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# ALLOMETRY OF AXIS LENGTH, DIAMETER, AND TAPER IN THE DEVIL'S WALKING STICK (*ARALIA SPINOSA*; ARALIACEAE)[1]

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The allometry of axis length, diameter, and taper is described for the trunk, rachis, and rachilla of nonbranching ramets of *Aralia spinosa*. Significant log-linear relationships were found between length and diameter for all axis categories, and in all cases, scaling was negatively allometric. Linear models best described the relationship between length and diameter for the rachis and rachilla, while a quadratic model best described this relationship for the trunk. During the trunk-building stage, the safety factors for trunk height were size dependent, with larger trunks exceeding their predicted critical buckling height. Taper was described by a linear relationship between diameter and position along the axis for all axis categories. All rachises and rachillas sampled exhibited taper along the length of the axis, however, only 51% of the trunks showed continuous taper. The trunk was less tapered than the rachis, but no differences in taper were found between the trunk and the rachilla, or the rachis and the rachilla. In unbranched ramets the large bipinnately compound leaves occupy the space normally occupied by lateral branches. We suggest that the rachis and rachilla are functionally equivalent to branches, that is, acting as axes of exploration and exploitation of the environment.

**Key words:** allometry; *Aralia spinosa*; Araliaceae; critical buckling height; pinnately compound leaf; taper.

The aboveground portion of most arborescent plants is composed of a branch system upon which leaves (simple or compound) are arranged. In plants such as palms, cycads, and tree ferns, which rarely if ever branch, the "crown" is composed only of large pinnately compound leaves. Pinnately compound leaves can be viewed as structurally and functionally analogous to relatively short-lived leafy branches (Givnish, 1978; Fisher, 1984). Leafy branches and pinnately compound leaves are both composed of an axial support system (stem/rachis), which is roughly circular in cross section, and a laminar photosynthetic system (leaves/leaflets). Stems and pinnately compound leaves may also be branched (higher order branches/rachillas), however, in most cases branches are indeterminate and persistent, while leaves are determinate and deciduous (Givnish, 1978). Some leaves are, however, perennial and possess an apical meristem that continues to produce new leaflets as the leaf elongates (indeterminate growth). This is the case in the tropical genera *Guarea* and *Chisocheton* (Corner, 1964; Fisher, 1984; Fisher and Rutishauser, 1990; Miesch and Barnola, 1993). Recent evidence has also shown that determinate pinnately compound leaves may also resemble stems in their early development (Sattler and Rutishauser, 1992; Jeune and Lacroix, 1993; Lacroix and Sattler, 1994; Lacroix, 1995).

*Aralia spinosa* L. (Araliaceae) is an unusual shrub/small tree present in the deciduous forests of the eastern United States, from New York and New Jersey south to Florida and Texas (Little, 1980). Branching is uncommon and the permanent woody framework of this species often consists only of a single axis, the trunk, which is covered with prickles (sensu Bell, 1991) (White, 1984, 1988). Along the trunk on the current year's growth, and on short shoots, are large deciduous bipinnately to tripinnately compound leaves, also often covered with prickles, and ranging in length from 40 to 100 cm (Fig. 1) (Smith, 1982; White, 1983, 1988). The temporary axial system of plagiotropically oriented compound leaves acts as a replacement for the "missing" branch system. This species therefore provides an ideal model for the study of plant organs that appear to be functionally and morphologically intermediate between branches and leaves. Our objective was to compare the allometry of axis length and diameter, and axis taper for the trunk, rachis, and rachilla of nonbranching ramets of *Aralia spinosa* in order to determine whether: (1) the allometric scaling exponents for these axes are similar to those values predicted by theoretical models describing the scaling of $L$ and $D$ in tree trunks and branches, (2) the allometric scaling exponents and taper coefficients vary as a function of ramet and leaf size, and (3) the axes of compound leaves scale and taper like woody branches or exhibit unique values exclusive to compound leaves. This is the first quantitative analysis of the allometry of the trunk and supporting axes of pinnately compound leaves for this species.

## MATERIALS AND METHODS

***Sampling***—Ramets of *Aralia spinosa* were sampled at five sites in Wicomico and Worcester County, on Maryland's Eastern Shore. Fifteen axes from each axis category: trunk, leaf rachis, and leaf rachilla (Fig. 1) (terminology from Bell, 1991) were randomly sampled at three sites

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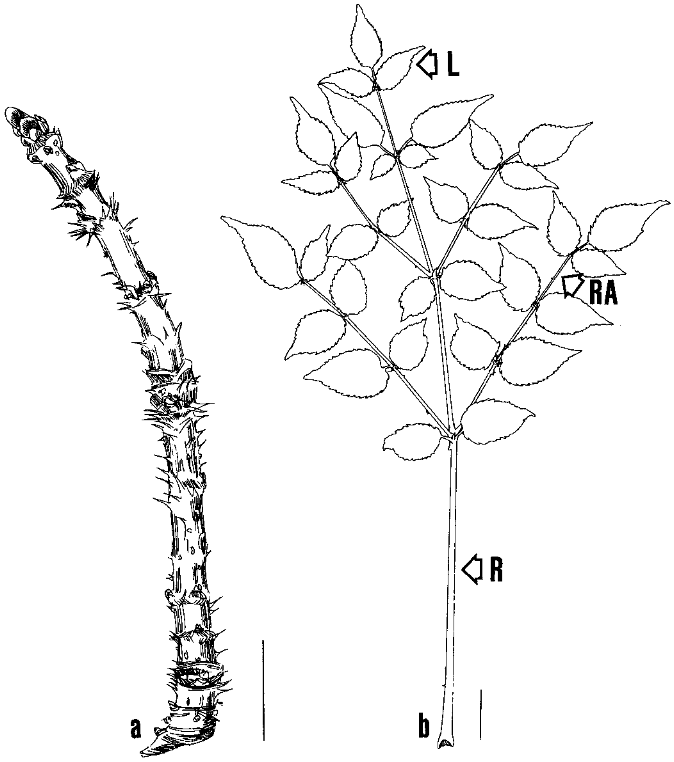

Fig. 1. Illustration of (a) the trunk, and (b) a bipinnately compound leaf of *Aralia spinosa*. L, leaflet; R, rachis; RA, rachilla (scale bars = 5 cm).

($N = 45$ for each axis category). For the trunk, only unbranched ramets (one growing tip, excluding short shoots) were sampled, and no distinction was made between monopodial and sympodial trunks. Trunks were cut at the level of the soil, after removal of the leaf litter, while both rachises and rachillas were cut as close to their supporting axis as possible. The length ($L$) and diameter ($D$) (at 10% of the length from the base) of each axis and the diameter at 10–13 equally spaced intervals along the length of each axis were determined. The most proximal diameter measurement for all axis orders was excluded from the taper analyses as this region was often considerably swollen, i.e., rachis phyllopodium. Diameter measurements were made with vernier calipers (trunk) or after hand sectioning, with an ocular micrometer fitted in an Olympus SZ40 dissecting microscope (rachis and rachilla).

TABLE 1. Summary data of axis length ($L$) and diameter ($D$) of *Aralia spinosa.*

| Axis | Variable | Mean ± 95% CI (cm) | Range (cm) |
|---|---|---|---|
| Trunk | $L$ | $93.9 \pm 17.2^{A*}$ | 9.6–222.0 |
| Rachis | $L$ | $53.7 \pm 6.0^{A}$ | 19.0–91.8 |
| Rachilla | $L$ | $17.2 \pm 2.9^{B}$ | 5.4–46.5 |
| Trunk | $D$ | $1.20 \pm 0.12^{a}$ | 0.48–2.05 |
| Rachis | $D$ | $0.38 \pm 0.03^{b}$ | 0.20–0.63 |
| Rachilla | $D$ | $0.16 \pm 0.01^{c}$ | 0.09–0.30 |

* Means with the same superscripts are not significantly different (Tukey test, $\alpha = 0.05$)

***Statistical analyses***—The relationship between $L$ and $D$ (both log transformed) for each axis category and among sites within an axis category was determined by ordinary least-squares (OLS) and reduced major axis (RMA) regression. Both the experimental lack-of-fit test ($\alpha = 0.10$) (Burns and Ryan, 1983) and an examination of the relationship between the standardized residuals and the fitted values were made in order to detect curvature. The scaling exponent (slope of the RMA regression: $b_{RMA}$) was determined by dividing the slope from the OLS regression by the correlation coefficient ($r$) (Bertram, 1989; Niklas, 1994a). Variation of slopes among axis categories and among sites within axis categories was explored using ANCOVA and a Tukey test for multiple comparisons (Zar, 1984). Taper was determined by regressing (OLS regression) diameter against position along the length of the axis (both untransformed). Variation of taper among axis categories and among sites within axis categories was assessed using nested ANOVA. Axis category was treated as a fixed effect, while site within axis category was treated as a random effect. With the exception of the experimental lack-of-fit test, the significance level was set at $\alpha = 0.05$ for all tests. Statistical analyses were performed using Minitab (Minitab, 1992) and Quattro Pro (Novell, 1994).

***Critical buckling height***—The critical buckling height ($H_{crit}$) of *Aralia spinosa* trunks was estimated using Greenhill's (1881) formula for a vertical columnar mechanical support:

$$H_{crit} = C(E/\rho)^{1/3}D^{2/3} \tag{1}$$

where $C$ is the constant of proportionality, $E$ is Young's modulus, $\rho$ is the bulk density, and $D$ is the diameter of the column. This formula assumes that the column is untapered, therefore values obtained for tapered columns such as tree trunks must be interpreted with some caution. We assume that the force which induces elastic buckling is distributed over the length of the stem, therefore $C = 0.792$ (McMahon, 1973), and that the column is composed entirely of wood, therefore $(E/\rho)^{1/3} = 125\ \mathrm{m}^{+1}$ (Niklas, 1994b). The safety factor for each trunk was calculated as $H_{crit}/H$, with values $< 1.0$ indicating that the trunk has surpassed its critical buckling height. Log $H_{crit}/H$ was plotted against log $D$, and a correlation coefficient was calculated in order to determine whether safety factors were independent of, or dependent on, stem diameter (Niklas, 1994b).

## RESULTS

***Axis size***—Summary data of axis length ($L$) and diameter ($D$) for the trunk, rachis, and rachilla of *Aralia spinosa* are presented in Table 1. Nested ANOVA revealed that there were significant differences between axis types with respect to $L$ ($P < 0.001$) and $D$ ($P < 0.001$). Length did not differ, on average, between the trunk and the rachis, however, both the trunk and the rachis were significantly longer than the rachilla. The diameter of the trunk, rachis and rachilla all, however, differed significantly from each other (Tukey tests). Some variation among sites within axis categories was evident with regards to $D$ ($P = 0.024$) but not $L$ ($P = 0.055$).

***Scaling of length and diameter***—At all sites $L$ and $D$ of the trunk ($r = 0.818$–$0.894$; $P < 0.001$), rachis ($r = 0.784$–$0.914$; $P < 0.001$), and rachilla ($r = 0.839$–$0.927$; $P < 0.001$) were highly correlated. As anticipated, there was a significant log-linear relationship between $L$ and $D$ for each axis type at each site, and when pooled for all sites (Table 2). There was evidence for lack-of-fit of the log-linear model for the relationship between trunk $L$ and $D$ at sites Elberta ($P = 0.045$) and Riverside ($P = 0.009$), but not Zion Church ($P > 0.100$). There was also evidence of possible curvature at Riverside ($P = 0.026$). The quadratic term was significant at Riverside ($t = -4.20$, $P = 0.001$), but not at Elberta ($t = -1.99$, $P = 0.070$). Overall, for all sites pooled, there was also evidence for

TABLE 2. Ordinary least squares (OLS) and reduced major axis (RMA) regression statistics for the relationship between axis length ($L$) and diameter ($D$): $\log L = \log a + b \log D$, where $a$ is the intercept and $b$ is the slope.

| Axis | Site | $b_{\mathrm{OLS}}$ | $b_{\mathrm{RMA}}$ | 95% CI | $r$ | $P$ |
|---|---|---|---|---|---|---|
| Trunk | Elberta | 1.95 | 2.37 | ± 0.80 | 0.826 | <0.001 |
| | Riverside | 1.93 | 2.05 | ± 0.42 | 0.939 | <0.001 |
| | Zion Church | 2.23 | 2.65 | ± 0.86 | 0.842 | <0.001 |
| | Pooled | $2.03^{A*}$ | 2.28 | ± 0.32 | 0.893 | <0.001 |
| Rachis | Liberty | 1.50 | 1.66 | ± 0.43 | 0.904 | <0.001 |
| | Riverside | 1.26 | 1.50 | ± 0.48 | 0.842 | <0.001 |
| | Twilley | 0.91 | 1.11 | ± 0.38 | 0.824 | <0.001 |
| | Pooled | $1.20^{B}$ | 1.38 | ± 0.21 | 0.869 | <0.001 |
| Rachilla | Elberta | 1.44 | 1.66 | ± 0.50 | 0.864 | <0.001 |
| | Riverside | 1.87 | 2.52 | ± 1.01 | 0.744 | 0.001 |
| | Zion Church | 1.49 | 1.63 | ± 0.40 | 0.914 | <0.001 |
| | Pooled | $1.49^{B}$ | 1.79 | ± 0.31 | 0.833 | <0.001 |

* Means with the same superscripts are not significantly different (Tukey test, $\alpha = 0.05$).

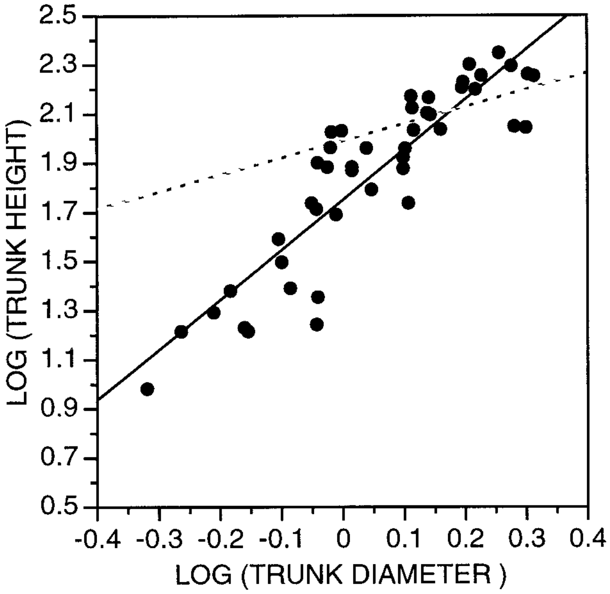

Fig. 2. The relationship between log(trunk height [cm]) and log(trunk diameter [cm]) for *Aralia spinosa*. The solid line represents the ordinary least-squares linear regression for log(height) vs. log(diameter), while the dashed line represents the ordinary least squares linear regression for log($H_{\mathrm{crit}}$) vs. log(diameter) for a free standing untapered column composed of wood.

lack of fit ($P = 0.079$) and curvature ($P = 0.079$). The quadratic term was significant ($t = -2.52$, $P = 0.016$), and therefore the relationship between trunk $L$ and $D$ was estimated by the quadratic regression: $\log L = 1.80 + 2.18 \log D - 2.06[\log D]^2$ ($r^2_{\mathrm{adj}} = 0.815$, $P < 0.001$). For both the rachis and rachilla, quadratic terms were not included as there was no indication of lack of fit for the linear models ($P > 0.100$), and an examination of the plots of residuals vs. fitted values for each regression gave no indication of curvature.

Testing for homogeneity of slopes revealed that the relationship between $L$ and $D$ varied among the axis types ($P < 0.001$), but not among sites within an axis type ($P > 0.05$). The slope describing the relationship between $L$ and $D$ for the trunk was significantly different than the slopes for the rachis and rachilla. There was, however, no significant difference in slope between the rachis and rachilla (Tukey test, Table 2).

***Taper***—Of the 45 trunks sampled, 23 (51.1%) exhibited taper along the length of the entire trunk (negative linear relationship between trunk diameter and position along the length of the trunk) ($r = -0.632$ to $-0.955$, $P < 0.05$). The percentage of tapered trunks varied among sites, with Zion Church having considerably fewer (2/15, 13.3%) than Elberta (8/15, 53.3%) or Riverside (13/15, 86.7%). The average taper coefficient (slope of the LS regression) was $-0.00266 \pm 0.00086$ (mean ± 95% CI) (range: $-0.01092$ to $0.00417$). When untapered trunks were excluded, the average taper coefficient was $-0.00442 \pm 0.00090$ (range: $-0.00210$ to $-0.01092$). No relationship was found between the degree of taper (taper coefficient) and either trunk $L$ ($P = 0.694$) or $D$ ($P = 0.575$).

For all rachises ($r = -0.945$ to $-0.997$, $P < 0.001$), and rachillas ($r = -0.694$ to $-0.994$, $P < 0.001$) there was a moderate to strong negative linear relationship between $D$ and position along the length of the axes. The average taper coefficient for the rachis was $-0.00655 \pm 0.00048$ (range: $-0.00365$ to $-0.01089$), while that of the rachilla was $-0.00524 \pm 0.00030$ (range: $-0.00343$ to $-0.00805$). A positive linear relationship was found between the taper coefficient and rachis $L$: taper coefficient $= -0.00819 + 0.0000307L$ ($r^2_{\mathrm{adj}} = 0.128$, $P = 0.009$). The rachis of small leaves had a tendency to have a larger degree of tapering than large leaves. No relationship was found between the taper coefficient and rachis $D$ ($P = 0.644$), rachilla $L$ ($P = 0.126$) or rachilla $D$ ($P = 0.793$).

Nested ANOVA revealed that taper varied among both axis categories ($P = 0.018$), and sites within axis categories ($P < 0.001$). The trunk was, on average, less tapered than the rachis, but no differences in taper were found between the trunk and the rachilla, or the rachis and the rachilla (Tukey test). The trunks of the ramets at Zion Road showed considerably less taper (taper coefficient $= -0.00040$) than at either Elberta (taper coefficient $= -0.00331$) or Riverside (taper coefficient $= -0.00425$). There was, however, no difference in trunk taper between the latter two sites. Significant site-to-site variation in taper did not occur for either the rachis or rachilla (Tukey tests).

***Trunk safety factors***—Thirty-five percent (16/45) of the ramets sampled exceeded the predicted critical buckling height ($H_{\mathrm{crit}}$) for an untapered column composed entirely of wood (Fig. 2). The average safety factor calculated as $H_{\mathrm{crit}}/H$ was $1.86 \pm 0.21$ (range: 0.66–6.32). The safety factor was size dependent, decreasing with increasing plant size ($r = -0.798$, $P < 0.001$) (Fig. 3).

## DISCUSSION

***Scaling of length and diameter***—A comparison of the slopes describing the relationship between $L$ and $D$ revealed that the rachis and rachilla were closest in form, with the trunk being least like the other axes. The scaling of $L$ and $D$ in the trunk, rachis, and rachilla was in all

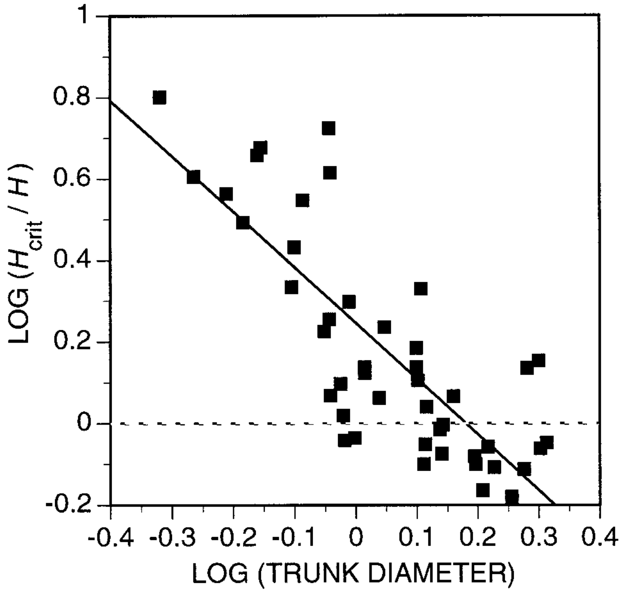

Fig. 3. The relationship between log[$H_{\mathrm{crit}}/H$] and log(diameter [cm]) for the trunk of *Aralia spinosa*. The solid line represents the ordinary least squares linear regression for log[$H_{\mathrm{crit}}/H$] vs. log(diameter), while the dashed line represents $H_{\mathrm{crit}}/H = 1.0$. Values that fall below the dashed line exceed the predicted $H_{\mathrm{crit}}$ and are at risk of elastic buckling.

cases negatively allometric ($b_{\mathrm{RMA}} > 1$), indicating that longer axes had a smaller diameter relative to their length than shorter axes. The trunk and rachilla had the smallest relative diameter, while the rachis had the largest relative diameter in relation to its length. A number of scaling models have been proposed to explain the scaling of $L$ and $D$ in tree trunks and branches. In the stress similarity model, $L$ is proportional to $D^{1/2}$, that is $b_{\mathrm{RMA}} = \frac{1}{2}$. A constant maximum stress level is maintained throughout the length of the axis, and deflection of the free end decreases with increasing $L$. In axes that conform to the elastic similarity model, $L$ is proportional to $D^{2/3}$, that is $b_{\mathrm{RMA}} = \frac{2}{3}$. Deflection of the free end of the axis is constant relative to $L$. Form becomes more robust as size increases (growth in girth occurs at a relatively faster rate than growth in height) when axes conform to either the stress similarity or elastic similarity model. Length is proportional to $D$ in axes that exhibit geometric similarity; form is the same regardless of size, and therefore $b_{\mathrm{RMA}} = 1.0$ (McMahon, 1973, 1975; McMahon and Kronauer, 1976; Bertram, 1989; Niklas, 1994a).

The allometric exponent for trunk length was dependent on trunk diameter (quadratic equation is best-fitting model), while the allometric exponents for rachis and rachilla length were not (linear equations provide best-fitting models). Again the rachis and rachilla were closest in form, with the trunk being least like the other axes. For the trunk, the slope of the regression at any diameter can be estimated by: $\Delta(\log L)/\Delta(\log D) = b_1 + 2b_2 \log D$ (Niklas, 1994b). Therefore, the diameter when the allometric exponent of trunk length exhibits stress similarity ($b_{\mathrm{RMA}} = \frac{1}{2}$), elastic similarity ($b_{\mathrm{RMA}} = \frac{2}{3}$), and geometric similarity ($b_{\mathrm{RMA}} = 1$) can be estimated from the equation: $\Delta(\log L)/\Delta(\log D) = 2.18 + (2[-2.06])\log D$. From this equation the trunk is predicted to exhibit stress similarity when $\log D = 0.408$ ($D = 2.55$ cm), elastic similarity when $\log D = 0.367$ ($D = 2.33$ cm), and geometric similarity when $\log D = 0.286$ ($D = 1.93$ cm). The allometric exponent that describes the relationship between $L$ and $D$ is therefore dependent on the size and presumably the age of the trunk. As the largest trunks sampled had a diameter of only 2.05 cm, none of the ramets exhibited either elastic or stress similarity during the trunk-building phase. *Aralia spinosa* has been reported to reach a diameter at breast height of 24 cm (White, 1984), therefore elastic and stress similarity might be attained in larger older ramets if growth remains on the same trajectory predicted by the quadratic model. Several reports indicate that rather than a single static relationship between $L$ and $D$ holding throughout the life of a tree ($b_{\mathrm{RMA}} = \frac{1}{2}$, $b_{\mathrm{RMA}} = \frac{2}{3}$, or $b_{\mathrm{RMA}} = 1$), the allometric exponent is size and age dependent, with $b_{\mathrm{RMA}}$ declining with increasing size and age (Rich et al., 1986; Niklas, 1995). Thus, saplings exhibit relatively narrow trunks in relation to their height, while older trees exhibit relatively massive trunks in relation to their height. The relative allocation of resources to vertical and lateral growth changes during the life span of the tree. This may be the result of a decline in trunk extension growth, an increase in lateral growth, or a combination of both. A decrease in the length of annual increments with increasing ramet age was reported for the trunk of *Aralia spinosa* (White, 1984).

***Taper***—A comparison of the taper coefficients indicated that large-scale differences in taper were not apparent between the trunk and the leaf axes. Trunk taper was only significantly different from rachis taper. The trunk, rachis, and rachilla can be thought of as more or less tapered cantilever beams (fixed at the base). A tapered support is mechanically advantageous as maximum stress occurs at the base during bending, where diameter is greatest (Mosbrugger, 1990; Speck, Spatz, and Vogellehner, 1990; Niklas, 1997a). Also, a tapered support is more economical to construct than a non-tapered support with the same basal diameter (Niklas, 1997b).

The rachis and rachilla were closest in form as their taper coefficients did not vary significantly and all rachises and rachillas were tapered. It has previously been shown that the petioles of pinnately compound leaves are tapered, while the petioles of simple and palmately compound leaves are untapered (Niklas, 1994a). Only about half of the sampled trunks were tapered along their entire length. The lack of continuous taper in trunks may result indirectly from the perennial nature of the trunk vs. the annual nature of the rachis and rachilla. Damage to the shoot apical meristem of normally monopodial trunks of *Aralia spinosa* usually results in the outgrowth of at least one distal axillary bud. The resulting branch grows orthotropically forming a new "leader." This replacement may have a basal diameter greater than the distal diameter of its subtending axis. If this event occurs a number of times, diameter can decline and increase a number of times along the length of the axis (sympodium), resulting in an overall lack of detectable taper.

***Trunk critical buckling height***—The safety factors for trunk height during the trunk-building stage of *Aralia spinosa* were size dependent, with larger trunks exceeding the predicted critical buckling height for untapered wooden columns. Casual observations tend to support this, as large specimens appear to bend under their own mass, and in some cases fall over, although this may also result from windthrow. In contrast, McMahon (1973) and Niklas (1994b) reported that safety factors were size independent for most angiosperm and gymnosperm trees. A size-dependent decrease in safety factors was reported for large palm trees and arborescent cacti, with the palms but not the cacti exceeding their predicted critical buckling height (Rich et al., 1986; Niklas, 1994b; Niklas and Buchman, 1994).

***Comparison of pinnately compound leaves and shoots***—Recent developmental evidence suggests that pinnately compound leaves resemble shoots, especially during early ontogeny. Sattler and Rutishauser (1992), Lacroix and Sattler (1994), and Lacroix (1995) reported that the apex of developing pinnately compound leaves in a number of species may be histologically differentiated into a tunica and corpus, much like the shoot apical meristem, and that leaflet primordia are initiated on the flank of the leaf apex in a similar fashion to leaf primordia on a shoot exhibiting more or less distichous phyllotaxy.

In *Aralia spinosa*, the compound leaves are deciduous and determinate (both the rachis and rachillas bearing a terminal leaflet; Fig. 1). A comparison of the allometric scaling exponents for the relationship between $L$ and $D$ of the leaf axes with published values for herbaceous and woody stems is illuminating. The allometric scaling exponent for the rachis of *Aralia spinosa* was 1.38 ± 0.13, while that of the rachilla was 1.79 ± 0.31. Previous work has indicated that the allometric scaling exponent for tree trunks averages 0.69, for the peripheral axes of trees, 1.39, the woody axes of shrubs, 1.27, and nonwoody plants, 1.32–1.46 (Bertram, 1989; Niklas, 1994a). It appears that the allometric scaling exponent of the rachis and rachilla of *Aralia spinosa* most closely resembles that of the peripheral axes (ultimate branches) of trees, and the axes of shrubs and nonwoody plants. A comparison with other compound leaves is not possible as these data do not exist. Our work supports Niklas' (1991, 1992, 1993) contention that mechanically the rachis of a compound leaf is equivalent to a branch, because it serves the same function, although for a more limited time. Givnish (1978) views compound leaves as throw-away branches. In nonbranched ramets of *Aralia spinosa* the rachises represent the axes of lateral exploration, while the rachillas represent the axes of exploitation (bearing the bulk of the photosynthetic tissue: leaflets) sensu Edelin (1977).

***Adaptive growth form***—The design of a tree is largely the result of natural selection operating within the constraints imposed by the genome. Mattheck (1991) suggests that selection favors the "compromise tree," that is, the design of a tree represents a compromise between maximizing physiological processes such as uptake, transport, and photosynthesis, while minimizing investments for mechanical support. As ". . . each species is presumed to be adapted to the environment at a particular stage" (Horn, 1971), one may ask what is the adaptive significance of the design of a particular species. *Aralia spinosa* is an obligate initial community species (classification: Sullivan, 1992). Early-successional species usually exhibit rapid stem elongation, quickly raising their crown and shading out competitors. Extension growth of *Aralia spinosa* ramets is very high, especially during the first two years of growth where it averages 75 cm/yr (White, 1984). King (1991) suggests that rapid growth in height can be obtained with minimum biomass by producing a small crown supported by a thin stem composed of low-density wood. During the trunk-building phase, the crown of *Aralia spinosa* is composed entirely of compound leaves, thus minimizing support costs. Givnish (1978) suggests that compound leaves also help to pay for themselves, as their axes are photosynthetic. In *Aralia spinosa* lateral growth of the stem does not keep up with extension growth, again minimizing support costs, but with the added risk of elastic buckling and stem failure. *Aralia spinosa* also has relatively light wood. Wiemann and Williamson (1989) reported that the specific gravity of *Aralia spinosa* wood (0.34) was the lowest for 17 arborescent angiosperm species sampled in Mississippi. The design of *Aralia spinosa* ramets appears to result from adaptation to life as an early-successional species.

## LITERATURE CITED

BELL, A. 1991. Plant form. Oxford University Press, Oxford.

BERTRAM, J. E. A. 1989. Size-dependent differential scaling in branches: the mechanical design of trees revisited. *Trees* 4: 241–253.

BURNS, D. A., AND T. A. RYAN, JR. 1983. A diagnostic test for lack of fit in regression models, 286–290. American Statistical Association. Statistical Computing Section. Proceedings of the Statistical Computing Section. American Statistical Association, Washington, DC.

CORNER, E. J. H. 1964. The life of plants. The University of Chicago Press, Chicago, IL.

EDELIN, C. 1977. Images de l'architecture des conifères. Thèse de doctorat, 3$^{e}$ cycle, Biologie végétale, Université de Montpellier II, France.

FISHER, J. B. 1984. Tree architecture: relationships between structure and function. *In* R. A. White and W. C. Dickison [eds.], Contemporary problems in plant anatomy, 541–589. Academic Press, Orlando, FL.

FISHER, J. B., AND R. RUTISHAUSER. 1990. Leaves and epiphyllous shoots in *Chisocheton* (Meliaceae): a continuum of woody leaf and stem axes. *Canadian Journal of Botany* 68: 2316–2328.

GIVNISH, T. J. 1978. On the adaptive significance of compound leaves, with particular reference to tropical trees. *In* P. B. Tomlinson and M. H. Zimmerman [eds.], Tropical trees as living systems, 351–380. Cambridge University Press, Cambridge.

GREENHILL, G. 1881. Determination of the greatest height consistent with stability that a vertical pole or mast can be made, and the greatest height to which a tree of given proportions can grow. *Proceedings of the Cambridge Philosophical Society* 4: 65–73.

JEUNE, B., AND C. R. LACROIX. 1993. A quantitative model of leaflet initiation illustrated by *Murraya paniculata* (Rutaceae). *Canadian Journal of Botany* 71: 457–465.

HORN, H. S. 1971. The adaptive geometry of trees. Princeton University Press, Princeton, NJ.

KING, D. A. 1991. Tree allometry, leaf size and adult tree size in old-growth forests of western Oregon. *Tree Physiology* 9: 369–381.

LACROIX, C. R. 1995. Changes in leaflet and leaf lobe form in developing compound and finely divided leaves. *Botanische Jahrbücher für Systematik* 117: 317–331.

———, AND R. SATTLER. 1994. Expression of shoot features in early leaf development of *Murraya paniculata* (Rutaceae). *Canadian Journal of Botany* 72: 678–687.

LITTLE, E. L. 1980. The Audubon Society field guide to North American trees: eastern region. Alfred A. Knopf, New York, NY.

MATTHECK, C. 1991. Trees: the mechanical design. Springer-Verlag, Berlin.

MCMAHON, T. A. 1973. Size and shape in biology. *Science* 179: 1201–1204.

———. 1975. The mechanical design of trees. *Scientific American* 233: 92–102.

———, AND R. E. KRONAUER. 1976. Tree structures: deducing the principle of mechanical design. *Journal of Theoretical Biology* 59: 443–466.

MIESCH, R., AND P. BARNOLA. 1993. Croissance rythmique endogène de la feuille de *Guarea guidonia* (Méliacées): étude préliminaire expérimentale. *Canadian Journal of Botany* 71: 558–564.

MINITAB. 1992. Minitab reference manual, release 9. Minitab, State College, PA.

MOSBRUGGER, V. 1990. The tree habit in land plants. Springer-Verlag, Berlin.

NIKLAS, K. J. 1991. Flexural stiffness allometries of angiosperm and fern petioles and rachises: evidence for biomechanical convergence. *Evolution* 45: 734–750.

———. 1992. Plant biomechanics: an engineering approach to plant form and function. The University of Chicago Press, Chicago, IL.

———. 1993. Testing 'economy in design' in plants: are the petioles and rachises of leaves 'designed' according to the principle of uniform strength? *Annals of Botany* 71: 33–41.

———. 1994a. Plant allometry: the scaling of form and process. The University of Chicago Press, Chicago, IL.

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

———. 1995. Size-dependent allometry of tree height, diameter and trunk-taper. *Annals of Botany* 75: 217–227.

———. 1997a. Mechanical properties of black locust (*Robinia pseudoacacia* L.) wood. Size- and age-dependent variations in sap- and heartwood. *Annals of Botany* 79: 265–272.

———. 1997b. The evolutionary biology of plants. The University of Chicago Press, Chicago, IL.

———, AND S. L. BUCHMAN. 1994. The allometry of saguaro height. *American Journal of Botany* 81: 1161–1168.

NOVELL. 1994. Quattro Pro V 6.0 user's guide. WordPerfect, Novell Applications Group, Orem, UT.

RICH, P. M., K. HELENURM, D. KEARNS , S. R. MORSE, M. W. PALMER, AND L. SHORT. 1986. Height and stem diameter relationships for dicotyledonous trees and arborescent palms of Costa Rican tropical wet forest. *Bulletin of the Torrey Botanical Club* 113: 241–246.

SATTLER, R., AND R. RUTISHAUSER. 1992. Partial homology of pinnate leaves and shoots. Orientation of leaflet inception. *Botanische Jahrbücher für Systematik* 114: 61–79.

SMITH, E. B. 1982. Juvenile and adult leaflet phases in *Aralia spinosa* (Araliaceae). *SIDA Contributions to Botany* 9: 330–332.

SPECK, T., H.-C. SPATZ, AND D. VOGELLEHNER. 1990. Contributions to the biomechanics of plants. I. Stabilities of plant stems with strengthening elements of different cross-sections against weight and wind forces. *Botanica Acta* 103: 111–122.

SULLIVAN, J. 1992. *Aralia spinosa*. *In* W.C. Fisher [compiler], The Fire Effects Information System [Data base]. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Intermountain Fire Sciences Laboratory, Missoula, MT.

WHITE, P. S. 1983. 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.

———. 1984. The architecture of devil's walking stick, *Aralia spinosa* (Araliaceae). *Journal of the Arnold Arboretum* 65: 403–418.

———. 1988. Prickle distribution in *Aralia spinosa* (Araliaceae). *American Journal of Botany* 75: 282–285.

WIEMANN, M. C., AND G. B. WILLIAMSON. 1989. Radial gradients in the specific gravity of wood in some tropical and temperate trees. *Forest Science* 35: 197–210.

ZAR, J. H. 1984. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, NJ.