiphyte	18°35′N, 95°07′W	*T*, *D*, N, A	1
12	*Dialium guianense* (Aubl.) Sandw.	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
22	*Dipteryx panamensis* (Pitt.) Record & Mell. [3]	Tree	10°46′N, 84°02′W	*T*, *D*	3
17	*Drimys winteri* L.	Tree	9°34′N 83°41′W	*T*, *D*	2
80	*Dryandra sessilis* (Knight) Domin	Shrub	33°57′S, 120°07′E	*T*, *D*	1
43	*Dryobalanops aromatica* Gaertn. f.[3]	Tree	3°9′N, 101°43′E	*T*, *D*	5
12	*Dussia mexicana* (Standl.) Harms.	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
43	*Endospermum malaccense* M.A.[3]	Tree	3°9′N, 101°43′E	*T*, *D*	5
66, 71	*Eucalyptus baxteri* (Benth.) J. Black	Tree	34°59′S, 138°40′E	*T*, *D*, N	1
66, 71	*Eucalyptus behriana* F. v. Muell	Tree	33°55′S, 147°12′ E	*T*, *D*, N	1
66, 71	*Eucalyptus diversifolia* Bonpl.	Tree	35°35′S, 139°46′E	*T*, *D*, N	1
66, 71	*Eucalyptus foecunda* Schauer	Tree	36°06′S, 140°31′E	*T*, *D*, N	1
71	*Eucalyptus incrassata* Labill.	Tree	33°59′S, 145°43′E	*T*, *D*, N	1
66, 71	*Eucalyptus incrassata* Labill.	Tree	34°11′S, 139°59′E	*T*, *D*, N	1
66, 71	*Eucalyptus incrassata* Labill.	Tree	36°06′S, 140°31′E	*T*, *D*, N	1
66, 71	*Eucalyptus leucoxylon* F. v. Muell	Tree	34°57′S, 138°38′E	*T*, *D*, N	1
66, 71	*Eucalyptus microcarpa* Maiden	Tree	34°57′S, 138°38′E	*T*, *D*, N	2
66, 71	*Eucalyptus obliqua* L'Hérit	Tree	34°59′S, 138°40′E	*T*, *D*, N	1
66, 71	*Eucalyptus socialis* Miq.	Tree	34°11′S, 139°59′E	*T*, *D*, N	1
66, 71	*Eucalyptus socialis* Miq.	Tree	34°17′S, 141°10′E	*T*, *D*, N	1
66, 71	*Eucalyptus socialis* Miq.	Tree	34°23′S, 139°20′E	*T*, *D*, N	1
80	*Eucalyptus tetragona* (R. Br.) F. v. Muell	Tree	33°57′S, 120°07′E	*T*, *D*	2
66, 71	*Eucalyptus viminalis* Labill.	Tree	34°57′S, 138°38′E	*T*, *D*, N	1
63	*Euphorbia arnottiana* Endl.[3,5,9,15]	Shrub	38°34′N, 121°44′W	*T*, *D*, N	1
63	*Euphorbia celastroides* Boiss.[3,5,9,15]	Shrub	38°34′N, 121°44′W	*T*, *D*, N, A	1
63	*Euphorbia clusiaeifolia* Hook & Arn.[3,5,9,15]	Shrub	38°34′N, 121°44′W	*T*, *D*, N	1
63	*Euphorbia degeneri* Sherff[3,5,9,15]	Shrub	38°34′N, 121°44′W	*T*, *D*, N, A	1
63	*Euphorbia forbesii* Sherff[3,5,9,15]	Shrub	38°34′N, 121°44′W	*T*, *D*, N, A	1
63	*Euphorbia halemanui* Sherff[3,5,9,15]	Shrub	38°34′N, 121°44′W	*T*, *D*, N	1
63	*Euphorbia hillebrandii* Levl.[3,5,9,15]	Shrub	38°34′N, 121°44′W	*T*, *D*, N	1
63	*Euphorbia multiformis* Hook & Arn.[3,5,9,15]	Shrub	38°34′N, 121°44′W	*T*, *D*, N, A	1
63	*Euphorbia olowaluana* Sherff[3,5,9,15]	Shrub	38°34′N, 121°44′W	*T*, *D*, N	1
63	*Euphorbia remyi* Gray ex Boiss.[3,5,9,15]	Shrub	38°34′N, 121°44′W	*T*, *D*, N, A	1
63	*Euphorbia skottsbergii* Sherff[3,5,9,15]	Shrub	38°34′N, 121°44′W	*T*, *D*, N, A	1
40	*Fagus crenata* Blume[3,5]	Tree	42°58′N, 141°23′E	*T*, *D*, A, P	1
35	*Fagus japonica* Maxim.[3,5]	Tree	36°58′N, 140°36′E	*T*, *D*, A	1
47, 48	*Fagus sylvatica* L.	Tree	49°00′N, 8°23′E	*T*, *D*, A	4
11	*Fagus sylvatica* L.	Tree	48°46′N, 6°17′E	*T*, *D*, A	8
15	*Fagus sylvatica* L.	Tree	43°44′N, 11°32′E	*T*, *D*, A	3
77	*Fagus sylvatica* L.[3,5]	Tree	44°30′N, 11°20′E	*T*, *D*, A, P	8
16	*Fagus sylvatica* L.	Tree	43°44′N, 11°32′E	*T*, *D*, N	10
12	*Faramea occidentalis* (L.) A. Rich.	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
9, 79	*Fatsia japonica* Decne & Planck[3,5,10]	Shrub	41°30′N, 2°6′E	*T*, *D*, N, A, P	3
67	*Ficus benjamina* L.[3,5,11]	Shrub	40°30′N, 74°27′W	*T*, *D*	4
86	*Ficus citrifolia* P. Mill.	Hemiepiphyte	9°10′N, 79°51′W	*T*, *D*, N	1
12	*Ficus colubrinae* Standl.	Shrub	18°35′N, 95°07′W	*T*, *D*, N, A	1
12	*Ficus insipida* Willd.	Shrub	18°35′N, 95°07′W	*T*, *D*, N, A	1
88	*Ficus macbridei* Standl.	Hemiepiphyte	8°43′N, 82°14′W	*T*, *D*	1
31	*Ficus nymphaeifolia* P. Mill.	Hemiepiphyte	8°37′N, 70°12′W	*T*, *D*, A	1
31	*Ficus obtusifolia* H. B. K.	Hemiepiphyte	8°37′N, 70°12′W	*T*, *D*, A	2
31	*Ficus pertusa* L. f.	Hemiepiphyte	10°12′N, 84°42′W	*T*, *D*, A	4
31	*Ficus trigonata* L.	Hemiepiphyte	8°34′N, 67°35′W	*T*, *D*, A	2
52	*Flourensia thurifera* (Mol.) DC.	Shrub	33°30′S, 70°45′W	*T*, *D*	1
4	*Fraxinus americana* L.	Tree	43°33′N, 89°27′W	*T*, *D*	2
6	*Fraxinus americana* L.	Tree	40°48′N, 77°51′W	*T*, *D*	1
8	*Fraxinus americana* L.	Tree	40°49′N, 77°56′W	*T*, *D*, N, P	2
40	*Fraxinus mandschurica* Rupr.	Tree	42°58′N, 141°23′E	*T*, *D*, A, P	1
4	*Fraxinus nigra* Marsh.	Tree	43°33′N, 89°27′W	*T*, *D*	2
6	*Fraxinus nigra* Marsh.	Tree	40°48′N, 77°51′W	*T*, *D*	1
7	*Fraxinus pennsylvanica* Marsh.[3,5]	Tree	40°48′N, 77°52′W	*T*, *D*, P	5
51	*Gautheria shallon* Pursh	Shrub	48°40′N, 123°37′W	*T*, *D*	2

1B. Broad-leaved species (cont.)

Citation	Species	Life form	Sample location	Variables analysed	*n*
12	*Guarea glabra* Vahl.	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
12	*Guarea grandifolia* A. DC.	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
23	*Guarea guidonia* (L.) Sleumer[3,12]	Tree	25°45′N, 80°12′W	*T*, *D*	6
80	*Hakea lasianthoides* B. L. Rye[3,5,13]	Shrub	37°25′N, 122°09′W	*T*, *D*	7
28	*Hakea trifurcata* (Smith) R. Br.	Shrub	31°59′S, 116°04′E	*T*, *D*, A, P	1
80	*Hakea victoriae* J. L. Drumm	Shrub	33°57′S, 120°07′E	*T*, *D*	1
29	63 broad-leaved *Hakea* species [14]	Shrub	31°59′S, 115°53′E	*T*, *D*	6
4	*Hamamelis virginiana* L.	Tree	43°33′N, 89°27′W	*T*, *D*	2
12	*Hampea nutricia* Fryxell	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
86	*Havetiopsis flexilis* Spruce ex Planch. & Tr.	Hemiepiphyte	9°10′N, 79°51′W	*T*, *D*, N	1
12	*Heliocarpus appendiculatus* Turcz.	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
22	*Heliocarpus appendiculatus* Turcz. [3]	Tree	10°46′N, 84°02′W	*T*, *D*	3
70	*Heteropteris* sp.	Tree	1°54′N, 67°03′W	*T*, *D*, N, A	1
43	*Hopea wrightiana* Wall.[3]	Tree	3°9′N, 101°43′E	*T*, *D*	5
88	*Inga punctata* Willd.	Tree	8°43′N, 82°14′W	*T*, *D*	1
12	*Inga* sp.	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
80	*Isopogon attenuatus* R. Br.	Shrub	33°57′S, 120°07′E	*T*, *D*	1
40	*Juglans ailanthifolia* Carr.	Tree	42°58′N, 141°23′E	*T*, *D*, A, P	1
6	*Juglans nigra* L.	Tree	40°48′N, 77°51′W	*T*, *D*	1
52	*Kagneckia oblonga* R. & Pav.	Shrub	33°30′S, 70°45′W	*T*, *D*	1
68	*Kalmia latifolia* L.	Shrub	39°18′N, 76°38′W	*T*, *D*	1
40	*Kalopanax pictus* Nakai	Tree	42°58′N, 141°23′E	*T*, *D*, A, P	1
53	*Laurus azorica* (Seub.) Franco	Tree	28°27′N, 16°24′W	*T*, *D*	9
20	*Laurus nobilis* L.	Shrub	37°58′N, 23°45′E	*T*, *D*, A	1
67	*Leea coccinia* L.[3,5,15]	Shrub	40°30′N, 74°27′W	*T*, *D*	4
67	*Leea rubra* L.[3,5,15]	Shrub	40°30′N, 74°27′W	*T*, *D*	4
66, 71	*Leptospermum myrsinoides* Schldl.	Shrub	34°59′S, 138°40′E	*T*, *D*, N	1
66	*Leptospermum myrsinoides* Schldl.	Shrub	36°06′S, 140°31′E	*T*, *D*, N	1
52	*Lithraea caustica* (Mol.) Hook and Arn.	Shrub	33°30′S, 70°45′W	*T*, *D*	1
12	*Lonchocarpus guatemalensis* Benth.	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
49	*Lonicera maackii* (Rupr.) Herder [3]	Shrub	39°02′N, 84°28′W	*T*, *D*, A, P	3
12	*Lunania mexicana* Brandegee	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
70	*Macairea rufescens* DC.	Tree	1°54′N, 67°03′W	*T*, *D*, N, A	1
40	*Macckia amurensis* Rupr. et Maxim.	Tree	42°58′N, 141°23′E	*T*, *D*, A, P	1
40	*Magnolia obovata* Thunb.	Tree	42°58′N, 141°23′E	*T*, *D*, A, P	1
66, 71	*Melaleuca lanceolata* R. Baker	Shrub	33°55′S, 147°12′E	*T*, *D*, N	2
66	*Melaleuca sieberi* Schauer	Shrub	26°21′S, 153°00′E	*T*, *D*, N	1
44	*Monstera adansonii* Schott.[14]	Woody vine	10°28′N, 84°02′W	*T*, *D*, A	2
76	*Mora excelsa* Bentham[3]	Tree	5°13′N, 58°48′W	*T*, *D*, A	1
76	*Mora gonggrijpii* (Kleinhoonte) Sandwith [3]	Tree	5°13′N, 58°48′W	*T*, *D*, A	1
12	*Mortoniodendron guatemalense* Standl. & Steyerm.	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
20	*Morus alba* L.	Tree	38°14′N, 23°48′E	*T*, *D*	1
53	*Myrica faya* Ait.	Tree	28°27′N, 16°24′W	*T*, *D*	11
12	*Myriocarpa longipes* Liebm.	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
20	*Myrtus communis* L.	Shrub	38°14′N, 23°48′E	*T*, *D*, A	1
20	*Nerium oleander* L.	Shrub	37°58′N, 23°45′E	*T*, *D*, A	1
39	*Nothofagus menziesii* (Hook f.) Oerst.	Tree	44°38′S, 169°01′E	*T*, *D*, N, A	4
70	*Ocotea esmeraldana* Moldenke	Tree	1°54′N, 67°03′W	*T*, *D*, N, A	1
20	*Olea europea* L.	Tree	38°14′N, 23°48′E	*T*, *D*, A	1
12	*Omphalea oleifera* Hemsl.	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
12	*Orthion oblanceolatum* Lundell	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
40	*Ostrya japonica* Sarg.	Tree	42°58′N, 141°23′E	*T*, *D*, A, P	1
4	*Ostrya virginiana* (Mill.) K. Koch	Tree	43°33′N, 89°27′W	*T*, *D*	1
43	*Parkia javanica* (Lamk.) Merr. [3]	Tree	3°9′N, 101°43′E	*T*, *D*	5
60	*Pentaclethra macroloba* (Willd.) Kuntze[3,7]	Tree	10°28′N, 84°02′W	*T*, *D*	4
59, 61	*Pentaclethra macroloba* (Willd.) Kuntze	Tree	10°28′N, 84°02′W	*T*, *D*, P	6
53	*Persea indica* (L.) Spreng.	Tree	28°27′N, 16°24′W	*T*, *D*	10
20	*Phillyrea media* L.	Shrub	38°14′N, 23°48′E	*T*, *D*, A	1
9	*Philodendron scandens* Koch & Sell[3,5,17]	Shrub	41°30′N, 2°6′E	*T*, *D*, N, A	1
66, 71	*Phyllota remota* J. H. Willis	Shrub	36°06′S, 140°31′E	*T*, *D*, N	1
12	*Piper amalugo* L.	Shrub	18°35′N, 95°07′W	*T*, *D*, N, A	1
19	*Piper arieianum* C. DC.[3]	Shrub	10°26′N, 83°59′W	*T*, *D*, N, A, P	1
12	*Piper auritum* H. B. K.	Shrub	18°35′N, 95°07′W	*T*, *D*, N, A	1
12	*Piper hispidum* Sw.	Shrub	18°35′N, 95°07′W	*T*, *D*, N, A	1
19	*Piper sancti-felicis* Trel. [3]	Shrub	10°26′N, 83°59′W	*T*, *D*, N, A, P	1

1B. Broad-leaved species (*cont.*)

Citation	Species	Life form	Sample location	Variables analysed	*n*
20	*Pistacia lentiscus* L.	Shrub	38°14′N, 23°48′E	*T*, *D*, A	1
20	*Pistacia terebinthus* L.	Shrub	38°14′N, 23°48′E	*T*, *D*	1
20	*Platanus orientalis* L.	Tree	38°14′N, 23°48′E	*T*, *D*	1
12	*Pleuranthodendron lindenii* (Turcz.) Sleumer	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
4	*Populus deltoides* Marsh.	Tree	43°33′N, 89°27′W	*T*, *D*	2
20	*Populus deltoides* Marsh.	Tree	38°14′N, 23°48′E	*T*, *D*	1
4	*Populus grandidentata* Michx.	Tree	43°33′N, 89°27′W	*T*, *D*	2
8	*Populus grandidentata* Michx.	Tree	40°49′N, 77°56′W	*T*, *D*, N, P	2
40	*Populus maximowiczii* A. Henry	Tree	42°58′N, 141°23′E	*T*, *D*, A, P	1
40	*Populus sieboldii* Miq.	Tree	42°58′N, 141°23′E	*T*, *D*, A, P	1
4	*Populus tremuloides* Michx.	Tree	43°33′N, 89°27′W	*T*, *D*	2
12	*Poulsenia armata* (Mig.) Standl.	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
12	*Pouteria durlandii* (Standl.) Baehni	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
12	*Pouteria* sp.	Shrub	18°35′N, 95°07′W	*T*, *D*, N, A	1
50	*Protea arborea* Houttuyn.	Shrub	33°59′S, 19°44′E	*T*, *D*, N, A	1
52	*Proustia cinerea* Phil.	Shrub	33°30′S, 70°45′W	*T*, *D*	1
6	*Prunus pensylvanica* L. f.	Tree	40°48′N, 77°51′W	*T*, *D*	1
40	*Prunus sargentii* Rehd.	Tree	42°58′N, 141°23′E	*T*, *D*, A, P	1
3	*Prunus serotina* Ehrh.^{3,5}	Tree	40°48′N, 77°52′W	*T*, *D*, P	4
4	*Prunus serotina* Ehrh.	Tree	43°33′N, 89°27′W	*T*, *D*	2
6	*Prunus serotina* Ehrh.	Tree	40°48′N, 77°51′W	*T*, *D*	1
8	*Prunus serotina* Ehrh.	Tree	40°49′N, 77°56′W	*T*, *D*, N, P	2
40	*Prunus ssiori* Fr. Schn.	Tree	42°58′N, 141°23′E	*T*, *D*, A, P	1
4	*Prunus virginiana* L.	Tree	43°33′N, 89°27′W	*T*, *D*	2
12	*Pseudolmedia oxyphyllaria* Donn. Sm.	Shrub	18°35′N, 95°07′W	*T*, *D*, N, A	1
12	*Psychotria faxlucens* Lorence & Dwyer	Shrub	18°35′N, 95°07′W	*T*, *D*, N, A	1
12	*Psychotria flava* Oerst. & Standl.	Shrub	18°35′N, 95°07′W	*T*, *D*, N, A	1
12	*Psychotria simiarum* Standl.	Shrub	18°35′N, 95°07′W	*T*, *D*, N, A	1
12	*Pterocarpus rohrii* Vahl.	Shrub	18°35′N, 95°07′W	*T*, *D*, N, A	1
66	*Pultenaea myrtoides* Benth.	Shrub	26°21′S, 153°00′E	*T*, *D*, N	1
20	*Pyrus communis* L.	Tree	38°14′N, 23°48′E	*T*, *D*	1
83	94 *Pyrus* cultivars	Tree	38°14′N, 139°50′E	*T*, *D*	1
12	*Quararibea guatemalteca* (Donn. Sm.) Standl.	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
4	*Quercus alba* L.	Tree	43°33′N, 89°27′W	*T*, *D*	2
18	*Quercus coccifera* L.	Shrub	42°18′N, 1°27′W	*T*, *D*, N	1
20	*Quercus coccifera* L.	Shrub	38°14′N, 23°48′E	*T*, *D*, A	1
17	*Quercus copeyensis* C. H. Muller	Tree	9°34′N, 83°41′W	*T*, *D*	2
17	*Quercus costaricensis* Liebm.	Tree	9°34′N, 83°41′W	*T*, *D*	2
4	*Quercus ellipsoidalis* E. J. Hill	Tree	43°33′N, 89°27′W	*T*, *D*	2
18	*Quercus faginea* Lam.	Tree	42°18′N, 1°27′W	*T*, *D*, N	1
75	*Quercus ilex* L.	Tree	41°46′N, 2°24′E	*T*, *D*	2
18	*Quercus ilex* L.	Tree	42°18′N, 1°27′W	*T*, *D*, N	1
20	*Quercus ilex* L.	Shrub	38°14′N, 23°48′E	*T*, *D*, A	1
30	*Quercus ilex* L.	Tree	42°46′N, 11°6′E	*T*, *D*	4
4	*Quercus macrocarpa* Michx.	Tree	43°33′N, 89°27′W	*T*, *D*	2
6	*Quercus macrocarpa* Michx.	Tree	40°48′N, 77°51′W	*T*, *D*	1
40	*Quercus mongolica* Fisch.	Tree	42°58′N, 141°23′E	*T*, *D*, A, P	1
37, 38	*Quercus prinus* L.	Tree	40°49′N, 77°56′W	*T*, *D*, P	2
46	*Quercus pyrenaica* Willd.	Tree	41°7′N, 5°48′W	*T*, *D*, N, A, P	1
25	*Quercus robur* L.	Tree	50°30′N, 37°56′E	*T*, *D*, A	2
46	*Quercus rotundifolia* Lam.	Tree	41°7′N, 5°48′W	*T*, *D*, N, P	3
41	*Quercus rubra* L.^{3,5}	Tree	40°48′N, 77°52′W	*T*, *D*, P	2
4	*Quercus rubra* L.	Tree	43°33′N, 89°27′W	*T*, *D*	2
11	*Quercus sessiliflora* Salisb.	Tree	48°46′N, 6°17′E	*T*, *D*, A	4
21	*Quercus suber* L.^{3,5}	Tree	38°48′N, 9°16′W	*T*, *D*	2
4	*Quercus velutina* Lam.	Tree	43°33′N, 89°27′W	*T*, *D*	2
6	*Quercus velutina* Lam.	Tree	40°48′N, 77°51′W	*T*, *D*	1
37, 38	*Quercus velutina* Lam.	Tree	40°49′N, 77°56′W	*T*, *D*, P	2
70	*Remijia morilloi* Steyerm.	Tree	1°54′N, 67°03′W	*T*, *D*, N	1
70	*Retiniphyllum concolor* (Spruce ex Benth.) Muell. Arg.	Tree	1°54′N, 67°03′W	*T*, *D*, N, A	1
68	*Rhododendron catawbiense* Michx.	Shrub	39°18′N, 76°38′W	*T*, *D*	1
68	*Rhododendron indicum* Sweet	Shrub	39°18′N, 76°38′W	*T*, *D*	1
68	*Rhododendron myrtifolium* Lodd.	Shrub	39°18′N, 76°38′W	*T*, *D*	1
68	*Rhododendron nudiflorum* Torr.	Shrub	39°18′N, 76°38′W	*T*, *D*	1

1B. Broad-leaved species (*cont.*)

Citation	Species	Life form	Sample location	Variables analysed	*n*
68	*Rhododendron viscosum* Torr.	Shrub	39°18′N, 76°38′W	*T*, *D*	1
50, 70	*Rhodognaphalopsis discolor* A. Robyns	Tree	1°54′N, 67°03′W	*T*, *D*, N	2
4	*Robinia pseudacacia* L.	Tree	43°33′N, 89°27′W	*T*, *D*	2
12	*Robinsonella mirandae* Gomez-Pompa	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
40	*Salix hultenii* Floderus	Tree	42°58′N, 141°23′E	*T*, *D*, A, P	1
12	*Sapranthus microcarpus* (Donn. Sm.) R. E. Fr.	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
6	*Sassafras albidum* (Nutt.) Nees	Tree	40°48′N, 77°51′W	*T*, *D*	1
37, 38	*Sassafras albidum* (Nutt.) Nees	Tree	40°49′N, 77°56′W	*T*, *D*, P	2
10	*Scheelea zonensis* Bailey	Palm	9°10′N, 79°51′W	*T*, *D*, A	2
17	*Schefflera rodriguesiana* Frodin	Tree	9°34′N, 83°41′W	*T*, *D*	2
43	*Shorea singkawang* (Miq.) Burch [3]	Tree	3°9′N, 101°43′E	*T*, *D*	5
43	*Sindora echinocalyx* (Benth.) Prain [3]	Tree	3°9′N, 101°43′E	*T*, *D*	5
10	*Socratea exorrhiza* (Martinus) H. A. Wendland	Palm	9°10′N, 79°51′W	*T*, *D*, A	2
40	*Sorbus alnifolia* C. Koch	Tree	42°58′N, 141°23′E	*T*, *D*, A, P	1
40	*Sorbus commixta* Hedl.	Tree	42°58′N, 141°23′E	*T*, *D*, A, P	1
86	*Souroubea sympetala* Gilg.	Hemiepiphyte	9°10′N, 79°51′W	*T*, *D*, N	1
12	*Spondias radlkoferi* Donn. Sm.	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
80	*Spyridium globulosum* (Labill.) Benth.	Shrub	33°57′S, 120°07′E	*T*, *D*	1
66	*Spyridium subochreatum* Reisseck	Shrub	36°06′S, 140°31′E	*T*, *D*, N	1
12	*Stemmadenia donnell-smithii* (Rose) Woodson	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
44	*Syngonium rayii* Croat & Grayum	Woody vine	10°28′N, 84°02′W	*T*, *D*, A	2
4	*Tilia americana* L.	Tree	43°33′N, 89°27′W	*T*, *D*	2
6	*Tilia americana* L.	Tree	40°48′N, 77°51′W	*T*, *D*	1
25	*Tilia cordata* Mill.	Tree	50°30′N, 37°56′E	*T*, *D*, A	2
40	*Tilia japonica* Simonkai	Tree	42°58′N, 141°23′E	*T*, *D*, A, P	1
40	*Tilia maximowicziana* Shrisawa	Tree	42°58′N, 141°23′E	*T*, *D*, A, P	1
12	*Trema micrantha* L. Blume	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
12	*Trichilia martiana* C. DC.	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
12	*Trichospermum mexicanum* (DC.) Baill.	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
12	*Trophis mexicana* (Liebm.) Bur.	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
12	*Turpinia occidentalis* (Swartz) G. Don	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
40	*Ulmus davidiana* Planch var. *japonica* Nakai	Tree	42°58′N, 141°23′E	*T*, *D*, A, P	1
40	*Ulmus laciniata* Mayy.	Tree	42°58′N, 141°23′E	*T*, *D*, A, P	1
4	*Ulmus rubra* Muhl.	Tree	43°33′N, 89°27′W	*T*, *D*	2
6	*Ulmus rubra* Muhl.	Tree	40°48′N, 77°51′W	*T*, *D*	1
25	*Ulmus scabra* Mill.	Tree	50°30′N, 37°56′E	*T*, *D*, A	3
89	*Uncaria tomentosa* (Willd.) DC	Woody vine	9°10′N, 79°51′W	*T*, *D*, N, P	1
12	*Urera elata* (Sw.) Griseb.	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
17	*Vaccinium consanguineum* Klotzch	Tree	9°34′N, 83°41′W	*T*, *D*	2
82	*Vaccinium myrtillus* L.	Shrub	56°25′N, 6°1′W	*T*, *D*, N, P	3
12	*Vatairea lundellii* (Standl.) Killip	Shrub	18°35′N, 95°07′W	*T*, *D*, N, A	1
12	*Vochysia guatemalensis* (Donn.) Smith	Shrub	18°35′N, 95°07′W	*T*, *D*, N, A	1
17	*Weinmannia pinnata* L.	Tree	9°34′N, 83°41′W	*T*, *D*	1
12	*Zanthoxylum kellermanii* P. Wilson	Tree	18°35′N, 95°07′W	*T*, *D*, N, A	1
6	6 mesic species	Tree	40°48′N, 77°51′W	*T*, *D*, P	1
6	6 wet-mesic species	Tree	40°48′N, 77°51′W	*T*, *D*, P	1
6	5 xerix species	Tree	40°48′N, 77°51′W	*T*, *D*, P	1

[1] Cross-section geometry (cf. 33) was approximated by circle or ellipsoid (C, terete-leaved species), rhomb (R), sector (K), segment (S) or triangle (T); [2] Data available for leaf thickness (*T*), density (*D*), volume to total leaf area ratio (V/A_T), nitrogen content (N), photosynthesis (P) or for several other leaf anatomical variables (A, e.g., the fractional investments of leaf in various tissues). Data for leaf dry mass per area were available in all studies, and whenever not directly reported in the original study, *D* was calculated from leaf dry mass per area and *T*; [3] Seedlings; [4] Seedlings and adult plants; [5] Plants grown in a naturally lit greenhouse; [6] seeds obtained from a native stand at Eneabba, Western Australia, 29°53′S, 115°17′E); [7] Plants grown in a growth chamber at constant environmental conditions; [8] seeds from Bangladesh; [9] C_4species; [10] native to Japan; [11] native to Burma and India; [12] seeds from 18°22′N, 66°37′W; [13] seeds from 33°57′S 120°07′E; [14] seedlings and adult plants; [15] seeds from Hawaii (20–22°N, 157–159°W); [16] native to Caribbean Islands; [17] native to E-Mexico.

Appendix 2. References to the data used in the analysis

2A. Works providing information on leaf density, thickness, nitrogen and photosynthesis (Appendix 1)

1. **Abrams MD. 1986.** *Canadian Journal of Forest Research* **16**: 1170–1174.
2. **Abrams MD. 1988.** *Forest Science* **34**: 200–207.
3. **Abrams MD, Kloeppel BD, Kubiske ME. 1992.** *Tree Physiology* **10**: 343–355.
4. **Abrams MD, Kubiske ME. 1990.** *Forest Ecology and Management* **31**: 245–253.
5. **Abrams MD, Kubiske ME. 1990.** *Functional Ecology* **4**: 727–733.
6. **Abrams MD, Kubiske ME, Mostoller SA. 1994.** *Ecology* **75**: 123–133.
7. **Abrams MD, Kubiske ME, Steiner KC. 1990.** *Tree Physiology* **6**: 305–315.
8. **Abrams MD, Mostoller SA. 1995.** *Tree Physiology* **15**: 361–370.
9. **Araus JL, Alegre L, Tapia L, Calafell R, Serret MD. 1986.** *American Journal of Botany* **73**: 1760–1770.
10. **Araus JL, Hogan KP. 1994.** *American Journal of Botany* **81**: 726–738.
11. **Aussenac G, Ducrey M. 1977.** *Annales des Sciences Forestières* **34**: 265–284.
12. **Bongers F, Popma J. 1990.** *Botanical Gazette* **151**: 354–365.
13. **Bongers F, Popma J, Iriarte-Vivar S. 1988.** *Functional Ecology* **2**: 379–390.
14. **Brewer JF, Hinesley LE, Snelling LK. 1992.** *HortScience* **27**: 920–925.
15. **Bussotti F, Bottacci A, Bartolesi A, Grossoni P, Tani C. 1995.** *Environmental and Experimental Botany* **35**: 201–213.
16. **Bussotti F, Grossoni P, Bottacci A. 1997.** *Forestry* **70**: 267–271.
17. **Camacho M, Bellefleur P. 1996.** *Revista de Biologia Tropical* **44**: 71–79.
18. **Castro-Díez P, Villar-Salvador P, Pérez-Rontomé C, Maestro-Martínez M, Montserrat-Martí G. 1997.** *Trees: Structure and Function* **11**: 127–134.
19. **Chazdon RL, Kaufmann S. 1993.** *Functional Ecology* **7**: 385–394.
20. **Christodoulakis NS, Mitrakos KA. 1987.** In: Tenhunen JD, Catarino FM, Lange OL, Oechel WC, eds. *Plant response to stress. Functional analysis in Mediterranean ecosystems*. Berlin: Springer-Verlag. 547–551.
21. **Faria T, Wilkins D, Besford RT, Vaz M, Pereira JS, Chaves MM. 1996.** *Journal of Experimental Botany* **47**: 1755–1761.
22. **Fetcher N, Strain BR, Oberbauer SF. 1983.** *Oecologia* **58**: 314–319.
23. **Fisher JB. 1986.** *Botanical Gazette* **147**: 84–89.
24. **García-Núñez C, Azócar A, Rada F. 1995.** *Trees: Structure and Function* **10**: 114–124.
25. **Goryshina TK, Zabotina LN, Pruzhina EG. 1979.** *Vestnik Leningradskogo Gosudarstvennogo Universiteta, ser. Biologiya* **3**: 67–76.
26. **Gries C, Lösch R, Kappen L. 1987.** In: Steubing L, ed. *Verhandlungen der Gesellschaft für Ökologie*. Göttingen: Gesellschaft für Ökologie. 227–230.
27. **Groom PK, Lamont BB. 1997.** *The New Phytologist* **136**: 231–237.
28. **Groom PK, Lamont BB, Kupsky L. 1994.** *Australian Journal of Botany* **42**: 307–320.
29. **Groom PK, Lamont BB, Markey AS. 1997.** *Australian Journal of Botany* **45**: 827–838.
30. **Grossoni P, Bussotti F, Tani C, Gravano E, Santarelli S, Bottacci A. 1998.** *Chemosphere* **36**: 919–924.
31. **Holbrook NM, Putz FE. 1996.** *Plant, Cell and Environment* **19**: 631–642.
32. **Johnson JD, Zedaker SM, Hairston AB. 1985.** *Forest Science* **31**: 891–898.
33. **Jordan DN, Smith WK. 1993.** *Tree Physiology* **13**: 29–39.
34. **Kamaluddin M, Grace J. 1993.** *Tree Physiology* **13**: 189–201.
35. **Kimura K, Ishida A, Uemura A, Matsumoto Y, Terashima I. 1998.** *Tree Physiology* **18**: 459–466.
36. **Kloeppel BD, Abrams MD. 1995.** *Tree Physiology* **15**: 739–746.
37. **Kloeppel BD, Abrams MD, Kubiske ME. 1993.** *Canadian Journal of Forest Research* **23**: 181–189.
38. **Kloeppel BD, Kubiske ME, Abrams MD. 1994.** *International Journal of Plant Sciences* **155**: 73–79.
39. **Körner C, Bannister P, Mark AF. 1986.** *Oecologia* **69**: 577–588.
40. **Koike T. 1988.** *Plant Species Biology* **3**: 77–87.
41. **Kubiske ME, Abrams MD. 1992.** *Canadian Journal of Forest Research* **22**: 1402–1407.
42. **Lee DW. 1988.** *Journal of Tropical Ecology* **4**: 281–292.
43. **Lee DW, Krishnapilay B, Mansor M, Mohamad H, Yap SK. 1996.** *Ecology* **77**: 568–580.
44. **Lee DW, Richards JH. 1991.** In: Mooney HA, Putz FH, eds. *The biology of vines*. New York: Cambridge University Press. 205–243.
45. **Lei TT, Lechowicz MJ. 1990.** *Oecologia* **84**: 224–228.
46. **Leßner A. 1994.** Die Beziehung zwischen Gaswechsel, Blattdemographie und Stickstoffhaushalt an immer- und wechselgrühnen mediterranen Holzgewächsen. Diploma Thesis, Fakultät für Biologie, Chemie und Geowissenschaften der Universität Bayreuth. 92 p.
47. **Lichtenthaler HK. 1981.** In: Akoyunoglou G, ed. *Photosynthesis and productivity, photosynthesis and environment*. Philadelphia: Balaban International Science Services. 273–287.
48. **Lichtenthaler HK, Buschmann C, Döll M, Fietz H-J, Bach T, Kozel U, Meier D, Rahmsdorf U. 1981.** *Photosynthesis Research* **2**: 115–141.
49. **Luken JO, Tholemeier TC, Kuddes LM, Kunkel BA. 1995.** *Canadian Journal of Botany* **73**: 1953–1961.
50. **Medina E. 1981.** *Nitrogen content, leaf structure and photosynthesis in higher plants. A report to the United Nations Environmental Program study group on Photosynthesis and Bioproductivity*. Caracas: Instituto Venezolano de Investigaciones Cientificas.
51. **Messier C, Mitchell AK. 1994.** *Forest Ecology and Management* **68**: 263–271.
52. **Mooney HA, Kummerow J. 1971.** *Botanical Gazette* **132**: 245–252.
53. **Morales D, Gonzalez-Rodriguez AM, Čermák J, Jimenez MS. 1996.** *Phyton – Annales Rei Botanicae* **36**: 251–263.
54. **Niinemets Ü. 1988.** Specific leaf area (SLA) of Estonian woody species. Manuscript at ENSV TA Zooloogia ja Botaanika Instituut. Tartu.
55. **Niinemets Ü. 1997.** *Tree Physiology* **17**: 723–732.
56. **Niinemets Ü. 1997.** *Trees: Structure and Function* **11**: 144–154.

57. **Niinemets U, Kull O. 1995.** *Tree Physiology* **15**: 307–315.
58. **Nygren M, Kellomäki S. 1983–1984.** *Forest Ecology and Management* **7**: 119–132.
59. **Oberbauer SF, Strain BR. 1985.** *Journal of Tropical Ecology* **1**: 303–320.
60. **Oberbauer SF, Strain BR. 1986.** *American Journal of Botany* **73**: 409–416.
61. **Oberbauer SF, Strain BR, Riechers GH. 1987.** *Oecologia* **71**: 369–374.
62. **Pääkkönen E, Holopainen T. 1995.** *The New Phytologist* **129**: 595–603.
63. **Pearcy RW, Osteryoung K, Randall D. 1982.** *Oecologia* **55**: 333–341.
64. **Perterer J, Körner C. 1990.** *Forstwissenschaftliches Centralblatt* **109**: 220–241.
65. **Roberts DA, Nelson BW, Adams JB, Palmer F. 1998.** *Trees: Structure and Function* **12**: 315–325.
66. **Rundel PW, Specht RL, Hopkins AJM, Montenegro G, Margaris NS. 1988.** In: Specht RL, ed. *Mediterranean-type ecosystems. A data source book.* Dordrecht: Kluwer Academic Publishers. 63–80.
67. **Sarracino JM, Merritt R, Chin CK. 1992.** *HortScience* **27**: 400–403.
68. **Schratz E. 1932.** *Planta* **16**: 17–69.
69. **Shelton MG, Switzer GL. 1984.** *Forest Science* **30**: 355–363.
70. **Sobrado MA, Medina E. 1980.** *Oecologia* **45**: 341–345.
71. **Specht RL, Rundel PW. 1990.** *Australian Journal of Botany* **38**: 459–474.
72. **Steele MJ, Coutts MP, Yeoman MM. 1989.** *The New Phytologist* **113**: 367–375.
73. **Syvertsen JP. 1984.** *Journal of the American Society for Horticultural Science* **109**: 812–817.
74. **Syvertsen JP, Smith ML Jr. 1984.** *Journal of the American Society for Horticultural Science* **109**: 807–812.
75. **Terradas J, Savé R. 1992.** *Vegetatio* **99–100**: 137–145.
76. **ter Steege H. 1994.** *Oecologia* **100**: 356–367.
77. **Tognetti R, Minotta G, Pinzauti S, Michelozzi M, Borghetti M. 1998.** *Trees: Structure and Function* **12**: 326–333.
78. **Tucker GF, Emmingham WH. 1977.** *Forest Science* **23**: 195–203.
79. **Vidal D, Griera E, Marin P, Sabido J. 1990.** *American Journal of Botany* **77**: 1149–1158.
80. **Witkowski ETF, Lamont BB. 1991.** *Oecologia* **88**: 486–493.
81. **Witkowski ETF, Lamont BB, Walton CS, Radford S. 1992.** *Australian Journal of Botany* **40**: 849–862.
82. **Woodward FI. 1986.** *Oecologia* **70**: 580–586.
83. **Yamamoto T, Itoh H, Nobori H, Sasaki H. 1997.** *Journal of the Japanese Society of Horticultural Science* **66**: 45–57.
84. **Young DR, Yavitt JB. 1987.** *American Journal of Botany* **74**: 1487–1491.
85. **Zhelawski W, Kinelska G, Lotocki A. 1968.** *Acta Societatis Botanicorum Poloniae* **37**: 505–518.
86. **Zotz G, Patiño S, Tyree MT. 1997.** *Flora* **192**: 143–150.
87. **Zotz G, Tyree MT, Patiño S. 1997.** *Tree Physiology* **17**: 359–365.
88. **Zotz G, Tyree MT, Patiño S, Carlton MR. 1998.** *Trees*: *Structure and Function* **12**: 302–309.
89. **Zotz G, Winter K. 1996.** In: Mulkey SS, Chazdon RL, Smith AP, eds. *Tropical forest plant ecophysiology*. New York: Chapman & Hall. 89–113.

2B. Additional studies used to develop the correlations between leaf thickness and foliar anatomy (Fig. 3e–h)

1. **Ashton PMS, Berlyn GP. 1994.** *American Journal of Botany* **81**: 589–597. (3 species)
2. **Aussenac G. 1973.** *Annales des Sciences Forestières* **30**: 375–392. (3 species)
3. **Boeger MRT, Alves de Brito CJF, Negrelle RRB. 1997.** *Arquivos de Biologia e Tecnologia* **40**: 493–503. (7 species)
4. **Bostrack JM. 1993.** *Annals of Botany* **72**: 341–347. (4 species)
5. **Choong MF. 1996.** *Functional Ecology* **10**: 668–674. (1 species)
6. **Cooper WS. 1922.** *Carnegie Institution of Washington Publications* **319**: 1–127. (33 species)
7. **Cormack RGH, Gorham AL. 1953.** *Canadian Journal of Botany* **31**: 537–541. (2 species)
8. **Day JS, Gould KS, Jameson PE. 1997.** *Annals of Botany* **79**: 617–624. (1 species)
9. **Dean TJ, Pallardy SG, Cox GS. 1982.** *Canadian Journal of Forest Research* **12**: 725–730. (1 species)
10. **De Lillis M, Valletta A. 1985.** *Annali di Botanica* **43**: 209–225. (21 species)
11. **Dzyarugina TF, Luchkoi AI. 1987.** *Bestsi AN BSSR. Ser. Biyal. N.* **5**: 18–23. (9 species)
12. **Hunt JE, Kelliher FM, McNeil DL. 1996.** *New Zealand Journal of Botany* **34**: 401–410. (5 species)
13. **Körner C, Pelaez Menendez-Riedl S. 1990.** In: Lambers H, Cambridge ML, Konings H, Pons TL, eds. *Causes and consequences of variation in growth rate and productivity of higher plants*. The Hague: SPB Academic Publishing. 141–157. (1 species)
14. **Kovalyev AG. 1980.** *Lesovedeniye* **6**: 30–35. (1 species)
15. **Krause D, Kummerow J. 1977.** *Acta Oecologica/Oecologia Plantarum* **12**: 133–148. (4 species)
16. **Leal ME, Kappelle M. 1994.** *Revista de Biologia Tropical* **42**: 473–478. (32 species)
17. **Luken JO, Tholemeier TC, Kuddes LM, Kunkel BA. 1995.** *Canadian Journal of Botany* **73**: 1953–1961. (2 species)
18. **Luken JO, Kuddes LM, Tholemeier TC, Haller DM. 1997.** *The American Midland Naturalist* **138**: 331–343. (1 species)
19. **McLaughlin SB, Madgwick HAI. 1968.** *The American Midland Naturalist* **80**: 547–550. (1 species)
20. **Oláh R, Masarovičová, Shamaj J, Ovečá M, Bobák M, Krishtín J, Egedová V. 1997.** *Biologia Plantarum* **39**: 271–280. (1 species)
21. **Pääkkönen E, Holopainen T, Kärenlampi L. 1995.** *Annals of Botany* **75**: 285–294. (1 species)
22. **Philpott J. 1956.** *Botanical Gazette* **118**: 88–105. (25 species)
23. **Powers HO. 1967.** *The American Midland Naturalist* **78**: 301–323. (43 species)
24. **Pyykkö M. 1966.** *Annales Botanici Fennici* **3**: 453–622. (111 species)
25. **Riveros F, Hoffmann A, Avila G, Aljaro ME, Araya S, Hoffmann AE, Montenegro G. 1976.** *Flora* **165**: 223–234. (2 species)
26. **Rôças G, Barros CF, Scarano FR. 1997.** *Trees: Structure and Function* **11**: 469–473. (1 species)
27. **Schramm R. 1912.** *Flora* **4**: 225–295. (11 species)
28. **Schulz S. 1984.** Anatomisch-morphologische Untersuchungen an Blättern immergrüner Arten der Mediterranean Hartlaubformation. Diploma Thesis, Universität Würzburg. 143 p. (5 species)

29. **Smith WK, Nobel PS. 1978.** *American Journal of Botany* **65**: 429–432. (1 species)
30. **Stover EL. 1944.** *Botanical Gazette* **106**: 12–25. (3 species)
31. **Wylie RB. 1949.** *Proceedings Iowa Academy of Science* **56**: 189–198. (1 species)
32. **Wylie RB. 1951.** *American Journal of Botany* **38**: 355–361. (10 species)