

CONVERGENCE AND CORRELATIONS AMONG LEAF SIZE AND FUNCTION IN SEED PLANTS: A COMPARATIVE TEST USING INDEPENDENT CONTRASTS¹

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Prior studies of a broad array of seed plants have reported strong correlations among leaf life span, specific leaf area, nitrogen concentration, and carbon assimilation rates, which have been interpreted as evidence of coordinated leaf physiological strategies. However, it is not known whether these relationships reflect patterns of evolutionary convergence, or whether they are due to contrasting characteristics of major seed plant lineages. We reevaluated a published data set for these seven traits measured in over 100 species, using phylogenetic independent contrasts calculated over a range of alternative seed plant phylogenies derived from recent molecular systematic analyses. In general, pairwise correlations among these seven traits were similar with and without consideration of phylogeny, and results were robust over a range of alternative phylogenies. We also evaluated relationships between these seven traits and lamina area, another important aspect of leaf function, and found moderate correlations with specific leaf area (0.64), mass-based photosynthesis (0.54), area-based nitrogen (−0.56), and leaf life span (−0.42). However, several of these correlations were markedly reduced using independent contrasts; for example, the correlation between leaf life span and lamina area was reduced to close to zero. This change reflects the large differences in both these traits between conifers and angiosperms and the absence of a relationship between the traits within these groups. This analysis illustrates that most interspecific relationships among leaf functional traits, considered across a broad range of seed plant taxa, reflect significant patterns of correlated evolutionary change, lending further support to the adaptive interpretation of these relationships.

Key words: comparative method; correlated evolution; independent contrasts; leaf life span; leaf size; photosynthesis; seed plants; specific leaf area.

Research on a broad array of terrestrial seed plants has revealed strong relationships among a suite of leaf functional traits, in particular leaf life span, specific leaf area, leaf nitrogen concentrations, carbon assimilation rates, and leaf conductance (Reich, Walters, and Ellsworth, 1992, 1997; Reich et al., 1999). In general, species with short leaf life span exhibit high specific leaf area, mass-based nitrogen concentration, and carbon assimilation rates; in log-log analyses, these relationships are linear with $r^2 > 0.5$ over a broad range of values. This suite of attributes is also broadly associated with high allocation to leaves, rapid growth rates, rapid attainment of reproductive age, and regeneration in high resource or disturbed environments (Bazzaz, 1979; Reich, Walters and Ellsworth, 1992; Cornellison, Castro-Diez, and Carnelli, 1998; van der Werf et al., 1998). Recently, it has been found that the scaling functions among leaf traits (slopes of log-log relationships) are similar across a range of contrasting biomes representing a diverse array of conifer and angiosperm taxa (Reich, Walters, and Ellsworth, 1997). These relationships have been interpreted as evidence of coordinated leaf physiological strategies, reflecting adaptive and/or biomechanical constraints. For example, the inverse relationship between leaf life span and assimilation rate indicates that two trait combinations are

not generally observed: high assimilation rates in long-lived leaves and low rates in short-lived leaves. The former combination would appear to be highly adaptive (high carbon gain sustained over long periods of time), but may be impossible as leaf longevity may require both thickness to resist damage, creating internal self-shading, which reduces assimilation, as well as investment in protective physical or chemical traits, which reduces resources invested in the photosynthetic apparatus. In contrast, a species with short-lived leaves and low assimilation rates would presumably be eliminated by selection due to low growth and fecundity. Optimality models, based on maximizing carbon gain and plant growth, also predict an inverse relationship between assimilation and leaf life span (Kikuzawa, 1991; Ackerly, 1999b). It is important to note, however, that up to threefold variation in physiological traits may be observed at a particular level of leaf life span, so correlations among these traits may be weak or nonapparent in samples that do not span a great range of values (cf. Diemer, Körner, and Prock, 1992; Reich, 1993).

In addition to these patterns in leaf physiological traits, considerable attention has been focused on the ecological significance of leaf size variation (Parkhurst and Loucks, 1972; Givnish and Vermeij, 1976; Chiariello, 1984). Leaf size directly affects light interception, light penetration through the canopy, and leaf energy balance, and leaves are often smaller in species occupying habitats with high light, low nutrients, or low moisture availability (e.g., Hamann, 1979; Körner et al., 1989; Niinemets and Kalevi, 1994; see references in Givnish, 1987), conditions that are also associated with thick leaves, low nitrogen con-

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centrations, and low photosynthetic rates (Reich, Walters, and Ellsworth, 1992). In cool-temperate forests, it has also been suggested that the predominance of conifers is due to the association between evergreenness and small, steeply angled leaves (i.e., conifer needles), which enhance light penetration and low-temperature canopy photosynthesis (Sprugel, 1989; but see Smith and Brewer, 1994). Leaf size also varies considerably among species within habitats, partly in association with architectural traits and reproductive morphology (White, 1983; Midgley and Bond, 1989; Ackerly and Donoghue, 1998). However, relationships among leaf size and the physiological traits listed above have not been systematically examined.

Adaptive interpretations of relationships such as these suggest that the traits have exhibited correlated evolutionary changes, as selection combined with biophysical constraints would maintain certain trait combinations as outlined above. However, the use of cross-species correlations in comparative ecology has come under intense scrutiny in recent years, particularly in relation to the question of adaptive correlations, due to the potential problem of similarity among related species and the statistical independence of species as data points (Harvey and Pagel, 1991). Though it is not always explicitly stated, independence in this context is based on a null model of the independence of evolutionary changes (Felsenstein, 1985). Thus we may pose the question in the following way: do the trait relationships observed among contemporary species reflect or provide evidence of statistically significant patterns of correlated evolutionary changes leading up to the present day? Alternatively, correlations among extant species may arise due to a small number of initial divergence events, in which biologically independent changes in two traits happen to be correlated, and these changes are passed on to descendent species. This will lead to correlations between traits among extant taxa despite the independence of evolutionary changes in the past. This question has been addressed in recent years through the development of a number of statistical techniques that incorporate the phylogenetic relationships among species in order to estimate the evolutionary patterns underlying present-day trait distributions. The most powerful of these is the method of independent contrasts, which calculates the standardized differences in trait values between sister taxa descended from each node of a phylogeny and then evaluates trait correlations or regressions between these contrasts (Felsenstein, 1985; Garland, Harvey, and Ives, 1992). This contrast correlation is quantitatively equivalent to the correlation between the evolutionary changes that have occurred along each branch of the phylogeny (Pagel, 1993).

In recent years, a number of proposed trait relationships in plant functional ecology have been reevaluated in a phylogenetic context, and in several cases the phylogenetically structured correlations have been reported as considerably weaker and nonsignificant (e.g., seed size in relation to establishment conditions: Kelly and Purvis, 1993; Kelly, 1995; stomatal density in relation to life form: Kelly and Beerling, 1995). These reexaminations have shown that many data sets may contain only a few appropriate contrasts from a phylogenetic perspective, greatly reducing the power of the analyses. The problem

is particularly compounded in comparisons between a continuous and a categorical variable (e.g., seed size vs. gap/nongap regeneration), as there may be few contrasts for the categorical trait between related species. Further loss of power occurs when taxonomic schemes (e.g., Cronquist, 1981) are used to construct a phylogeny, because of the lack of resolution.

In contrast to these case studies, meta-analyses of published results in both animal and plant ecology suggest that there is often little quantitative difference in the correlation coefficients or regression slopes resulting from cross-species and independent contrast analyses (Ricklefs and Starck, 1996; Price, 1997; Ackerly, 1999a). These cases primarily involve associations between pairs of continuous traits (e.g., leaf size and branching density, body size and home range) combined with the use of fully resolved phylogenies, both of which maximize the number of available contrasts. Recently Ackerly and Donoghue (1998) demonstrated quantitatively that substantial discrepancies between cross-species and independent contrast correlations only arise for traits that are very highly conserved from a phylogenetic perspective, i.e., when closely related species are also very similar in the functional and ecological traits of interest.

The objectives of this study were to reevaluate previously published analyses of leaf trait relationships for the functional traits described above, together with previously unpublished data for lamina area, based on the data set for 108 species presented in Reich, Walters, and Ellsworth (1997) and Reich et al. (1999). A perusal of the data suggests that these relationships hold up across different phylogenetic groups and that most traits exhibit considerable convergence among the taxa in this study (Reich et al., 1999). However, both leaf life span and lamina area exhibit consistent differences between conifers and angiosperms that might result in correlations across species that are not observed in independent contrasts. Here, we address the following questions: (1) Which of these traits exhibit the highest levels of evolutionary convergence (i.e., similarity among distantly related species)? (2) Is there a relationship across species between lamina area and leaf functional traits (i.e., specific leaf area, leaf life span, nitrogen concentration, or gas exchange rates)? (3) To what extent are trait correlations observed across species similar or different using phylogenetically independent contrasts, based on recent molecular phylogenetic analyses of seed plants? (4) What are the consequences of alternative seed plant phylogenies, and alternative approaches to resolving uncertainty in these phylogenies, for the conduct of comparative analyses?

METHODS

Leaf traits—The following eight traits were considered in this study: (1) lamina area (LA), (2) leaf life span (LL), (3) specific leaf area (SLA), (4) mass-based leaf nitrogen concentration (N_{mass}), (5) area based leaf N (N_{area}), (6) mass-based, light-saturated assimilation rates (A_{mass}), (7) area-based assimilation rates (A_{area}), and (8) leaf conductance (G_s). Methods of data collection for traits 2 through 8 are described in detail in Reich et al. (1999). Lamina area was measured for the entire leaf for simple-leaved species, and for the leaflet in compound-leaved species. Analyses of trait correlations focused on the relationships between leaf area and the other seven traits, as these have not been previously re-

TABLE 1. Polytomies arising from pasting the 108 species in this study onto a phylogenetic framework provided by the seed plant consensus phylogenies based on *rbcL* (Chase et al., 1993; Rice, Donoghue, and Olmstead, 1997) or 18S sequences (Soltis et al., 1997). Polytomies arose either from lack of resolution in the underlying tree or from addition of taxa that were not present in these two analyses; families were assigned to the *rbcL* tree based on Bremer et al. (1998), and to the smaller 18S tree following Chase et al. (1993), or Bremer et al. (1998) if not present in the Chase analysis. All but four polytomies were resolved using the sources at right. All possible combinations of the remaining four were constructed, resulting in 540 systematically resolved trees for comparative analyses (see text).

N	Taxa	Source for resolution
	<i>Families—unresolved in rbcL and 18S</i>	
1	Betulaceae, Juglandaceae, Fagaceae	Manos and Steele, 1997
2	Clusiaceae, Euphorbiaceae, Salicaceae, Chrysobalanaceae	unresolved
	<i>Families—unresolved in rbcL only</i>	
3	Diapensiaceae/Sapotaceae, Ericaceae, Sarraceniaceae	Kron, 1996
4	Rhamnaceae, Eleagnaceae, Moraceae/Ulmaceae	Swensen, 1996
5	Solanaceae, Oleaceae, Apocynaceae/Rubiaceae	Olmstead et al., 1993
6	Celastraceae, Violales, Fabales/Fagales clade	unresolved
	<i>Families—unresolved in 18S only</i>	
7	Eleagnaceae, Rhamnaceae, Bombacaceae/Moraceae, Ulmaceae, Fagales	Chase et al., 1993; Swensen, 1996
8	Fabaceae/Sapindales/etc., Urticales/Fagales/etc., Zygophyllaceae	Chase et al., 1993
	<i>Genera</i>	
9	Pinaceae: <i>Abies</i> , <i>Larix</i> , <i>Picea</i> , <i>Pinus</i>	Tsumura et al., 1995
10	Liliaceae: <i>Erythronium</i> , <i>Trillium</i> , <i>Veratrum</i>	Kato et al., 1995
11	Ericaceae: <i>Andromeda</i> , <i>Arctostaphylos</i> , <i>Chamaedaphne</i> , <i>Kalmia</i> , <i>Lyonia</i> , <i>Rhododendron</i> , <i>Vaccinium</i>	P. Stevens, University of Missouri, personal communication
12	Asteraceae: <i>Baccharis</i> , <i>Echinacea</i> , <i>Eupatorium</i> , <i>Gutierrezia</i> , <i>Helianthus</i> , <i>Pterocaulon</i> , <i>Silphium</i>	Bremer, 1994, 1996; Jansen and Kim, 1996
13	Melastomataceae: <i>Bellucia</i> , <i>Clidemia</i> , <i>Miconia</i>	S. Renner, University of Missouri, personal communication
14	Fabaceae: <i>Baptisia</i> , <i>Eperua</i> , <i>Prosopis</i> , <i>Robinia</i>	Doyle, 1995; Lavin, 1995
	<i>Species</i>	
15	<i>Pinus</i> - nine species	Schwilk and Ackerly, unpublished data
16	<i>Picea engelmannii</i> , <i>P. glauca</i> , <i>P. mariana</i>	Smith and Klein, 1994
17	<i>Vaccinium arboreum</i> , <i>V. corymbosum</i> , <i>V. myrtilus</i>	unresolved
18	<i>Protium</i> - three undetermined species	unresolved
19	<i>Quercus</i> - six species	P. Manos, Duke University, person- al communication
20	<i>Populus deltoides</i> , <i>P. fremontii</i> , <i>P. tremuloides</i>	Smith and Sytsma, 1990

ported and between leaf life span and the remaining six functional traits for comparison.

Phylogenetic trees—Data were collected for 108 species representing 78 genera and 45 families of seed plants, distributed over six distinct biomes. Four species were measured twice independently either within or across distinct biomes, resulting in 112 total records (see Reich et al., 1999).

The construction of phylogenetic trees for broad ecological surveys such as this poses various difficulties. First, the species sampled in ecological surveys rarely coincide with those used in molecular phylogenetic analyses, necessitating extensive substitution of taxa based on taxonomic affiliation at the genus and family level. Secondly, uncertainty in the phylogeny at various levels (in part due to the substitution process just mentioned) may lead to numerous polytomies, which potentially reduce the number of contrasts and the power of statistical analyses. Finally, the necessity for combining information from various sources makes it impossible to obtain consistent branch lengths, in terms of the amount of evolutionary time represented along each branch. Recognizing these problems, we used the following procedure to generate a robust set of phylogenetic trees that combine high levels of resolution with extensive sensitivity testing to examine the consequences of phylogenetic uncertainty (cf. Donoghue and Ackerly, 1996). This procedure is spelled out in detail to provide guidance for future comparative studies addressing broad samples of seed plants.

First, the strict consensus trees from two distinct analyses of seed plant phylogeny (*rbcL*: Chase et al., 1993; Rice, Donoghue, and Olmstead, 1997; 18S: Soltis et al., 1997) were pruned to show relationships among families represented in each analysis. Next, these trees were

pruned to show only the families represented in the ecological data set in this study. Families that were present in the ecological data set but not represented in these phylogenetic analyses (four families for *rbcL*; 12 families for 18S) were then joined to affiliated taxa based on Chase et al. (1993) for the smaller 18S analysis or, if not present in the Chase analysis, based on the classification presented by Bremer et al. (1998). The resulting *rbcL*-based tree had six polytomies for family-level relationships, while the 18S-based tree had four family-level polytomies (Table 1). Figure 1 shows the resulting trees for *rbcL* and 18S, and the correspondence between them. Species within each family were then attached to the tree, with genera within families and species within genera shown as polytomies. The four species with two independent measurements were represented as two adjacent branches at the tips of the trees. Both trees had six polytomies for generic relationships and six polytomies at the species level (Table 1).

At this point, polytomies were resolved in two ways to obtain a range of alternative fully bifurcating trees for comparative analyses. (1) A set of 250 “randomly resolved trees” was generated separately for the *rbcL*- and 18S-based trees, using the “randomly resolve current tree” option in MacClade (Maddison and Maddison, 1992), which resolves polytomies while preserving the remainder of the topology. This step provides a rapid approach to obtaining alternative, fully resolved phylogenies for sensitivity analyses. (2) Alternatively, “systematically resolved trees” were constructed based on extensive searches of the literature and consultation with experts for various groups to resolve the polytomies as listed in Table 1. Four polytomies remained unresolved for the *rbcL* tree and three of these also for 18S: three species of *Vaccinium*, three species of *Protium*, four families of the Violales (Chrysobalanaceae, Euphorbiaceae, Salicaceae, and Clusiaceae), and (*rbcL*

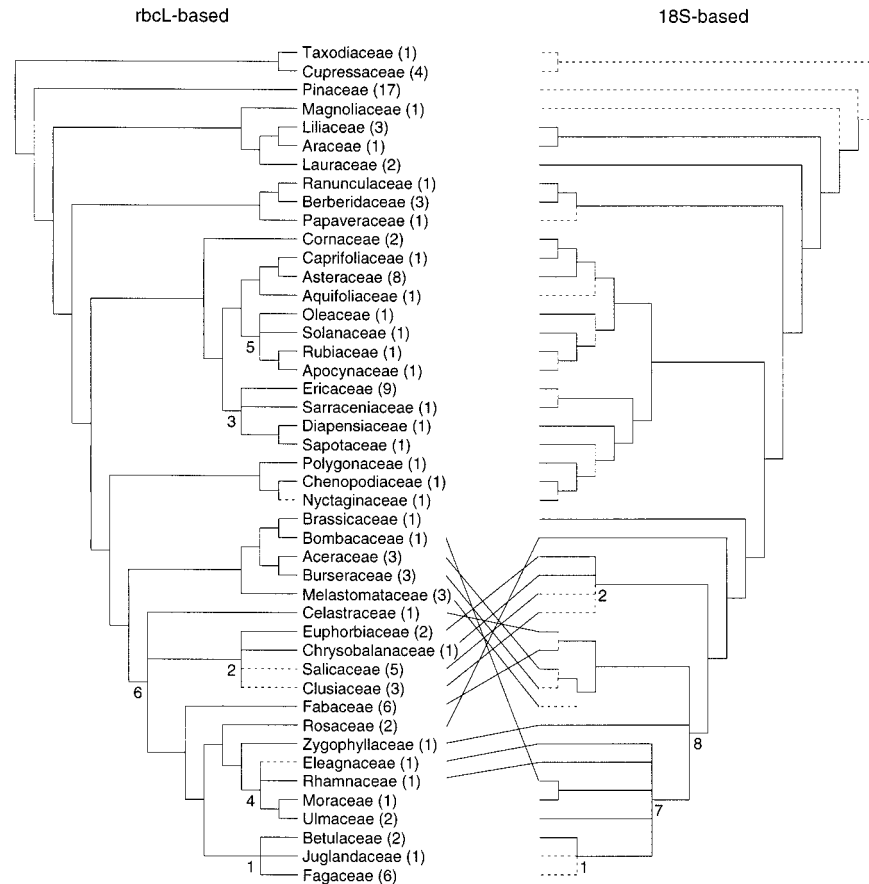


Fig. 1. Family-level relationships for the 45 families present in this analysis, based on consensus trees derived from *rbcL* (Chase et al., 1993; Rice, Donoghue, and Olmstead, 1997) or 18S (Soltis et al., 1997) sequences. Families connected with a dashed line were not present in the original analyses and were joined to the 18S tree based on the *rbcL* analysis, and to the *rbcL* tree following Bremer et al. (1998). Numbers in parentheses after each family indicate the number of species present in the ecological data set. Numbered polytomies correspond to the list in Table 1.

only) relationships among Celastraceae, Violales, and a large clade including Fagaceae and Fabaceae. Polytomies of three and four taxa have three and 15 binary resolutions, respectively, so all possible resolutions of these polytomies produced 135 alternative phylogenies for the 18S-based tree and 405 alternatives for the *rbcL*-based tree, resulting in a final set of 540 systematically resolved trees for analysis.

Finally, a set of 250 fully random trees was created using MacClade's equiprobable trees algorithm, in order to evaluate the potential range of outcomes for the comparative analyses (cf. Maddison and Slatkin, 1991; Losos and Adler, 1995; Donoghue and Ackerly, 1996).

Comparative methods—Comparisons of relative levels of evolutionary convergence were made using the Quantitative Convergence Index (QVI), introduced by Ackerly and Donoghue (1998) for the analysis of continuous characters (convergence is abbreviated "V" to avoid confusion with the Consistency Index, CI; see Maddison and Maddison, 1992). The QVI is based on linear parsimony algorithms for ordered discrete characters (see Swofford and Maddison, 1987) and is equivalent to 1–Retention Index (Farris, 1989); values range from 0, for traits in which closely related species are phenotypically most similar, to 1 for traits in which similar species are distantly related and closely related species are most dissimilar (see Ackerly, 1999a). Trait relationships were evaluated based on correlation analyses, using phylogenetically independent contrasts (Felsenstein, 1985) based on the various alternative phylogenies. In order to evaluate the robustness of the results, branch lengths were calculated with all lengths assumed to be equal, or following Grafen's (1989) method, which assigns branch lengths based

on the number of species in each clade such that the total branch lengths from the root to each terminal taxon are equal.

Comparative analyses were conducted with ACAP v2 (Ackerly and Donoghue, 1998), which calculates QVI values and independent contrasts and their correlations over multiple fully resolved phylogenetic trees. Independent contrasts represent differences between the trait values of two sister taxa. As a result each contrast may be negative or positive depending on the direction chosen to calculate the difference between taxa, but the same direction must be used for all traits at each node. For graphical presentation, the contrasts in the trait plotted along the horizontal axis are all made positive by convention, and those for the trait on the vertical axis are positive or negative depending on whether the changes in the two traits covary positively or negatively, respectively (Garland, Harvey, and Ives, 1992). In addition, due to the symmetry arising from the arbitrary direction of contrasts all correlation and regression analyses must be centered on the origin. In this paper, we focus on correlations rather than regressions to avoid a priori assignment of independent and dependent variables, but it is important to note that these correlations are centered on the origin, not on the means of the two variates as is customary.

RESULTS

Convergence Index—Values of the Quantitative Convergence Index ranged from 0.450 for leaf size to 0.686 for A_{area} (Table 2). In contrast, mean QVI values calculated over 250 fully randomized trees (testing the null

TABLE 2. Summary of convergent evolution measures for the eight characters in this data set. Minimum and maximum values represent the range for all species, in original units. Tree length is the reconstructed total amount of evolutionary change, based on linear parsimony, and QVI is the quantitative convergence index (for all taxa and for angiosperms separately), both based on log-transformed trait values; these were calculated for an arbitrarily selected fully resolved tree based on the *rbcL* phylogeny. Results for other trees were very similar and are not shown. QVI results calculated over random trees test the null hypothesis that the distribution of values for each trait is independent of phylogenetic relationships (see text).

Trait (abbreviation)	Units	N	Species values		Tree length (log units)	QVI		QVI for random trees (N = 250)		
			Minimum	Maximum		All	Angiosperms	Mean	Min.	Max.
Leaf size (LA)	cm ²	102	0.1	408	34.15	0.450	0.621	0.850	0.742	0.936
Leaf life span (LL)	mo	109	1.2	98	22.37	0.493	0.706	0.831	0.708	0.929
Specific leaf area (SLA)	cm ² /g	111	12.1	469	15.15	0.581	0.736	0.866	0.761	0.950
N_{mass}	mg/g	110	6.8	63.6	11.31	0.586	0.619	0.857	0.767	0.938
A_{mass}	nmol·g ⁻¹ ·s ⁻¹	108	11.5	467.9	18.92	0.592	0.708	0.838	0.754	0.928
N_{area}	g/m ²	109	0.71	9.14	10.80	0.667	0.732	0.856	0.760	0.940
A_{area}	μmol·m ⁻² ·s ⁻¹	107	2.92	18.7	11.06	0.686	0.654	0.837	0.745	0.930
Leaf conductance (G_s)	mmol·m ⁻² ·s ⁻¹	101	67	2272	15.24	0.637	0.669	0.842	0.746	0.927

hypothesis of no phylogenetic similarity) ranged from 0.831 to 0.866, and the lowest observed value across all eight characters was 0.708. Therefore, the observed values were significantly lower than null expectation. The low values for leaf size and leaf life span, and to a lesser extent the other traits as well, primarily reflect the differences between conifer and angiosperm species in this study (leaf size mean \pm SD = 2.09 \pm 2.84 and 90.6 \pm 85.8 cm², respectively, Table 3); large differences between major clades lead to more conserved trait distributions, which lower QVI values (see Ackerly, 1999a). QVI values were higher within angiosperms considered separately, reinforcing this conclusion (Table 2; values were not calculated for conifers alone because they are paraphyletic in the *rbcL* phylogeny). QVI values were virtually identical over the 540 alternative phylogenies based on the 18S and *rbcL* trees (range of <0.05 between the lowest and highest values for all eight characters). Note that for this analysis, we have tested the null hypothesis that relationships among species are random with respect to their functional traits, leading to very high null expectations of convergence levels. In contrast Ackerly and Donoghue (1998) randomized reconstructed changes over the branches of the tree, which leads to a null expectation of greater similarity among species, and much lower QVI values, as the phylogenetic structure of trait evolution is conserved. The difference between these two approaches to significance testing of evolutionary

convergence is currently being further explored (D. Ackerly and D. Schwilk, unpublished data).

Leaf size relationships—Conifers and angiosperms exhibited significant differences for all eight traits (Table 3). Conifers have smaller leaves with longer life span, lower SLA, N_{mass} , A_{mass} , A_{area} , and G_s and higher N_{area} . For the entire data set leaf size showed significant cross-species correlations with all functional traits except A_{area} ; the strongest relationship was a positive correlation with SLA, indicating that larger leaved species were also thinner (Table 3, Fig. 2). However, none of these correlations were significant among conifer species and only relationships with SLA and N_{area} were significant among angiosperms. This suggests that most of the relationships observed across all species were due to the overall differences between the two groups. In contrast, correlations between leaf life span and the remaining six functional traits were generally similar in magnitude across all species and among species of conifers and angiosperms, respectively (Table 3). Interestingly, the rank order of the correlation coefficients with leaf life span was very similar in conifers and angiosperms (Spearman Rho = 0.71), while there was no correspondence for the leaf size correlations (Rho = -0.04). Thus, functional correlates with leaf size, though weak in both cases, are distinctive in these two groups.

TABLE 3. Comparison of trait values and cross-species correlations (R) with leaf size and leaf life span, for all species and for all angiosperms and conifers treated separately. Differences between means for conifers vs. angiosperms were significant in all cases (t test, $P < 0.0001$, except for A_{area} ; $P = 0.012$). Sample sizes (and corresponding critical values for significance at $P = 0.05$) were 99-108 for all species correlations ($R_{\text{crit}} = 0.19$), ~ 20 for conifers ($R_{\text{crit}} = 0.44$) and ~ 85 for angiosperms ($R_{\text{crit}} = 0.21$), depending on missing values (see data table in Reich et al., 1999).

Trait (abbreviation)	Trait means \pm 1 SD (log ₁₀ -transformed)		Correlations with leaf size			Correlations with leaf life span		
	Conifers	Angiosperms	All	Conifers	Angiosperms	All	Conifers	Angiosperms
Leaf size (LA)	0.019 \pm 0.533	1.681 \pm 0.624	—	—	—	—	—	—
Leaf life span (LL)	1.529 \pm 0.373	0.885 \pm 0.415	-0.424	-0.145	0.042	—	—	—
Specific leaf area (SLA)	1.616 \pm 0.259	2.063 \pm 0.243	0.644	0.080	0.412	-0.754	-0.736	-0.620
N_{mass}	1.074 \pm 0.106	1.284 \pm 0.218	0.293	-0.030	-0.008	-0.770	-0.548	-0.748
A_{mass}	1.466 \pm 0.271	2.009 \pm 0.286	0.538	-0.147	0.183	-0.885	-0.761	-0.852
N_{area}	0.433 \pm 0.218	0.227 \pm 0.165	-0.564	0.002	-0.536	0.230	0.533	-0.095
A_{area}	0.805 \pm 0.161	0.941 \pm 0.177	0.113	-0.225	-0.203	-0.600	-0.392	-0.574
Leaf conductance (G_s)	2.216 \pm 0.230	2.540 \pm 0.272	0.430	-0.261	0.193	-0.551	-0.683	-0.372

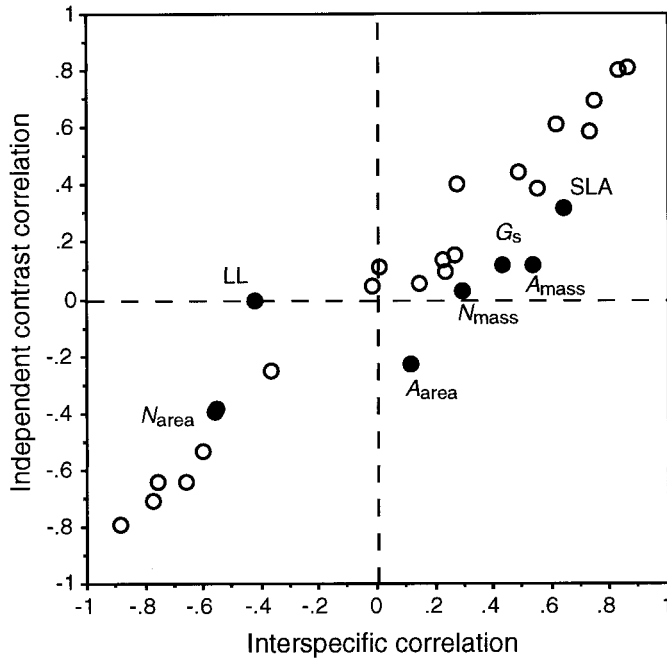


Fig. 2. Scatterplot of interspecific correlations vs. independent contrast correlations, based on a fully resolved *rbcL*-based phylogeny for the species in this analysis. Closed circles: correlations between leaf size and the seven other traits (abbreviations follow Table 2); open circles: all other pairwise correlations among the seven functional traits. Critical values for significance for both correlations are approximately $R > 0.19$ and $R < -0.19$, based on $N \approx 100$.

Phylogenetic correlations—Results of evolutionary correlations using independent contrasts are presented for one systematically resolved *rbcL*-based tree; results over alternative trees were generally similar (see below). Overall, evolutionary correlations were similar in magnitude to the ahistorical, interspecific correlations (Fig. 2). This was especially true for all of the pairwise correlations involving the seven functional traits, excluding leaf size. Figure 3 illustrates three of the pairwise correlations, with the scatterplot of species values on the left, and of independent contrasts on the right, plotted following the conventions described in the Methods. The correlation between leaf life span and specific leaf area was -0.754 between species and -0.642 for independent contrasts ($N = 108$, both $P < 0.001$; Fig. 3A, D). As noted above, the negative relationship between these traits was observed both within and between the angiosperms and conifers, and angiosperms with long leaf life span also had low SLA values, similar to the values for comparable conifers (Fig. 3A). The relationship between leaf size and SLA was also significant based on independent contrasts ($N = 102$, $R = 0.323$, $P < 0.001$; Fig. 3C, F). The most significant discrepancies in interspecific vs. independent contrast analyses involved relationships among leaf size and several other ecophysiological traits. Four of these relationships (with LL, N_{mass} , A_{mass} and G_s), which would be considered significant based on cross-species analyses were not significant based on independent contrasts (Fig. 2, critical value for significance is ~ 0.2 in all cases). In particular, in the association between leaf size and leaf life span, a negative correlation

of -0.424 across species disappeared completely using independent contrasts (see Fig. 2). This occurred because the interspecific correlation reflects the differences in both traits between angiosperms and conifers (Fig. 3B), as reflected in their low QVI values. In the analysis of independent contrasts, these differences are revealed in the large contrast between the Pinaceae branch and the angiosperms, while there is no significant correlation between these traits within each of these groups (Fig. 3E). In contrast to SLA, leaf size was similar for angiosperms across the entire range of leaf life span, and leaves were larger than comparable conifers.

Sensitivity to the phylogeny—All correlations of independent contrasts were extremely similar based on equal branch lengths or branch lengths adjusted following Grafen (1989). The results were also very robust over the alternative phylogenies constructed for this analysis. For example, for leaf life span vs. specific leaf area, the mean correlations over the systematically resolved trees based on *rbcL* ($N = 435$) and 18S ($N = 105$) were -0.64 and -0.62 , respectively, with a range of ± 0.005 in each case (Table 4). Results were only slightly more variable in the two sets of 250 randomly resolved trees, with slightly lower means and a range of ± 0.05 . Similar patterns were observed for leaf life span vs. leaf size. These analyses were also repeated on an angiosperm phylogeny based on a combined analysis of *rbcL* sequences and morphology (Nandi, Chase, and Endress, 1998), which appeared after this study had been completed, and the results were very similar to the *rbcL*-based analyses reported here (results not shown). In contrast, the average evolutionary correlations over random trees were virtually identical to the cross-species correlation (see Abouheif, 1998). For leaf life span vs. SLA, the results over random trees barely overlapped the *rbcL* and 18S results, while for life span vs. leaf size the results were completely divergent, as expected due to the large differences between the cross-species and independent-contrast results in this case.

DISCUSSION

The objective of this paper was to reexamine interspecific correlations among leaf physiological traits in the context of phylogenetic relationships among species. The primary result was to demonstrate that these relationships are generally quite robust and that previous analyses and interpretations based on cross-species patterns (e.g., Reich, Walters, and Ellsworth, 1997; Reich et al., 1999) are supported from a phylogenetic perspective. In addition, there were weak associations among leaf size and function, but several of these were primarily due to differences between conifers and angiosperms, not to relationships observed within each of these groups. The analysis of quantitative convergence levels also demonstrates significant phylogenetic structuring of these physiological traits, especially leaf size and leaf life span (Table 2). This illustrates that even in this phylogenetically diverse set of species there is a pattern of functional similarity among related species. This pattern is primarily driven by the overall similarities among conifers and angiosperms, relative to the divergence between these two

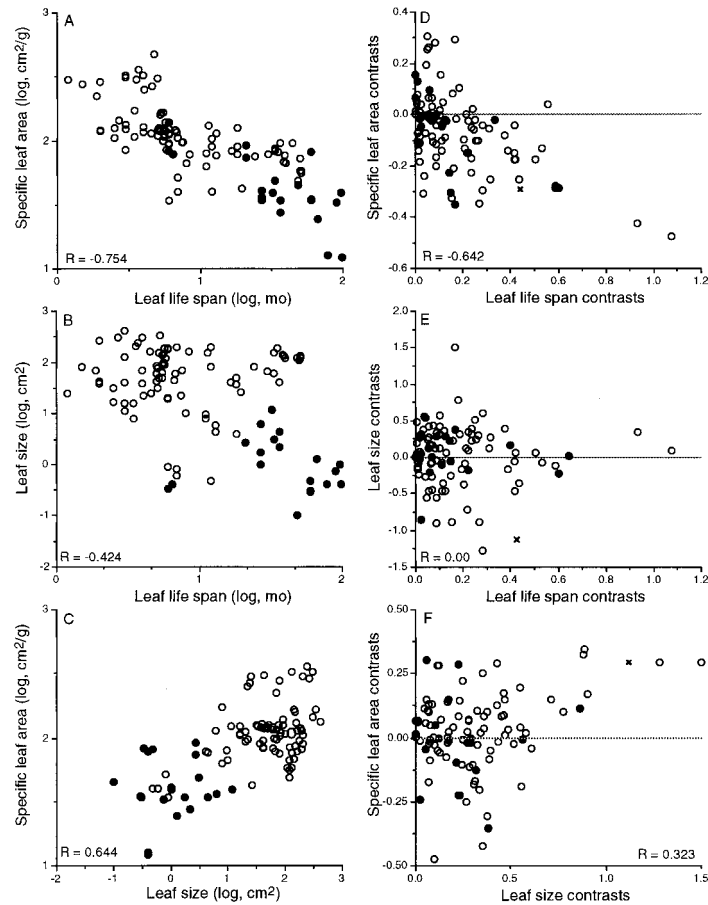


Fig. 3. Scatterplots of species trait values and independent contrasts of leaf life span vs. specific leaf area (A, D), leaf life span vs. leaf size (B, E), and leaf life span vs. specific leaf area (C, F). Independent contrasts were calculated based on an arbitrarily selected *rbcL*-based phylogeny. Each contrast represents the difference in the corresponding trait values between two sister taxa. Correlation analyses using independent contrasts are calculated through the origin, because the sign of each pair is arbitrary (see text for details). Open symbols: species values or contrasts for angiosperms; closed symbols: values for conifers; cross: contrast between the Pinaceae branch and angiosperms (see Fig. 1).

groups; QVI values within angiosperms (Table 2) indicate considerable convergence in this subset of flowering plant species.

Various studies have documented interspecific leaf size variation both within and across habitats in association with light levels, nutrient and moisture availability, and

temperature (Givnish, 1987), and it was suggested that parallel variation in leaf ecophysiology would lead to associations among these traits. This hypothesis is partially supported by these data, in particular by the positive correlation among angiosperm species and among independent contrasts for the entire data set between leaf size and

TABLE 4. Sensitivity of trait correlations analyzed over alternative phylogenies (cf. Fig. 3). Phylogenetic relationships among families were based on *rbcL* or 18S analyses; polytomies in family, generic, and specific relationships were resolved systematically, following Table 1, or at random in MacClade. Correlations of independent contrasts were calculated using equal branch lengths.

Phylogenetic trees used for correlation	Leaf life span vs. SLA (<i>N</i> = 108)			Leaf life span vs. leaf size (<i>N</i> = 102)		
	Mean	Minimum	Maximum	Mean	Minimum	Maximum
Interspecific correlation	-0.754			-0.424		
Independent contrasts						
<i>rbcL</i>						
Systematic (435)	-0.640	-0.645	-0.634	-0.005	-0.018	0.006
Random (250)	-0.620	-0.684	-0.563	-0.002	-0.058	0.047
18S						
Systematic (105)	-0.620	-0.625	-0.614	0.002	-0.014	0.011
Random (250)	-0.592	-0.650	-0.529	0.005	-0.077	0.048
Random trees (250)	-0.752	-0.811	-0.648	-0.417	-0.562	-0.272

specific leaf area, i.e., smaller leaves tended to be thicker. Of all the traits, leaf size shows the greatest variation among communities in this study, with the smallest mean leaf size in the dry New Mexico site, and the largest mean size in Venezuelan rain forest (cf. Reich et al., 1999). However, the species in this study were not sampled to compare mean trait differences between communities, and it is possible that random sampling of species from contrasting habitats would show stronger associations among leaf size and ecophysiological traits than those observed here. On the other hand, it is understandable that leaf size and function relationships, which reflect parallel responses to abiotic conditions, will be weaker than the functional relationships among specific leaf area, assimilation, nitrogen, and leaf life span, which reflect adaptive and/or physiological constraints on coordinated leaf function. Leaf size exhibits considerable variation among ecologically similar species and may be associated with other aspects of plant function. For example, in tropical rain forests variation in leaf size among pioneer and late-successional species is much greater than average differences between these groups (Ackerly, 1996). Leaf size is strongly associated with canopy architecture and branching morphology, and to a lesser extent with reproductive morphology (White, 1983; Midgley and Bond, 1989; Ackerly and Donoghue, 1998), and these traits may influence leaf size evolution independently of ecophysiological function. Despite the long-standing interest in leaf size, variation among species within habitats is still poorly explained (cf. Givnish, 1987).

The results of the comparative analysis of leaf functional traits do provide strong additional support for broad patterns of convergence in leaf trait correlations. In addition, this study highlights several methodological points regarding comparative analyses of functional and ecological traits. As in many comparative ecological studies, the species in this data set are drawn from a broad phylogenetic spectrum. In this analysis, we constructed highly resolved "supertrees" for these species by substituting the species of interest onto appropriate locations of seed plant phylogenies based on *rbcL* and 18S sequences, pruning extraneous portions of the trees, and then resolving the numerous polytomies based on relevant published studies (see Table 1). This relatively time-consuming procedure left us with just four unresolved polytomies, but even this small number led to over 500 distinct phylogenies for examination. However, the results of both the convergence and correlation analyses were extremely similar over all of these trees, suggesting that reasonable results could be accomplished by picking any one resolution at random. Donoghue and Ackerly (1996) also showed that the variations among the numerous alternative parsimonious trees of the seed plant *rbcL* phylogeny (Rice, Donoghue, and Olmstead, 1997) have little influence on analyses of trait correlations.

Of more practical relevance, results of this study were also fairly similar when the families, genera, and species were pasted onto the *rbcL* and 18S trees and the resulting polytomies were resolved at random in MacClade. This is a very rapid procedure which provides fully bifurcating trees, maximizing the power of comparative analyses. The results of this study suggest that alternative random

resolutions of uncertain portions of the phylogeny (cf. Losos and Adler, 1995) are superior to the treatment of each polytomy as a single contrast (Pagel, 1992), which results in a rapid loss of degrees of freedom and power. To facilitate the construction of phylogenies for comparative analyses, a simple utility has been written that prunes and pastes branches in order to partially automate this process (D. Ackerly and B. Bennett, unpublished data). Although much remains to be learned about seed plant phylogeny, the current state of knowledge coupled with these approaches to phylogenetic uncertainty provide ample basis to conduct phylogenetically structured analyses of ecological data. The rationalization that phylogenies are still too crude for these analyses is not justified.

The results of this study also illustrate that in many cases the results of phylogenetically structured correlation analyses are quite similar to traditional cross-species correlations (Fig. 2; cf. Ackerly, 1999a). However, it is very important to pay attention to those cases in which results of the two approaches are quantitatively different from each other, especially when the difference is not due to a loss of power as discussed in the Introduction. In this study we found an example of such divergence in the relationship between leaf life span and leaf size (Fig. 3B, E). The negative relationship between these two traits results entirely from the divergence between the angiosperms and the conifers, and there is no relationship observed within either group nor in the analysis of independent contrasts for the entire set of species. How should this difference in the results be interpreted? One view is that evolutionary changes in trait values along particular phylogenetic lineages may occur for many reasons or even at random, and the fact that both leaf size and leaf life span exhibit a shift along the branch leading to the angiosperms does not provide statistical evidence of a biological association between the two traits. It represents a single event, so there is no support for a repeated pattern of correlated evolutionary change. From this perspective, the correlation observed at the species level might be considered spurious and biologically meaningless, and the results of cross-species analyses positively misleading. From another view, the changes in both of these traits may in fact be related to the shifts in physiology and life history accompanying the evolution of angiosperms (cf. Bond, 1989). Larger laminas and shorter leaf life span of angiosperms may be two functional traits associated with increased hydraulic conductance, enhanced photosynthetic rates, and rapid growth, relative to conifers as a whole. And, as Sprugel (1989) argued, the combination of small leaves and evergreenness in conifers may in fact be related to their success in cold environments. In this sense, the divergence event between these groups does represent an instance of biologically significant coordinated evolutionary change, which at the very least has influenced the subsequent success of each group. Furthermore, the maintenance of the differences between the groups may reflect continued stabilizing selection within each group, rather than "phylogenetic inertia" due to lack of genetic variation or directional selection (Hansen, 1997). Each of these traits exhibits high levels of convergence within angiosperms and conifers, suggesting rapid evolution and minimal

constraints for response to selective pressures. While this may be true, it is still worth noting that there is no relationship between leaf size and leaf life span within conifers or angiosperms, supporting the notion that there is no intrinsic biological linkage between evolutionary changes in these two traits. The choice between the two alternative views above cannot be made simply based on the quantitative results themselves. Ultimately, the biological and evolutionary interpretation of these correlative patterns depends on both functional understanding of the traits, as well as a philosophical decision about the significance and interpretation of unique historical events (Donoghue, 1989).

One final aspect of this analysis that deserves attention is the problem of species sampling in relation to the phylogeny. The species in this study were drawn from a very broad phylogenetic range, with individual species serving as representatives of lineages with hundreds or thousands of taxa. On the one hand, this sampling means that the patterns observed may be safely inferred to apply across all seed plants; they are not idiosyncrasies of one family or one biological community (cf. Reich, Walters, and Ellsworth, 1997). On the other hand, this sparse sampling from a phylogenetic perspective seriously draws into question the meaning of the trait reconstructions used to calculate convergence indices and independent contrasts. For example, *Acomastylis* (= *Geum*) *rosii* and *Prunus serotina* are the only two Rosaceae in this study and appear as sister taxa in the phylogeny, and they also exhibit relatively similar functional traits (deciduous leaves with moderately high SLA and assimilation rates). Based only on this sample, these values are interpreted as phylogenetically conserved in these two taxa and representative of the Rosaceae, contributing to lower convergence values. However, there is no question that each of these species has numerous closer relatives with contrasting functional traits (e.g., *Prunus serotina* is more closely affiliated with evergreen chaparral species, such *Prunus ilicifolia* and *Adenostema fasciculata*; see Morgan, Soltis, and Robertson, 1994), so the similarity of the two species in this study is clearly misleading as a representation of Rosaceae as a whole. Analyses of independent contrasts are robust to random species sampling, but may be biased if the associations in question are stronger within the communities sampled in a particular study, relative to the entire evolutionary distribution of the traits (D. Ackerly, unpublished data). Such biases are probably minimized in these data as they have been drawn from six widely contrasting habitats. However, reconstructions of the sequence and timing of evolutionary changes, especially in these relatively labile physiological traits, require greater study of closely related species to complement the broad comparative approach employed here.

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