THE ARCHITECTURE OF DEVIL'S WALKING STICK, ARALIA SPINOSA (ARALIACEAE)

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ARALIA SPINOSA L., a small tree of moist sites in eastern deciduous forests, is striking in appearance. Among its distinctive traits are large, two- or threetimes compound leaves (often over 1 m long and with more than 100 leaflets), abundant prickles, large terminal inflorescences (over 6000 flowers), and a relatively unbranched pachycaulous habit. Several of these characteristics are treated in the empirical observations known as Corner's rules (Hallé *et al.*, 1978), which state that the thicker the annual increment, the larger the leaf borne on the increment and the fewer the ultimate number of branches. A test of Corner's rules in eastern deciduous trees (P. S. White, 1983) confirmed that *Aralia* is extreme in form: it had larger leaves, thicker annual increments, and fewer branches per unit leaf area than any of the other 47 species considered. The ecological role of *Aralia* is also of interest. Although trees of this species sometimes persist in shade, they occur primarily in disturbed areas (where they appear after fire, windstorm, or gap creation) and in old fields.

The relationship between the architecture and the ecological role of a tree has been the subject of a growing literature (e.g., Horn, 1971; Whitney, 1976; Givnish, 1978a; Hallé *et al.*, 1978). *Aralia* was selected for study because several of its morphological traits (large annual increment (Marks, 1975), high numbers of leaves and extensive total leaf area per annual increment (P. S. White, 1983), and larger leaf size with compound organization (Givnish, 1978a, 1978b)) have been hypothesized to be correlates of shade intolerance.

In this study I investigated the gross morphology and life history of *Aralia* ramets. Of primary interest were the growth in height and in diameter of individual ramets, the accumulation of branches in *Aralia* crowns over time, and the leaf area carried by these branches.

METHODS

Three populations of *Aralia spinosa* occupying moist, low-elevation (500–600 m) sites in the Great Smoky Mountains, Sevier County, Tennessee, were sampled. These populations were irregular in extent due to past agricultural disturbances. Since *Aralia spinosa* is clonal, individual stems are ramets; genets were not distinguished here because this would have greatly disturbed the populations. A random-numbers table was used to sample 114 ramets—one-fourth of all stems encountered.

Because leaf scars, terminal bud-scale scars, and inflorescence axes all persist

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for ten to fifteen years, the developmental history of each ramet could be reconstructed. For each year of growth, the amount of extension growth (the annual increment, or the length of axis produced per year), the number of leaves (on stems older than one year, the number of leaf scars), and the presence or absence of flowering (as shown by the position of old inflorescence axes) were recorded. Analysis of architectural development was facilitated because flowering and branching are intimately related: each flowering event terminates the growth of the axis, with branching occurring the following year from axillary buds that develop below the old inflorescence axis.

Each year's increment was numbered starting at the base of the ramet (annual increment no. 1) and working to the tips of the branches (the most recent year's growth) (see FIGURE 1). Yearly increments were also numbered from the base of each branch order. In this way, the increment formed each year could be analyzed as a function of age and crown position.

The numbering system was used to divide annual increments into trunk increments ("T" in the figures; the unbranched parts of the ramet) and firstand subsequent-order branch increments ("B" in the figures). Spur branches ("Sp"; short, slow-growing, suppressed branches) were so morphologically distinctive that they were segregated from other branches in the analysis, as were inflorescence axes ("F").

Part of one population had been cut during roadside mowing the previous season (1980). The trunks that sprouted after this grew more vigorously than did uninjured trunks. Shaded stems, on the other hand, grew less vigorously than did uninjured ones. Hence, for the trunk-building phase of growth, three states could be contrasted: injured, open-grown ("I" in the figures), uninjured, open-grown ("T"), and uninjured, shaded ("S"). For comparisons between trunks and branches, only open-grown, uninjured trunks ("T") were used. Note that the "T" (uninjured, unsuppressed trunks) in the figures was used twice: once in the "T" vs. "B" (branches), "F" (inflorescences), and "Sp" (spur branches) comparison. The data labeled "T" are identical in these separate comparisons.

Bifurcation ratios (Whitney, 1976) were computed for ramets. This is the average number of daughter branches per branch, using a branch-ordering scheme similar to that used in stream ordering (Whitney, 1976). Branch angles were measured at the base of each branch. Due to distal, adaxial bending of the branch, however, effective branch spread was less than that predicted from basal branch angles. Hence, effective branch angle (in degrees) was computed from branch length and the spread of the branch tip away from the axis of the next lower branch order.

Since *Aralia spinosa* is deciduous, leaves could only be measured on the most recent year's growth. A random-numbers table was used to select one leaf from each of the leafy shoots present. This leaf was characterized in terms of the annual-increment numbering system described above; leaf length and width (outer points of the outline of the compound leaf) and number of leaflets were recorded. Fifty trunk and fifty branch leaves were sampled. A subsample

ANNUAL INCREMENT NUMBERING SYSTEM



FIGURE 1. Annual increment ("AI") numbering system used to model growth and branching of Aralia spinosa.



FIGURE 2. Mean length of increment (extension growth) and mean number of leaves (nodes) borne per year in *Aralia spinosa* as function of annual increment number. Mean diameters of 3 lowermost and 3 uppermost annual increments shown beneath figure; standard errors indicated above and below means.

of leaflets was used to establish a regression between leaflet blade area and dry weight.

Diameters of the most recent year's growth (one-year-old shoots) and of the basal increment of the ramet (annual increment no. 1) were measured. A subsample of ramets was harvested for determination of biomass of wood, leaves (divided into leaflet blades and rachides), inflorescences, and infructescences. These biomass samples were randomly selected from within the different age classes of the ramets studied. They were oven dried at 105°C until their weight stabilized (usually after 48 hours) and then weighed.

RESULTS

Extension Growth, Diameter, Biomass, and Number of Leaves per Shoot

For each of the first two years, extension growth in *Aralia* averaged more than 75 cm; this was followed by a decline, so that by the eighth to tenth years extension growth averaged less than 25 cm annually (a 67% decline; FIGURE 2). The average diameter of annual increments also decreased (FIGURE 2, below). Additionally, the number of leaves borne per year ("nodes" or leaf scars present; FIGURE 2) declined, but the decline—ca. 40 percent—was less steep

1984]



FIGURES 3, 4. 3, characteristics of annual increments as function of position on plant (T = trunk, B = branches, Sp = spurs, F = inflorescence axes): a, mean extension growth; b, mean number of nodes; c, mean diameter; d, mean woody biomass. 4, characteristics of trunk increments as function of shading and injury (T = open-grown, uninjured trunks, I = trunk segments sprouting after injury during previous season, S = shaded plants): a, mean length of increment; b, mean number of nodes; c, mean diameter; d, mean woody biomass. Standard errors indicated above and below means.

than that for extension growth (early growth averaged about 10 leaves per increment, while later increments had about 6). This decrease in extension growth and leaf number with age corresponded to the first flowering and branching of the stem. The stage of rapid height growth, high leaf numbers per annual increment, and sterility was termed the "trunk-building phase." Growth is strictly erect and unbranched during this phase.

Mean differences between trunks and branches for extension growth, and for number of leaves, diameter, and biomass per (new) annual increment, were all significant at the .001 level (FIGURE 3). Trunk annual increments averaged .7 m in extension growth, 10.7 leaves, 1.8 cm in diameter, and 56.2 g woody biomass; branch annual increments averaged .31 m in extension, 7.01 leaves, 1 cm in diameter, and 15.1 g. Spur branches showed the lowest extension growth (.02 m), the lowest number of leaves (2.9), and the lowest first-year woody biomass (.5 g). Diameters of branches, spurs, and inflorescence axes were not significantly different (FIGURE 3).

Trunks that resprouted after injury grew to larger dimensions than uninjured ones (FIGURE 4): they averaged almost twice the extension growth (1.4 m) in



FIGURE 5. Mean surface area of individual leaf blades: a, open-grown individuals (T = trunks, B = branches, Sp = spurs); b, trunks (T = open-grown trunks, I = ramets sprouting after injury during previous season, S = shaded ramets). Standard errors shown above and below means.



FIGURE 6. Mean total leaf area per annual increment: a, open-grown individuals (T = trunks, B = branches, Sp = spurs); b, trunks (T = open-grown, uninjured trunks, I = ramets sprouting after injury during previous season, S = shaded ramets). Standard errors shown above and below means.



FIGURE 7. Mean leaf biomass per annual increment (left) and leaf biomass as percentage of total annual increment biomass (right). Data for open-grown, uninjured ramets (T = trunks, B = branches, Sp = spurs). Standard errors shown above and below means.

the first year after injury, and they had greater leaf numbers (12.6), diameters (1.9 cm), and woody biomass (97.9 g). Shaded ramets had the lowest values for these characteristics (.4 m extension, 7.2 leaves, 1.1 cm diameter, and 10 g woody biomass). These means were significantly different at the .01 level.

LEAF CHARACTERISTICS

Leaves borne on trunks averaged 3333 cm² in area—significantly larger (P < .001) than those borne on either branches (2295 cm²; a 31% decline) or spurs (only 300 cm²; FIGURE 5, a). For trunks, leaves were smaller on shaded individuals (1850 cm²) than on open-grown ones, but trunks growing after injury were not significantly different than uninjured ramets (FIGURE 5, b). Trunk leaves (uninjured, open grown) averaged 1.02 m long (SD = .2) and 95.1 leaflets (SD = 27.8), while branch leaves averaged .86 m long (SD = .18) and 77.3 leaflets (SD = 27).

Total leaf area per annual increment (mean area per leaf times mean number of leaves per increment) showed the same trends: trunk increments bore over 35,000 cm² total leaf area, while branch increments bore ca. 17,000 cm², and spurs bore less than 1000 cm² (differences significant at the .001 level; FIGURE 6, a). Injured ramets had a greater total leaf area per increment than uninjured ones because of higher leaf numbers per increment (FIGURE 6, b).

BRANCH ORDER*	Mean number of branches borne	SE	
1 (N = 42)	2.7	.17	
2(N = 116)	1.6	.06	
3 (N = 125)	1.4	.05	
4 (N = 121)	1.5	.06	
5(N = 82)	1.3	.07	
6(N = 47)	1.4	.15	
7(N = 22)	1.2	.09	
8 (N = 5)	1.4	.27	

TABLE 1. Mean number of branches borne as a function of branch order.

*Branch order 1 is the first branching event.

Total leaf biomass per annual increment, therefore, declined from trunks to branches (FIGURE 7). However, woody biomass per successive annual increment decreased more quickly than leaf weight; hence, if leaf biomass is expressed as a percentage of total biomass per annual increment (FIGURE 7, right), relative leaf biomass actually increased from trunks to branches and was highest in spur branches. It should also be borne in mind that branched plants had several to many new shoots; hence, total leaf biomass per ramet (as opposed to leaf biomass per annual increment as discussed above) increased through the life of the plant with the increase in the number of branches in the crown.

Three tissues were weighed separately in one-year-old annual increments: leaflet blades, rachides, and wood. There was an average of 2.5 g of leafletblade tissue and 1.3 g of rachides per g of woody tissue. Total leaf biomass was thus 3.8 g per g of woody tissue. Leaflet-blade biomass per g of supportive biomass (rachides plus wood) was 1.1 g.

FLOWERING AND BRANCHING

At first flowering, the mean age was 3.54 years and the mean height (to the base of the inflorescence) 2.6 m. This marked the end of the trunk-building

Branch age at flowering† (years)	Percent flowering			
	All branches (N = 686)	First-order branches (N = 127)	All sub- sequent-order branches (N = 559)	
1	57.5	26.8	64.4	
2	39.6	73.2	32.4	
3	2.3		2.9	
4	0.6	_	0.4	

TABLE 2. Frequency of flowering in branches as a function of age.*

*No spurs were included in these data.

[†]Branch age was determined as follows: the first annual increment of a particular branch order was year 1 for that branch, the second annual increment was year 2, and so on, until flowering.



FIGURE 8. Accumulation of live (above) and dead (below) branches in *Aralia spinosa* as function of ramet age. Spurs not included. Straight line labeled 2^x corresponds to theoretical addition of 2 branches each year, characterizing early life history of *Rhus typhina*; that labeled 1.35^x corresponds to model for *Aralia spinosa*, $b = 1.35^x$ (b = number of branch tips, x = ramet age in years).

phase; the apex died and lateral buds below the inflorescence were the source of branches and hence of extension growth the following year. Two factors controlled the rate of branch increase as the ramets aged: the number of branches (axillary buds) that developed the year after flowering, and the number of years that these branches remained sterile before they flowered and produced higher-order branching. The first branching event was unlike the others in both of these characteristics (TABLES 1, 2). The year following the first time an individual ramet flowered, an average of 2.7 branches were produced. Subsequent flowering events produced only 1 or 2 branches (mean = 1.2-1.6—significantly different from means for primary branches at the .01 level; TABLE 1). First-order branches usually remained sterile for at least one year (26.8% flowered the first year), while later ones were more likely (64.4%) to flower their first year of development.

Branch longevity (before flowering) and branches per flowering event controlled accumulation of branches over time (FIGURE 8). Two reference lines are shown: *Rhus typhina* L., in its early life, accumulated branches at the rate



FIGURE 9. Accumulation of live branches (above) and branching trajectories (below) in *Aralia spinosa* as function of number of years since first branching event. Spurs not included. Straight line in upper figure corresponds to model $b = 1.35^x$ (b = number of branch tips, x = ramet age in years). Arrows represent effect of adding dead branches to live ones for selected older ramets (this addition does not take into account any calculated increase in branches if dead branches were alive, flowering and branching). Branching trajectories (lower figure) constructed by superimposing developmental accumulation of branches in all *Aralia* individuals sampled.

of 2^(age in years) (plants of this species show strict bifurcation every year for the first several years; J. White, 1980). For *Aralia* this early exponential increase of branch number (as determined from regression of the logarithm of branch number on the logarithm of age in years for the first 6 years of branching) approximated 1.35^(age in years). There was a marked slowing in branch accumulation after this early phase. By age 5, dead branches began to appear in *Aralia* crowns (FIGURE 8, below); these (since they eliminated later branch generations) and the lower number of branches produced per flowering event resulted in a leveling off of branch number after about 10 years. Since the first branching event was so distinctive, the data of FIGURE 8 were recast in FIGURE 9 to show branch accumulation as a function of time after the first branching event. The overall decrease in branch accumulation with age is seen in FIGURE 9 (below), where the individual branching trajectories of all *Aralia* ramets in this data set 1984]



FIGURE 10. Diameter (above) and height (below) growth in *Aralia spinosa* as function of age (GRSM, largest known individual in Great Smoky Mountains National Park; National Champion, largest known individual in U. S. A., based on scalar integrating diameter, height, and spread). Curves fitted by eye.

have been superimposed. The oldest (14 years) individual ramets had approximately 25 to 30 living branches (not including spurs).

BRANCH ANGLES AND CROWN SPREAD

Branch angles (for all orders of branches) averaged 30° when measured between the distal part of the recently terminated axis and the branch base. Because the branch tips curved toward the vertical, the effective branch angle was $5-25^{\circ}$ (mean = 15°).

Branched ramets had an overall Y shape, with the crown diameter equal to

77 percent (SD = 52) of crown height (as measured from the first branch). The angle of overall crown spread at the first branch is 42°, giving an effective trunk-to-first-order-branch angle of 21° for each side of the crown—an angle generally larger than that of the higher-order branches.

The shape of the crown as seen from above was determined by the phyllotaxy of nodes (axillary buds) below the first inflorescence and by the number of branches that developed after the first flowering event. The phyllotaxy was 2/5, and the first-order branches were thus separated by 144° on a horizontal plane. The mean number of first-order branches was 2.7. The shape of the crown was initially narrowly elliptic (when two first-order branches developed) to circular (when three first-order branches developed).

Internodal distances increased regularly from the base of each annual increment to its midpoint and then decreased in a similar way to the increment tip. This was true for both fertile and sterile increments, but in the former the upper, more crowded nodes bore the inflorescence branches. The year after flowering, leafy branches developed from axillary buds near the annual increment's midpoint, in the area where the nodes were farthest apart. Together with phyllotaxy, this vertical distance tended to separate the main crown branches.

BIFURCATION RATIOS

The mean bifurcation ratio was 3.0 if spurs were included and 2.5 if they were not. This ratio was positively and significantly correlated with ramet age ($\mathbf{R} = .71$, P = .05). In older ramets the bifurcation ratio averaged 4 (spurs included).

HEIGHT GROWTH, DIAMETER GROWTH, AND LONGEVITY

Aralia grew uniformly in diameter (mean = .73 cm per yr) as it aged (FIGURE 10, above). However, growth in height slowed (FIGURE 10, below), with most (ca. 50–60%) occurring in the first 3–4 years (or ca. 10%) of the life span, during the trunk-building phase of growth. Thereafter, extension growth decreased and was no longer concentrated in erect, upward growth. Maximum height in the sampled populations was 7 m; the largest recorded individuals were over 10 m tall (FIGURE 10). Average height was about 1.5 to 2 times height before flowering. Average stem longevity was ca. 25–30 years; record ages were 40–50 years.

INFLORESCENCE AND FRUIT BIOMASS

There was an average of 6360 flowers per inflorescence, with an average total inflorescence weight of 22.5 g, and 905 mature fruits per infructescence, with 5 seeds per fruit (for a total of 4525 seeds per inflorescence). Infructescences averaged 79.4 g dry weight, and their biomass was thus similar in magnitude to total leaf and stem biomass of branch annual increments (ca. 90 g) (note that no estimate was made of the biomass or number of fallen flowers or flower parts). Total biomass (leaves, stems, infructescences) of branch annual incre-

ments was 169.5 g per increment, similar to that of sterile trunk segments (about 200 g per annual increment).

DISCUSSION

The architectural development of Aralia ramets was nonstationary (J. White, 1979, 1980; Waller & Steingraeber, in press). In stationary models of growth, the probability of branching and the number of branches produced per branching event are constant. In nonstationary models, the rules of growth vary with time (for example, as a function of plant age or crown development). As long as more than one daughter branch is produced in each branching event, stationary branching results in an exponential increase in branch number over time. Stationary models have been applied to early phases of tree branching and to rhizomatous herbs; in both cases it has been suggested (Waller & Steingraeber, in press) that daughter branches can increase exponentially as long as they do not interfere with one another. Computer simulation of branching in older tree crowns has required the probability of branching to be nonstationary and to decrease as branch order increases (Fisher & Honda, 1977). These simulations produce behavior similar to the logistic model of population growth, with an early exponential increase in branch number followed by a decreasing rate of branching (J. White, 1980; Waller & Steingraeber, in press).

In Aralia the number of branches per order decreased as branch order increased. Hence, the rate of branch accumulation in Aralia crowns also decreased over time. When compared to higher-order branches, first-order ones also differed in usually remaining sterile for one year (vs. tending to flower the first year), in having greater angles to the parent axis, and in having their points of origin along the parent axis farther apart. Thus the first-order branches are well separated. Among branch orders, the first-order branches are most responsible for the three-dimensional spread of Aralia crowns. With the decrease in rate of branch accumulation over time, there was a decrease in height growth rate. Fifty to 60 percent of the total height of Aralia shoots was attained during the first three to four years.

The trunk-building and branching phases of growth in *Aralia* differed in ways other than height growth and branching rate. During the trunk-building phase, annual increments were longer, thicker, and heavier (dry weight) than the annual increments of branches. Further, when compared with leaves of branch increments, those of trunk increments were more numerous and longer, with more leaflets and a greater total leaf area. Prickle distribution also differed, with prickles denser on trunk annual increments than on branch annual increments (P. S. White, unpubl. data).

Borchert and Slade (1981) have shown that reduced branch length and reduced rates of branching over time are both necessary to prevent daughter branches from interfering with one another (i.e., in leaf display). Such interference was not measured in the present study; however, data on annualincrement length and branching in *Aralia* lends empirical support to Borchert and Slade's conclusion. A decreasing branching rate was correlated with decreasing length of the annual increments. Decreases in branch length with increasing branch order have been reported for several tree species (J. White, 1980; Honda, 1971). A decreasing rate of branching over time has been reported for *Acer rubrum* L. (J. White, 1980). Further, decreases in height growth rates over time may be a common property of trees. Site index curves from the forestry literature frequently show a decrease in height growth rate, although the timing of the decrease and the precise shape of the curves vary with species and site quality (see, for example, Trimble & Weitzman, 1956).

Borchert and Slade (1981) also argued that realistic simulations of tree branching require absolute measures of tree morphology (e.g., absolute branch length or leaf size). For example, they predicted that trees with large leaves would experience an earlier decrease in branching rate than trees with small leaves. *Aralia spinosa* has the largest leaves in the arborescent flora of the study area (P. S. White, 1983). The early decrease in branching rate (after the firstorder branches developed) is qualitatively compatible with Borchert and Slade's (1981) prediction. A complication in *Aralia* is that leaf size decreases with ramet age. Smaller leaves on the branches decrease branch interference independently of other morphological characteristics.

Bifurcation ratios were nonstationary in Aralia spinosa. This has also been reported for Acer saccharum Marsh. (Steingraeber et al., 1979), Lindera benzoin (L.) Blume (Pickett & Kempf, 1980), and Populus deltoides Bartram and Tabebuia rosea DC. (Borchert & Slade, 1981). The bifurcation ratio has been criticized as a measure of tree branching because of this nonstationary behavior (Waller & Steingraeber, in press). A second criticism is that the ratio measures only relative attributes of branching (Borchert & Slade, 1981; P. S. White, 1983). For example, Aralia spinosa has a bifurcation ratio similar to that of Acer saccharum (Whitney, 1976), yet the two species are very different in gross morphology: Aralia has larger leaves, has fewer branches at a given leaf area, and displays a given total leaf area in a shorter time than Acer (P. S. White, 1983).

Rhus typhina, which also has nonstationary branching and increment length that decreases with increasing branch order (J. White, 1980), is architecturally similar to *Aralia spinosa*. *Rhus* conforms to Leeuwenberg's architectural model (Hallé *et al.*, 1978). Although *A. spinosa* fits this model better than any other one, Leeuwenberg's model is characterized by two or more branches per module; *Aralia* has only one or two branches per module in all except first-order branches.

Aralia initially accumulated branches at a rate slower than *Rhus*. In addition, Aralia remained sterile and in the trunk-building phase for three to four years, while *Rhus* flowers in the first one to two years (Waller, pers. comm.). Aralia also continued to produce sterile annual increments in its crowns, whereas *Rhus* shoots usually flower more regularly. The result is that Aralia ramets grew taller but accumulated branches more slowly than those of *Rhus*. The comparison of these two relatively simple woody plants suggests that gross morphological traits (size of leaves, number of leaves per annual increment, length of annual increment, rate of branch accumulation, and number of branches) are differently adjusted in different trees, resulting in a range of possible morphological forms within one architectural model (Hallé *et al.*,

1978). The architectural models themselves are based on relative position and development of meristematic tissue (Hallé *et al.*, 1978); like bifurcation ratios, their definition is independent of absolute measures of morphology (e.g., leaf size, annual-increment length, branch-accumulation rates). Differences in gross morphology within architectural models are then to be expected.

In Aralia, growth during the trunk-building phase was strongly erect. This phase is keyed to stem establishment. During this period, total leaf area was a function of the number of leaves per annual increment and the amount of leaflet area per leaf. Leaves of the trunk phase differed in both characteristics from those of the branch phase: there were more per increment, and they had a greater total leaflet area. Givnish (1978a, 1978b) has argued that in trees with large leaves, the spread of photosynthetic tissue is partly due to the branched nature of the leaf itself. He predicted that such trees would have fewer woody branches and greater extension growth than smaller-leaved trees. The unbranched phase of growth in Aralia lends support to this suggestion. Annual increments during this period of growth were relatively long; however, early successional trees with simple leaves also have long annual increments (Marks, 1975).

In the life history of *Aralia*, the branched phase is also a time of sexual maturity. Fruit production contributed nearly as much late-summer biomass to the annual increments of branches as did first-year stems and leaves. This fruit production may result in a constraint on branching, in addition to the limits imposed by architectural development, as discussed above. Fruit production coincided with decreasing annual-increment length. *Aralia* is short lived; after a tree was in the branched phase ten to twenty years, senescence was marked.

In summary, the life history of *Aralia spinosa* ramets includes a period of unbranched, erect growth (with a high leaf area per increment), a period of first-order branching (with a relatively high rate of branching), and a period of higher-order branching (with a decreasing rate of branch accumulation and frequent flowering). This sequence of events results in nonstationary height growth and branching as a function of ramet age. The three periods are correlated, respectively, with rapid stem establishment, three-dimensional crown spread, and consistent fruit production. This leads to the hypothesis that nonstationary growth in trees is generally a result of trade-offs between the requirement for establishment (i.e., competitive pressure for an early exponential increase in leaf area or branch number) and the branch interference that exponential growth must eventually produce.

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