

Architectural differences in saplings of temperate versus tropical angiosperms; consequences of the deciduous habit?

David A. King

Abstract: The architecture of saplings of temperate deciduous species of the southeastern United States was compared with that of tropical evergreen species of Central America, Borneo, and northeastern Australia. The deciduous species were more planar in the understory than were the tropical species, because of (i) more planar leaf displays within branches, (ii) a high frequency of arching, plagiotropic main stems (associated with greater plasticity in crown symmetry in relation to light), and (iii) a lower height of first branching. The deciduous species also had more planar branches than did subtropical and temperate evergreen angiosperms. This greater planarity in temperate deciduous understories may be associated with the simultaneous positioning of most leaves during a single flush in the spring. In contrast, saplings in tropical understories typically bear multiple leaf cohorts and position new leaves at the peripheries of existing leaf displays. These results and those of other studies suggest that there are adaptive links between plant architecture and phenology. Other factors, such as latitudinal variation in sun angles, may influence crown shape in overstory trees, but did not seem to be involved here, possibly because the filtering effect of the canopy results in smaller latitudinal shifts in understory illumination angles during the growing season. Thus, by favouring the deciduous habit, the cold winters and warm, humid summers of the eastern deciduous biome of North America appear to have had a notable influence on sapling architecture.

Key words: morphological plasticity, plagiotropy, stem orientation, tree architecture.

Résumé : Les auteurs ont comparé l'architecture de jeunes arbres d'espèces décidues tempérées du sud-est des États-Unis, avec celle d'espèces sempervirentes tropicales de l'Amérique Centrale, de Bornéo et du nord-est de l'Australie. Les espèces décidues de sous-étages sont plus planaires que ne le sont les espèces tropicales, dû à : (i) une disposition plus planaire des feuilles, sur la branche; (ii) une fréquence plus grande de tiges principales voûtées, plagiotropiques (associée avec une plus grande plasticité dans la symétrie du houppier, en relation avec la lumière) et; (iii) des premières branches plus basses. Les espèces décidues ont également plus de branches planaires que les angiospermes subtropicales sempervirentes tempérées. Cette planarité plus forte, dans les sous-étages des espèces décidues tempérées, peut être associée au positionnement simultané de la plupart des feuilles au cours d'une même poussée au printemps. D'autre part, les jeunes arbres des sous-étages des forêts tropicales portent typiquement de nombreuses cohortes foliaires, et placent les nouvelles feuilles aux périphéries de l'étagage des feuilles existantes. Ces résultats et ceux de d'autres études suggèrent qu'il y aurait des liens adaptatifs entre l'architecture des plantes et la phénologie. D'autres facteurs, comme la variation latitudinale des angles solaires, peuvent influencer la forme du houppier chez les arbres dominants, mais ne semblent pas impliqués ici, possiblement parce que l'effet filtrant de la canopée conduit à des déplacements latitudinaux plus petits des angles d'illumination, en sous-étage, au cours de la saison de végétation. Ainsi, en favorisant le port décadu, les hivers froids et les étés chauds et humides du biome oriental décadu de l'Amérique du Nord, semblent exercer une influence notable sur l'architecture des jeunes arbres.

Mots clés : plasticité morphologique, plagiotropie, orientation des tiges, architecture des arbres.

[Traduit par la Rédaction]

Introduction

A striking feature of temperate deciduous trees is that they often produce most of their leaves over a short interval in late spring. Alterations of this pattern occur in sun-grown saplings, which flush new leaves over longer periods, partic-

ularly in shade-intolerant species (Marks 1975; Kikuzawa 1983, 1984). This prolonged flushing increases juvenile growth rates via the rapid reinvestment of photosynthate in the productive system, a strategy that is more effective when relative growth rates are high, i.e., for small, fast-growing plants, and in dense thickets, where older leaves are soon shaded by new growth (Kikuzawa 2003). However, slow-growing, shaded saplings often expand all or most of their leaves over a short time span, adjusting the size and shape of these leaves to form planes of nonoverlapping foliage (Wilson 1966; Zimmermann and Brown 1971; Givnish 1979). This pattern results in efficient light interception, but requires that the entire canopy be refoliated over a short interval.

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Table 1. Study areas.

Site	Location	Elevation (m)	Architectural characteristics
Danum Valley, Sabah, Malaysia	4°58'N, 117°51'E	200	1
Barro Colorado Island, Panama	9°8'N, 79°51'W	140	1, 2, 3
La Selva, Costa Rica	10°26'N, 83°59'W	50	1, 2, 3
Davies Creek, North Queensland, Australia	17°5'S, 145°34'E	850	1, 3
Lamington National Park, South Queensland	28°14'S, 153°10'E	900	1
Lilley Cornett Woods, Kentucky, USA	37°5'N, 83°0'W	350–550	2, 3
Mountain Lake Biological Station, Virginia, USA	37°20'N, 80°30'W	600–1200	1, 2, 3
Albermarle Co., Virginia, USA	38°N, 78°30'W	200	2
Bloomington, Indiana, USA	39°10'N, 86°30'W	250	1, 2, 3
Tasmania, Australia	42°S, 146°E	100–900	1

Note: The studied architectural characteristics include: 1, shape of branch leaf display (branch depth to width ratio); 2, stem orientation and crown symmetry; 3, first branch height. See Martin (1975), Stephenson et al. (1991), King (2001), and King and Maindonald (1999) for detailed site descriptions. New, previously unpublished data are included for branch shape at Lamington National Park, Mountain Lake Biological Station, Albermarle Co., Bloomington, and Tasmania, stem orientation at Barro Colorado Island, La Selva, Albermarle Co., and Bloomington, and first branch height at Lilley Cornett Woods, Mountain Lake Biological Station, and Bloomington.

In contrast, evergreen saplings vary between continuous leaf production (typical of shade-intolerant saplings) and the production of distinct leaf flushes with the retention of multiple leaf cohorts, particularly in shade (Coley 1983). Shaded leaves of evergreen species are commonly retained for 1–4 years in tropical forests (Coley 1988) and even longer in temperate rain forests (Lowman 1992; Lusk 2002). Thus, evergreen saplings usually have leaves arrayed along their twigs at all times, shedding the innermost leaves and adding new ones at the twig tips. As a result, new leaves must be placed beyond or above existing leaves, and only a fraction of the total current leaf area is produced in one flush. These differences between evergreen and deciduous tree phenologies may lead to differences in crown construction and leaf display, because of adaptive links between tree architecture and phenology (Kikuzawa et al. 1996). For example, temperate deciduous saplings exhibit greater plasticity in stem orientation and crown symmetry than do evergreen species (Cao 2001; King 2001). Deciduous saplings often vary between arching, planar forms with dorsiventral symmetry when grown in shade, and erect, radially symmetric forms when grown in sun; this shift being particularly apparent among short-petioled species (e.g., Paillet 1984). Such shifts in stem orientation seem less common in evergreen species, although their branches may shift from steeply inclined in sun to horizontal in shade (King 1998a, 2001; Cao 2001). This difference in plasticity may reflect greater costs of self-shading in shaded deciduous saplings, where all leaves are flushed over a short interval, leading to similar photosynthetic capacities among successive leaves within a shoot. As photosynthetic capacities generally decline with leaf age, particularly when older leaves become more shaded (Kikuzawa 1991; Ackerly 1999), the shading of older leaves by new ones should have less of an effect on whole-plant carbon balance in evergreen species.

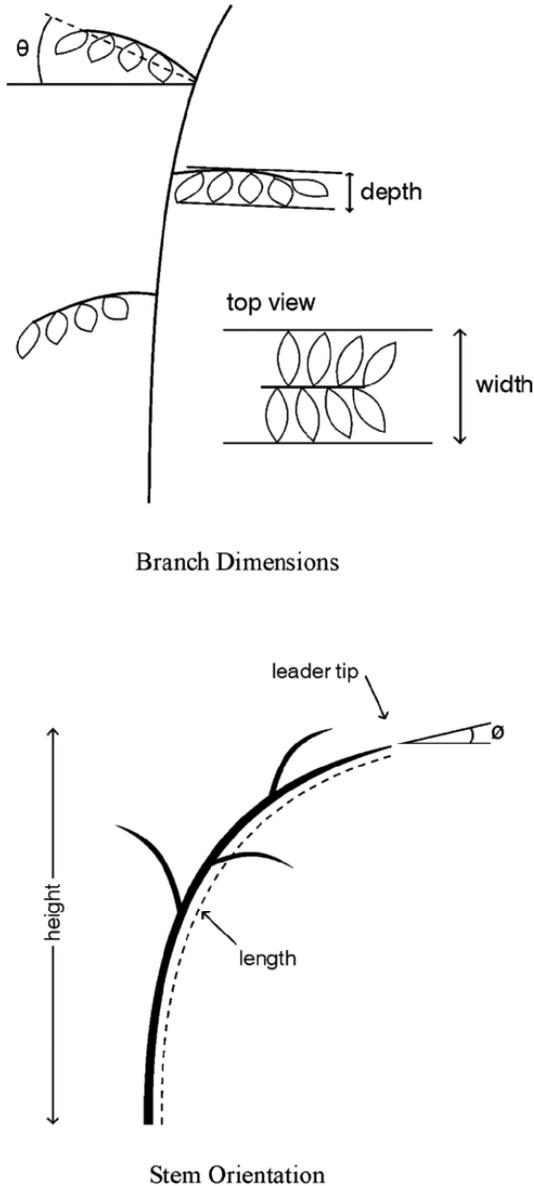
Other traits, such as the flatness of branch leaf displays and the height of first branching, may also vary with leaf habit, because of adaptive linkages with phenology. The height of the first produced branch is the height at which a sapling can display leaves away from the main axis. Because evergreen saplings have some leaves attached along

the upper stem at all times, new branch leaves must be extended beyond the shade of existing stem leaves, or branch initiation must be delayed until the current leaves have been shed from the stem section in question. But in deciduous saplings, which are bare in winter, the leaves of newly extending branches and the terminal leader can be positioned simultaneously to avoid overlap. With less impedance from existing leaves, lower first branch heights may be favoured in deciduous species.

However, our knowledge of the architectural differences between deciduous and evergreen saplings is incomplete, because many traits have not been measured and only a small number of species have been compared. Previous studies have controlled for environmental variation other than phenology by comparing co-occurring deciduous and evergreen species (Cao 2001; King 2001; Kikuzawa 2003), but this approach limits the number of species that can be compared, because the two leaf habits have differing geographic distributions. In North America, deciduous angiosperms attain their greatest vigour and diversity in the central-eastern to southeastern United States where warm, moist summers promote growth, but winters are sufficiently cold to exclude most evergreen angiosperms, in part because of intense Arctic cold fronts (Wolfe 1987). In contrast, evergreen angiosperms attain their maximum diversity and development in wet lowland forests of the equatorial tropics.

This study of temperate deciduous and tropical evergreen saplings compares the two leaf habits from their respective regions of dominance, recognizing that latitudinal differences in sun angle and climate also influence tree architecture (Terborgh 1985; Kuuluvainen 1992; King and Maindonald 1999). The flatness of the leaf display within branches is compared over a wide latitudinal gradient among evergreen species to provide a partial assessment of latitudinal effects on leaf display, independent of leaf habit. The comparison offered here examines (i) the flatness of branch leaf displays, (ii) stem orientation and crown symmetry, and (iii) the height of the first produced branch, all characteristics that may be adaptively linked to phenology. The results of this and previous studies are then interpreted with respect to overall sapling leaf display in relation to leaf habit and other

Fig. 1. Measured branch characteristics include branch depth, width, and angle to the horizontal (θ). Measured sapling characteristics include height, length, and terminal leader angle to the horizontal (ϕ), as shown for an arched sapling.



environmental factors. In so doing, the study provides strong evidence that the cold winters of temperate North America substantially influence sapling architecture via effects on leaf phenology.

Methods

The comparisons made use of previously published data on branch dimensions and first branch height of tropical evergreen saplings (King 1998a, 1998b) and stem orientation in temperate deciduous saplings (King 2001). Extensive additional measurements of all three characters were made on temperate deciduous saplings, and stem orientation was assessed for tropical evergreen species of two Central American forests (Table 1). Unpublished data on branch dimensions in subtropical and temperate evergreen angiosperms of

Fig. 2. Illustration of radial symmetry in a rapidly extending, sunlit sapling of *Castanea dentata* (top) and dorsiventral symmetry in a slow-growing, shaded sapling (bottom) of this deciduous species at Mountain Lake Biological Station, Virginia, USA.

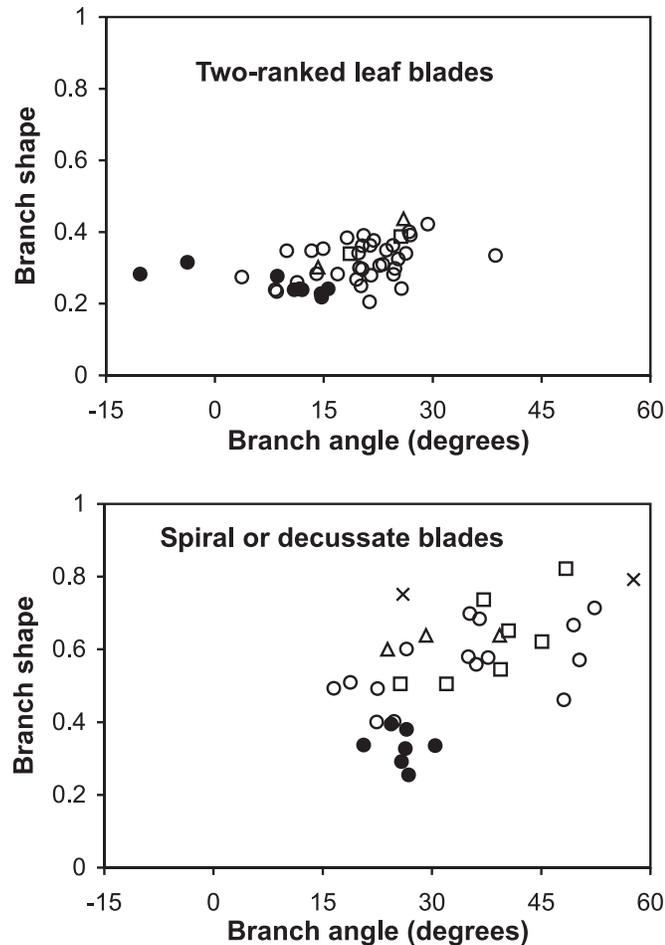


Australia from the sites of King and Maindonald (1999) were also included in the analyses.

Study areas

Saplings were measured in four tropical forests in Costa Rica, Panama, Sabah Malaysia, and northeastern Queensland, Australia, and in a subtropical rain forest in southeastern Queensland, temperate rain forests in Tasmania, Australia, and deciduous forests of the eastern and southeastern United States in Indiana, Kentucky, and Virginia (Table 1). The sites outside the United States were in old-growth forests dominated by evergreen angiosperms, with

Fig. 3. Mean branch shape (leaf display depth/width) versus mean branch angle to the horizontal for shaded saplings of evergreen angiosperms of tropical (○), subtropical (□), south temperate (△), and north temperate forests (×) as compared with temperate deciduous angiosperms (●). Each point corresponds to a species.



most sampled saplings located in or adjacent to forest dynamics plots (King 1998a; King and Maindonald 1999). The temperate deciduous saplings were mostly growing in mature second-growth forests, but also included individuals from old-growth forests (Table 1; Martin 1975; Stephenson et al. 1991; King 2001).

Classification of leaf arrangement

For all species, leaf arrangement was assessed as follows for shaded saplings. Species were classified as having “two-ranked leaf blades” if the leaf blades on branches were borne on opposite sides of the leaf-bearing axes, forming rough planes of foliage parallel to these axes. Species with “spiral leaf blades” had more three-dimensional arrangements of leaves about the branch axes, associated with spiral phyllotaxies. Species with “decussate leaf blades” had opposite leaves with the blades of successive leaf pairs borne at 90° angles to the previous pair. The species with “two-ranked leaf blades” frequently had precisely distichous leaves (i.e., with 180° angles between subsequent petiole bases), but also included species with spiral or irregular phyllotaxies, but two-ranked blades associated with twists

of the petioles and leaf-bearing axes to achieve planar orientations (Fisher 1986).

The species with “two-ranked leaf blades” correspond with the “monopodial plagiotropic” or “sympodial plagiotropic” species of King (1998b); those with “spiral” or “decussate leaf blades” correspond with “orthotropic” species (King 1998b). Less frequently encountered species of intermediate or other leaf arrangements were not included in the present comparison.

Species with two-ranked versus spiral or decussate leaf blades (as assessed in shade) were analysed separately with respect to branch shape, as these two groups differed substantially in this regard. Stem orientation and first branch height were expressed as a function leaf size, which incorporated most of the differences between the typically small-leaved, two-ranked species and the often larger-leaved spiral or decussate species.

Branch shape

Comparisons of branch dimensions were made among saplings of 50 tropical species (all but the “secondarily plagiotropic” species of King (1998b)) and 15 species of eastern deciduous forests of the US (Appendix A). Saplings (1–3 m tall) were selected for measurement as encountered within forest sites, excluding those with broken branches or in recent tree fall gaps, which would not have had time to respond to increases in light. Tropical sapling vigour was assessed by measuring the distance from the branch tip to the innermost leaf along the branch axis on that branch having the greatest length of directly attached leaves along it (King and Clark 2004). Suppressed saplings, for which this maximum leaved branch length was <8 cm, were generally rejected, as these individuals were considered to have too few leaves per axis for meaningful assessments of branch shape. In the case of temperate deciduous saplings, individuals were included if at least one axis had a current year extension of >8 cm, as determined from the position of the terminal bud scale scars of the previous winter.

The following measurements were made on the upper and mid-crown branches of each sapling: branch angle to the horizontal and the width and depth of the branch foliage (Fig. 1). Branch width was defined as the distance (perpendicular to the branch axis) from the leftmost to rightmost leaf edge. Branch depth was defined as the distance from the bottommost to topmost leaf surface, measured perpendicular to the surface defined by the upper or lower leaf surfaces (Fig. 1). Branch shape was then defined as the ratio of depth to width. Mean branch angles and shapes were computed for each sapling, omitting minor branches with fewer than five leaves. Species means were computed for the three to six measured saplings per species.

Stem orientation and crown symmetry

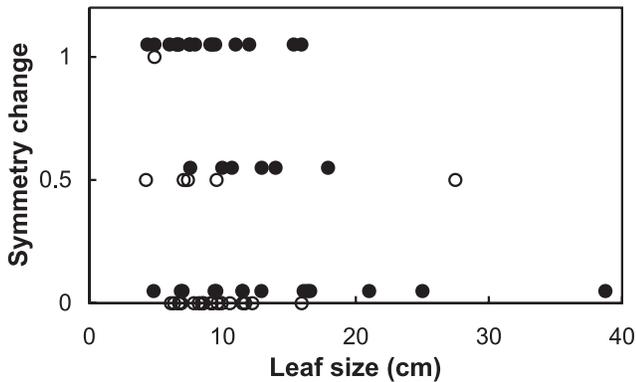
Stem orientation of shaded, slow-growing saplings was measured for 21 temperate deciduous species and 24 tropical lowland forest species. To simplify the comparison, only simple-leaved species were chosen. The temperate deciduous species included members of common genera of the eastern United States (*Acer*, *Betula*, *Fagus*, *Liriodendron*, *Quercus*, *Tilia*, and *Ulmus*), as well as other genera. The tropical species were the 24 most common simple-leaved

Table 2. Mean ratios of branch depth to width for forest-grown saplings of tropical evergreen, subtropical evergreen, south temperate evergreen (Tasmania), north temperate evergreen, and north temperate deciduous angiosperms.

Branch leaf display	Tropical	Subtropical	S. temperate	N. temperate	N. temperate deciduous
Two-ranked blades	0.32b (35)	0.36ab (2)	0.37ab (2)		0.26a (8)
Spiral or decussate blades	0.56b (15)	0.63bc (7)	0.63bc (3)	0.77c (2)	0.33a (7)

Note: Values within a row not sharing the same letter differ significantly ($P < 0.01$, with Bonferroni correction for multiple comparisons). Bonferroni $P > 0.05$ for all other comparisons. Number of species per category is given in parentheses.

Fig. 4. Plasticity in crown symmetry versus leaf size (blade length \times width)^{0.5} for the 24 most common simple-leaved species on the 50 ha plot on Barro Colorado Island, Panama (○) and 36 simple-leaved temperate deciduous species (●). A value of 1 indicates species whose saplings are arched and dorsiventrally symmetric in shade and erect and radially symmetric in sun; 0.5 indicates species that are either intermediate between these symmetries in shade and radially symmetric in sun, or dorsiventrally symmetric in shade and intermediate in sun; 0 indicates no change in symmetry with light. The temperate species points are plotted slightly above those of the tropical species for clarity.



species on the 50 ha forest dynamics plot on Barro Colorado Island (BCI), Panama (Condit et al. 1996).

The following measurements were made on 3–20 (mean, 8) saplings per species, as described by King (2001) for temperate species and shown in Fig. 1.

1. Vertical height to the highest twig in nonerect saplings or to the tip of the central stem (terminal leader) in erect saplings with radially symmetric crowns.
2. Length along the main stem from the base to the tip of the terminal leader. In arched saplings, where the highest point was a lateral branch on a substantially longer, more vigorous axis, the latter was taken as the terminal leader (Fig. 1).
3. Angle to the horizontal of the upper section of the terminal leader. In deciduous species, this angle was measured along the current year's extension of the terminal leader. In the tropical species, this angle was measured along the upper half of the leaved stem length, which would on average be equal to the current year's extension in species with a leaf life span of 2 years, approximately the average among saplings of shade-tolerant species at BCI (Coley 1988).

Ratios of height to length were then calculated for each

sapling, with erect saplings having ratios approaching 1, and arched saplings having substantially lower ratios.

Crown symmetry in low versus high light in relation to leaf size was assessed for the above 24 Panamanian species and for 36 temperate deciduous species, including those for which shaded stem orientation was measured. The symmetry of a sapling was classified as dorsiventral, if the leaves of the terminal leader and uppermost lateral branches lay in a common plane (Fig. 2). Radially symmetric saplings had a spiral or decussate arrangement of the upper leaves and branches and a circular or elliptical foliage display, as viewed down the length of the terminal leader. Dorsiventrally symmetric saplings were usually arched and spreading, while radially symmetric saplings were typically erect stemmed (Fig. 2). Saplings conforming to neither of these two groups were classified as intermediate in symmetry. Symmetry was assessed for saplings ranging from shaded understory to large openings. Leaf blade lengths, widths, and petiole lengths were measured on five average-sized leaves of each of three 1–3 m tall understory saplings per species.

Crown symmetry in relation to light (but not leaf size) was assessed for additional common simple-leaved species at BCI, Panama, La Selva, Costa Rica, and the southeastern United States, to provide a more comprehensive comparison of crown symmetry among 112 tropical versus 38 temperate deciduous species. In addition, stem orientation and crown symmetry were assessed for three deciduous and evergreen congeneric pairs to provide a limited assessment of plasticity in relation to leaf habit among closely related species.

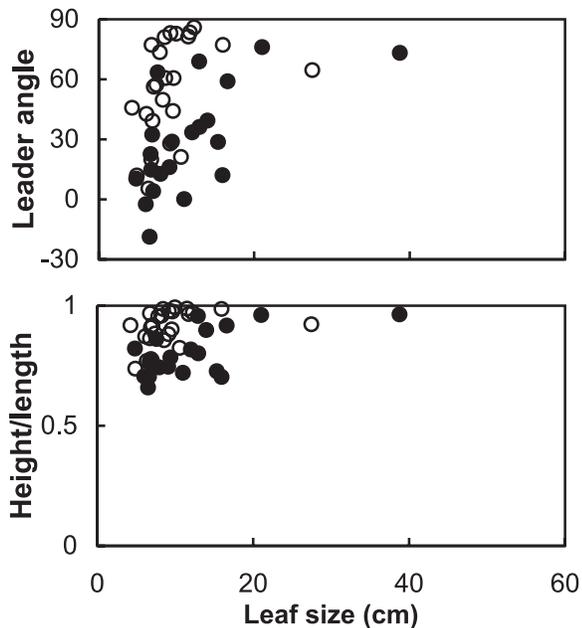
First branch height

The height of the first produced branch was measured on forest-grown seedlings or saplings of 70 tropical forest species, as described by King (1998a), and for 15 species of eastern deciduous forests of the United States (Table 1). Species of a wide range in leaf size, with both simple and compound leaves, were included in both groups. The selected species typically had erect stems to the first branch, though the upper stems of larger saplings were often arched in several of the deciduous species. First branch height was measured on all suitable individuals encountered, ranging from recently branched plants to older plants that were several times the height of first branching. Saplings that were too large and old for identification of the first produced branch were rejected, as were saplings for which the first branches were produced after stem breakage or dieback. Thus, juveniles of 0.2–0.4 m heights were measured for small-leaved species with low first branching points, while

Table 3. Percentages of common simple-leaved species with the listed sapling leader symmetry in sun versus shade (most of the remaining species not included in these three groups had intermediate crown symmetries in shade).

Region	Sapling symmetry in sun vs. shade (% species)			N
	Radial in both sun and shade	Radial in sun / dorsiventral in shade	Dorsiventral in both sun and shade	
Barro Colorado Island, Panama	51	5	17	59
La Selva, Costa Rica	66	0	17	53
Southeastern United States, deciduous spp.	16	45	24	38

Fig. 5. Leader angle to the horizontal and height/length versus leaf size (blade length \times width)^{0.5} for shaded, slow-growing, simple-leaved saplings of the 24 most common simple-leaved species on the 50 ha plot on Barro Colorado Island, Panama (○) and 21 temperate deciduous species (●). Vertical saplings have a leader angle of 90° and height/length ratio of 1.



trees exceeding 10 m in height were measured for the largest-leaved tropical species with correspondingly high first branching heights. Height of first branching was measured on at least 3 and an average of 10 plants per species. Leaf blade lengths and widths and petiole lengths were measured on 1–4 m tall saplings. Four or five leaves, close to the visually estimated average size, were measured on two or more saplings per species.

Log (first branch height) was then regressed against log (petiole length) and log (leaf size), where leaf size = (blade length \times width)^{0.5}, as either of the latter two variates explained much of the variation in log (first branch height) within both the temperate and tropical species. The predicted first branch heights for a leaf blade length of 25 cm and petiole length of 5 cm (the geometric means for the temperate deciduous species) were calculated by back-transforming the corresponding log-log regression value and correcting for logarithmic bias (Snowdon 1991) by multiplying by $\Sigma y_{\text{observed}} / \Sigma y_{\text{predicted}}$, where $\Sigma y_{\text{predicted}}$ is the sum of the back-transformed predicted values from the regression.

Plasticity in leaf phenology

To verify the perception that shaded temperate deciduous saplings produce most of their leaves at the beginning of the season, phenological plasticity was assessed for two species (*Acer pensylvanicum* L. and *Betula lenta* L.) showing clear differences between early and later produced leaves. These species exhibit the intermediate heterophyllous leaf emergence pattern of Kikuzawa (1983). In the case of *B. lenta*, two quite closely spaced early leaves are flushed initially, followed by more widely spaced leaves on the extending long shoots, as described by Kozłowski and Clausen (1966) for *B. alleghaniensis*. In *A. pensylvanicum*, a pair of large, broad leaves is flushed initially, followed by smaller, often narrower leaf pairs on the more vigorous axes (Wilson and Fischer 1977). In both species, short shoots bear only the two early leaves. The early and late leaves were counted on the upper crowns of shade- and sun-grown saplings in late August 2001, after flushing had ceased on all but the most vigorous, sunlit axes. For each sapling, the early leaf fraction (no. of early leaves/total no. of leaves) was then related to the mean extension growth rate over the past 3 years (past 2 years for the fastest-growing saplings), as determined from overwintering bud scale scars.

Results

Branch shape

The temperate deciduous saplings had more flattened leaf displays than the evergreen saplings of all latitudes, differences that were significant in all cases for the spiral or decussate-leaved species group (Fig. 3; Table 2). The difference in shape (branch foliage depth/width) between temperate and tropical saplings was small but significant for the species with two-ranked leaf blades and more substantial for the spiral or decussate group. In the case of the temperate decussate species, *Acer rubrum* L., *A. saccharum* Marsh., and *Aesculus flava* Soland., systematic variation in petiole length and orientation among successive leaf pairs tended to place the leaves in horizontal planes, resulting in leaf displays that were as flattened as those of species with two-ranked blades (Appendix A). For all species, the leaf displays, as measured on shaded saplings, were at least somewhat flattened compared with the 1:1 depth to width ratio expected for an undistorted, radially symmetric leaf display (Fig. 3).

Stem orientation and crown symmetry

The temperate deciduous saplings differed substantially from the tropical saplings in stem orientation and crown

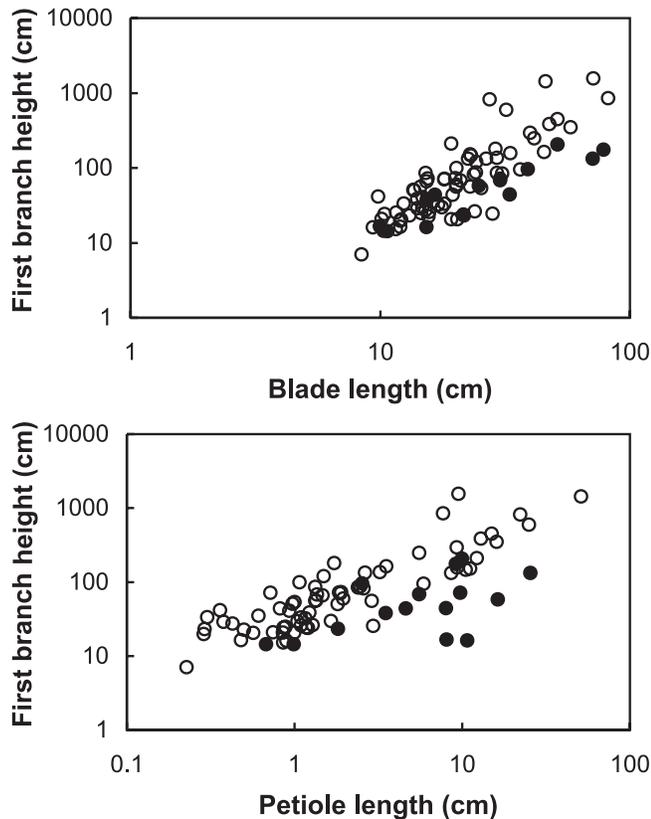
Table 4. Congeneric comparisons of sapling stem orientation in deciduous versus evergreen angiosperms.

Species	Symmetry in sun	Symmetry in shade	Shaded sapling		
			Leader angle (°)	Height/length	N
<i>Diospyros virginiana</i> L. ^a	Radial	Dorsiventral	16	0.746	7
<i>D. pentamera</i> (F. Muell.) F. Muell.	Radial	Radial	70	0.961	14
<i>Ilex montana</i> (T. & G.) Gray ^a	Radial	Dorsiventral	15	0.767	9
<i>I. opaca</i> Ait.	Radial	Intermediate	59	0.919	19
<i>Lindera benzoin</i> (L.) Blume ^a	Radial	Dorsiventral	23	0.704	6
<i>L. queenslandica</i> Hyland	Radial	Intermediate	48	0.909	4

Note: Leader angles to the horizontal and height/length ratios differed significantly between congeners ($P < 0.001$) for all comparisons except for *Lindera* leader angle, where $P = 0.051$, as determined by pairwise t tests, not assuming equal variance. *Diospyros virginiana* and *D. pentamera* (Ebenaceae) were measured in Indiana, USA (39°N), and South Queensland, Australia (28°S), respectively; *Ilex montana* and *I. opaca* (Aquifoliaceae) were measured in Virginia, USA (37°N); *Lindera benzoin* and *L. queenslandica* (Lauraceae) were measured in Virginia (37°N) and North Queensland (17°S), respectively.

^aDeciduous species.

Fig. 6. Height of first branch initiation versus leaf blade length and versus petiole length for 70 tropical (○) and 15 temperate deciduous species (●), plotted on a log–log scale.



symmetry (Fig. 4). The qualitative assessment of 150 species determined that over half of the more common tropical species were radially symmetric in both sun and shade, while only 1/6 of the temperate deciduous species were in this group (Table 3). In contrast, nearly half of the deciduous species were radially symmetric in sun and dorsiventrally symmetric in shade, while only 3% of the tropical species were in this category (Table 3). This difference in frequencies resulted in leader angles and sapling height to length ratios that were substantially lower for the temperate deciduous species than the tropical species, as computed for shaded saplings (Fig. 5). Among species of leaf size (blade

width \times length)^{0.5} < 16 cm, the mean leader angles and height/length ratios of shaded saplings were 22° versus 55° and 0.78 versus 0.92, respectively, for the temperate versus tropical species. These means differed significantly from each other ($P < 0.001$) in both cases. For the three congeneric comparisons, the deciduous species was less erect in shade and showed a more pronounced shift in symmetry than the evergreen species in every case (Table 4). Large-leaved species tended to be more erect in shade, particularly among the temperate deciduous species, as the symmetry changers were concentrated among deciduous species with small- to medium-sized leaves (Fig. 4). All of the deciduous symmetry changers had two-ranked leaf blades in shade, except for two decussate-leaved species (*Acer rubrum* and *A. saccharum*). Among slow-growing saplings, both leader angle and height/length ratio were significantly correlated ($P < 0.05$) with log (leaf size) for the temperate deciduous species and for the 24 Panamanian species.

First branch height

Among the tropical species, the height of first branching increased markedly with both leaf blade and petiole length (Fig. 6; Table 5). Among the temperate deciduous species, the height of first branching showed less of an increase with increasing leaf dimensions, with large-leaved deciduous species initiating branches at a fraction of the height of tropical species of similar leaf size. The first branch heights for the tropical species were, respectively, 2.6 \times and 3.3 \times those for the temperate species, compared at a blade length of 25 cm and petiole length of 5 cm, the geometric mean dimensions for the sampled temperate species (Table 5).

Plasticity in leaf phenology

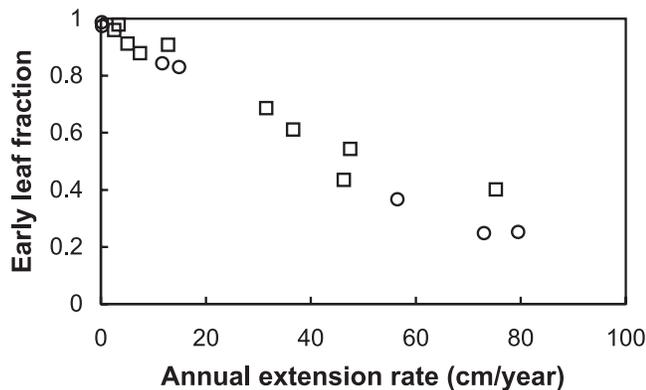
Plasticity in the fraction of early- versus late-produced leaves was observed in the two heterophyllous temperate species, where early leaves could be easily distinguished. Slow-growing, shaded saplings produced almost all of their leaves during the initial flush in spring, while fast-growing saplings of large openings produced more than half of their leaves in an extended period following the initial flush (Fig. 7). Both species showed plasticity in stem orientation in relation to light, having dorsiventral symmetry in shade and radial symmetry in sun.

Table 5. Regression coefficients of the form $\log y = b_0 + b_1 \log x$.

Sample	b_0	b_1	r^2	Predicted first branch height (cm) for	
				blade length = 25 cm	petiole length = 5 cm
Log (first branch height) vs. log (blade length)					
Temperate	-0.069	1.252	0.86	50	
Tropical	-0.740	1.959**	0.70	131***	
Log (first branch height) vs. log (petiole length)					
Temperate	1.311	0.503	0.32		59
Tropical	1.604	0.832ns	0.76		195***

Note: Values for the slopes and first branch heights that differed significantly between temperate deciduous species and tropical species according to a two-tailed test at $P < 0.05$, $P < 0.01$, and $P < 0.001$ are indicated after the tropical values by *, **, and ***, respectively. ns, not significant. The listed blade and petiole lengths for which first branch height was predicted are the respective geometric means of the values for the temperate deciduous species.

Fig. 7. Fraction of upper-crown leaves, which are early leaves, versus terminal leader extension rate for saplings of *Acer pensylvanicum* (□) and *Betula lenta* (○), two heterophyllous temperate deciduous species.



Discussion

General patterns

The results of this comparison indicate substantial morphological differences between temperate deciduous and evergreen tropical saplings, as assessed in forest understories. Juvenile plants initiate their first branches at lower heights among deciduous species, particularly when large-leaved species are compared (Fig. 6; Table 5). Temperate deciduous saplings show greater plasticity in crown symmetry and stem orientation in relation to growth rate and light intensity than do evergreen saplings of both temperate and tropical forests (Table 3; Figs. 4 and 5; Cao 2001; King 2001; Kikuzawa 2003). However, evergreen saplings do show substantial plasticity in leaf arrangement and the orientation and spacing of their lateral branches (Kohyama 1980; Fisher and Hibbs 1982; Steingraeber 1982; Tucker et al. 1987; Valladares et al. 2000).

The deciduous saplings had flatter leaf displays, as measured in shade, than did evergreen saplings of all latitudes, particularly for the comparison between species with decussate or spirally arranged leaf blades (Fig. 3; Table 2). While the number of species sampled was small for the subtropical and temperate evergreen sites, the pattern of more planar branches in shaded temperate deciduous saplings was consistently observed for all comparisons. In the *Quercus* spe-

cies, studied in the United States, most leaves of shaded saplings were borne in planar pseudowhorls at the twig tips, in contrast with the longer and more even distributions of leaves along twigs in open-grown saplings. Thus, the presence of multiple leaf cohorts among evergreen broad-leaved species is associated with less planarity in branch foliage, a lower frequency of planar terminal leaders, and a higher frequency of saplings with erect, unbranched stems.

Broader context of the results

The observation of greater planarity in temperate deciduous species pertains to shaded saplings of forest understories, as open-grown saplings are generally more erect and three dimensional in leaf display in both temperate and tropical regions (Table 3; Steingraeber et al. 1979; King 1998b, 2001). Trees also show ontogenetic shifts in architecture (Sterck and Bongers 2001) and leaf phenology (Seiwa 1999) that may vary with leaf habit. Within temperate deciduous forests, seedlings and subcanopy trees (of canopy species) tend to be more erect than the 1–3 m tall saplings studied here (Millet et al. 1998). Less plasticity in architecture may occur in small deciduous shrubs, such as *Vaccinium hirtum*, which produces successive branches by the extension of erect, orthotropic axes whose leaders then reorient to produce spreading, plagiotropic planes of foliage (Kawamura and Takeda 2004). Conversely, greater plasticity in the angle of the terminal leader was observed in the small evergreen shrub *V. bracteatum* than in *V. hirtum* (Kawamura and Takeda 2002).

Traits decreasing self-shading in deciduous saplings

The more planar leaf display of shaded deciduous species is associated with several traits allowing suppressed saplings to maintain planes of foliage in the same position from one year to the next, including arched leaders, the production of short shoots, and coordinated variation in leaf size, petiole length, and orientation (Wilson 1966; Niklas 1994). The production of most leaves early in the season, even in species with prolonged flushing in sun (Fig. 7), increases the mean duration of understory leaves, providing more time to pay off associated leaf, stem, and root construction costs (Chabbot and Hicks 1982; Kikuzawa 2003). Thus, the replacement of leaves over a short interval and associated architectural traits facilitate the development of monolayered

crowns, the most efficient arrangement of foliage for photosynthesis under low light levels (Horn 1971; Givnish 1988).

Other latitudinal influences on architecture

Environmental differences between tropical and temperate regions have direct influences on tree form, as well as effects associated with the resultant phenological differences studied here. Among canopy trees, crown shape varies with latitude from rounded spreading forms in the tropics to the narrow spires of boreal forest conifers. This pattern increases the efficiency of light interception at the respective latitude of the tree (Kuuluvainen 1992), and narrow, pointed crowns reduce snow loads in evergreen conifers of high latitudes (Petty and Worrell 1981).

However, mid-latitude deciduous trees show less difference in crown form from tropical trees (Terborgh 1985), and the distributions of summer sun angles at the temperate site latitudes of 37°–39° are not much different from those of the tropics, because of the 23.5° tilt of the Earth's axis towards the sun at the summer solstice. Understory saplings receive less light from lower angles than do canopy trees in both temperate and tropical forests, because of longer path lengths through tree crowns for lateral light (Canham et al. 1990). Mean midsummer temperatures at the lower elevation temperate sites also approximate those of the tropics (United States Geological Survey 1970). These trends, along with the observations that temperate, as well as tropical, evergreen species show less plasticity in stem orientation (Cao 2001; King 2001; Kikuzawa 2003) and that flatness of leaf display did not vary with latitude among evergreen species (Fig. 3), are all consistent with the hypothesis that the more planar appearance of shaded deciduous saplings is related to their rapid flushing of a single cohort of leaves.

On the other hand, the density of vegetation in the 1–3 m high layer studied here may be greater in tropical than temperate deciduous forests, as inferred from reports of greater sapling densities in tropical versus temperate forests (Muller 1982; Condit et al. 1999). The associated lower vertical gradients in light would also favour arched, spreading forms in deciduous understories, where the additional height gained by erect forms would provide little extra light (Kikuzawa 2003).

Shade tolerance

The greater planarity of deciduous saplings does not imply that they are more shade tolerant than evergreen species, as the longer leaf life spans of the latter should offset minor reductions in light interception efficiency associated with less planar arrangements of multiple leaf cohorts. Although leaf mass per unit area (LMA) also increases with leaf life span, thereby increasing the cost of producing long-lived leaves, this increase in LMA is generally proportionately less than the increase in leaf life span, resulting in somewhat greater ratios of cumulative carbon gain/LMA in long-lived leaves (Reich et al. 1997). Furthermore, the translocation of nutrients from older, more shaded leaves to new leaves results in gradients in photosynthetic capacity across leaf cohorts that increase whole-plant carbon gain and nutrient use efficiency (Field 1983; Ackerly 1999). Hence, evergreen saplings may be as or more shade tolerant than deciduous

saplings, with the greater planarity of the latter offsetting their higher annual costs of leaf replacement.

Evolutionary considerations

Large changes in plant architecture can be achieved by variation in shoot elongation and the differential activation of bud meristems (Honda et al. 1981; Fisher 1986). Thus, the coordination of leaf and branch traits should be readily attainable (Honda and Fisher 1978; White 1983; Givnish 1987; Kikuzawa et al. 1996). The coordinated evolution of leaf and branch characteristics in a single genus (*Acer*) has been convincingly demonstrated by Ackerly and Donoghue (1998). The finding that congeneric deciduous and evergreen species conformed to the general pattern of greater plasticity in the former (Table 4) suggests that this pattern is not due to phylogenetic constraints. Comprehensive analyses using modern phylogenetic methods are needed to confirm this surmise (Ackerly et al. 2000).

Thus, by favouring the deciduous habit, the cold winters and warm, humid summers of the eastern deciduous biome appear to have had a notable influence on crown architecture, often imparting a more planar appearance to temperate forest understories than those of tropical rain forests. This greater planarity is due to (i) flatter displays of leaves on branches, particularly in saplings with spiral or decussate phyllotaxis, (ii) the prevalence of arching stems in shade, associated with greater plasticity in stem orientation in temperate deciduous saplings, and (iii) a lower height of first branching, which also imparts a more planar appearance to temperate forest understories. However, these characteristics of individual sapling crowns may be less apparent in vertical distributions of leaf density, where variation in height among neighbours blurs the larger-scale expression of within-crown leaf display (Parker and Brown 2000).

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Appendix A

Table A.1. Branch attributes of forest-grown juveniles of temperate deciduous species, listed as follows: branch angle to the horizontal, branch shape (leaf display depth/width), sapling leaf blade length and petiole length, and height of first initiated branch.

Species	Family	Branch angle (°)	Branch shape	Blade length (cm)	Petiole length (cm)	First branch height (cm)
<i>Acer pensylvanicum</i> L.	Aceraceae	10.9	0.239	16.5	4.61	44
<i>Acer rubrum</i> L.	Aceraceae	26.8	0.255			
<i>Acer saccharum</i> Marsh.	Aceraceae	25.8	0.292			
<i>Aesculus flava</i> Soland.	Hippocastaneaceae	30.4	0.335	24.8	16.3	58.2
<i>Aralia spinosa</i> L.	Araliaceae			71.0	25.4	133
<i>Betula lenta</i> L.	Betulaceae	8.6	0.277			
<i>Carya ovata</i> (Mill.) K. Koch	Juglandaceae	26.4	0.328			
<i>Carya tomentosa</i> (Poir.) Nutt.	Juglandaceae			30.2	9.73	71.6
<i>Castanea dentata</i> (Marsh.) Borkh.	Fagaceae	15.6	0.242			
<i>Cornus florida</i> L.	Cornaceae			10.3	0.677	14.5
<i>Fagus grandifolia</i> Ehrh.	Fagaceae	−10.3	0.283			
<i>Fraxinus americana</i> L.	Oleaceae			33.0	8.00	44.4
<i>Gymnocladus dioica</i> (L.) K. Koch	Fabaceae			78.3	9.14	176
<i>Liquidambar styraciflua</i> L.	Hamamelidaceae			10.0	8.07	16.7
<i>Liriodendron tulipifera</i> L.	Magnoliaceae	26.5	0.380	15.3	10.7	16.3
<i>Magnolia acuminata</i> (L.) L.	Magnoliaceae	14.7	0.219	21.7	1.81	23.3
<i>Magnolia fraseri</i> Walt.	Magnoliaceae			30.2	5.53	68.4
<i>Magnolia macrophylla</i> Michx.	Magnoliaceae			51.3	9.97	207
<i>Magnolia tripetala</i> L.	Magnoliaceae			39.0	2.53	96.2
<i>Nyssa sylvatica</i> Marsh.	Nyssaceae			10.7	0.987	14.4
<i>Oxydendrum arboreum</i> (L.) DC.	Ericaceae	12.0	0.219			
<i>Prunus serotina</i> Ehrh.	Rosaceae	−3.8	0.316			
<i>Quercus alba</i> L.	Fagaceae	24.4	0.395			
<i>Quercus rubra</i> L.	Fagaceae	20.6	0.337			
<i>Sassafras albidum</i> (Nutt.) Nees	Lauraceae			15.3	3.49	38.1
<i>Tilia heterophylla</i> Vent.	Tiliaceae	14.6	0.228			