Leaf Size, Sapling Allometry, and Corner's Rules: Phylogeny and Correlated Evolution in Maples (*Acer*)

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ABSTRACT: We studied the evolution of leaf size, sapling canopy allometry, and related traits in 17 *Acer* species growing in the understory of temperate deciduous forests, using parsimony methods, randomization tests, and independent contrasts calculated on a phylogeny inferred from nuclear ribosomal internal transcribed spacer (ITS) sequences. Bivariate correlations and multivariate analyses indicated two independent suites of coevolving traits, and the results were robust over a range of alternative phylogenies. The first suite consisted of strong positive correlations among twig thickness, leaf size, inflorescence length, and branch spacing (Corner's rules). Seed size and mature height were also weakly correlated with these traits. The second suite reflected aspects of sapling crown allometry, including crown size, stem diameter, and total leaf area, which appear to be related to shade tolerance. There was a weak negative correlation between sapling crown size and mature height, but no correlation with leaf or seed size. Most correlations were similar in magnitude for ahistorical and independent contrasts analyses, and discrepancies between these two measures were greater in traits with lower levels of convergent evolution. The evolutionary correlations among twig, leaf, seed, inflorescence, and canopy dimensions emphasize the need for integrated theories of evolution and function of these disparate traits.

Keywords: tree life history, canopy architecture, independent contrasts, internal transcribed spacer, randomization methods, convergent evolution.

Plant canopies are complex structures, reflecting a large number of component traits at several levels of organization, including the leaf, the leaf cluster and individual shoot, branch systems, and the entire crown. The ecological consequences of traits at each level (e.g., leaf size, branching density, or crown shape and allometry) cannot be considered in isolation. Rather, these characteristics interact with each other and with environmental conditions to influence plant performance. As a consequence, marked patterns of correlated evolution are observed among traits at various levels, resulting in constellations or suites of characteristics in species of different habitats and life histories (e.g., Horn 1971; Givnish 1984; Kikuzawa et al. 1996). Studies of leaf and canopy form have identified two important trait constellations that covary in forest trees. First, Corner (1949) argued that twig thickness, leaf size, and inflorescence size are positively correlated in the evolution of tree morphology and inversely related to the density of branching in the crown ("Corner's rules," Hallé et al. 1978; see also Sinnott 1921; Troll 1937, 1939). These patterns have been confirmed in several quantitative studies (White 1983*a,* 1983*b;* Midgley and Bond 1989; Chazdon 1991), though the implications for interactions among vegetative and reproductive evolution have received little attention (Primack 1987; Bond and Midgley 1988). Second, the allometry of sapling crown dimensions in relation to tree life history and understory regeneration has been studied from theoretical and empirical perspectives (Horn 1971; King 1981, 1990, 1991; Givnish 1986, 1988; Kohyama 1987; Kohyama and Hotta 1990; Sakai 1995). These studies suggest there is a trade-off in sapling growth between investment in lateral crown extension, to maximize light interception and persistence in the shade, and investment in height growth, which enhances the opportunistic utilization of light following disturbance. Givnish (1988) and King (1990) suggested that sapling allometry is associated with a species' mature height, with broader crowns in understory species than in equivalent height saplings of canopy species. In addition, King (1991) found evidence of an inverse relationship between leaf size and lateral crown extension in temperate trees, a trend that is apparent in tropical species as well (King 1990; Kohyama and Hotta 1990).

These studies raise two intriguing questions, which are the focus of this article. First, are these two suites of traits

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independent of each other or, as suggested by overlapping relationships with leaf size, are they parts of a larger constellation of leaf and canopy characteristics in forest tree species? Second, do the phenotypic correlations observed among species reflect historical patterns of correlated evolutionary change? Most studies of leaf size and canopy function have examined coexisting species within a particular community, and studies of related species (e.g., White 1983*a;* Givnish 1987; Chazdon 1991) have not formally incorporated phylogenetic information into comparative analyses. In recent years, advances in comparative biology have made it possible to conduct explicit tests of correlated evolution, based on patterns of character variation coupled with information on phylogenetic relationships among species (e.g., Harvey and Pagel 1991). For the study of continuous characters, Felsenstein's (1985*b*) method of independent contrasts provides the most powerful quantitative tool to test for correlated evolutionary change underlying contemporary trait variation and covariation (Garland et al. 1992; Pagel 1993).

In this article, we present the first phylogenetic comparative study of correlated evolution among leaf traits, canopy allometry, and tree life history, based on field studies and phylogenetic analyses of temperate, deciduous tree species in the genus *Acer*. We have two primary empirical objectives. The first is an explicit test of a small number of a priori hypotheses of correlated evolution related to Corner's rules and sapling allometry, and a sensitivity analysis of these results with respect to uncertainty in the phylogeny. Second is a multivariate analysis, based on principal components analysis of independent contrasts, to evaluate the predominant suites of coevolving traits and their relationship to two morphological proxies of tree life history: mature height and seed size. Simultaneously, we illustrate and explore several problems of methodology and interpretation that arise in phylogenetic tests of comparative ecological hypotheses. Our methodological objectives include exploration of methods for handling multiple alternative phylogenetic hypotheses in comparative studies, in particular the role of sensitivity analyses and random phylogenetic trees, and the introduction of the Quantitative conVergence Index (QVI) to assess levels of parallel and convergent evolution (i.e., homoplasy) in continuous traits, and the relationship between levels of homoplasy and the overall amount of evolutionary change in a trait. Randomization tests were also used to test for levels of homoplasy significantly less than or greater than expected by chance.

Background on Maple Systematics and Ecology

The genus *Acer* includes approximately 125 species, primarily deciduous shrubs and trees of temperate forest regions of the Northern Hemisphere, with a few species extending into the subtropics (van Gelderen et al. 1994). Based on morphological cladistic analyses, *Acer* and its sister group *Dipteronia* (one to two species in China and Tibet), which make up the Aceraceae, are nested within the Sapindaceae and are most closely affiliated with the genera *Diatenopteryx, Serjania,* and *Bridgesia* (Judd et al. 1994). A phylogeny based on *rbc*L sequences also identifies a clade composed of Sapindaceae, Aceraceae, and Hippocastanaceae but suggests that the latter are sister taxa (Gadek et al. 1996). The fossil record of *Acer* dates to the late Cretaceous (100 m.y.b.p.) and implies a spread from the Pacific Rim around the Northern Hemisphere during the Tertiary (Wolfe and Tanai 1987; Boulter et al. 1996). Morphological systematic studies of *Acer* have arranged the species into a number of well-supported sections (taxonomy in this article follows van Gelderen et al. 1994, unless otherwise noted). However, previous treatments based on overall morphology (Delendick 1981; van Gelderen et al. 1994), leaf venation (Wolfe and Tanai 1987), and restriction fragment length polymorphisms (M. Hasebe, personal communication), as well as a provisional phylogenetic analysis of morphological data (D. Ackerly, unpublished analyses of data in Delendick 1981), provide inconsistent or inconclusive results regarding the relationships among sections. Molecular phylogenetic analyses have been conducted for a small number of *Acer* taxa, predominantly from Korea (Suh et al. 1996; Cho et al. 1997), but these are insufficient to resolve overall phylogenetic relationships within the genus.

Maples exhibit considerable diversity in life history, regeneration ecology, seed size, leaf size, and canopy structure. Mature height ranges from 6–10 m in understory species (e.g., *A. spicatum* in North America; *A. crataegifolium* in Japan) to 25–35 m in canopy species (e.g., *A. saccharum, A. rubrum* in North America; *A. palmatum* in Japan), and there are both early and late successional species (e.g., *A. rubrum* and *A. saccharum,* respectively). Seed size spans over two orders of magnitude, from 20 mg in *A. rubrum* to over 255 mg in the closely related riparian species *A. saccharinum* (Olson and Gabriel 1974); in all species, seeds are wind dispersed. There is considerable variation in growth strategies within the genus; branch growth may be determinate (section *Palmata*) or indeterminate (e.g., *A. rubrum*), branch orientation plagiotropic or orthotropic, and apical dominance of lateral branch growth strong or weak (Sakai 1990). Leaf length ranges from 5–10 cm (*A. rubrum, A. palmatum*) to >40 cm in *A. negundo* and in the aptly named *A. macrophyllum. Acer* species are important components of forests in eastern North America and Japan and have been the subject of numerous studies in community ecology and regeneration biology (e.g., Naka-

shizuka et al. 1995). Comparative studies of *Acer* have documented significant interspecific variation in life history, morphology, and physiology and in the plasticity of these traits in relation to forest light environments (Lei and Lechowicz 1990, 1997; Sipe and Bazzaz 1994, 1995; Tanaka 1995). Such variation among closely related species, occupying broadly similar habitats, makes *Acer* an excellent system to explore evolutionary correlations among ecological traits.

Methods

Choice of Species

Our study of ecological and morphological traits related to canopy structure focused on a set of 17 focal taxa, all of which exhibit natural regeneration in forest understory in temperate deciduous forests of eastern North America and Japan. The decision to restrict the ecological component of this study to understory-regenerating species was based on two considerations. First, canopy development and sapling allometry exhibit considerable phenotypic plasticity in relation to light environments (e.g., Bonser and Aarssen 1994). Differences observed among species living in the common environment of the understory primarily reflect interspecific, evolutionary differentiation rather than environmentally dependent variation. Second, the functional significance of leaf and canopy traits is dependent on environmental conditions, so comparisons of values obtained in the understory are more ecologically meaningful. As described below, there is considerable life-history variation among the selected species, although species that regenerate primarily in high light environments (e.g., *Acer negundo, A. tschonoskii*) were excluded. In order to minimize bias in species selection with respect to the ecological hypotheses tested here, all species encountered in each study site were included in the study if sufficient sample sizes were available (see Westoby 1998; Westoby et al. 1998).

Phylogenetic Analysis

In order to conduct a comparative study of trait evolution in a sample of species selected from a larger clade of interest, one would like to obtain the best estimate of phylogenetic relationships among those species. Short of including all species of the clade in question in a phylogenetic analysis (which is neither practical for a large group nor necessary in order to obtain a robust hypothesis of relationships), the best estimate of relationships among the focal taxa may be achieved by sampling a broad array of species, representing the major lineages within the clade. Our phylogenetic analysis of *Acer* was based on DNA sequence data from 39 accessions representing 32 *Acer* species, and one species of its presumed sister group *Dipteronia* (see appendix). *Acer* accessions included representatives of 12 of the 16 sections of the genus (van Gelderen et al. 1994; sections *Wardiana, Trifoliata, Hyptiocarpa,* and *Pubescentia,* with a total of 10 species, were not represented). Emphasis was placed on selection of species included in the comparative study of sapling allometry, as well as on those included in previous comparative ecophysiological studies (e.g., Lei and Lechowicz 1997).

Sequences of the internal transcribed spacer (ITS) region of nuclear ribosomal DNA were utilized for phylogenetic analysis. The two ITS regions flanking the 5.8S nrDNA show moderately high levels of sequence divergence and have proven useful for intrageneric phylogenetic analysis in flowering plants (Baldwin et al. 1995). DNA extraction, amplification, and sequencing followed standard protocols, as described elsewhere (Eriksson and Donoghue 1997). Sequences were obtained using an Applied Biosystems 377 automated fluorescence sequencer (Applied Biosystems, Foster City, Calif.), and sequence output was captured and processed with Applied Biosystems software (Applied Biosystems 1992). Twenty-five accessions were newly sequenced as part of this study (in collaboration with S. Wiegrefe, Morton Arboretum, Lisle, Ill.), and 14 sequences were obtained from GenBank (including six duplicate accessions of species included in the sequencing above; Suh et al. 1996; Cho et al. 1997). Sequences of three distant outgroups (Fabaceae: *Vicia faba,* Yokota et al. 1989; Malvaceae: *Hibiscus costatus,* Seelanan et al. 1996; and Malvaceae: *Gossypium trilobum,* Wendel et al. 1995) were also obtained from GenBank to test the assumption of *Acer* monophyly with respect to *Dipteronia.*

Sequences for the 39 Aceraceae accessions were assigned numeric codes by a third party to prevent any bias during alignment. Sequences were aligned using Clustal W (Thompson et al. 1994), and subsequently modified by visual inspection, resulting in an aligned sequence length of 643 base pairs (bp; aligned lengths of 259, 164, and 220 bp for ITS1, 5.8S, and ITS2, respectively). Eight distinct shared insertion/deletion ("indel") regions were recognized in the final alignment and were coded as binary characters for phylogenetic analysis (Baldwin et al. 1995). One 60-bp region of ITS2 with ambiguous alignment was identified for inclusion/exclusion experiments. After completing the alignment of Aceraceae sequences, sequences of the three distant outgroups (*Vicia, Hibiscus,* and *Gossypium*) were added to the data set and visually aligned; this required the addition of 75 gaps within the Aceraceae alignment, but alignments among the Aceraceae sequences themselves were not altered. Parsimony analyses were conducted with PAUP 3.1.1 (Swofford

1993). Heuristic searches were conducted with at least 10 random addition replicates, and TBR branch swapping, MULPARS, and steepest descent options in effect. All sequence positions and inferred base changes, as well as the indel characters, were weighted equally. Support for the resulting clades was evaluated with bootstrap (Felsenstein 1985*a*) and decay analyses (Bremer 1988; Donoghue et al. 1992), the latter using the reverse constraint option in PAUP and AutoDecay software (Eriksson 1995). DNA sequences have been deposited in GenBank (appendix) and the aligned matrix has been deposited in TreeBASE (Sanderson et al. 1994).

For comparative analyses, the resulting *Acer* phylogenies were pruned to show relationships among the 17 taxa for which we obtained the set of morphological measurements described above (two of the 17 species were added to the phylogeny based on independent morphological evidence; see below). Methods have been developed to handle polytomies resulting from the consensus of equally parsimonious trees (e.g., Grafen 1989; Pagel 1992); we opted to approach this problem by choosing one fully resolved tree for illustration (designated tree number 1), and then to conduct sensitivity analyses over all alternative equally parsimonious trees, as described below (cf. Losos 1994; Donoghue and Ackerly 1996).

Comparative Data

Based on the following procedures, a total of 32 traits were obtained from field and herbarium samples and published sources, including mature height and seed size as proxies of tree life history; eight shoot-level characters related to leaf, twig, and inflorescence size; bifurcation angle and dominance index of the terminal shoot in saplings (Sakai 1987); and estimates of slope and predicted value (= elevation) based on 10 allometric analyses of sapling crown dimensions. (The full data set is available on request from D. D. Ackerly or see Ackerly 1998*a*).

Life-History Variables. Maximum height presents an important axis of life-history variation in forest trees, with important implications for light environments, physiology, and allocation (Givnish 1988; Thomas 1996). Mature height values were obtained from floras and tree manuals (Canada Department of Forestry 1963; Ogata 1965; Phillips 1978), and averages were used where multiple values were reported for a species.

Seed size is an important aspect of tree regeneration and dispersal biology, and variation among species is associated with capacity to survive defoliation and physical damage, drought, and extended periods in deep shade or darkness (Westoby et al. 1996). However, there is not a simple relationship between seed size and overall shade tolerance or establishment environment (Foster and Janson 1985; Kelly 1995; Grubb and Metcalfe 1996). Here, we treat seed size as a potential correlate of seedling establishment ecology and conduct nondirectional tests of relationships with leaf size and canopy structure. Seed sizes were obtained from published sources (Olson and Gabriel 1974; Tanaka 1995) supplemented by nondestructive measurements of herbarium specimens combined with a calibrated regression of seed mass versus locule volume ($r^2 = 0.72$, $N = 12$, details not shown).

Sapling Allometry. The allometry of canopy structure was studied in naturally regenerating saplings of 17 species growing in forest understory in two sites in eastern North America and six sites in Japan (see locations in appendix). At least 40 individuals of each species were selected for study (except *A. palmatum,* $N = 16$), and 13 of the 17 species were sampled at two or more sites (appendix). Saplings selected for study had at least one lateral branch (generally >0.5 m tall) and were up to 2.5 m in height. The distribution of sizes was inspected during sampling to guarantee a broad representation within this height range. Damaged individuals and saplings growing in or at the edge of large canopy gaps were excluded. Individual leaf area was estimated for each sapling based on the length of three leaves and independently derived regressions of leaf area versus length. The following parameters of sapling height and canopy size were measured on each individual (fig. 1): HT: plant height, measured verti-

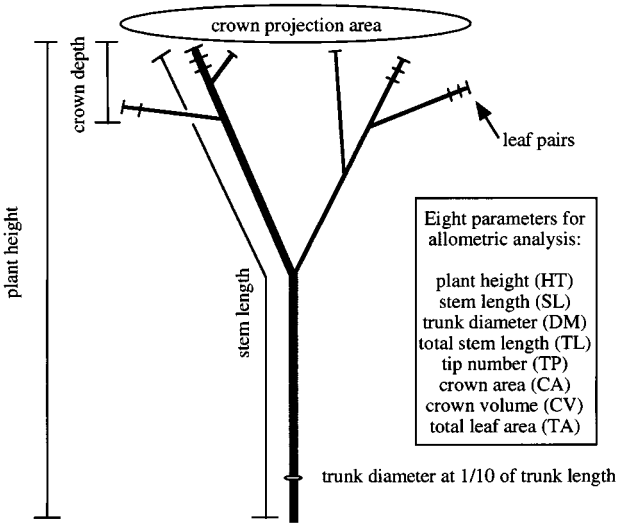

Figure 1: Measurements of sapling size and crown dimensions utilized for study of sapling allometry. Bivariate allometric relationships derived from these measurements are summarized in table 1.

cally from the ground to the highest leaf; SL: primary stem length, measured along the trunk to the uppermost growing tip; DM: basal stem diameter, measured at 1/10 of stem length; TL: total length of the trunk and all branches; TP: number of active growing tips (apical meristems) in the crown; CA: projected crown area, based on the area of an ellipse, where d_1 and d_2 are the diameter of the crown in the major and minor axes (respectively) and $CA = \pi d_1 d_2/4$; CV: crown volume, based on an ellipsoid, where d_3 is the depth of the foliage and $CV = \pi d_1 d_2 d_3/6$; and TA: total leaf area, the product of number of leaves and mean individual leaf area.

Allometric analysis was used to assess the trajectory of sapling development and canopy structure and as an analog of the ratios frequently used to describe plant form. For example, leaf area index for an individual plant can be calculated as the ratio of total leaf area to the projected crown area; here we use the allometric relationship between these traits (leaf area vs. crown area) rather than their ratio (Coleman et al. 1994). Type I regression was used for these analyses, with an explicit assignment of a dependent and independent variable, due to ease of statistical analyses, and the parallel to a ratio with numerator and denominator. (As discussed below, the r^2's of these regressions were generally high, so the choice of regression model is not expected to alter strongly the results). Ten allometric relationships were chosen from the 28 pairwise combinations of the eight variables, based on the following considerations (table 1): CA, CV, DM, SL, TA, TL, and TP versus height (HT), providing a standard basis for comparing canopy development in relation to sapling growth and vertical position in the understory; TA and TP versus CA, providing allometric analogs of leaf area index and growing tip density, respectively; and TA versus DM, as a measure of leaf area display relative to stem conductive potential.

Allometric relationships are identified by concatenation of the *X* and *Y* variable codes, with an S or P appended to indicate the slope or predicted value, respectively (e.g., CATA-S indicates the slope of the regression with crown area as the independent and total area as the dependent variable). All variables were ln-transformed, and separate regression equations were calculated for each species. For 44 of the 170 cases (10 relationships × 17 species), nonlinear regression was used due to significant quadratic regression terms. Based on the regressions developed for each species, the predicted value of the *Y* variable was calculated at the grand mean of the independent variable to provide a comparison of the elevation of the regression lines across species (for nonlinear regressions, the slope was calculated as the first derivative of the polynomial regression equation, evaluated at the grand mean). For HTCA, the predicted value of CA at a sapling height of 2.5 m (HTCA@2.5) was calculated instead of HTCA-P, to facilitate direct comparison with previous studies (King 1990, 1991; Kohyama and Hotta 1990). ANCOVA, using linear regression for all species and designating species as fixed effects, was used to test for significance of differences in elevation and slope for each relationship.

Branch Angles. Sakai (1987) studied canopy form in 20 Japanese *Acer* species, 14 of which were included in the present study. He measured the bifurcation angle of the

Table 1: Summary of 10 allometric relationships used in this study

Relationship: X, Y	*Sample size*	*Grand mean of* X *variable*	*Species* r^2 *values*			*Nonlinear*
			Mean	*Minimum*	*Maximum*	
CA, TA	740	.28 m^2	.927	.842	.982	2
CA, TP	794	.29 m^2	.910	.806	.982	3
DM, TA	738	8.2 mm	.927	.845	.927	5
HT, CA	794	76.9 cm	.838	.658	.961	3
HT, CV	780	77.0 cm	.888	.769	.976	4
HT, DM	792	76.9 cm	.880	.752	.972	9
HT, SL	794	76.9 cm	.948	.836	.989	5
HT, TA	740	75.2 cm	.871	.795	.969	2
HT, TL	735	75.3 cm	.906	.823	.982	5
HT, TP	794	76.9 cm	.853	.706	.967	6

Note: Sample size is the total number of all saplings; there were 17 species in all cases. The grand mean of the *X* variable is the value at which the elevations of the allometric lines were compared (see text and fig. 4). Values of r^2 show mean, minimum, and maximum r^2 of the individual regressions for each allometric relationship across the 17 species. Nonlinear: number of individual species' allometric regressions that were significantly nonlinear (see text). For abbreviations, see figure 1.

terminal shoot (Bif, the angle between the leader and the dominant lateral) and the leader dominance index (Dom, the length of the leader divided by the sum of the leader and the lateral; it ranges from 0.5 for equal length branches to almost 1 when the lateral is very short). There was a negative relationship between these two parameters among the species in his study, and the two values were used to parameterize a simple model of canopy architecture that predicted characteristic differences in sapling form. For this study, the same variables were measured for the three North American species (*A. pensylvanicum, A. saccharum,* and *A. spicatum*) and were combined with Sakai's published values for comparative analysis.

Leaf, Inflorescence, and Seed Size. Leaf, twig, seed, and inflorescence size were measured from herbarium specimens, as it was not possible to obtain reproductive material for all species in the field. Five specimens of each species were selected from the collections of the Harvard University Herbaria, with at least one complete reproductive shoot present, and the following measurements were obtained: number of leaf pairs subtending the inflorescence; basal twig diameter at the bud scars below the current year growth; leaf length, leaf width, and petiole length on a representative leaf; inflorescence length (from the first branch to the most distal fruit); and peduncle length. In studies of leaf energy balance, effective leaf size (the diameter of the largest circle that can be inscribed in the leaf outline) is more relevant than total size (Horn 1971; Givnish 1978). In this study, we utilized leaf length and individual leaf area, which are more appropriate for light interception and the study of shoot allometry.

A Priori Hypotheses

A set of 11 prior predictions was chosen for explicit tests of correlated evolution among the characters available in this study; the direction of the predicted relationships was specified (positive/negative) to allow one-tailed significance testing, and sequential Bonferroni correction was employed to maintain table-wide $\alpha = 0.05$ error levels (Rice 1989). All analyses were based on correlations, as it is impossible to designate dependent and independent traits from a biological perspective.

Five relationships arising from Corner's rules were examined: H_1, twig thickness versus growing tip density per unit crown area (CATP-P, negative); H_2, twig thickness versus shoot leaf area (positive); H_3, twig thickness versus individual leaf area (positive); H_4, twig thickness versus inflorescence length (positive); and H_5, leaf + petiole length versus inflorescence + peduncle length (positive). For H_5, (leaf + petiole) and (inflorescence + peduncle) length were used to represent the length of the entire vegetative and reproductive appendages.

Four relationships between leaf size, tree height, and sapling allometry were examined as a test of whether these traits vary independently or are linked as suggested in the introduction to this article: H_6, leaf size versus crown area (HTCA@2.5, negative); H_7, mature height versus crown area (HTCA@2.5, negative); H_8, leaf area index (CATA-P) versus crown area (HTCA@2.5, negative); and H_9, leaf size versus leaf area index (CATA-P, positive). Hypotheses 6 and 7 test whether crown breadth in 2.5 m tall saplings is negatively correlated with leaf size or tree height (Givnish 1988; King 1990, 1991; Kohyama and Hotta 1990). Hypothesis 8 tests whether leaf overlap (total area vs. crown area, the allometric equivalent of leaf area index) is lower in species with the putative broad crown, shade persistence strategy (Horn 1971), and H_9 is a corollary of H_6 and H_8.

Finally, the negative correlation between sapling leader dominance and bifurcation angle (Sakai 1987) was reanalyzed, and the prediction that greater leader dominance should be correlated with narrower crowns was tested: H_{10}, leader dominance versus bifurcation angle (negative); and H_{11}, leader dominance versus crown area (HTCA@2.5, negative).

Comparative Methods

Three types of comparative analyses were conducted for this study: the quantitative convergence index (QVI, see below) was used to quantify levels of convergent evolution for each trait, based on the hypothesized phylogeny(ies); comparisons of pairs of traits, using independent contrasts, were conducted to test for correlated evolutionary change, based on a priori hypotheses as described above; and a multivariate analysis was conducted based on principal components analysis of independent contrasts to determine the primary constellations of coevolving traits among these species. Sensitivity analyses were conducted for all analyses, by examining the range of outcomes over two sets of trees (cf. Richman and Price 1992; Losos 1994; Donoghue and Ackerly 1996; Martins 1996; Abouheif 1998): a set of 16 equally parsimonious trees resulting from the phylogenetic analysis, and a set of 1,000 random trees generated by the MacClade equiprobable trees algorithm (Maddison and Maddison 1992). The Macintosh software program ACAP (Ackerly 1998*b*) was used for all analyses. ACAP calculates independent contrasts, ahistorical and contrast correlations between pairs of traits and values of QVI, and conducts significance testing of QVI based on randomization of trait values and/or trait changes; it also facilitates sensi-

tivity analyses by allowing batch processing of analyses over multiple phylogenies, using slightly modified "nexus-format" files generated by PAUP (Swofford 1993) or MacClade (Maddison and Maddison 1992).

Single Character Analyses. For each of the 32 traits, linear parsimony methods, which minimize the sum of reconstructed changes over the entire tree (Swofford and Maddison 1987), were used to calculate the minimum amount of evolutionary change (L) for each trait over the phylogeny (this is the equivalent for continuous characters of the minimum number of steps for a discrete character). For continuous traits, the algorithms for these reconstructions are identical to those for ordered, discrete traits. We define a new index, the quantitative convergence index (QVI), to quantify the amount of convergent evolution in each trait. The QVI is based on methods for ordered, discrete traits and is equivalent to 1—Retention Index (RI; Farris 1989; see review in Archie 1996). It is calculated as:

$$\mathrm{QVI}_{ik} = \frac{L_{ik} - m_i}{M_i - m_i}, \tag{1}$$

where L_{ik} is the tree length of character i on tree k, and M_i and m_i are the maximum and minimum amounts of change, respectively, given the same set of trait values over any conceivable phylogeny. These are calculated as:

$$M_i = \sum_{j=1}^{N} |X_{ij} - X_{\mathrm{median}(i)}| \tag{2}$$

and

$$m_i = X_{\max(i)} - X_{\min(i)}, \tag{3}$$

where X_{ij} is the trait value for character i and terminal taxon j, N is the number of terminal taxa, and $X_{\max(i)}$, $X_{\min(i)}$, and $X_{\mathrm{median}(i)}$ are the maximum, minimum, and median values, respectively, for trait i over all terminal taxa (Swofford and Maddison 1987). QVI varies from 0, for a trait in which phenotypically similar species are also closely related, to 1, for a trait in which similar species are distantly related and convergent evolution is maximized (cf. Maddison and Maddison 1992). In addition, for ln-transformed trait values, L_i provides a directly comparable measure of the amount of evolutionary change, as each change of one unit is equivalent to a proportional change of 2.718 times in the absolute trait value. As all traits were evaluated over the same phylogeny, differences in the total amount of evolution correspond to differences in mean rate of change among traits, though the total amount of evolutionary time represented on this phylogeny is not known.

Significance of QVI was examined using parsimony-based randomization methods, to test for levels of homoplasy greater or less than expected by chance (cf. Maddison 1990). The set of evolutionary changes for each trait was calculated from the trait values reconstructed by linear parsimony, based on the differences between basal and apical nodes of each branch. Trait evolution was then simulated by selecting changes from this set and randomly assigning them to the branches of the tree, generating a set of trait values among terminal taxa. Simulations were repeated 1,000 times, calculating QVI for each run, in order to calculate mean QVI and two-tailed critical values ($\alpha = 0.05$) to test for significant conserved and convergent trait evolution, relative to the null model. Results reported here are based on MINSTATE reconstructions (Maddison and Maddison 1992) and sampling of changes with replacement; the use of MAXSTATE reconstructions and sampling without replacement did not alter the outcomes. We also examined randomizations of the original trait values across the tips of the tree, rather than randomizing reconstructed changes. However, this approach does not incorporate the phylogenetic structure inherent in trait evolution (T. Garland, personal communication), resulting in a null expectation of very high levels of convergent evolution.

Calculation of Independent Contrasts. Phylogenetic independent contrasts (Felsenstein 1985*b*) were calculated in order to test for patterns of correlated evolutionary change among particular pairs of traits and among the entire suite of traits using principal components analysis. Independent contrasts are calculated as the difference between the trait values of sister taxa (at either terminal or internal nodes; N taxa provide $N - 1$ contrasts), providing a measure of evolutionary divergence in a trait that is independent of the divergence taking place among all other pairs of sister taxa. In order to meet the assumptions of parametric statistics, independent contrasts are usually standardized by dividing them by the standard deviation of the expected amount of change along each branch (the branch length; Garland et al. 1992). However, the determination of appropriate branch lengths is difficult, as it depends on the specification of an appropriate model of trait evolution (Garland et al. 1992). For the results reported here, contrasts were calculated on the basis of equal branch lengths; branch lengths based on Grafen's (1989) clade diversity method, on topological node depth, and on trait changes calculated with squared-change parsimony (Maddison 1991) were also examined, but in each case results were quite similar to those reported here (results not shown).

Pairwise Trait Correlations. The Pearson correlation coefficient was calculated from the species data, without considering the phylogeny, as a descriptive statistic measur-

ing the degree of association between the traits among contemporary taxa (AC = ahistorical correlation). To test the hypothesis of correlated evolution between pairs of traits, correlations of independent contrasts (CC = contrast correlation or evolutionary correlation) were calculated using the coefficient of correspondence (a correlation analysis forced through the origin, because the sign of the contrasts of each pair of data points is arbitrary; see Garland et al. 1992 for details of computation). CC in this article corresponds to the FL1P statistic in Martins and Garland (1991). Exact significance values for CC results, which were needed for Bonferonni corrections, were determined by Monte Carlo simulation, based on 1,000 randomizations of independent contrast values, to obtain null distributions for the coefficient of correspondence. Alternative null models that incorporate phylogenetic structure into the randomization process are currently under development (T. Garland, personal communication).

Principal Components Analysis. Finally, patterns of multivariate correlated evolution were examined using Principal Components Analysis (PCA, DataDesk 5.0; Velleman 1995), with independent contrasts as the raw input data. Because the sign of each contrast is arbitrary, the contrasts corresponding to each node were entered into two data rows, with the signs reversed in the second entry. This is a simple technique to guarantee that the principal components axes will pass through the origin, as required for independent contrasts. The loadings from the unrotated factor matrix were used to identify the suites of coevolving characters associated with the first two principal components.

Results

Phylogenetic Analysis

Preliminary analyses were conducted using all taxa, ITS sequence positions and indels, with and without the region of ambiguous alignment, using *Vicia, Gossypium,* and *Hibiscus* for rooting purposes. These analyses resulted in a total of 61 trees, and in the strict consensus of these trees all *Acer* species formed a clade (united by 10 unambiguous synapomorphies), with *Dipteronia* as the sister group. In all subsequent analyses, only *Dipteronia* was included for rooting purposes.

Parsimony analysis of the *Acer* ITS data set, excluding the region of ambiguous alignment and including the indel characters, resulted in 36 equally parsimonious trees of length 623 and CI = 0.58. The strict consensus of these trees indicates consistent support for several higher level lineages (e.g., sections *Palmata* and *Platanoidea*), with weak support for deeper nodes. In order to select a tree for illustration, the parsimony analysis was repeated with the ambiguous alignment region included; this resulted in two equally parsimonious trees of length 707, both of which were among the 36 trees found in the initial analysis. The consensus of these two trees, with bootstrap ($N = 100$) and decay values for each node (based on the entire sequence data set), is shown in figure 2. All branches with decay values = 1 collapse in the strict consensus of the 36 trees found in the initial analysis. Two additional species that were included in field sampling, but from which we were unable to obtain ITS sequences, were added to the phylogeny based on morphological taxonomy: *A. amoenum* was added as the sister taxon of *A. palmatum* (these are considered subspecies by van Gelderen et al. 1994), and *A. tenuifolium* was added as the sister taxon of *A. shirasawanum* (these are also considered subspecies by van Gelderen et al. 1994 and were identified as sister taxa in a morphometric analysis by Chang 1991). Note that the placement of these taxa, while based on morphological criteria, was not influenced by the ecological and allometric traits analyzed here.

The results of our phylogenetic analysis are consistent with many aspects of *Acer* morphological systematics but suggest several novel relationships. Three well-supported clades in this analysis correspond to sections *Palmata, Rubra,* and *Platanoidea* (van Gelderen et al. 1994). The species of section *Macrantha* fall into two lineages, corresponding to the series *Tegmentosa* and *Micrantha* proposed by Pojárkova (1949); these are directly linked in trees requiring one additional step. The relationships between sections *Rubra* and *Acer* (including *A. saccharum*) and between *A. macrophyllum* and section *Platanoidea* were suggested by Mai (1984). In contrast, the connections between *A. distylum* and *A. ginnala,* and between *A. spicatum* and *A. negundo,* have not been previously suggested. Our analysis also strongly supports the placement of *A. oblongum* within section *Palmata* (cf. Cho et al. 1997). Four of the six pairs of duplicate accessions (*A. buergerianum, A. platanoides, A. spicatum,* and *A. ginnala*) were strongly supported as monophyletic, while in two cases the accessions did not appear together. In the case of *A. mono,* this may reflect extensive intraspecific variation and difficulty in establishing species limits in section *Platanoidea.* The separation of *A. japonicum* accessions requires further attention; for our comparative analyses we chose our accession (number 1) because it is of Japanese origin and because the voucher specimen was available to us. Many of the deeper nodes in our ITS trees were weakly supported, highlighting the importance of sensitivity analyses that incorporate phylogenetic un-

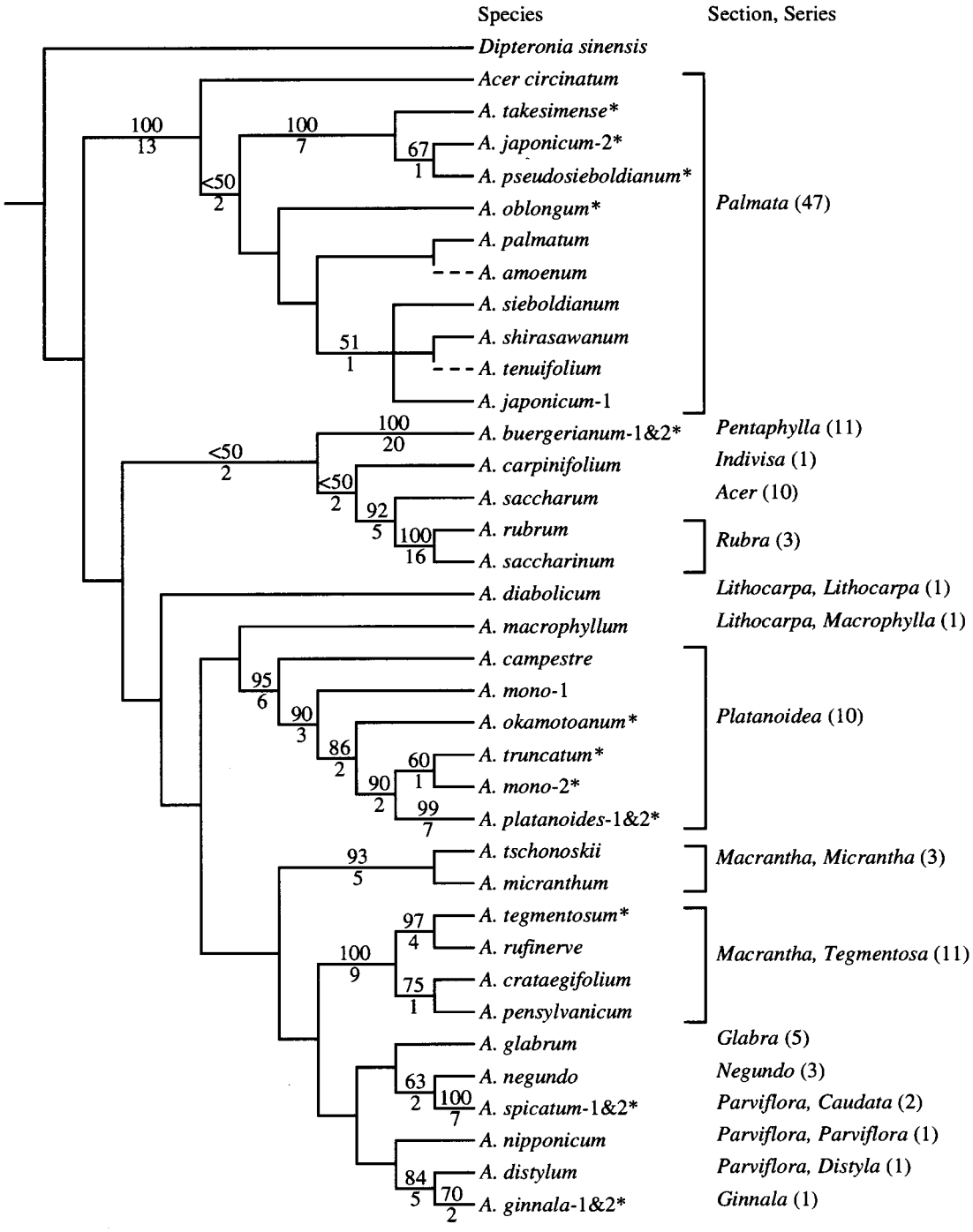

Figure 2: Consensus of two most parsimonious ITS trees representing 34 *Acer* species and *Dipteronia sinensis* (accession information is provided in appendix; accessions marked with * were obtained from GenBank). Numbers above and below branches are bootstrap ($N = 100$) and decay values, respectively; unlabeled branches had bootstrap <50 and decay = 1. Taxonomic sections and series, following van Gelderen (1994), are listed on the right, with the total number of species in parentheses. Series *Micrantha* and *Tegmentosa* of section *Macrantha* were recognized by Pojárkova (1949) but were not included in van Gelderen et al. (1994). ITS sequences were not obtained for two species included in our comparative studies (*A. amoenum* and *A. tenuifolium;* see the dashed branches), and these were added based on morphological taxonomy (see text). Four sections with a total of 10 species (*Wardiana, Trifoliata, Hyptiocarpa,* and *Pubescentia*) were not represented in the analysis.

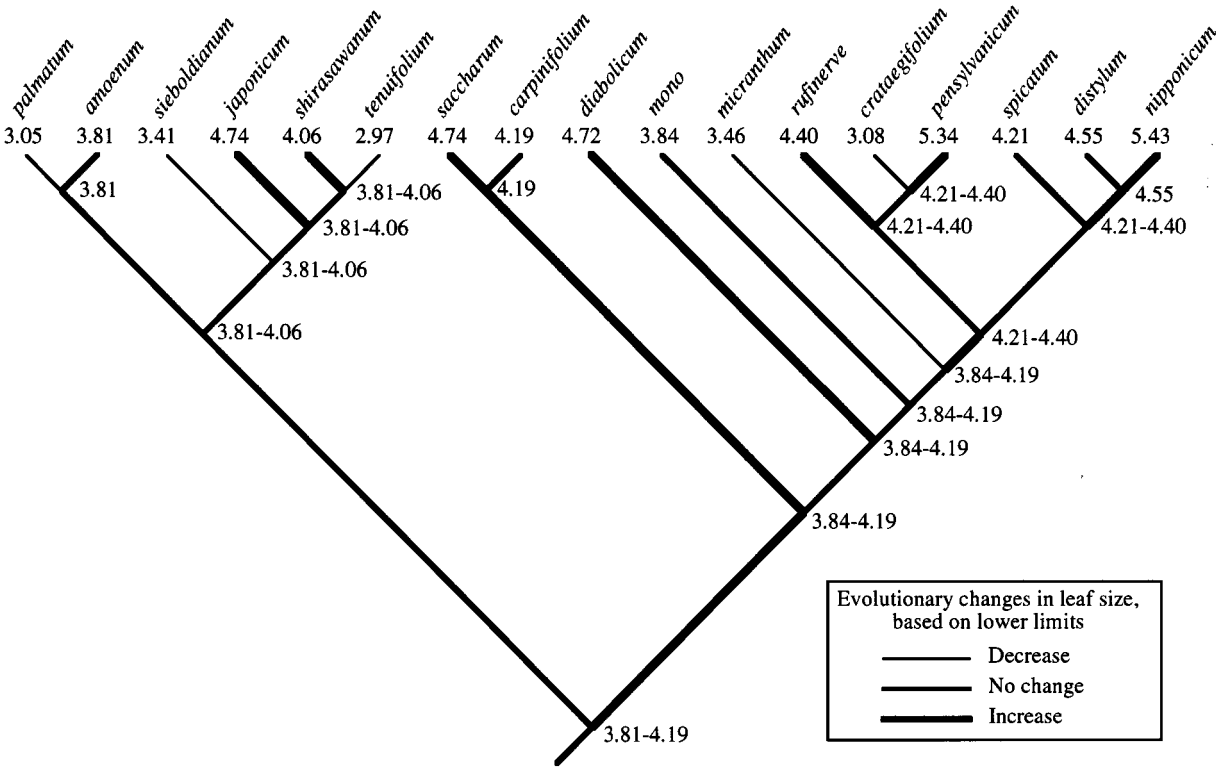

Figure 3: Tree number 1 of 16 most parsimonious trees for the 17 taxa included in the comparative study of canopy architecture. Evolution of leaf size (ln-transformed) is illustrated on this tree, based on linear parsimony. For nodes with a range of values, there are alternative solutions to the linear parsimony algorithm spanning this range. Thickness of branches indicates decrease, no change, or increase in leaf size, based on the lower limit (MINSTATE) of the parsimony reconstructions of ancestral states (obtained from MacClade, Maddison and Maddison 1992). The minimum amount of evolutionary change under linear parsimony is 8.33 ln units, corresponding to a 4,000-fold cumulative change in leaf size over the phylogeny (see text).

certainty. Definitive answers to many questions in *Acer* systematics await further study with additional genes and taxa.

For our comparative analyses, the 36 trees obtained in the analysis described above were pruned to show only the 17 species for which we obtained morphological measurements. After pruning, there were 16 topologically distinct trees. Figure 3 shows the first of these 16 trees; this corresponds to one of the two trees supported by the entire sequence data set and is designated tree number 1 for illustration. All analyses were conducted over the entire set of 16 trees to assess the sensitivity of the results to phylogenetic uncertainty.

Interspecific Character Variation

Size related traits at the leaf, inflorescence, and branch level exhibited at least a fourfold range of variation, and both seed size and leaf size varied by over an order of magnitude between species (table 2: characters 1–13). For all traits in which intraspecific variation was available to permit statistical testing, differences between species means were highly significant (ANOVA results not shown). Figure 4 illustrates intraspecific allometric relationships, in this case the regression of growing tip number on crown area for four species with contrasting tip density. Elevation of each regression line was calculated at the grand mean X value, indicated by the vertical dashed line. For the entire study, the r^2 of the individual species regressions ranged from 0.658 to 0.989, and the mean r^2 for the 10 allometric relationships ranged from 0.841 to 0.948 (table 1). The elevation values are expressed in the units of the respective Y variables (ln-transformed), so comparisons of the absolute values across the different relationships are not meaningful. The slopes express the allometric coefficients for each relationship (table 2). Values range from around 1, for isometric relationships in which the two variables increase

Table 2: Summary statistics for amount of evolutionary change (L), convergent evolution (QVI), expectation of QVI under a null model (randomized changes), and sensitivity analyses of QVI on alternative parsimonious trees and on random trees

					Species means		*Tree no. 1 (fig. 3)*			*Randomized changes, $QVI_{i,RI}$*		*Alternative parsimonious trees, $QVI_{i,j}$*		*Random trees, QVI_{RT}*			
i	*Character*	*Abbreviation*	*Units*	*Trans*	*Min*	*Max*	$L_{i,1}$	$QVI_{i,1}$	P	*Mean*	*SD*	*Min*	*Max*	*Mean*	*SD*	*Min*	*Max*
1	Mature height	MtHt	m	ln	7.0	35.0	5.94	.87*	.04	.49	.197	.62	1.00	.78	.114	.36	1
2	Seed size	SdSz	mg	ln	11.7	217	8.59	.76	.14	.47	.190	.40	.98	.78	.115	.38	1
3	Leaf + petiole length	LfPt	mm	ln	65.2	289	4.26	.76	.14	.48	.187	.56	.94	.82	.102	.42	1
4	Inflorescence + peduncle length	InfPd	mm	ln	30.6	125	3.53	.78	.11	.46	.195	.76	.96	.87	.104	.48	1
5	Petiole length	Pet	mm	ln	13.0	147	6.60	1.00*	<.001	.44	.194	.35	1.00	.86	.096	.42	1
6	Twig cross-sectional area	TCSA	mm^2	ln	.68	12.4	8.47	.78	.14	.48	.191	.71	.99	.82	.108	.35	1
7	Inflorescence length	Infl	mm	ln	14.0	97.0	5.34	.54	.71	.46	.186	.52	.94	.81	.105	.46	1
8	Leaf pairs per shoot	LfPr	count	···	1.00	3.80	6.00	1.00*	.004	.36	.258	.72	1.00	.91	.139	.22	1
9	Individual leaf area	IndLA	cm^2	ln	19.6	227	9.40	.87*	.036	.48	.186	.62	.98	.83	.105	.46	1
10	Shoot leaf area	ShLA	cm^2	ln	39.1	823	11.39	.85	.064	.47	.193	.50	.96	.84	.102	.43	1
11	Bifurcation angle	Bif	degree	···	42.7	80.3	86.80	.35	.61	.46	.188	.35	1.00	.80	.112	.37	1
12	Leader dominance	Dom	ratio	···	.57	.91	.95	.37	.81	.43	.188	.37	.90	.79	.117	.34	1
13	CATA-P	···	m^2	ln	.11	.34	2.28	.71	.16	.42	.195	.57	.96	.86	.100	.45	1
14	CATA-S	···	···	···	.86	1.03	.50	.54	.75	.46	.193	.54	.93	.80	.106	.38	1
15	CATP-P	···	count	ln	7.91	92.9	9.49	.68	.24	.45	.192	.67	.99	.80	.113	.32	1
16	CATP-S	···	···	···	.77	.96	.74	.67	.26	.45	.189	.67	.95	.81	.103	.29	1
17	DMTA-P	···	m^2	ln	.13	.31	3.15	.77	.092	.44	.186	.45	.99	.83	.105	.42	1
18	DMTA-S	···	···	···	1.96	2.62	2.04	.78	.12	.46	.192	.74	1.00	.84	.099	.46	1
19	HTCA@2.5m	···	m^2	ln	1.51	7.64	5.04	.75	.17	.46	.196	.64	1.00	.84	.102	.41	1
20	HTCA-S	···	···	···	1.44	2.17	2.44	.79	.09	.47	.184	.75	.93	.83	.103	.49	1
21	HTCV-P	···	m^3	ln	.05	.17	4.38	.72	.16	.44	.193	.62	.97	.85	.099	.39	1
22	HTCV-S	···	···	···	2.36	3.47	3.10	.70	.24	.46	.196	.70	.98	.83	.099	.47	1
23	HTDM-P	···	mm	ln	6.38	12.6	1.66	.58	.57	.47	.190	.58	1.00	.80	.107	.41	1
24	HTDM-S	···	···	···	.65	.93	1.05	.94*	.006	.47	.183	.58	.95	.79	.111	.36	1
25	HTSL-P	···	cm	ln	86.4	119	1.30	.87*	.018	.41	.186	.66	.96	.83	.101	.37	1
26	HTSL-S	···	···	···	.91	1.17	.95	.62	.43	.47	.193	.62	.97	.85	.096	.50	1
27	HTTA-P	···	m^2	ln	.09	.48	4.09	.63	.35	.44	.191	.62	.99	.87	.090	.45	1
28	HTTA-S	···	···	···	1.54	2.24	2.83	.84*	.036	.48	.187	.51	.92	.81	.106	.44	1
29	HTTL-P	···	cm	ln	143	861	4.54	.51	.65	.42	.187	.51	.94	.78	.114	.34	1
30	HTTL-S	···	···	···	1.42	2.01	2.66	.73	.13	.40	.204	.73	.96	.85	.102	.43	1
31	HTTP-P	···	count	ln	4.51	193	11.07	.64	.39	.46	.198	.49	.92	.78	.116	.32	1
32	HTTP-S	···	···	···	1.28	2.09	3.66	.83	.072	.45	.196	.76	.98	.84	.111	.35	1
Minimum		···	···	···	···	···	···	.35	···	.36	.183	.35	.90	.78	.090	.22	1
Maximum		···	···	···	···	···	···	1.00	···	.49	.258	.76	1.00	.91	.139	.50	1
Average		···	···	···	···	···	···	.73	···	.45	.193	.59	.97	.83	.106	.40	1

Note: Units: slopes of allometric equations are unitless because both axes were ln-transformed. Min, max: minimum and maximum species values; back transformed for ln-transformed variables; $L_{i,1}$, $QVI_{i,1}$: tree length and quantitative convergence index for character *i* on tree number 1 (fig. 3). *P*: two-tailed probability values for departure of $QVI_{i,1}$ from random expectation. $QVI_{i,RI}$ (mean, SD): QVI for 1,000 randomizations of trait changes on tree number 1. $QVI_{i,j}$ (min and max): QVI values over 16 alternative equally parsimonious *Acer* phylogenies. QVI_{RT} (mean, SD, min, and max): QVI values over 1,000 random phylogenies.

* $P < .05$.

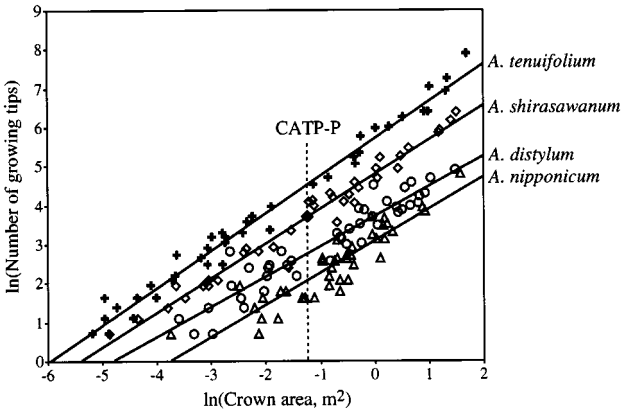

Figure 4: Illustration of allometric relationships for growing tip number (TP) versus crown area (CA) for four species with contrasting tip density. The dotted line indicates the weighted mean value of crown area for all species, where the elevation of each allometric regression was calculated to determine CATA-P. The r^2 for the four relationships illustrated here were (top to bottom) 0.982, 0.970, 0.895, and 0.820.

in proportion to each other (e.g., HTDM, stem diameter vs. height), to around 3, indicating that the dependent variable increases in proportion to the third power of the independent variable (e.g., HTCV, crown volume vs. height). ANCOVA (not taking into account nonlinear relationships) indicated that there were highly significant differences among species in both the slope and elevation of all 10 relationships. Due to the significant differences among slopes, differences in the elevation of the species regressions may not be maintained over the entire range of the independent variables.

Character Evolution and Homoplasy

The calculation of minimum, maximum, and reconstructed amount of evolutionary change, under linear parsimony, is illustrated for leaf size (fig. 3; character 9 in table 2). Among the 17 species included in this study, mean individual leaf area (ln-transformed) ranged from 2.97 (ln[19.5 cm^2]) in *A. tenuifolium* to 5.43 (ln[227 cm^2]) in *A. nipponicum*. The minimum amount of evolution that could account for this variation (m_i, eq. [1]) is the range of values, equal to 2.46 or a 12-fold range in leaf size. The maximum amount of change (M_i, eq. [2]) that could have occurred given the observed leaf size value is 10.43, corresponding to cumulative changes of 34,000-fold. This maximum change, representing the highest possible level of convergent evolution, would be observed on a phylogeny in which the species with the most disparate leaf sizes (*A. tenuifolium* and *A. nipponicum*) were sister taxa, then the next most disparate taxa (*A. palmatum* and *A. pensylvanicum*) were paired, and so on to construct the overall phylogeny (Maddison and Maddison 1992). The reconstructed evolution of leaf size on tree number one ($L_{9,1}$) was 8.33 ln units, corresponding to a 4,000-fold cumulative change over all lineages. Therefore, $QVI_{9,1} = 0.87$, suggesting a very high level of convergent evolution in leaf size. The null expectation of QVI based on 1,000 randomizations of reconstructed evolutionary changes in leaf size on tree number 1 ($QVI_{9,R1}$) was 0.48 ($\pm$0.186 SD), and the observed value of 0.87 was significant relative to the null distribution at $P = .036$. Values of QVI over the 16 parsimonious trees ranged from 0.62 to 0.98, indicating that estimates of convergence are highly sensitive to alternative trees. Over the 1,000 random trees, QVI ranged from 0.46 to 1, with a mean of 0.83 ($\pm$0.11 SD).

Table 2 provides summary statistics for the evolution of all 32 traits. Overall, the convergence index ($QVI_{i,1}$) ranged from 0.35 (for bifurcation angle) to 1 (for petiole length and the number of leaf pairs per shoot), with an average of 0.72, based on tree number 1. Values based on randomized trait changes ($QVI_{i,1}$ R1) ranged from 0.36 to 0.49, with an average of 0.45. Seven traits (including mature height and leaf size; see table 2) exhibited significantly elevated convergence, but no traits were significantly conserved, based on a two-tailed, $P = .05$ significance level. However, for all 32 traits, there was a wide range of QVI values over the 16 parsimonious trees, and there was no case where significant trait convergence was observed across all of the alternative trees. Means and standard deviations of QVI over 1,000 random trees were much higher than those for the randomized changes, and in fact were identical to the values obtained by randomizing trait values themselves across the tips of a single phylogeny (results not shown). Minimum and maximum values of QVI over random trees ranged from $\leq$0.5 to 1 in all cases, again illustrating the enormous importance of the phylogenetic hypothesis for estimating levels of convergent evolution.

Minimum, maximum, and reconstructed amounts of change can be compared among traits measured in similar units or on a proportional scale as provided by ln-transformed data. For the 19 ln-transformed size traits (including the predicted values of the allometric relationships) the minimum amount of evolution (m_i), ranged from 0.42 (1.5-fold, for HTSL-P) to 3.73 (41.6-fold, for HTTP-P). The reconstructed amount of evolutionary change on tree number 1 ($L_{i,1}$) ranged from 1.13 (3.1-fold, again for HTSL-P) to 13.02 (4.5×10^5–fold, again for HTTP-P). Among these 19 traits, there was no correlation between $QVI_{i,1}$ and $L_{i,1}$ ($R = -0.035$, $P > .5$), the level of convergent evolution, and the amount of evolutionary change, respectively. For the slopes of the 10 allo-

Table 3: Tests of 11 predictions of correlated character evolution in species of *Acer*

				Tree no. 1 (fig. 3)			*Alternative parsimonious trees*					
							CC		*Number*	*Over 1,000 random trees, CC_{RT}*		
Test	*Trait 1*	*Trait 2*	*Pred*	*AC*	*CC*	P	*Minimum*	*Maximum*	*Significant*	$\bar{X}$ (±*SD*)	*Minimum*	*Maximum*
H_1	TCSA	CATP-P	−	−.936	−.924	<.001**	−.935	−.920	16	−.935 (±.018)	−.974	−.863
H_2	TCSA	ShLA	+	.946	.943	<.001**	.931	.955	16	.944 (±.016)	.878	.978
H_3	TCSA	IndLA	+	.889	.885	<.001**	.882	.909	16	.888 (±.030)	.728	.952
H_4	TCSA	Infl	+	.621	.590	.010[a]	.484	.657	11	.617 (±.085)	.278	.857
H_5	LfPt	InflPd	+	.680	.742	<.001**	.663	.769	15	.677 (±.074)	.373	.871
H_6	IndLA	HTCA@2.5	−	−.316	−.123	.235[a]	−.137	−.015	0	−.312 (±.124)	−.698	.102
H_7	MatHt	HTCA@2.5	−	−.195	−.453	.060[a]	−.453	−.223	0	−.190 (±.122)	−.564	.224
H_8	CATA-P	HTCA@2.5	−	.113	.083	.488[a]	.040	.186	0	.109 (±.136)	−.371	.542
H_9	IndLA	CATA-P	+	.614	.718	.001*	.718	.803	16	.611 (±.082)	.324	.832
H_{10}	Bif	Dom	−	−.796	−.287	.088[a]	−.407	−.025	0	−.793 (±.053)	−.924	−.537
H_{11}	Dom	HTCA@2.5	−	−.450	−.120	.330[a]	−.190	.078	0	−.449 (±.112)	−.759	.007

Note: Character abbreviations follow table 2. Pred: direction of the predicted correlation. AC: ahistorical correlation. CC: correlation of independent contrasts based on the phylogeny shown in figure 3. *P:* one-tailed significance of CC calculated by randomization. Critical values for significance testing based on sequential Bonferroni correction (Rice 1989); $N = 17$ for all tests. CC, minimum and maximum: minimum and maximum values of CC over 16 alternative phylogenies. Number significant: number of significant CC correlations over 16 alternative phylogenies, based on randomization tests. CC_{RT}: $\bar{X}$ (±SD), minimum, and maximum values of CC calculated over a set of 1,000 randomly generated trees.

[a] Not significant; $P >$ corrected critical value.

* $P <$ corrected value.

** $P < 1/10$ of corrected value.

metric relationships, m_i ranged from 0.17 (1.18-fold, for CATA-S) to 1.4 (4.0-fold, for HTTL-S), and L_i ranged from 0.64 (1.6-fold, again for CATA-S) to 3.8 (45-fold, for HTTP-S). There was a positive but nonsignificant correlation between $QVI_{i,1}$ and $L_{i,1}$ ($R = 0.40$, $P < .3$).

Pairwise Trait Correlations

Significant correlations were observed for five of the 11 a priori tests, based on independent contrasts calculated on tree number 1 (table 3). Correlations related to Corner's rules were significant as predicted (H_1–H_3, H_5): positive correlations between twig thickness and both shoot leaf area (fig. 5*A, B*) and individual leaf area; a negative correlation between twig area and density of growing tips; a positive correlation between the length of vegetative and reproductive appendages (leaf + petiole vs. inflorescence + peduncle) (fig. 5*C, D*). The correlation between twig thickness and inflorescence length (H_4, CC = 0.59) was not significant on tree number 1 following Bonferroni correction, but was significant on 11 of the 16 alternative phylogenies. In addition, there was a highly significant positive correlation between leaf size and leaf area index (H_9). In contrast to predictions based on previous studies of allometry and tree life history, there was no correlation between leaf size and crown breadth (H_6) or between crown breadth and leaf area index (H_8), and only a weak, nonsignificant correlation between tree height and crown breadth (H_7, fig. 5*E, F*). For the first nine tests, the ahistorical correlations (AC) were generally comparable to the evolutionary correlations (CC) resulting from the comparative analysis.

The negative correlation between leader dominance index and bifurcation angles (H_{10}), as reported by Sakai (1987), was strong for the ahistorical analysis (AC = −0.796), but the magnitude of the correlation was markedly reduced in tests of independent contrasts, and the contrast correlation (CC = −0.287) was not significant (fig. 5*G, H*). Leader dominance was not correlated with crown breadth (H_{11}). The reduction in the magnitude of these correlations occurred because a low dominance index and high bifurcation angles were observed only in *A. carpinifolium* and in the five species of section *Palmata;* consequently, marked evolutionary change was concentrated in only two divergence events, subtending these taxa, providing weak evidence for a statistical association in the evolutionary changes of these traits. The strong evolutionary conservation of these two traits is confirmed by their low values of the QVI (0.37 and 0.35, respectively; table 2).

Sensitivity analyses indicated that the results of these tests were generally robust over the set of 16 parsimonious trees; the minimum and maximum values of CC measured over the alternative trees were generally within 0.1 of the value on tree number 1. Significant results remained significant over at least 11 of the 16 alternative

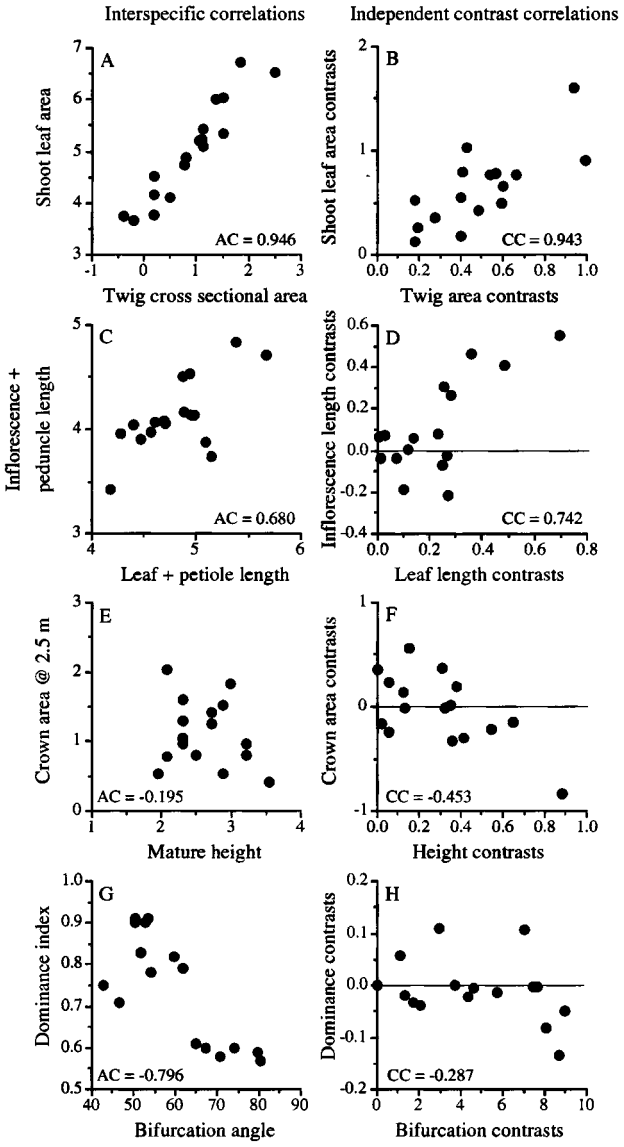

Figure 5: Illustrations of pairwise correlations between traits for species values (*AC* correlations, on left), and corresponding plots for independent contrasts (*CC* correlations, on right). *A, B,* H_2, twig cross-sectional area versus shoot leaf area; *C, D,* H_5, leaf + petiole length versus inflorescence + peduncle length; *E, F:* H_7, mature height versus crown area of 2.5-m-tall saplings (in *F,* the outlier in the lower right is the contrast between *A. saccharum* and *A. carpinifolium;* if this point is excluded *CC* declines to −0.13); *G, H,* H_9, bifurcation angle versus leader dominance index. Correlation coefficients correspond to results in table 3. All traits in *A–F* were ln-transformed, and original measurement units are listed in table 2.

trees, and the nonsignificant results were nonsignificant over all alternatives (table 3). In contrast, a wide range of evolutionary correlations was observed over the 1,000 random trees, in particular for correlations that were initially lower in magnitude. For example, for H_6 the CC on the parsimonious trees ranged from −0.14 to −0.02, but on the random trees the corresponding range was −0.70 to 0.1. This wide range illustrates that alternative phylogenies do exist that lead to markedly different conclusions regarding some of these tests. Furthermore, the mean value of CC calculated over the 1,000 random trees was virtually identical to AC, the ahistorical correlation in the absence of a phylogeny. In other words, the mean correlation over all possible phylogenies is equivalent to the correlation in the absence of any phylogenetic information, suggesting that random trees provide little guidance in estimating evolutionary correlations (Abouheif 1998; cf. Martins 1996).

Character Constellations: Principal Components Analysis

Principal components analysis of independent contrasts provides an overall picture of multivariate patterns of correlated evolution among traits (Bauwens et al. 1995; cf. Faith and Belbin 1994). The first and second axes of the PCA explained 39% and 17%, respectively, of the variation in the independent contrasts for the 32 traits in this study. The variation explained by each axis and the weightings of individual characters were quite similar for contrasts calculated over all 16 alternative trees, and the results in figure 6 show the mean (±1 SE) of the unrotated factor scores for each trait on the first two axes.

The first axis reflected Corner's rules, with very strong positive covariation among twig thickness, shoot leaf area, leaf size, and, to a lesser extent, both inflorescence length and seed size (fig. 6). These traits were negatively associated with number of growing tips per unit crown area and height (CATP-P, HTTP-P), total shoot length versus height (HTTL-P), and main stem length versus height (HTSL-P; i.e., large-leaved species had more vertically oriented saplings). The second axis of variation involved covariation in sapling crown dimensions; 12 of the top 15 variables associated with this axis were allometric parameters. The four most important traits were HTDM-P, HTTA-P, HTCV-P, and HTCA@2.5, all with negative scores, indicating covariation in stem diameter, crown area, crown volume, and total leaf area in saplings of equivalent height. Seed size was positively associated with the first axis, and negatively with the second. Mature height was positively associated with both axes, but the individual loading factors were lower than those for seed size. This reflects the weak negative relationship, as discussed above (H_7), between sapling crown size and

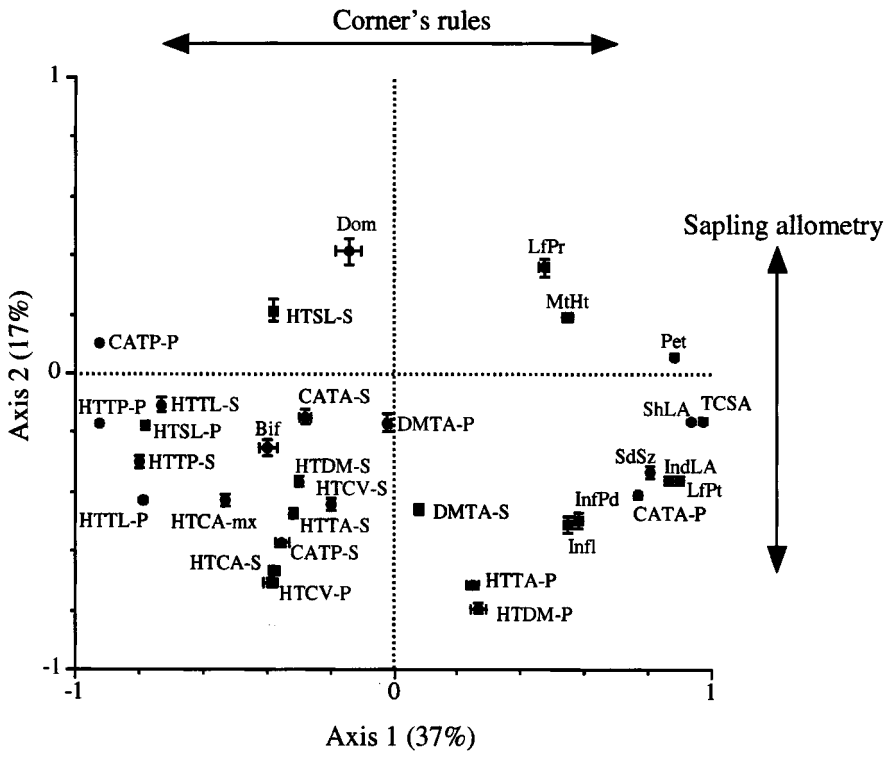

Figure 6: Arrangement of 32 traits in this study along first two principal components axes, constructed from independent contrasts. Points represent the mean factor loading (±1 SE) resulting from analyses over 16 alternative parsimonious phylogenies. Axis 1 (37% of the variation) corresponds to Corner's rules with associations among twig thickness, shoot leaf area, tip density, and related traits. Axis 2 (17%) reflects evolution of sapling allometry, particularly crown breadth, canopy leaf area, and trunk diameter, for saplings compared at a similar height. Trait abbreviations follow table 2, figure 1, and text.

species stature. Contrast correlations between individual leaf size and HTDM-P were positive and significant over eight of the 16 parsimonious trees, indicating a possible relationship between leaf size and trunk diameter; no other correlations between leaf size and these four allometric parameters were significant. As discussed below, the second axis of the PCA may be related to sapling shade tolerance, though the evidence is not conclusive.

Discussion

Allometry of Leaf, Twig, and Inflorescence Size

The most striking patterns in the evolution of canopy structure in *Acer* involve the constellation of traits associated with Corner's rules (the first axis of the PCA results). The strongest relationship was the positive correlation between twig diameter and shoot leaf area (leaf number × individual leaf size); significant positive correlations were also observed between twig diameter and both individual leaf area and inflorescence length, corresponding to Corner's second rule regarding the size of appendages (Hallé et al. 1978). Consequently, there was also a positive correlation between the evolution of leaf size and inflorescence size (we examined leaf + petiole and inflorescence + peduncle length as these are more indicative of the space these appendages occupy in the crown). There was also a very strong negative correlation, corresponding to Corner's first rule, between twig diameter and branching density, which we determined from the allometry of number of growing tips in relation to sapling height and crown area. These results confirm previous studies addressing twig thickness, leaf size, and branch density (e.g., White 1983*a*) and regarding the associations between leaf and inflorescence size (Midgley and Bond 1989). The evolution of larger leaves, thicker twigs, and sparser branching was also correlated with greater seed size and, to a lesser extent, with maximum tree height (fig. 6).

Early work on branch and appendage size in plants focused on developmental constraints and ontogenetic changes related to meristem size, which would result in large inflorescences and leaves on large shoots (Sinnott 1921; Troll 1937, 1939; see discussion in Chazdon 1991). However, there are various exceptions of plants with large axes producing narrow, often strap-like leaves (e.g., some *Espeletia* species), suggesting that meristem size

may put an upper limit on leaf size, but not a lower limit. A variety of adaptive explanations have also been considered (White 1983*a;* Primack 1987; Chazdon 1991), including the following: twig thickness should scale with the total mass of leaves and reproductive structures to maintain biomechanical stability under the stress of weight and wind (Niklas 1993, 1994); larger leaf area requires greater xylem area for supply of water, also leading to a larger twig (Shinozaki et al. 1964); and if the leaves on a branch are the primary carbon source for fruit maturation, then leaf size (scaled by photosynthetic rate) may be directly related to inflorescence size and total fruit mass (Primack 1987). It is likely that all of these factors play a role, depending on the particular environmental and life-history characteristics of different groups of species, but critical tests to distinguish their relative importance have not been conducted.

In addition, none of the hypotheses above explain the correlation of leaf and branch size with branching density. The number of growing tips on a plant limits the number of locations for production of both leaves and inflorescences (particularly if inflorescences are terminal on the branches). As a result, there may be simultaneous size/number trade-offs for leaves and inflorescences in relation to whole plant leaf area and reproductive output, respectively (cf. Venable 1996). Thus strong selection on either leaf size or inflorescence size could drive the evolution of this constellation of characters. Inflorescence size and number can influence both male and female reproductive success, depending on pollination mechanisms and breeding system (Schoen and Dubuc 1990; Fishbein and Venable 1996). In the dioecious South African genus *Leucadendron,* Bond and Midgley (1988) observed marked sexual dimorphism in inflorescence size, twig thickness, and leaf size and suggested that the dimorphism is the result of sexual selection on floral display and pollination success. *Acer* exhibits a complex array of breeding systems (de Jong 1976) and pollination biology (Matsui 1991). It is possible that the evolution of these reproductive traits, and their effects on inflorescence size, have been important factors in the evolution of leaf size and canopy architecture, but we do not have direct evidence for this hypothesis at this point.

Seed size and maximum tree height in *Acer* were also positively correlated with twig diameter and associated traits (fig. 6, pairwise correlations not shown). Positive interspecific correlations between seed size and leaf size have been reported in several genera (Primack 1987; Andersson 1993), but these relationships have not figured prominently in the literature on the comparative ecology of seed size (e.g., Westoby et al. 1996). Seed size in *Acer* was also positively correlated with species height (pairwise correlation based on independent contrasts, results not shown). Thompson and Rabinowitz (1989) hypothesized that in species with wind-dispersed seeds (such as *Acer*), larger plants would potentially have larger seeds because the greater height of release would compensate for the reduced dispersability of the larger seed. Rees (1996) found a significant correlation (based on the analysis of independent contrasts) between seed size and plant height in wind-dispersed species of the Sheffield flora, but not in animal-dispersed ones, supporting this hypothesis.

Sapling Allometry and Tree Life History

The traits associated with the second PCA axis are all related to the allometry of sapling crown dimensions, including positive correlations among total leaf area, projected crown area, and trunk diameter (the pairwise contrast correlation for HTTA-P and HTDM-P was 0.75). These are precisely the traits that various authors have suggested are related to dynamic strategies of light harvesting in the forest understory (Kohyama 1987; Kohyama and Hotta 1990; Givnish 1988; King 1990, 1991). Species with broad crowns (relative to height) maximize current light harvesting in the shade; those with narrow crowns reduce light interception but maximize the opportunity to exploit increases in light availability associated with gap formation (Kohyama and Hotta 1990; cf. Sakai 1995). On the basis of our quantitative results alone, we cannot identify the life-history significance of this variation. However, based on knowledge of the individual species ecology, it does appear that crown size is related to shade tolerance. (Note that here we address trait values in the terminal taxa, rather than the independent contrasts that are the inputs to the PCA.) Four of the five species with smallest canopy leaf area, *A. crataegifolium, A. mono, A. micranthum,* and *A. saccharum,* are understory to canopy species that grow rapidly in gaps and either reproduce at small stature (Ogata 1965; D. Ackerly, unpublished observations) or reach maturity in the canopy after several gap opening and closure events (Canham 1985; Peters et al. 1995). The five species with the largest canopy leaf area are *A. shirasawanum, A. tenuifolium, A. carpinifolium, A. japonicum,* and *A. pensylvanicum,* all considered moderately to strongly shade tolerant (e.g., Ogata 1965; Hayashi 1969; Hibbs and Wilson 1980). Correlations with leaf thickness provide additional, though weak, support for this interpretation. In temperate species, leaves are generally thinner in more shade-tolerant species (Givnish 1988; Niinemets and Kalevi 1994; but see Reich et al. 1992). For 12 of the species in this study, which were also included in Powers's (1967) study of leaf thickness in Aceraceae species growing in a common environment, the correla-

tion between leaf thickness and total crown leaf area (HTTA-P) was −0.4 (not significant based on this small sample size), suggesting that broad crown species have thinner leaves. Based on these considerations, we tentatively conclude that the second PCA axis is associated with shade tolerance, supporting earlier studies of the importance of sapling allometry in relation to forest tree life history.

The importance of these results is that the first and second axes of the principal components analysis are, by definition, orthogonal and independent of each other. There was no correlation between leaf size and crown area, and only weak negative correlations of crown area, canopy leaf area, and stem diameter with tree height and seed size (results not shown). If the second axis is in fact connected to shade tolerance, this means that the evolution of leaf size and seed size are largely independent of shade tolerance in *Acer*. This runs counter to the view that high light environments favor smaller leaves, but in fact the relationship between leaf size and light environments is highly variable. Within species, smaller leaves are almost always observed in high light, due to direct responses to environment (except in very deep shade as overall growth declines). Across species, patterns are less consistent. In forest herbs, Givnish (1987) demonstrated that spring ephemerals, which experience high light before canopy closure, have smaller leaves than summer-growing species. However, in temperate woody plant species, Niinemets and Kalevi (1994) found only a very weak negative correlation between leaf size and growth light levels. In tropical forest trees, a wide and largely overlapping range of leaf size is observed across early and late successional species; in fact, the largest and smallest leaved species in tropical forests are often found among high light, early successionals (Ashton 1978; cf. Ackerly 1996). The large-leaved species are apparently found on sites with higher moisture and soil fertility (T. Givnish, personal communication) and possibly with less wind (P. Ashton, personal communication), but these patterns have not been carefully examined.

Overall, the results of this study suggest the relatively independent evolution of two suites of traits in *Acer,* one related to leaf size and twig thickness, and the other involving various aspects of sapling allometry. Maximum height and seed size are more strongly associated with the first set of traits, while shade tolerance and regeneration ecology may be more closely correlated with the second. Further research to resolve these patterns should focus on studies of leaf structure and function and on field studies of seedling growth and regeneration. Reich et al. (1997) have documented consistent patterns of covariation, in widely contrasting habitats, among leaf mass per area, leaf nitrogen content, leaf life span, and light saturated photosynthetic rate. These traits are also associated with whole plant allocation patterns and seedling growth rates (Reich et al. 1992) and with light environments in forest tree species (e.g., Williams et al. 1989). However, leaf size was not correlated with these functional traits (P. Reich, personal communication), again suggesting that leaf size evolution may be largely independent of these regeneration-related characteristics and that more attention must be paid to the allometric relations among leaf size, inflorescence size, branch thickness, and branching density.

Variation and Convergent Evolution

In this study, we have introduced the quantitative convergence index (QVI), a parsimony-based method derived from the consistency and retention indices (Farris 1989; Archie 1989, 1996), to evaluate levels of convergent evolution (i.e., homoplasy) in continuous ecological and morphological characters. We have introduced QVI to distinguish its application to continuous characters and to emphasize our interest in evolutionary convergence rather than the ''retention'' or ''consistency'' of traits on a phylogeny. For continuous characters, it is not possible to map discrete instances of character change or homoplasy onto the phylogeny, but the total amount of evolutionary change (analogous to number of steps) can be calculated based on either linear (Swofford and Maddison 1987; fig. 3) or squared change parsimony (Maddison 1991). We have chosen linear parsimony methods due to the simplicity of calculating minimum and maximum tree lengths; we do not suggest that this provides an intrinsically superior model of trait evolution.

QVI ranged from a low of 0.35 for leader bifurcation angle to a high of 1 in petiole length and number of leaf pairs per shoot. Traits related to Corner's rules (twig area, leaf size, etc.) and the life-history traits seed size and mature height all had relatively high QVI values, suggesting high levels of convergent evolution. The lowest values were observed for the shoot bifurcation angle and dominance index, inflorescence length, and several allometric traits (including some associated with the second axis of the PCA). The low QVI for bifurcation angle and shoot dominance reflects the evolutionary shift in branching architecture shared among species in section *Palmata.* Growth in these species is determinate and sympodial, as the apical meristem either flowers or aborts at the end of the growing season and lateral branches extend from the uppermost node. This leads to high bifurcation angles between the two laterals (65°–80°), and low dominance values (approximately 0.6) as they tend to be similar in length. In contrast, extension growth in most other species (except *A. carpinifolium,* in this study) is

monopodial, with bifurcation angles of 40°–60° and dominance values of 0.7–0.9 (Sakai 1990).

Significant convergent evolution was only detected for seven traits, and no traits were significantly conserved. Mean QVI values based on randomized changes were relatively low (0.36–0.49), due to the similarity among close relatives that occurs under a phylogenetically structured null model. In this study of 17 taxa, critical values (two-tailed, $\alpha = 0.05$) for detection of significant conserved or convergent traits were approximately 0.19 and 0.85, respectively, reflecting the broad distribution of outcomes for randomized changes. Critical values based on randomizations of an artificial data set were 0.25–0.77 on a 32-taxon tree, and 0.23–0.59 on a 100-taxon tree, indicating that the critical significance values become less stringent with increasing number of taxa. Results of randomizations are also sensitive to tree topology and the distribution of trait changes (results not shown), so simulation methods are the only reliable approach to significance testing. It is important to note that randomization of trait values on the tips of the tree, rather than randomization of changes on the branches, led to much higher values of QVI as there is no tendency for close relatives to be phenotypically similar. Analyses over random trees resulted in an identical outcome because species are paired with each other in the phylogeny without respect to their phenotypic resemblance.

For traits measured on a ln-transformed scale, and for the slopes of the allometric relationships, there was not a significant relationship between QVI and the total amount of reconstructed evolutionary change (L). Thus, for these traits the amount of convergent evolution is independent of the total amount of evolutionary change (and hence the mean rate of evolution, since all traits were evaluated over the same phylogeny). This contrasts with simulations of discrete character evolution, in which greater rates of evolution result in more frequent reversals among the limited set of states and thus greater homoplasy (Givnish and Sytsma 1997).

Independent Contrasts and Correlations

The discussion of trait correlations above focused on the correlations between traits derived from the analysis of independent contrasts. Overall, the results obtained from the phylogenetic analyses were comparable to ahistorical correlations calculated directly from the species values (cf. values of AC with CC in table 3). Ricklefs and Starck (1996) and Price (1997) recently reviewed applications of the independent contrast method and also found a strong correspondence of the results of both correlation and regression analyses conducted with and without consideration of phylogeny. These results are consistent with theoretical expectations under the Brownian motion model. If two traits evolve with a correlation ρ between the changes occurring in each generation, then the expected value of both the ahistorical and the contrast correlations will also equal ρ. However, the variance in the correlation coefficients resulting from multiple evolutionary "runs" will be much greater for the ahistorical correlation (Martins and Garland 1991). As a result, discrepancies between the ahistorical correlations and evolutionary correlations are to be expected, although there is little or no overall bias in the direction of the differences (cf. Price 1997). On the one hand, divergences in deep nodes, coupled with reduced divergence within the descendent lineages, can create strong correlations among traits in extant taxa, even if the correlations in the underlying evolutionary changes are weak. This is the pattern that is illustrated by Felsenstein (1985*b*, fig. 7) and Maddison and Maddison (1992, p. 28) and that is most frequently invoked to justify the importance of calculating independent contrasts. On the other hand, the converse can also happen, where a deep divergence masks subsequent correlated evolutionary change such that correlations among extant taxa are weakened. The differences in the outcome of analyses conducted with and without a phylogeny are of considerable interest and may reveal important patterns in the evolution of a trait or potential departures from the Brownian motion model that deserve further attention (Price 1997).

Several authors have argued that if there is no significant "phylogenetic effect" on variation in a particular trait, then analyses using independent contrasts or other phylogenetic methods are not necessary. For example, Gittleman and Luh (1992) suggested that traits of interest first be examined using hierarchical ANOVA, and if most variation is found at the species level, then the influence of common descent is low and the ahistorical correlations may be a reliable guide to correlated evolution. We have found some support for this proposition based on our calculations of QVI (which avoids the problems of taxonomic ranks associated with hierarchical ANOVA). Based on all 32 traits, we calculated 496 pairwise correlations with and without consideration of the phylogeny (AC vs. CC, fig. 7*A*), and then calculated the absolute value of the difference between the two coefficients as a measure of the discrepancy between the ahistorical and phylogenetic correlation analysis. A regression of this difference versus the mean QVI for the two traits involved in each correlation was negative and highly significant ($P < .001$), though it explained only a moderate portion of the variance ($r^2 = 0.249$, fig. 7*B*). Therefore, for traits with more homoplasy, the ahistorical and evolutionary correlations tended to be more similar, but individual cases can still vary considerably in their outcome. It is

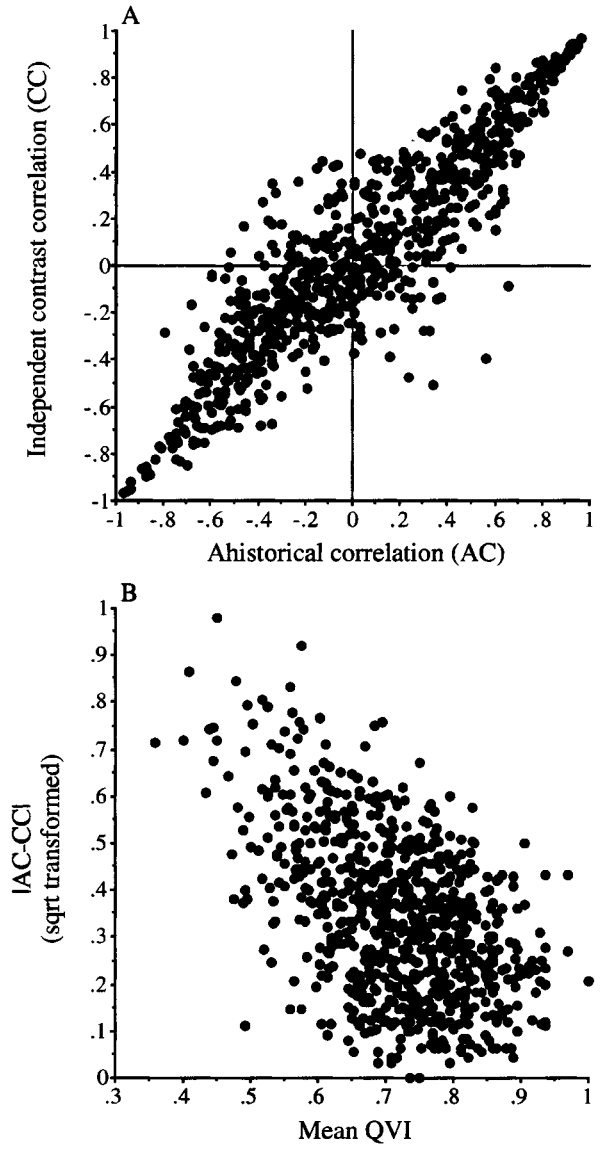

Figure 7: *A,* Scatterplot of the ahistorical correlation (*AC*) vs. contrast correlation (*CC*) for all 496 pairwise combinations of the 32 traits in this study (cf. Price 1997, fig. 1; and Ricklefs and Starck 1996, fig. 1). *B,* Plot of mean quantitative convergence index (QVI) of the two traits in each correlation versus the absolute value of the difference between *AC* and *CC* (square-root transformed, $r^2 = 0.25$, $N = 496$). This plot illustrates that for traits with greater homoplasy, the discrepancies between correlations calculated with and without consideration of the phylogeny are reduced.

worth remembering that the calculation of QVI or hierarchical ANOVA require a phylogenetic hypothesis to begin with (albeit a crude one for the latter approach), so we recommend incorporating whatever phylogenetic information is available into comparative tests.

Phylogenetic Sensitivity, Random Trees, and Randomization Tests

The correlation analyses conducted for this study were examined over a set of 16 alternative, equally parsimonious phylogenies resulting from the phylogenetic analysis of ITS sequence data and also over a set of 1,000 random trees generated by the MacClade equiprobable trees algorithm. The correlation results were quite robust over the alternative trees, similar to our results for over 7,000 alternative seed plant *rbc*L phylogenies (Donoghue and Ackerly 1996). One of the features of independent contrasts is that they are calculated from the tips down and are not influenced by changes in ancestral or sister lineages. As a result, the movement of a particular clade within the phylogeny will only alter the contrasts in nodes ancestral to the clade's former and subsequent position. Therefore, rearrangements of major groups within a phylogeny may have the least effect on the overall analysis because they will affect the fewest individual contrast values. This is of particular importance in this study, in which the deeper nodes of the phylogeny are least well supported. The results of the correlation analyses were also fairly robust to the alternative methods of calculating branch lengths and contrasts (results not shown; cf. Martins and Garland 1991; Diaz-Uriarte and Garland 1996).

In contrast, there was a fairly wide range of outcomes for tests conducted over the 1,000 randomly constructed trees (see table 3). Martins (1996) suggested that analyses over random trees could provide a provisional estimate of the evolutionary correlation between two traits, in the absence of a phylogenetic hypothesis. However, the mean correlation over a large set of random trees is equivalent to the ahistorical correlation calculated in the absence of a phylogeny (table 3; Donoghue and Ackerly 1996; Abouheif 1998); in addition, the confidence intervals calculated based on random trees are extremely broad, leading to very high Type II error rates if this approach is used for significance testing (Abouheif 1998). The distribution of contrast correlations on random trees emphasizes the potential range of outcomes, and this could prove useful when no phylogeny is available to help decide whether and how much phylogenetic information is needed (Losos 1994). We only observed one test in which the correlations on the most parsimonious trees fell outside the range of outcomes over the random trees (test H_{10}, table 3). Because the mean correlation on the ran-

dom trees approximates the ahistorical correlation, this occurs when there is a large discrepancy between the ahistorical and evolutionary correlations (AC and CC). As shown above, this discrepancy is most likely for traits with low homoplasy. Low levels of homoplasy may also suggest that the Brownian motion model of trait evolution is not a good choice; Brownian motion is inherently Markovian and should lead to repeated evolutionary reversals and parallelism. This suggests a paradoxical situation: if two traits do exhibit Brownian motion, the ahistorical and evolutionary correlations on average should generate the same result (Pagel 1993). On the other hand, if the two correlations are very different, then the underlying model of Brownian motion that was used to conduct the analysis is called into question, so the result may be least reliable in the very situation in which it is most interesting. Recently, Price (1997) provided an alternative model of correlated evolution based on niche partitioning that predicts consistent differences in the ahistorical and independent contrast correlations. Methods to distinguish random versus biologically meaningful variation between these measures of trait correlations need to be developed.

Overall, the development of explicit statistical models of character evolution in a phylogenetic context has been extremely valuable as it has sharpened the distinction between correlated evolutionary change and correlated phenotypic states in the resulting species. Further work is required to understand the relationship between correlated divergence, as measured by independent contrasts, and convergent evolution (e.g., the evolution of similar character state values from different ancestral conditions). Future work in this area needs to incorporate all of these components of evolution, the historical process and the resulting contemporary patterns, into analytical models for the analysis of trait variation and covariation.

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APPENDIX

Table A1: List of species included in this study

Family or section (series)	*Species**	*Range†*	*Study sites‡ (N)*	*Accession§*	*GenBank ID‖*
Aceraceae:					
Acer (Saccharodendron)	*A. saccharum*#	ENA	HF, L (78)	MOR 113-88	AF020363
Ginnala	*A. ginnala***–1	EAs	· · ·	MOR 308-83	AF020364
	A. ginnala–2	· · ·	· · ·	· · ·	U89912††
Glabra	*A. glabrum*	WNA	· · ·	AA 15-80-A	AF056017
Indivisa	*A. carpinifolium*#	J	S, C, O (43)	AA 10648	AF020365
Lithocarpa (Lithocarpa)	*A. diabolicum*#	J	C (36)	AA 2625-A	AF020366
Lithocarpa (Macrophylla)	*A. macrophyllum*	WNA	· · ·	MOR 545-83	AF020367
Macrantha	*A. crataegifolium*#	J	O (40)	MA 87-001-A	AF020368
	A. micranthum#	J	K, C, A (40)	WPA 848-40	AF020369
	A. pensylvanicum#	ENA	HF, L (76)	MOR 111-82	AF020370
	A. rufinerve#	J	S, K, C, O (48)	AA 1430-77-D	AF020371
	A. tegmentosum	EAs	· · ·	· · ·	U98807
	A. tschonoskii	EAs	· · ·	MOR 289-73	AF020372
Negundo	*A. negundo*	NA	· · ·	· · ·	U89909
Palmata (Palmata)	*A. amoenum*#‡‡	EAs	H, O (40)	· · ·	No sequence
	A. japonicum#–1	J	S, H (51)	MOR 572-53	AF020374
	A. japonicum–2	· · ·	· · ·	· · ·	U57776
	A. palmatum#	EAs	O, A (16)	AA 585-88	AF020375

Table A1 (*Continued*)

Family or section (series)	*Species**	*Range†*	*Study sites‡ (N)*	*Accession§*	*GenBank ID‖*
	A. shirasawanum#	J	C (40)	AA 270-81-A	AF020376
	A. sieboldianum#	J	S, O (40)	AA 3919-A	AF020377
	A. tenuifolium#,§§	J	O (40)	···	No sequence
	A. circinatum	WNA	···	AA 724-72-A	AF020373
	A. pseudosieboldianum	EAs	···	···	U57778
	A. takesimense‖‖	Kor	···	···	U57777
Parviflora (Caudata)	*A. spicatum*#–1	ENA	HF, L (78)	AA 945-79-C	AF020378
	A. spicatum–2	···	···	···	U89911
Parviflora (Distyla)	*A. distylum*#	J	K, C, O (42)	AA 1184-77-A	AF020379
Parviflora (Parviflora)	*A. nipponicum*#	J	K, A (40)	S. Tsugaru 13672##	AF020380
Pentaphylla (Trifida)	*A. buergerianum*–1	EAs	···	···	U89908
	A. buergerianum–2	···	···	MA 32-1676-A	AF020381
	A. oblongum	EAs	···	···	U89910
Platanoidea	*A. mono*#–1	EAs	S, K, H, O (69)	AA 5358-A	AF020383
	A. mono–2	···	···	···	U57775
	A. campestre	Eur	···	MOR 531-38	AF020382
	A. okamotoanum	EAs	···	···	U57772
	A. platanoides–1	Eur	···	MOR 153-57	AF020384
	A. platanoides–2	···	···	···	U57773
	A. truncatum	EAs	···	···	U57774
Rubra	*A. rubrum*	ENA	···	MOR 322-81	AF020385
	A. saccharinum	ENA	···	MOR 339-81	AF056018
	Dipteronia sinensis	CAs	···	WPA 500-70	AF020386
Fabaceae	*Vicia faba*	···	···	···	X17535
Malvaceae	*Gossypium trilobum*	···	···	···	U12723
	Hibiscus costatus	···	···	···	U56774

* Nomenclature follows van Gelderen et al. (1994), with exceptions as noted.

† ENA: Eastern North America; WNA: Western North America; J: Japan; EAs: East Asia; Kor: Korea; CAs: Central Asia; Eur: Europe.

‡ Study sites and sample size for allometric samples are listed. USA: HF: Harvard Forest, Petersham, Mass. (42°26′N, 72°11′W); L: Lyme Center, N.H. (43°50′N, 72°4′W); JAPAN: S: Sendai Botanic Garden, Sendai (38°11′N, 140°55′E); K: Mount Kurikoma National Park (38°53′N, 140°45′E); H: Mount Hakkoda Biological Station and Oirase Gorge (40°38′N, 140°54′E); C: Lake Chuzenji, Nikko National Park (36°44′N, 139°32′E); O: Ogawa Forest Reserve, National Forestry and Forest Products Research Institute (36°55′N, 140°35′E); A: Ashiu Forest Reserve, Kyoto University (35°19′N, 135°46′E).

§ Accession numbers for living collections from which DNA samples were obtained. AA: Arnold Arboretum, Boston, Mass.; MA: Morris Arboretum, Philadelphia, Pa.; MOR: Morton Arboretum, Lisle, Ill.; WPA: Washington Park Arboretum, Seattle, Wash.

‖ GenBank accession numbers starting with "AF" indicate new sequences obtained in this study. Accessions of *Acer* starting with "U" are from Suh et al. (1996) and Cho et al. (1997).

Species included in the comparative analyses.

** *A. tataricum* subsp. *ginnala* in van Gelderen et al. (1994).

†† Sequence accession U95779 appended to U89912 for analysis.

‡‡ *A. palmatum* subsp. *amoenum* in van Gelderen et al. (1994).

§§ *A. shirasawanum* subsp. *tenuifolium* in van Gelderen et al. (1994).

‖‖ *A. pseudosieboldianum* subsp. *takesimense* in van Gelderen et al. (1994).

Specimen in Arnold Arboretum Herbarium (A), Harvard University.

Literature Cited

Abouheif, E. 1998. Random trees and the comparative method: a cautionary tale. Evolution 52:1197–1204.

Ackerly, D. D. 1996. Canopy structure and dynamics: integration of growth processes in tropical pioneer trees. Pages 619–658 *in* S. S. Mulkey, R. L. Chazdon, and A. P. Smith, eds. Tropical forest plant ecophysiology. Chapman & Hall, London.

———. 1998*a*. Ackerly and Donoghue, *Acer* data. http://www.stanford.edu/~dackerly/acerdata.html.

———. 1998*b*. Another comparative analysis program, v2. http://www.stanford.edu/~dackerly/ACAP.html.

Andersson, S. 1993. Population differentiation in *Crepis tectorum* (Asteraceae): patterns of correlation among characters. Biological Journal of the Linnean Society 49:185–194.

Applied Biosystems. 1992. Data Collection 1.1.1, Analysis 1.1.1, Seq Ed 1.0.3. Applied Biosystems, Foster City, Calif.

Archie, J. W. 1989. Homoplasy excess ratios: new indices for measuring levels of homoplasy in phylogenetic systematics and a critique of the consistency index. Systematic Zoology 38:253–269.

———. 1996. Measures of homoplasy. Pages 153–188 *in* M. J. Sanderson and L. Hufford, eds. Homoplasy: the recurrence of similarity in evolution. Academic Press, San Diego, Calif.

Ashton, P. S. 1978. Crown characteristics of tropical trees. Pages 591–615 *in* P. B. Tomlinson and M. H. Zimmerman, eds. Tropical trees as living systems. Cambridge University Press, Cambridge.

Baldwin, B. G., M. J. Sanderson, J. M. Porter, M. F. Wojkiechowski, C. S. Campbell, and M. J. Donoghue. 1995. The ITS region of nuclear ribosomal DNA: a valuable source of evidence on angiosperm phylogeny. Annals of the Missouri Botanical Garden 82:247–277.

Bauwens, D., T. Garland, Jr., A. M. Castilla, and R. Van Damme. 1995. Evolution of sprint speed in Lacertid lizards: morphological, physiological and behavioral covariation. Evolution 49:848–863.

Bond, W., and J. Midgley. 1988. Allometry and sexual difference in leaf size. American Naturalist 131:901–910.

Bonser, S. P., and L. W. Aarssen. 1994. Plastic allometry in young sugar maples (*Acer saccharum*): adaptive responses to light availability. American Journal of Botany 81:400–406.

Boulter, M. C., J. N. Benfield, H. C. Fisher, D. A. Gee, and M. Lhotak. 1996. The evolution and global migration of Aceraceae. Philosophical Transactions of the Royal Society of London B, Biological Sciences 351: 589–603.

Bremer, K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. Evolution 42:795–803.

Canada Department of Forestry. 1963. Native trees of Canada. Duhamel, Ottawa.

Canham, C. D. 1985. Suppression and release during canopy recruitment in *Acer saccharum.* Bulletin of the Torrey Botanical Club 112:134–145.

———. 1988. Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. Ecology 69: 786–795.

Chang, C.-S. 1991. A morphometric analysis of genus *Acer* L., section *Palmata* Pax, series *Palmata.* Korean Journal of Plant Taxonomy 21:165–186.

Chazdon, R. L. 1991. Plant size and form in the understory palm genus *Geonoma:* are species variations on a theme? American Journal of Botany 78:680–694.

Cho, H.-J., S. Kim, Y. Suh, and C.-W. Park. 1997. ITS sequences of some *Acer* species and phylogenetic implication (in Korean). Korean Journal of Plant Taxonomy 26:271–291.

Coleman, J. S., K. D. M. McConnaughay, and D. D. Ackerly. 1994. Interpreting phenotypic variation in plants. Trends in Ecology & Evolution 9:187–191.

Corner, E. J. H. 1949. The Durian theory or the origin of the modern tree. Annals of Botany 13:367–414.

de Jong, P. C. 1976. Flowering and sex expression in *Acer* L.: a biosystematic study. Mededelingen Landbouwhogeschool Wageningen 76:1–201.

Delendick, T. 1981. A systematic review of the Aceraceae. Ph.D. thesis. City University of New York, New York.

Diaz-Uriarte, R., and T. Garland, Jr. 1996. Testing hypotheses of correlated evolution using phylogenetically independent contrasts: sensitivity to deviations from Brownian motion. Systematic Biology 45:27–47.

Donoghue, M. J., and D. D. Ackerly. 1996. Phylogenetic uncertainties and sensitivity analyses in comparative biology. Philosophical Transactions of the Royal Society of London B, Biological Sciences 351:1241–1249.

Donoghue, M. J., R. G. Olmstead, J. F. Smith, and J. D. Palmer. 1992. Phylogenetic relationships of Dipsacales based on *rbc*L sequences. Annals of the Missouri Botanical Garden 79:333–345.

Eriksson, T. 1995. AutoDecay, release 2.0. http://www.botan.su.se/systematik/folk/Torsten.html.

Eriksson, T., and M. J. Donoghue. 1997. Phylogenetic relationships of *Sambucus* and *Adoxa* (Adoxoideae, Adoxaceae) based on nuclear ribosomal ITS sequences and preliminary morphological data. Systematic Botany 22:555–573.

Faith, D. P., and L. Belbin. 1994. Distinguishing phylogenetic effects in multivariate models relating *Eucalyptus* convergent morphology to environment. Pages 169–188 *in* P. Eggleton and R. I. Vane-Wright, eds. Phylogenetics and ecology. Academic Press, London.

Farris, J. S. 1989. The retention index and the rescaled consistency index. Cladistics 5:417–419.

Felsenstein, J. 1985*a.* Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39:783–791.

———. 1985*b.* Phylogenies and the comparative method. American Naturalist 125:1–15.

Fishbein, M., and L. Venable. 1996. Evolution of inflorescence design: theory and data. Evolution 50:2165–2177.

Foster, S. A., and C. H. Janson. 1985. The relationship between seed size and establishment conditions in tropical woody plants. Ecology 66:773–780.

Gadek, P. A., E. S. Fernando, C. J. Quinn, S. B. Hoot, T. Terrazas, M. C. Sheahan, and M. W. Chase. 1996. Sapindales: molecular delimitation and infraordinal groups. American Journal of Botany 83:802–811.

Garland, T., Jr., P. H. Harvey, and A. R. Ives. 1992. Procedures for the analysis of comparative data using phy-

logenetically independent contrasts. Systematic Biology 41:18–32.

Gittleman, J. L., and H.-K. Luh. 1992. On comparing comparative methods. Annual Review of Ecology and Systematics 23:383–404.

Givnish, T. J. 1978. Ecological aspects of plant morphology: leaf form in relation to the environment. Acta Biotheoretika, Supplement 27:83–142.

———. 1984. Leaf and canopy adaptations in tropical forests. Pages 51–84 *in* E. Medina, H. A. Mooney, and C. Vázquez-Yanes, eds. Physiological ecology of plants of the wet tropics. Junk, The Hague.

———. 1986. Biomechanical constraints on self-thinning in plant populations. Journal of Theoretical Biology 119:139–146.

———. 1987. Comparative studies of leaf form: assessing the relative roles of selective pressures and phylogenetic constraints. New Phytologist 106:S131–S160.

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

Givnish, T. J., and K. J. Sytsma. 1997. Consistency, characters and the likelihood of correct phylogenetic inference. Molecular Phylogenetics and Evolution 7: 320–330.

Grafen, A. 1989. The phylogenetic regression. Philosophical Transactions of the Royal Society of London B, Biological Sciences 326:119–157.

Grubb, P. J., and D. J. Metcalfe. 1996. Adaptation and inertia in the Australian tropical lowland rain-forest flora: contradictory trends in intergeneric and intrageneric comparisons of seed size in relation to light demand. Functional Ecology 10:512–520.

Hallé, F., R. A. A. Oldeman, and P. B. Tomlinson. 1978. Tropical trees and forests: an architectural analysis. Springer, Berlin.

Harvey, P. H., and M. Pagel. 1991. The comparative method in evolutionary biology. Oxford University Press, Oxford.

Hayashi, Y. 1969. Illustrated guide to valuable trees in Japan (in Japanese). Seibundo Shinkosha, Tokyo.

Hibbs, D. E., and B. F. Wilson. 1980. Habitat requirements and growth of striped maple (*Acer pensylvanicum* L.). Ecology 61:490–496.

Horn, H. 1971. The adaptive geometry of trees. Princeton University Press, Princeton, N.J.

Judd, W. S., R. W. Sanders, and M. J. Donoghue. 1994. Angiosperm family pairs: preliminary phylogenetic analyses. Harvard Papers in Botany 5:1–51.

Kelly, C. K. 1995. Seed size in tropical trees: a comparative study of factors affecting seed size in Peruvian angiosperms. Oecologia (Berlin) 102:377–388.

Kikuzawa, K., H. Koyama, K. Umeki, and M. J. Lechowicz. 1996. Some evidence for an adaptive linkage between leaf phenology and shoot architecture in sapling trees. Functional Ecology 10:252–257.

King, D. 1981. Tree dimensions: maximizing the rate of height growth in dense stands. Oecologia (Berlin) 51: 351–356.

King, D. A. 1990. Allometry of saplings and understory trees of a Panamanian forest. Functional Ecology 4: 27–32.

———. 1991. Tree allometry, leaf size and adult tree size in old-growth forests of Western Oregon. Tree Physiology 9:369–381.

Kohyama, T. 1987. Significance of architecture and allometry in saplings. Functional Ecology 1:399–404.

Kohyama, T., and M. Hotta. 1990. Significance of allometry in tropical saplings. Functional Ecology 4:515–521.

Lei, T. T., and M. J. Lechowicz. 1990. Shade adaptation and shade tolerance in saplings of three *Acer* species from North America. Oecologia (Berlin) 84:224–228.

———. 1997. The photosynthetic light response of eight species of *Acer* to stimulated light regimes from the centre and edges of gaps. Functional Ecology 11: 16–23.

Losos, J. B. 1994. An approach to the analysis of comparative data when a phylogeny is unavailable or incomplete. Systematic Biology 43:117–123.

Maddison, W. P. 1990. A method for testing the correlated evolution of two binary characters: are gains or losses concentrated on certain branches of a phylogenetic tree? Evolution 44:539–557.

———. 1991. Squared-change parsimony reconstructions of ancestral states for continuous-valued characters on a phylogenetic tree. Systematic Zoology 40: 304–314.

Maddison, W. P., and D. R. Maddison. 1992. MacClade: analysis of phylogeny and character evolution, version 3. Sinauer, Sunderland, Mass.

Mai, D. H. 1984. Die Endokarpien bei der Gattung *Acer* L. Eine Biosystematische Studie. Gleditschia 11:17–46.

Martins, E. P. 1996. Conducting phylogenetic comparative studies when the phylogeny is not known. Evolution 50:12–22.

Martins, E. P., and T. Garland, Jr. 1991. Phylogenetic analyses of the correlated evolution of continuous characters: a simulation study. Evolution 45:534–557.

Matsui, K. 1991. Pollination ecology of four *Acer* species in Japan with special reference to bee pollinators. Plant Species Biology 6:117–120.

Midgley, J., and W. Bond. 1989. Leaf size and inflorescence size may be allometrically related traits. Oecologia (Berlin) 78:427–429.

Nakashizuka, T., S. Iida, T. Masaki, M. Shibata, and H. Tanaka. 1995. Evaluating increased fitness through dispersal: a comparative study on tree populations in a temperate forest, Japan. Ecoscience 2:245–251.

Niinemets, Ü., and K. Kalevi. 1994. Leaf weight per area and leaf size of 85 Estonian woody species in relation to shade tolerance and light availability. Forest Ecology and Management 70:1–10.

Niklas, K. J. 1993. The allometry of plant reproductive biomass and stem diameter. American Journal of Botany 80:461–467.

———. 1994. The allometry of safety-factors for plant height. American Journal of Botany 81:345–351.

Ogata, K. 1965. A dendrological study on the Japanese Aceraceae, with special reference to the geographical distribution. Bulletin of the Tokyo University Forests 60:1–99.

Olson, D. F., Jr., and W. J. Gabriel. 1974. *Acer* L. Maple. Pages 187–194 *in* C. S. Schopmeyer, ed. Seeds of woody plants of the United States. Agriculture Handbook 450. U.S. Department of Agriculture, Washington, D.C.

Pagel, M. D. 1992. A method for the analysis of comparative data. Journal of Theoretical Biology 156:431–442.

———. 1993. Seeking the evolutionary regression coefficient: an analysis of what comparative methods measure. Journal of Theoretical Biology 164:191–205.

Peters, R., H. Tanaka, M. Shibata, and T. Nakashizuka. 1995. Light climate and growth in shade-tolerant *Fagus crenata, Acer mono* and *Carpinus cordata.* Ecoscience 2: 67–74.

Phillips, R. 1978. Trees of North America and Europe. Random House, New York.

Pojárkova, A. I. 1949. Aceraceae. Flora USSR (English translation by Israel Program for Scientific Translation, Jerusalem) 14:443–476.

Powers, H. O. 1967. A blade tissue study of forty-seven species and varieties of Aceraceae. American Midland Naturalist 78:301–323.

Price, T. 1997. Correlated evolution and independent contrasts. Philosophical Transactions of the Royal Society of London B, Biological Sciences 352:519–529.

Primack, R. B. 1987. Relationships among flowers, fruits, and seeds. Annual Review of Ecology and Systematics 18:409–430.

Rees, M. 1996. Evolutionary ecology of seed dormancy and seed size. Philosophical Transactions of the Royal Society of London B, Biological Sciences 351:1299–1308.

Reich, P. B., M. B. Walters, and D. S. Ellsworth. 1992. Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. Ecological Monographs 62:365–392.

———. 1997. From tropics to tundra: global convergence in plant functioning. Proceedings of the National Academy of Sciences of the USA 94:13730–13734.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution 43:223–225.

Richman, A. D., and T. Price. 1992. Evolution of ecological differences in Old World warblers. Nature (London) 355:817–821.

Ricklefs, R. E., and J. M. Starck. 1996. Applications of phylogenetically independent contrasts: a mixed progress report. Oikos 77:167–172.

Sakai, S. 1987. Patterns of branching and extension growth of vigorous saplings of Japanese *Acer* species in relation to their regeneration strategies. Canadian Journal of Botany 65:1578–1585.

———. 1990. Sympodial and monopodial branching in *Acer* (Aceraceae): evolutionary trend and ecological implications. Plant Systematics and Evolution 171: 187–197.

———. 1995. Evolutionary stable growth of a sapling which waits for future gap formation under closed canopy. Evolutionary Ecology 9:444–452.

Sanderson, M. J., M. J. Donoghue, W. Piel, and T. Eriksson. 1994. Tree BASE: a prototype database of phylogenetic analysis and an interactive tool for browsing the phylogeny of life. American Journal of Botany 81: S183.

Schoen, D. J., and M. Dubuc. 1990. The evolution of inflorescence size and number: a gamete-packaging strategy in plants. American Naturalist 135:841–857.

Seelanan, T., J. F. Wendel, and A. Schnabel. 1996. Congruence and consensus in the cotton tribe: evidence from the nuclear and plastid genomes. Systematic Botany 22:259–290.

Shinozaki, K., K. Yoda, K. Hozumi, and T. Kira. 1964. A quantitative analysis of plant form—the pipe model theory. I. Basic analyses. Japanese Journal of Ecology 14:97–105.

Sinnott, E. W. 1921. The relation between body size and organ size in plants. American Naturalist 55:385–403.

Sipe, T. W., and F. A. Bazzaz. 1994. Gap partitioning among maples (*Acer*) in central New England: shoot architecture and photosynthesis. Ecology 75:2318–2332.

———. 1995. Gap partitioning among maples (*Acer*) in central New England: survival and growth. Ecology 76: 1587–1602.

Suh, Y., H.-J. Cho, S. Kim, and C.-W. Park. 1996. Comparative analysis of ITS sequences from *Acer* species (Aceraceae) in Korea. Journal of Plant Biology 39:1–8.

Swofford, D. 1993. PAUP: Phylogenetic analysis using parsimony, version 3.1.1. Smithsonian Institution Press, Washington, D.C.

Swofford, D. L., and W. P. Maddison. 1987. Reconstructing ancestral states under Wagner parsimony. Mathematical Biosciences 87:199–229.

Tanaka, H. 1995. Seed demography of three co-occurring

Acer species in a Japanese temperate deciduous forest. Journal of Vegetation Science 6:887–896.

Thomas, S. C. 1996. Asymptotic height as a predictor of growth and allometric characteristics in Malaysian rain forest trees. American Journal of Botany 83:556–566.

Thompson, J. D., D. G. Higgins, and T. J. Gibson. 1994. Clustal W: improving the sensitivity of progressive multiple sequence alignments through sequence weighting, position-specific gap penalties and weight matrix choice. Nucleic Acids Research 22:4673–4680.

Thompson, K., and D. Rabinowitz. 1989. Do big plants have big seeds? American Naturalist 133:722–728.

Troll, W. 1937. Vergleichende Morphologie der höheren Pflanzen. Erster Teil. Borntraeger, Berlin.

———. 1939. Vergleichende Morphologie der höheren Pflanzen. Zweiter Teil. Borntraeger, Berlin.

van Gelderen, D. M., P. C. de Jong, and H. J. Oterdoom. 1994. Maples of the world. Timber, Portland, Oreg.

Velleman, P. F. 1995. DataDesk, version 5.0. Data Description, Ithaca, N.Y.

Venable, D. L. 1996. Packaging and provisioning in plant reproduction. Philosophical Transactions of the Royal Society of London B, Biological Sciences 351:1319–1329.

Wendel, J. F., A. Schnabel, and T. Seelanan. 1995. An unusual ribosomal DNA sequence from *Gossypium gossypioides* reveals ancient, cryptic, intergenomic introgression. Molecular Phylogenetics and Evolution 4: 298–313.

Westoby, J., M. Leishmann, and J. Lord. 1996. Comparative ecology of seed size and dispersal. Philosophical Transactions of the Royal Society of London B, Biological Sciences 351:1309–1318.

Westoby, M. 1998. Generalization in functional plant ecology: the species-sampling problem, plant ecology strategy schemes, and phylogeny. Pages 00–00 *in* F. I. Pugnaire and F. Valladares, eds. Handbook of functional plant ecology. Dekker, New York.

Westoby, M., S. A. Cunningham, C. M. Fonseca, J. M. Overton, and I. J. Wright. 1998. Phylogeny and variation in light capture area deployed per unit investment in leaves: designs for selecting study species with a view to generalizing. Pages 539–566 *in* H. Lambers, H. Poorter, and M. M. I. Van Vuuren, eds. Inherent variation in plant growth: physiological mechanisms and ecological consequences. Backhuys, Leiden.

White, P. S. 1983*a*. Corner's rules in eastern deciduous trees: allometry and its implications for the adaptive architecture of trees. Bulletin of the Torrey Botanical Club 110:203–212.

———. 1983*b*. Evidence that temperate east North American evergreen woody plants follow Corner's rules. New Phytologist 95:139–145.

Williams, K., C. B. Field, and H. A. Mooney. 1989. Relationships among leaf construction cost, leaf longevity, and light environments in rain-forest plants of the genus *Piper*. American Naturalist 133:198–211.

Wolfe, J. A., and T. Tanai. 1987. Systematics, phylogeny, and distribution of *Acer* (maples) in the Cenozoic of western North America. Journal of the Faculty of Science of Hokkaido University, series 4, 22: 1–246.

Yokota, Y., T. Kawata, Y. Iida, A. Kato, and S. Tanifuji. 1989. Nucleotide sequences of the 5.8S rRNA gene and internal transcribed spacer regions in carrot and broad bean ribosomal DNA. Journal of Molecular Evolution 29:294–301.

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