

Leaf traits as indicators of resource-use strategy in floras with succulent species

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Summary

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- Associations between specific leaf area (SLA), leaf water content (LWC) and leaf thickness (LT) in 77 species were analysed to identify which of these traits gave a better indicator value of general plant resource-use strategy within the flora of central-western Argentina, in which succulent species are common.
- When all species were considered together, SLA and LWC were not significantly correlated. All high-SLA tender-leaved species showed high LWC. Low SLA, however, was associated both with low LWC (sclerophyllous species) and with high LWC (succulents). When succulents were excluded, the association between SLA and LWC was significant and positive. A similar trend was found for a mixed set of non-succulent species from other floras of the world.
- In the Argentine data set, SLA and LT, but not LWC, were significantly correlated with species' scores along a multivariate axis of plant resource-use strategy.
- Because of its clearer ecological interpretation and its applicability across different floras, SLA appears to be the best candidate for inclusion in large comparative databases.

Key words: comparative ecology, leaf thickness, leaf water content, plant functional types, sclerophylly, specific leaf area, succulence.

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Introduction

The identification of recurrent patterns of specialization in plants and the reduction of the enormous diversity of the natural world into a smaller number of categories have long been major foci of interest in comparative plant ecology (Grime *et al.*, 1997; Westoby, 1998). These have converged into the need to identify a small set of key plant traits. These traits should give maximum information on plant growth and resource-use strategy and, at the same time, should be simple enough to measure, so that they can be recorded for large numbers of species (Díaz & Cabido, 1997; Hodgson *et al.*, 1999; Weiher *et al.*, 1999). One of the most widely accepted of such key traits is specific leaf area (SLA), the light-catching area deployed per unit of previously photosynthesized dry mass allocated to the purpose (Westoby, 1998). SLA has been proven to be strongly linked to relative growth rate and resource use (Garnier, 1992; Lambers & Poorter, 1992; Reich,

1993; Garnier & Laurent, 1994; Grime *et al.*, 1997; Poorter & Van der Werf, 1998; Wilson *et al.*, 1999). Grime *et al.* (1997) reported that SLA was one of the major contributors to an axis of resource capture, usage and availability.

Variation in SLA depends on changes in leaf tissue density – or leaf water content (LWC), which is closely correlated with tissue density (Garnier & Laurent, 1994) – and leaf thickness (LT) (Witkowski & Lamont, 1991; Garnier & Laurent, 1994; Shipley, 1995; Cunningham *et al.*, 1999; Pyankov *et al.*, 1999; Wilson *et al.*, 1999). In cool-temperate predominantly herbaceous datasets, the lower SLA of slow-growing species tends to be related more to lower LWC than to higher LT (Dijkstra & Lambers, 1989; Garnier & Laurent, 1994; van Arendonk & Poorter, 1994; Shipley, 1995; Ryser & Aeschlimann, 1999). In datasets dominated by woody perennials, LT has been found to be equally influential (Witkowski & Lamont, 1991; Cunningham *et al.*, 1999; Wright & Cannon, 2001). The leaves of many slow-growing species have

thick epidermal walls and cuticle, abundant sclerification, high cell wall/cytoplasm ratio in tissues, and a high ratio of crude fibre to protein (Loveless, 1961, 1962; Fahn, 1982). In these leaves (sclerophyllous leaves) low SLA is accompanied by low LWC. By contrast, the leaves of fast-growing species (tender leaves) have few cell walls per unit leaf area and a high proportion of their volume is occupied by nitrogen-rich, photosynthetically active mesophyll protoplast. These traits are likely to favour carbon assimilation in fast-growing species (Reich, 1993; Garnier & Laurent, 1994). Shifts from tender to sclerophyllous leaves have been reported along regional productivity gradients. For example, along nutrient and water availability gradients in south-east Australia, SLA and LWC decreased and LT increased with decreasing resource availability (Cunningham *et al.*, 1999).

Wilson *et al.* (1999) have strongly advocated the use of LWC as an indicator of position on an axis of resource use because it is well correlated with SLA, shows less variability between samples, is simpler to measure and does not depend on LT, whose links with plant resource-use strategy are complex. Furthermore, in the British flora, LWC was a better predictor than SLA of position on an independently derived resource-use axis (Hodgson *et al.*, 1999). However, Wilson *et al.* (1999) based their preference for LWC on the study of a flora with very few succulents, and in which sclerophyllous tends to be the most common adaptation to the main source of stress, soil nutrient deficiency. The authors explicitly warn that their conclusions are valid for the flora of Western Europe, but may not necessarily apply to other floras, especially those of arid and semiarid areas in which succulents are common.

Succulents are plants that have thick water-storing tissues in their main photosynthetic organs, so that they can avoid desiccation when the soil is dry. Although some of the most conspicuous families are phylogenetically close (e.g. Cactaceae, Chenopodiaceae, Aizoaceae and Portulacaceae are all in the Order Caryophyllales), succulence appears in several distant clades (Gibson, 1996; The Angiosperm Phylogeny Group, 1998). They are most common in semiarid and arid ecosystems of warm regions (Gibson, 1996; Maberley, 1997). Most succulent species are perennials, have water contents of 90% or greater in a fully hydrated organ, and have crassulacean acid metabolism as the main photosynthetic pathway (Gibson, 1996). Accordingly, their photosynthetic organs consist of chlorenchyma with large, rounded cells that have a large vacuolar storage space for carboxylic acids and water (Larcher, 1995). The presence of such conspicuous vacuoles and large intercellular air spaces results in comparatively few chloroplasts per surface area (Kluge & Ting, 1978). In many succulents, photosynthetic organs also contain an internal, nonphotosynthetic parenchyma, with high capacity for water storage (Gibson, 1996). Consequently, succulent species are expected to have relatively low SLA (obviously high LT) but high LWC. The use of LWC as a predictor of plant functioning is based on the assumption that LWC is linked to leaf

nitrogen content and assimilatory capacity (Reich, 1993; Garnier & Laurent, 1994; Wilson *et al.*, 1999). That may be a wrong assumption in the case of succulents. Interestingly, variations of LWC between slow-growing and fast-growing species have been documented for floras in which succulence is absent or very rare. The analysis of leaf trait variation along a water availability gradient, considering a flora in which succulence is common, thus provides a good test for the universality of LWC as an indicator of plant resource-use strategy.

In this article, we aimed to: analyse the associations among SLA, LWC and LT in the flora of central-western Argentina, in which succulent species are common; to determine which of LWC, SLA or LT has better indicator value for general plant resource-use strategy in that region, and which of these appears to have greater potential for large-scale comparative screening programmes; and to compare the relationships between SLA and LWC in central-western Argentina with those in other regions of the world in which succulents are uncommon (Britain, France, Italy, south-east Canada, south-east Australia and Sri Lanka).

Materials and Methods

Study area

Plant material was collected along a climatic gradient in central-western Argentina (31°25'–32° S, 64°10'–68°37' W), with a difference in annual precipitation of > 800 mm, a difference in mean annual temperature of > 11°C and a difference in altitude of > 1500 m between extreme points. The area stretched from the subhumid high plateaux of the Córdoba Mountains to the western semiarid–arid plains of San Juan. Dry winters and rainfall heavily concentrated to the warm season are characteristic of the whole region (Capitanelli, 1979).

Collection of material

A total of 77 native and cultivated/naturalized angiosperm species were considered (Appendix 1). Native species selection was based on previous studies (Cabido, 1985; Cabido *et al.*, 1989, 1990, 1993). We also considered their abundance along the gradient described above and tried to include a wide range of plant functional types, including succulents.

The cultivated/naturalized species in our data set are succulents of the families Agavaceae, Asphodelaceae and Crassulaceae and thrive around human settlements along the gradient. We divided species into three leaf types: succulent, sclerophyllous and tender-leaved plants. Most authors agree on the main attributes that characterize these three types. Succulents tend to have well-developed water-storing tissues in the main photosynthetic organs (leaves and/or stems) (Font Quer, 1993; Gibson, 1996). Sclerophyllous species are characterized by tough, leathery leaves with moderate to high degree of sclerification, cutinization and/or silicification

(Schulze, 1982; Font Quer, 1993). Tender-leafed species lack both of these specializations. However, there are no precise, quantitative definitions of the three types in the literature. Turner (1994) and Fonseca *et al.* (2000) make clear that, although these leaf types are recognized as syndromes or constellations of traits by most botanists, exact definitions have not been agreed because different elements of the constellation often vary independently. This said, the distinction among these extreme types is usually clear in any given local flora, although transitional cases are not uncommon. In our particular case, we followed the descriptions in published floras and regarded species whose leaves were described as 'succulent' or 'fleshy' as succulents. Species typical of saline habitats, with fleshy leaves, no well-developed water-storing tissues and LWC of at least 65% were also included in this category. Species whose leaves were described as 'tough', 'fibrous' or 'leathery' were regarded as sclerophyllous. Species whose leaves were described as 'tender' or were not described as succulent, fleshy, leathery, fibrous or tough, were regarded as tender-leafed.

All material was collected from the field during the growing season (December–March) of 1998–99, during daytime, but avoiding the hours around noon. We collected separate leaf samples for all traits taken from the same species at the same site, but not necessarily from the same individuals. For each trait, six leaf samples (replicates) were collected from at least six randomly selected sexually mature, apparently healthy individuals of each species. Each replicate was a compound sample of at least four nonsenescent sun leaves. Despite the fact that leaves, petioles and stems are different organs, subjected to different constraints and allocation trade-offs, for practical purposes we considered a 'leaf' as the structure that carries out most of the photosynthesis, thus throughout this paper the term 'leaf' refers to photosynthetic stems, phyllodes, etc., as well as to true leaves. Following Westoby (1998), we considered all structures which are shed at abscission (e.g. petioles) as part of the leaf.

Leaf trait measurements

Leaf water content was measured as a rough indicator of leaf density and was calculated on a fresh mass basis 1-dry mass/fresh mass (1-dm/fm) (Garnier & Laurent, 1994; Shipley, 1995; Cunningham *et al.*, 1999). Trying to achieve full hydration of leaves by saturation, following the recommendations by Wilson *et al.* (1999) and Garnier *et al.* (2001b), proved operationally very difficult for many resinous and succulent xerophytes. Leaves of resinous species tended to expel their resin, making weighing impossible, while it was impossible to prevent succulents rapidly losing turgor. Therefore, full hydration was assured by collecting leaves in the morning immediately after rainfall. Samples were stored in sealed plastic bags (which were moistened in the case of mesophytic species, but not succulent and resinous species) and kept at 4°C in the dark during transport to the laboratory. In most cases, samples were measured on the day of collection. Samples were blotted

dry using tissue paper to remove any surface water and immediately weighed. Samples were then oven dried in paper bags at 70°C for 3 d and reweighed to produce a value for dry mass. Although lack of rehydration can alter the values of LWC and SLA obtained, especially in the case of high-SLA species (Garnier *et al.*, 2001b), in our judgement the errors that could arise from the rehydration of succulent and resinous species were potentially larger.

Some succulents store water in specialized, nonphotosynthetic parenchyma, within photosynthetic organs (Gibson, 1996). It is therefore debatable whether the whole photosynthetic organ or only the green tissue should be considered in the calculation of LWC. In order to account for this, for all those species in which it was possible to differentiate green tissue and inner, nonphotosynthetic, water-storing tissue with a $\times 20$ magnifying glass, we conducted two different measurements: one considering the whole leaf, and the other considering only the photosynthetically active tissue (Appendix 1). The photosynthetically active tissue was separated from the nonphotosynthetic tissue with a scalpel under a $\times 20$ magnifying glass. No distinction was made between water-storing and photosynthetic tissues in nonsucculent species, in which the whole leaf was considered.

The SLA was calculated as m^2 leaf area kg^{-1} dry mass. Samples were kept at 4°C in the dark in nylon bags until measurement. Leaves were then arranged between a white paper and a glass sheet and scanned with a manual scanner. Average leaf area of each replicate was calculated with Optimetrics software (Bioscan Inc., Edmonds, Washington, USA). Compound leaves were treated as a whole, without separating leaflets. Leaves were then oven dried at 70°C to constant mass. To estimate SLA of aphyllous species and some thick-stem succulents, fragments of photosynthetic tissue of known area were dry-weighed.

The LT was measured on the leaf lamina avoiding thick veins, by looking at cross-sectional leaf cuts under the microscope at $\times 3$ and $\times 10$ when necessary. In cylindrical leaves, the diameter was considered. On stem- and leaf-succulent species and aphyllous species, only the thickness of the photosynthetic tissue was measured when the latter was easy to identify in cross-sectional leaf or stem cuts with a magnifying glass.

In order to link SLA, LWC and LT with species resource-use strategy, we considered the score of each species along axis 1 of a Detrended Correspondence Analysis, as reported by Díaz & Cabido (1997). This axis, derived from 24 traits of the 100 most abundant species along a steep climatic gradient, represents a fundamental trade-off between investment in growth and resource acquisition at the lower extreme, and storage and defence at the higher extreme. It is analogous to a similar axis of resource use reported for the UK flora by Grime *et al.* (1997). The axis described by Díaz & Cabido (1997) was strongly and negatively correlated with plant relative growth rate measured under laboratory conditions ($r = -0.599$; $P < 0.001$; F. Vendramini, unpublished). It was also negatively

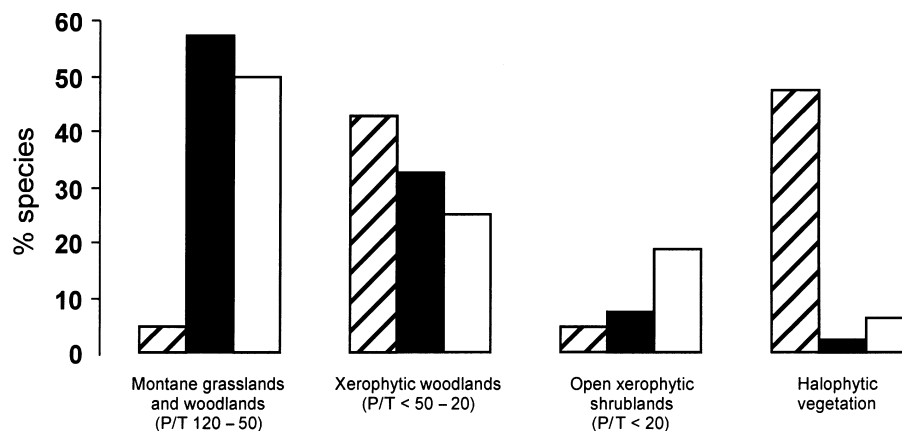


Fig. 1 Distribution of leaf types along a regional climatic gradient. Percentage of species refers to the percentage of species with preferential distribution at a given sector of the regional gradient, out of the total number of species with a certain leaf type considered in this study. Hatched bars, succulent species; solid bars, tender-leaved species; empty bars, sclerophyllous species. P/T, annual precipitation/mean annual temperature (Lang's rain factor). Saline lowlands are scattered across the semiarid–arid portion of the gradient, and soil characteristics exert a much stronger control over plant water balance than precipitation or temperature; therefore P/T values are not informative in this case.

correlated ($r = -0.523$; $P < 0.001$) with water availability at the sector of the regional climatic gradient in which the species were more abundant, as estimated by Lang's rain factor (annual precipitation/annual mean temperature; Lang, 1920). Despite the general negative association between plant resource acquisition rate and water availability, some short-lived, fast-growing plants with high SLA grow in very dry habitats, taking advantage of summer wet pulses, and some succulent and sclerophyllous slow-growing species thrive in stressful habitat patches in mesic environments (e.g. rock crevices, stony grasslands with very shallow soil) (Fig. 1).

Analysis of data

Data were checked for normal distribution and transformed when necessary. LWC, SLA and LT values were ln-transformed. Species' scores along the main resource-use strategy axis (DCA 1) defined by Díaz & Cabido (1997) were not transformed. Pearson's correlation analysis was used to test the relationships between traits, and between traits and resource-use strategy axis (Norušis, 1992).

Other data sources

Information on LWC and SLA in other floras of the world was obtained from unpublished data by P. J. Wilson *et al.* for the UK, and published reports (Gratani & Foti, 1998 for Italy; Shipley, 1995 for south-east Canada; Cunningham *et al.*, 1999 and Roderick *et al.*, 1999 for SE Australia; Garnier *et al.*, 2001a for the Mediterranean region of Southern France; Jayasekera 1992 for Sri Lanka).

We compared observed values of LWC and SLA with those expected on the basis of the Research School of Biological Sciences (RSBS)-model, a generic empirical model proposed by Roderick *et al.* (1999). To obtain a relation between LWC

and SLA, we calculated L_d (dry mass per unit area) and L_q (liquid mass per unit area) from expected values of z (thickness) in the regional flora following the equations $z = 1.50 \times 10^{-6} L_d + 141 \times 10^{-6}$ and $z = 2.27 \times 10^{-6} L_q - 92 \times 10^{-6}$, described by Roderick *et al.* (1999) and modified by Roderick *et al.* (2000b). LWC was calculated as $Q = L_q / (L_d + L_q)$ and SLA was calculated as $1/L_d$.

Results

Leaf water content of photosynthetic and nonphotosynthetic tissues of succulents from central-western Argentina

Not surprisingly, in succulents the photosynthetically active tissue had lower water content than the photosynthetic organ as a whole. However, they were strongly correlated (Fig. 2). Taking a conservative approach, in the case of those succulents in which the two types of tissue could be distinguished, we considered only photosynthetic tissue for the calculation of LWC in this article, whereas we considered the whole leaf in the case of other species. However, Fig. 2 suggests that the effort of separating it from the rest of the leaf may not be justifiable in many cases.

Associations between SLA, LWC and LT

When all species were considered together, SLA and LWC were not significantly correlated (Fig. 3a; Table 1). All high-SLA tender-leaved species showed high LWC (Fig. 3a). Low SLA, however, was associated with both low LWC (sclerophyllous species) and high LWC (succulents). These results did not match the patterns expected on the basis of the generic empirical model of leaf composition and morphology proposed by Roderick *et al.* (1999) (Fig. 3a).

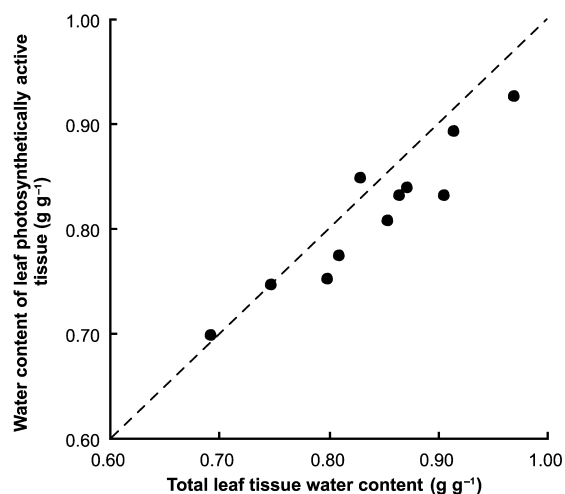


Fig. 2 Association between the water content of the whole photosynthetic organ and that of the photosynthetically active tissue of succulent species ($r = 0.937$; $P < 0.001$). The dashed line represents the 1 : 1 relationship.

When leaf and stem succulent species were excluded from the analysis, the association between SLA and LWC was significant and positive (Table 1). The results also matched more closely the patterns expected on the basis of the Roderick *et al.* (1999) model. SLA values expected from LWC values were significantly correlated with the measured SLA values ($r = 0.518$; $P < 0.001$). A similar trend was found for a mixed set of nonsucculent species from the UK, the Mediterranean region of Southern France, Italy, south-east Canada, south-east Australia and Sri Lanka (Fig. 4a).

When the three leaf types were analysed separately, we found significant and positive associations between SLA and LWC only in the case of tender-leafed species (Table 1).

The LT was significantly and negatively correlated with SLA, regardless the presence of succulent species in the dataset considered (Fig. 3b; Table 1). When different leaf types were analysed separately, this trend was maintained only in the case of sclerophyllous species (Table 1).

The LWC and LT were significantly and positively correlated across the whole dataset (Fig. 3c; Table 1), but this trend was lost when succulent species were excluded from the analysis (Table 1). When different leaf types were considered separately, a significant and positive association was found only in the case of tender-leafed species.

SLA, LWC and LT as predictors of plant position along a resource-use strategy axis

The SLA and LT were significantly correlated with species' scores along the main resource-use strategy axis (DCA 1) defined by Díaz & Cabido (1997) (Table 2). The correlation was negative in the case of SLA and positive in the case of LT. The LWC was not significantly correlated with species position along the resource-use strategy axis.

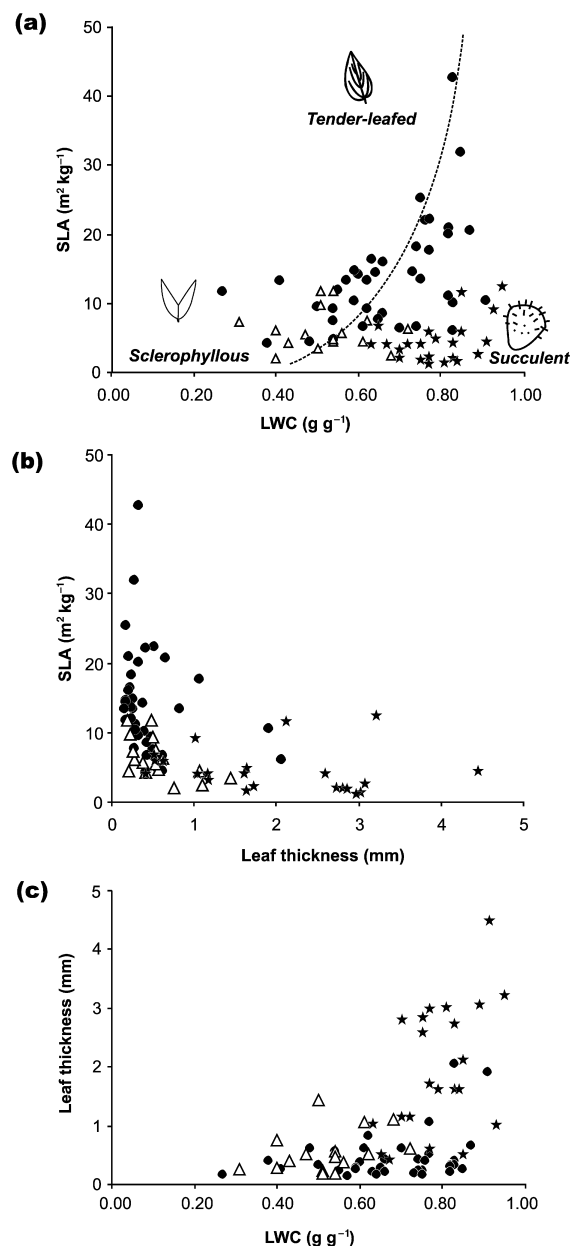


Fig. 3 Associations between specific leaf area (SLA), leaf water content (LWC) and leaf thickness (LT) among angiosperms from central-western Argentina. (a) Association between LWC and SLA ($r = 0.053$; $P = 0.648$). The dashed line shows expected values from the generic empirical model of leaf composition and morphology ('RSBS-model leaf') proposed by Roderick *et al.* (1999, 2000a,b). Expected values of SLA did not correlate with the measured values of SLA ($r = 0.091$; $P = 0.430$). (b) Association between LT and SLA ($r = 0.650$; $P < 0.001$). (c) Association between LWC and LT ($r = 0.463$; $P < 0.001$). Circles, tender-leafed species; triangles, sclerophyllous species; stars, succulent species.

Separate analyses of the three different leaf types (Table 2) showed that SLA was significantly and negatively correlated with DCA 1 in the case of tender-leafed species, but not in the case of sclerophyllous or succulent species. LT was significantly

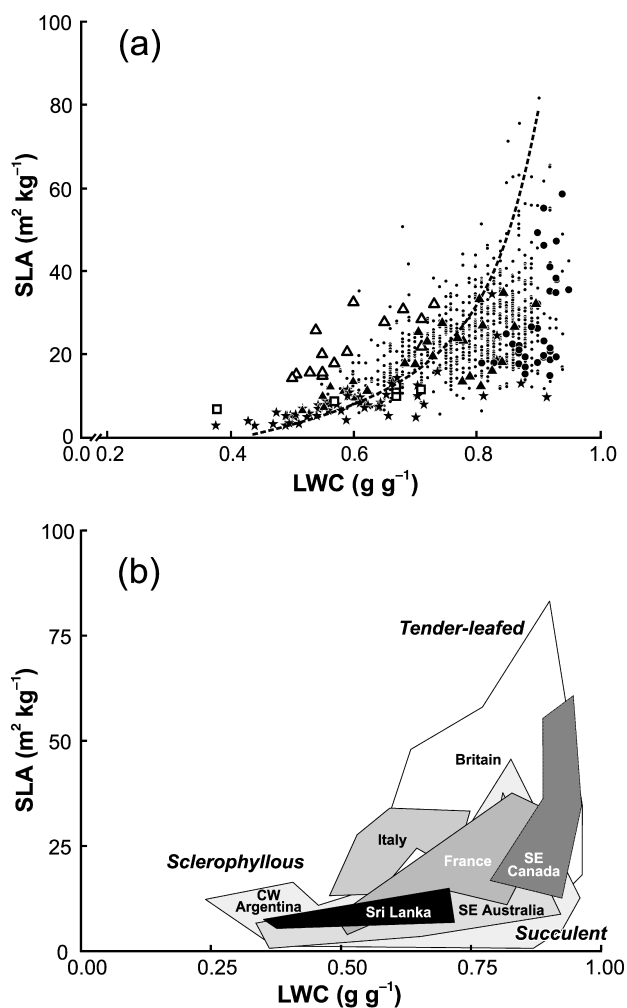


Fig. 4 Relationships between leaf water content (LWC) and specific leaf area (SLA) in different floras. (a) Association between LWC and SLA among nonsucculent species of the UK (Britain) (dots; $r = 0.587$; $P < 0.001$; $n = 768$ herbaceous and woody species; P. J. Wilson *et al.* unpublished), Mediterranean region of Southern France (closed triangles; $r = 0.811$; $P < 0.001$; $n = 17$ herbaceous and woody species; Garnier *et al.*, 2001a), Italy (open triangles; $r = 0.748$; $P < 0.001$; $n = 15$ deciduous broad-leaved woody species; Gratani & Foti, 1998), south-east Canada (circles; $r = 0.505$; $P = 0.002$; $n = 34$ mostly herbaceous species; Shipley, 1995), south-east Australia (stars; $r = 0.80$; $P < 0.001$; $n = 38$ perennial herbaceous and evergreen woody species with a wide range of leaf thickness (LT); Cunningham *et al.*, 1999; Roderick *et al.*, 1999) and Sri Lanka (squares; $r = 0.927$; $P = 0.008$; $n = 6$ woody species; Jayasekera, 1992). Whole dataset: $r = 0.694$; $P < 0.001$; $n = 955$. The dashed line shows expected values from the generic empirical model of leaf composition and morphology ('RSBS-model leaf') proposed by Roderick *et al.*, (1999, 2000a,b). SLA values expected from LWC values were significantly correlated with the measured SLA values in (a) and (b) ($r = 0.518$ and $r = 0.662$, respectively; $P < 0.001$ in both cases). (b) Diagrammatic representation of the range of SLA and LWC of species from central-western Argentina (including succulents, this study), and the six other floras mentioned in (a).

and positively correlated with DCA 1 in the case of succulents, but not in the case of tender-leafed or sclerophyllous species. More importantly, LWC was not correlated with DCA 1 in any of the three leaf types considered individually.

Discussion

In previous studies, slow-growing species with preferential allocation to storage and defence have shown low SLA associated with low water content. This tendency towards increased sclerophylly is common in nutrient-poor soils (Beadle, 1966; Monk, 1966; Small, 1973; Grime *et al.*, 1997) and also in drought-prone environments where succulents are rare (Cunningham *et al.*, 1999). In regions such as central-western Argentina, where the main proximate cause of low productivity is water deficiency, both sclerophylly and succulence are viable solutions, although short-lived tender-leafed species can also thrive if water deficiency is temporarily ameliorated by seasonal or sporadic precipitation. Our results also confirm the idea (Turner, 1994; Fonseca *et al.*, 2000) that, although the three leaf types represent well-defined constellations of traits, readily recognized by field botanists, there are transitional forms, apparent in Fig. 3 (e.g. succulents with very tough epidermis, such as *Agave americana*, or tender-leafed plants with rather thick leaves with a high water content, such as *Eryngium agavifolium* and *Carduus thoermeri*). Thus, objective definitions of the three types cannot be devised. Indeed, a discriminant analysis of our species, based on LT, LWC and SLA, was unable to reliably separate the three types in every case (results not shown).

Succulence and sclerophylly are different ways of dealing with low water availability, with succulents being more dependent on water pulses (Schwinning & Ehleringer, 2001, and references therein). However, they represent converging strategies in terms of carbon assimilation and nutrient conservation: both succulence and sclerophylly are related to preferential allocation to storage and defence, rather than to new growth (Díaz & Cabido, 1997). In the flora of central-western Argentina, both sclerophyllous and succulent species showed low SLA, but this was accompanied by a low LWC in sclerophyllous species and by a high LWC in succulent species. In the latter, high LWC did not directly reflect high content of photosynthetically active cytoplasm, since most of the water contained in the chlorenchyma is vacuolar water (Kluge & Ting, 1978; Larcher, 1995; Gibson, 1996). Water content was high both in high-SLA tender-leafed species (lower end of resource-use strategy axis) and in low-SLA succulents (higher end of the axis). As a consequence, SLA but not LWC was well correlated with the resource-use strategy axis described by Díaz & Cabido (1997). As pointed out by Wilson *et al.* (1999) and confirmed by Garnier *et al.* (2001a), SLA measurements tend to be less reproducible and more difficult to perform than those of LWC. In the British flora, LWC was the best predictor of position on an independently derived

Table 1 Associations between specific leaf area (SLA), leaf water content (LWC) and leaf thickness (LT) considering different subsets of species from central-western Argentina

	SLA-LWC	SLA-LT	LWC-LT
Whole dataset	0.053 (0.648)	-0.650 (< 0.001)	0.463 (< 0.001)
Pair of leaf types			
Sclerophyllous and tender-leafed	0.493 (< 0.001)	-0.455 (< 0.001)	0.185 (0.176)
Succulent and tender-leafed	-0.054 (0.682)	-0.703 (< 0.001)	0.472 (< 0.001)
Sclerophyllous and succulent	-0.191 (0.251)	-0.527 (0.001)	0.718 (< 0.001)
Individual leaf types			
Tender-leafed	0.480 (0.002)	-0.249 (0.126)	0.322 (0.045)
Sclerophyllous	-0.012 (0.964)	-0.563 (0.023)	0.345 (0.190)
Succulent	0.419 (0.059)	-0.190 (0.410)	0.380 (0.089)

Values are Pearson's correlation coefficients, with significance level in parenthesis.

Table 2 Correlations of specific leaf area (SLA), leaf water content (LWC) and leaf thickness (LT) with species scores along a resource-use strategy axis (DCA 1 defined by Díaz & Cabido, 1997)

	SLA	LWC	LT
All dataset	-0.587 (< 0.001)	-0.196 (0.088)	0.558 (< 0.001)
Tender-leafed species	0.356 (0.026)	0.234 (0.152)	0.056 (0.734)
Sclerophyllous species	0.479 (0.060)	0.220 (0.413)	0.480 (0.060)
Succulent species	0.192 (0.405)	0.141 (0.542)	0.484 (0.060)

Values are Pearson's correlation coefficients, with significance level in parenthesis.

resource-use axis (Grime *et al.*, 1997), either alone (for dicots) or combined with SLA (for graminoids; Hodgson *et al.*, 1999). However, our results suggest that SLA, which shows no monotonic association with LWC, appears as a better predictor of a species resource-use strategy than LWC in floras that contain succulent species.

In our data set, LT showed a clear pattern of association with SLA and the resource-use axis. Low-SLA plants, with differential allocation to storage and defence, and more typical of resource-poor habitats (sclerophyllous and succulent plants) tended to have thicker leaves than high-SLA plants with preferential allocation to photosynthesis and growth, more typical of resource-rich habitats (tender-leafed plants). This is in agreement with Cunningham *et al.* (1999), Meziane & Shipley (1999) and Roderick *et al.* (2000a). It can be argued, therefore, that in the case of the Argentine dataset, LT could be as useful as SLA as an indicator of plant resource-use strategy. However, Wilson *et al.* (1999) have suggested a non-monotonic relationship between LT and plant resource-use strategy in the Northern European flora. The LT can vary for reasons related more to light availability than the use of soil resources (Meziane & Shipley, 1999; Wilson *et al.*, 1999; Roderick *et al.*, 2000a), and both fast-growing plants from fertile habitats and slow-growing plants from shaded habitats can have thin leaves. This was not observed in our case, probably because soil resources represent a much stronger limitation to plant growth than the existence of a dense canopy. This suggests that the usefulness of LT as an indicator of resource use can vary from region to region, and for different ecological reasons. The SLA thus appears as a trait with more direct ecological interpretation in comparative studies. The LT may prove useful at a finer-scale analysis, for example in the

distinction between succulence and sclerophylly among low-SLA plants.

Our results did not match the patterns expected on the basis of the generic model linking SLA and LWC developed by Roderick *et al.* (1999, 2000a,b). This is not surprising, since that model was derived from an empirical dataset containing no succulents. When succulents were excluded from the analysis, there was a good association between SLA and LWC, in accordance with Wilson *et al.* (1999). This association was similar to those reported for species sets from the UK, Mediterranean region of southern France, Italy, south-east Australia, south-east Canada and Sri Lanka (Fig. 4b), in which succulents are absent or hardly present. The association between SLA and LWC seems to be particularly strong and consistent in floras where the main cause of stress is soil nutrient content, and in which tender-leafed species are common. The strength of the association decreases in floras more dominated by sclerophyllous species (e.g. south-east Australia; Fig. 4a), and disappears in floras with succulents (central-western Argentina; Fig. 4b). The results excluding succulents, both for Argentina and for other floras, matched reasonably well the model proposed by Roderick *et al.* (1999, 2000a,b).

The Argentine species set presented here encompasses the widest range of values reported to date along the sclerophylly-succulence axis. At the same time, its range of SLA is small and biased toward low SLA values. This situation may not be exceptional, and floras from other arid to semiarid, relatively warm, systems, such as those in Africa, North America, and the Middle East may show similar patterns. This suggests that, although SLA may not always be the best indicator of plant resource-use strategy (e.g. in cool temperate climates), it may be more widely applicable than LWC or LT. Also, the difficulties

involved in the measurement of SLA may be compensated by the fact that it is more directly relevant to carbon assimilation and nutrient conservation than LWC or LT (Garnier *et al.*, 2001a). Therefore, among the three leaf traits analysed in this study, SLA appears to be the best candidate for inclusion in large screening programs oriented to regional to global-scale comparisons.

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Appendix 1 Species set considered for specific leaf area (SLA), leaf water content (LWC) and leaf thickness (LT) measurements in central-western Argentina

Species	Family	SLA (m ² kg ⁻¹)	LWC (g g ⁻¹)	LT (mm)	Leaf type ¹
Perennial tussock grasses					
<i>Aristida achalensis</i>	Poaceae	9.85	0.51	0.23	SC
<i>Cortaderia rudiusscula</i>	Poaceae	4.68	0.54	0.56	SC
<i>Festuca tucumanica</i>	Poaceae	4.57	0.54	0.20	SC
<i>Pappophorum caespitosum</i>	Poaceae	9.65	0.50	0.33	TL
<i>Paspalum quadrifarium</i>	Poaceae	2.51	0.68	1.10	SC
<i>Poa stuckertii</i>	Poaceae	5.78	0.56	0.37	SC
<i>Schizachyrium condensatum</i>	Poaceae	14.53	0.64	0.17	TL
<i>Setaria pampeana</i>	Poaceae	18.21	0.74	0.24	TL
<i>Trichloris crinita</i>	Poaceae	11.87	0.54	0.48	SC
Perennial short graminoids					
<i>Carex fuscula</i>	Cyperaceae	16.47	0.63	0.22	TL
<i>Juncus uruguensis</i>	Juncaceae	6.39	0.72	0.62	SC
<i>Monanthochloë acerosa</i>	Poaceae	7.26	0.31	0.26	SC
<i>Neobouteloua lophostachya</i>	Poaceae	11.80	0.27	0.17	TL
<i>Nothoscordum gracile</i>	Liliaceae	20.69	0.87	0.66	TL
<i>Sorghum halepense</i>	Poaceae	13.48	0.62	0.83	TL
Annual short graminoids					
<i>Bouteloua aristidoides</i>	Poaceae	11.80	0.51	0.19	SC
<i>Muhlenbergia peruviana</i>	Poaceae	13.45	0.57	0.15	TL
Perennial herbaceous dicots					
<i>Alchemilla pinnata</i>	Rosaceae	13.61	0.75	0.24	TL
<i>Alternanthera pungens</i>	Amaranthaceae	22.30	0.77	0.51	TL
<i>Eryngium agavifolium</i>	Apiaceae	6.13	0.83	2.06	TL
<i>Hyptis mutabilis</i>	Lamiaceae	14.63	0.73	0.18	TL
<i>Oxalis conorrhiza</i>	Oxalidaceae	42.67	0.83	0.32	TL
<i>Pithecoctenium cynanchoides</i>	Bignoniaceae	6.73	0.74	0.43	TL
<i>Rhynchosia edulis</i>	Fabaceae	16.10	0.66	0.21	TL
<i>Taraxacum officinale</i>	Asteraceae	32.00	0.85	0.27	TL
<i>Trifolium repens</i>	Fabaceae	20.93	0.82	0.21	TL
Annual herbaceous dicots					
<i>Carduus thomereri</i>	Asteraceae	10.52	0.91	1.90	TL
<i>Gentianella parviflora</i>	Gentianaceae	20.06	0.82	0.32	TL
<i>Gomphrena pulchella</i>	Amaranthaceae	11.19	0.82	0.30	TL
Deciduous shrubs and trees					
<i>Acacia aroma</i>	Fabaceae	14.92	0.59	0.26	TL
<i>Acacia caven</i>	Fabaceae	12.04	0.55	0.24	TL
<i>Acalypha communis</i>	Euphorbiaceae	6.57	0.70	0.62	TL
<i>Buddleja brasiliensis</i>	Buddlejaceae	4.60	0.54	0.56	TL
<i>Celtis pallida</i>	Celtidaceae	8.55	0.66	0.43	TL
<i>Celtis tala</i>	Celtidaceae	7.58	0.54	0.50	TL
<i>Croton sarcopetalus</i>	Euphorbiaceae	22.25	0.76	0.41	TL
<i>Eupatorium viscidum</i>	Asteraceae	25.36	0.75	0.17	TL
<i>Flourensia campestris</i>	Asteraceae	6.75	0.61	0.62	TL
<i>Geoffroea decorticans</i>	Fabaceae	10.32	0.59	0.29	TL
<i>Mimozyanthus carinatus</i>	Fabaceae	13.32	0.41	0.25	TL
<i>Nicotiana glauca</i>	Solanaceae	10.26	0.83	0.40	TL
<i>Plectrocarpa tetraantha</i>	Zygophyllaceae	4.19	0.38	0.41	TL
<i>Prosopis flexuosa</i>	Fabaceae	14.15	0.60	0.37	TL
<i>Schinopsis haenkeana</i>	Anacardiaceae	9.32	0.54	0.49	TL
<i>Zizyphus mistol</i>	Rhamnaceae	9.28	0.62	0.48	TL
Evergreen shrubs and trees					
<i>Aspidosperma quebracho-blanco</i>	Apocynaceae	4.24	0.43	0.41	SC
<i>Capparis atamisquea</i>	Capparaceae	5.50	0.47	0.53	SC
<i>Heterothalamus alienus</i>	Asteraceae	7.48	0.62	0.53	SC
<i>Larrea divaricata</i>	Zygophyllaceae	6.05	0.40	0.28	SC

Appendix 1 *continued*

Species	Family	SLA (m ² kg ⁻¹)	LWC (g g ⁻¹)	LT (mm)	Leaf type ¹
<i>Lithraea molleoides</i>	Anacardiaceae	4.47	0.48	0.62	TL
<i>Polylepis australis</i>	Rosaceae	7.82	0.65	0.28	TL
Aphyllous shrubs and trees					
<i>Baccharis articulata</i>	Asteraceae	4.56	0.61	1.07	SC
<i>Bulnesia retama</i>	Zygophyllaceae	1.94	0.40	0.76	SC
<i>Senna aphylla</i>	Fubaceae	3.54	0.50	1.45	SC
Bromeliads					
<i>Bromelia urbaniana</i> ²	Bromeliaceae	3.98	0.75	2.59	SU
<i>Tillandsia capillaris</i>	Bromeliaceae	17.77	0.77	1.06	TL
<i>Tillandsia duratii</i>	Bromeliaceae	2.30	0.77	1.72	SU
Leaf succulents					
<i>Agave americana</i> ²	Fabacea	4.21	0.83	1.62	SU
<i>Allenrolfea patagonica</i> ²	Chenopodiaceae	11.51	0.85	2.12	SU
<i>Aloe vera</i> ²	Asphodelaceae	9.14	0.93	1.02	SU
<i>Atriplex argentina</i>	Chenopodiaceae	6.76	0.65	0.51	SU
<i>Cortesia cuneifolia</i>	Boraginaceae	3.23	0.70	1.16	SU
<i>Cyclolepis genistoides</i>	Asteraceae	4.01	0.72	1.16	SU
<i>Grahamia bracteata</i>	Portulacaceae	12.42	0.95	3.22	SU
<i>Heterostachys ritteriana</i>	Chenopodiaceae	3.99	0.63	1.04	SU
<i>Kalanchoe daigremontiana</i>	Crassulaceae	4.53	0.91	4.45	SU
<i>Lycium elongatum</i>	Solanaceae	5.83	0.77	0.62	SU
<i>Maytenus vitis-idaea</i>	Celastraceae	4.07	0.67	0.42	SU
<i>Suaeda divaricata</i>	Chenopodiaceae	4.87	0.79	1.63	SU
<i>Talinum polygaloides</i>	Portulacaceae	5.90	0.85	0.53	SU
Stem succulents					
<i>Cereus forbesii</i> ²	Cactaceae	2.05	0.83	2.73	SU
<i>Cleistocactus baumannii</i> ²	Cactaceae	1.57	0.84	1.63	SU
<i>Gymnocalycium monvillei</i> ²	Cactaceae	2.08	0.70	2.80	SU
<i>Harrisia pomanensis</i> ²	Cactaceae	2.68	0.89	3.07	SU
<i>Opuntia sulphurea</i> ²	Cactaceae	1.73	0.75	2.86	SU
<i>Stetsonia coryne</i> ²	Cactaceae	1.42	0.81	3.03	SU
<i>Tephrocactus articulatus</i> var. <i>articulatum</i> ¹	Cactaceae	1.19	0.77	2.99	SU

Nomenclature follows Zuloaga *et al.* (1994) and Zuloaga & Morrone (1996a,b). ¹Leaf types: TL, tender-leafed; SC, sclerophyllous; SU, succulent.

²Species in which it was possible to differentiate green tissue and inner, nonphotosynthetic, water-storing tissue with a ×20 magnifying glass.