Corner's Rules in Eastern Deciduous Trees: Allometry and Its Implications for the Adaptive Architecture of Trees

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WHITE, P. S. (Uplands Field Res. Lab., Great Smoky Mountains Nat. Park, Gatlinburg, TN 37738). Corner's rules in eastern deciduous trees: allometry and its implications for the adaptive architecture of trees. Bull. Torrey Bot. Club 110: 203-212. 1983.—The architecture of 48 eastern deciduous trees was examined using five characteristics: leaf size, leaf shape, twig cross-sectional area, leaf number per twig, and branching density. Although there was much intraspecific variability in these characteristics, broadscale interspecific trends were evident. As leaf size increased, the percentage of trees with lobed, and then compound, leaves increased, but simple, unlobed leaves ranged throughout. An allometric series of architectural forms resulted from correlations between three of the variables: as leaf size increased, twig cross-sectional area increased, and branching density decreased. This lends empirical support to "Corner's Rules," first formulated for tropical trees. Shade intolerant trees had more leaves per twig and bore a given total leaf area with fewer first-year shoots than shade tolerant trees. These data suggested that early successional trees bear their photosynthetically active tissue with lower investment in supportive, generally non-photosynthetic, tissue.

Key words: plant strategies, tree architecture, Corner's rules, Eastern deciduous trees

Corner's rules (Hallé et al. 1978, p. 82) suggested a spectrum of tropical tree forms in which the following relationships hold: (1) the thicker the plant axis (viz., the plant stem), the larger and more complicated the appendage (viz., leaf); and (2) the greater the ramification, the smaller the branches and their appendages (viz., leaves). These "rules" have remained untested; an unpublished work (Chuah 1977) cited by Hallé et al. 1978, and the work of deCastro e Santos 1980 lend indirect support, but their adaptive significance has not been explored. Givnish (1978a, 1978b, 1979) has, however, pointed to the possible adaptive significance of leaf size. He argued that trees with compound leaves or large simple leaves in humid temperate and tropical environments are able to economize on their woody frames: spreading photosynthetic surface in space is partly accomplished by the morphology of the leaf itself. In high light environments, such trees may invest in extension growth, and thus gain a com-petitive advantage over trees which must invest in lateral branches. Indeed, Marks (1975) has shown the importance of extension growth for early successional species and Whitney (1976) has shown that compound-leaved trees have lower bifurcation ratios than simple-leaved trees. Horn (1971) argued that early successional trees should have relatively small leaves because of constraints on leaf and branch spacing and problems with heat dissipation in high light environments (see also Parkhurst and Loucks 1972).

A survey of eastern deciduous trees was undertaken to test the correlations qualitatively summarized by Corner's rules and to investigate the adaptive significance of these rules with regard to successional role. Specific hypotheses included: (1) that leaf size and compoundedness are positively correlated to first-year shoot thickness; (2) that leaf size and compoundedness are negatively correlated with the number of first-year shoots in tree crowns; and (3) that successional role, as summarized by a shade tolerance index, is related to general tree form as described by (1) and (2) above.

Methods. Individuals of forty-eight deciduous tree species were located in mesic, open habitats in the Great Smokey Moun-

tains, Tennessee, at 500–1200 m elevation. Individuals sampled were uninjured, to rule out the sampling of vigorous injury sprouts, and well established (2.5 to 5 m tall; 4 to 10 cm dbh) to rule out sampling of seedlings and young saplings. Open, mesic habitats were used to examine morphological differentiation within common environments and to avoid the effects of suppression.

Fifteen leaves and first-year shoots ("twigs") were randomly selected from each of the forty-eight trees. A random numbers table was used to select a primary branch, then a secondary branch, and so on until a single twig had been selected. Leaves were then numbered and a random numbers table again used to select one leaf. Random numbers larger than the number of branches or leaves at any point in this hierarchy were ignored. The sample was thus random with regard to several factors which influence leaf and twig size (e.g., compass orientation and position within crowns). In effect, no attempt was made to control intra-tree or intraspecific variability; the present approach was used to survey interspecific differentiation rather than to model, intensively, the morphology of any one species.

Twig diameter was measured to the nearest 0.1 mm with dial callipers at the narrowest point on the internode below the attachment of a measured leaf. Leaf area for individual leaves was derived as follows (adapted from Dolph 1977): $LA = L \times W \times C \times N$, where LA is leaf area, L is leaf or leaflet length, W is leaf or leaflet width, C is a correction factor based on leaf shape (Dolph 1977), and N is the number of leaflets per leaf (N = 1 for simple-leaved species). "Leaf area per individual leaf" is used here interchangeably with "leaf size"; in all cases it refers to the leaf as a morphological unit. This usage should be contrasted with the "effective leaf size" of Givnish (1979) and Dolph (1977) in which individual leaflets of compound-leaved species are counted as the basic unit to be contrasted with simple-leaved species. Here I am interested directly, however, in the morphological organization of compound leaves. "Twig" is used as equivalent to "first-year shoot."

Branching density was measured in two ways. First, the number of leaves borne on each sampled first-year shoot was counted

and a mean value obtained for each species. This number was multiplied by the mean leaf area per leaf for that species to give the average total leaf area per first-year shoot. This value was used to compute the number of first-year shoots needed to bear 10^4 cm^2 total leaf area, which was near the maximum value recorded in this study for any single first-year shoot. A second measure of branching density was obtained by counting the number of first-year shoots on open grown, uninjured trees at 10 cm dbh. All twigs were counted, including released laterals, leaders, and spur branches.

A subset of the forty-eight species were used in the measures of branching density. Species included were all mesic site low elevation trees representative of the range of leaf sizes in the data set as a whole. Twenty species were used for the branching density counts based on 10^4 cm^2 leaf area; ten were used for the total twig counts.

Species were placed in three shade tolerance classes (shade tolerant, intermediate, and shade intolerant) based on Baker (1949). These classes were used to explore differences in leaf, twig, and branching characteristics among species with different successional roles.

The data were analyzed with statistical programs available in SAS (SAS Institute, 1979) at the University of Tennessee Computing Center. Nomenclature of trees follows Fernald (1950) except for southern species found in Radford et al. (1968).

Results. The difference between species in mean leaf area spanned three orders of magnitude, from 8.9 cm^2 (*Betula nigra*) to 904.3 cm^2 per leaf (*Magnolia macrophylla*) (Table 1). Differences in mean twig cross-sectional area spanned one and three-fourths orders of magnitude, from 0.01 cm^2 (*Carpinus caroliniana*, *Celtis tenuifolia*, *Ostrya virginiana*, *Ulmus alata*) to 0.78 cm^2 (*Aralia spinosa*). There was much intraspecific variability in both characteristics— coefficients of variation were usually between 25 and 80 percent for the species sampled (Table 1). Because of this variability, overall interspecific trends are stressed here, and not the precise location of any one species within the spectrum of tree forms reported. Plasticity of leaf size as a function of crown position and ontogenic

Table 1. Leaf area (LA) of individual leaves, twig cross-sectional area (TA), leaf shape, and shade tolerance class for 48 deciduous trees. Tolerance classes are: 1 (shade intolerant); 2 (intermediate); and 3 (shade tolerant) (adapted from Baker 1949).

Species	LA (cm^2)		TA (cm^2)		Shape	Tolerance Class
	MEAN	SD	MEAN	SD		
Acer negundo	117.5	59.0	.06	.03	Compd.	1
Acer pensylvanicum	105.1	57.6	.04	.02	Simp., lbd.	2
Acer rubrum	56.6	29.6	.03	.01	Simp., lbd.	2
Acer saccharum	53.2	24.0	.02	.01	Simp., lbd.	3
Acer spicatum	55.7	24.9	.06	.05	Simp., lbd.	2
Aesculus octandra	333.5	106.5	.22	.07	Cmpd.	2
Amelanchier laevis	18.0	6.2	.02	.01	Simp., unlbd.	2
Aralia spinosa	626.7	255.0	.78	.30	Cmpd.	1
Asimina triloba	117.1	47.9	.04	.02	Simp., unlbd.	3
Betula lenta	33.4	7.8	.03	.01	Simp., unlbd.	2
Betula lutea	35.0	21.6	.02	.01	Simp., unlbd.	2
Betula nigra	8.9	2.0	.01	.01	Simp., unlbd.	1
Carpinus caroliniana	14.2	7.9	.01	.01	Simp., unlbd.	3
Carya glabra	102.1	26.2	.06	.01	Cmpd.	2
Carya ovata	409.0	226.0	.16	.04	Cmpd.	2
Carya pallida	145.5	116.2	.06	.03	Cmpd.	1
Carya tomentosa	381.5	212.5	.24	.05	Cmpd.	2
Castanea dentata	77.7	24.9	.04	.02	Simp., unlbd.	2
Celtis tenuifolia	10.8	7.3	.01	.01	Simp., unlbd.	1
Cornus florida	39.6	8.8	.02	.01	Simp., unlbd.	3
Fagus grandifolia	33.3	11.8	.02	.01	Simp., unlbd.	3
Fraxinus americana	240.1	113.0	.14	.12	Cmpd.	2
Halesia carolina	45.0	18.3	.02	.01	Simp., unlbd.	2
Juglans nigra	276.9	103.9	.18	.09	Cmpd.	1
Liquidambar styraciflua	50.3	19.0	.04	.01	Simp., lbd.	1
Liriodendron tulipifera	69.9	31.1	.09	.04	Simp., lbd.	1
Magnolia acuminata	193.8	88.4	.08	.02	Simp., unlbd.	2
Magnolia fraseri	222.6	83.4	.19	.11	Simp., unlbd.	2
Magnolia macrophylla	904.3	684.0	.61	.27	Simp., unlbd.	2
Magnolia tripetala	327.3	143.8	.26	.13	Simp., unlbd.	2
Nyssa sylvatica	25.6	.1	.03	.01	Simp., unlbd.	2
Ostrya virginiana	17.5	7.7	.01	.01	Simp., unlbd.	3
Oxydendrum arboreum	62.0	16.9	.07	.03	Simp., unlbd.	2
Platanus occidentalis	135.9	65.0	.06	.03	Simp., lbd.	1
Prunus serotina	23.3	7.5	.01	.01	Simp., unlbd.	2
Quercus alba	39.2	14.1	.04	.02	Simp., lbd.	2
Quercus coccinea	75.0	31.4	.06	.01	Simp., lbd.	1
Quercus prinus	91.8	24.3	.05	.04	Simp., unlbd.	2
Quercus rubrum	102.3	36.0	.07	.05	Simp., unlbd.	2
Rhus glabra	262.5	73.6	.46	.12	Cmpd.	1
Rhus typhina	255.0	97.1	.29	.09	Cmpd.	1
Robinia pseudo-acacia	94.0	50.7	.06	.03	Cmpd.	1
Salix nigra	9.8	4.3	.02	.01	Simp., unlbd.	1
Sassafras albidum	61.9	55.0	.07	.07	Simp., lbd.	1
Tilia heterophylla	108.2	29.0	.05	.02	Simp., unlbd.	2
Ulmus alata	10.8	.06	.01	.01	Simp., unlbd.	2
Ulmus americana	32.3	4.0	.01	.01	Simp., unlbd.	2
Ulmus rubra	50.3	119.5	.03	.02	Simp., unlbd.	2

development (e.g., Jackson 1967, Critchfield 1960) was not analyzed for any one species.

The first premise of Corner's Rules was confirmed: there was a positive correlation between leaf size and twig cross-sectional area (Table 2 and Fig. 1). Correlations were stronger for species means than for raw data points not averaged by species, stronger for simple-leaved species than for compound-leaved species, and stronger for shade tolerant than for shade intolerant species. The correlations were also strong for selected genera (Table 2). Shade tolerance was not directly related to the leaf size–twig

Table 2. Correlations between leaf area and twig cross-sectional area for 48 deciduous trees. Correlations are shown for raw data (data not averaged by species) and for species means. (Significance levels: * = p < .05; ** = p < .01; *** = p < .001; **** = p < .0001).

Group	No. Species	Raw Data	Species Means
All species	48	.73****	.81****
Leaf morphology:			
Simple, unlobed, leaved species	26	.74****	.87****
Simple, lobed, leaved species	10	.70**	.79**
Compound-leaved species	12	.54***	.72**
Tolerance classes:			
Intolerant species	15	.69***	.83****
Intermediate species	27	.73***	.97****
Tolerant species	6	.72**	.98***
Carya	5	.74****	.96**
Magnolia	4	.52**	.98**
Betulaceae	5	.66**	.91**

thickness spectrum (Fig. 1); there was some suggestion, however, that at any given twig thickness, shade intolerant species bore smaller leaves than more shade tolerant species (Fig. 1).

Leaf shape was related to leaf size. As leaf size increased, the percentage of species with lobed, and then compound, leaves in-creased, but simple-leaved species ranged throughout (Fig. 1). The largest leaves be-longed to *Magnolia macrophylla,* a species with simple, unlobed leaves. There was an exponential decrease in the number of spe-cies present in the sample as leaf size in-creased (Fig. 1).
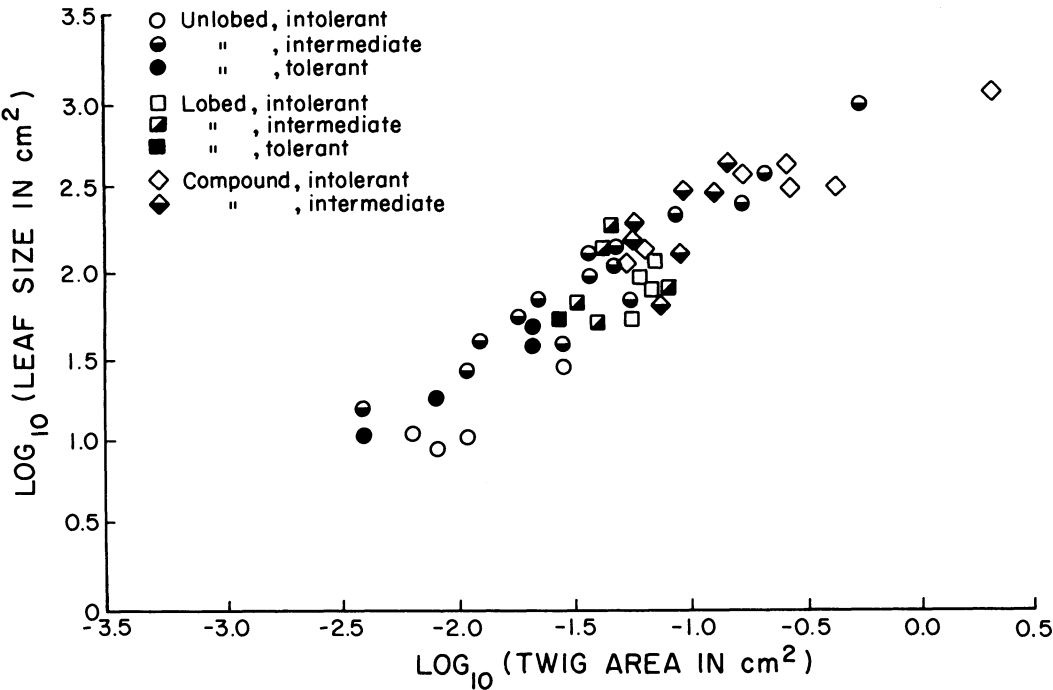
The second premise of Corner's Rules

Fig. 1. A plot of the relationship between leaf size (leaf area for individual leaves) and twig cross-sectional area for 48 deciduous trees. Data are taken from Table 1. Note log scales: there is an exponential decrease in the number of species in the data base as leaf size increases.

Table 3. Leaf area per leaf (LA), twig cross-sectional area (TA), number of leaves per shoot, total leaf area per shoot, and branching density. Species are arranged by tolerance class (taken from Baker 1949).

Species	Mean LA per leaf (cm^2)	Mean TA per twig (cm^2)	Mean No. Leaves/twig	Total LA/ twig	Branching Density No. twigs bearing 10^4 cm^2 Total LA	No. twigs at 10 cm dbh
INTOLERANT:						
Aralia spinosa	626.7	2.55	10.0	6267.0	1.6	42
Juglans nigra	276.9	.18	7.6	2104.4	4.8	256
Liquidambar styraciflua	50.3	.05	7.6	382.3	26.2	4026
Liriodendron tulipifera	69.9	.09	7.4	517.3	19.3	3135
Platanus occidentalis	135.9	.06	4.6	625.1	16.0	1290
Rhus typhina	255.0	.29	15.4	3927.0	2.6	76
Salix nigra	9.8	.02	18.8	183.2	54.6	—
All Intolerant SPP	203.5	.47	10.2	2000.9	17.9	1470.8
Standard Deviation	212.3	.94	5.1	2307.2	18.7	1720.1
INTERMEDIATE:						
Aesculus octandra	333.5	.22	7.3	2434.6	4.1	—
Betula lutea	35.1	.03	4.9	172.0	58.1	—
Fraxinus americana	240.1	.14	6.7	1608.7	6.2	—
Halesia carolina	45.0	.02	4.1	184.5	54.2	—
Magnolia macrophylla	904.3	.61	9.0	8138.7	1.2	—
Magnolia tripetala	327.3	.26	7.4	2422.0	4.1	86
Prunus serotina	023.3	.01	3.9	90.9	110.0	—
Tilia heterophylla	108.2	.05	4.6	497.7	20.1	—
Ulmus alata	10.9	.01	5.4	58.9	169.8	—
All Intermediate SPP	225.3	.15	5.9	1734.2	47.5	86
Standard Deviation	285.6	.20	1.8	2595.1	58.5	—
TOLERANT:						
Acer saccharum	53.2	.02	3.8	202.2	49.5	4324
Carpinus caroliniana	14.2	.01	5.1	72.4	138.1	7590
Cornus florida	39.6	.02	3.6	142.6	70.1	7344
Fagus grandifolia	33.3	.02	3.8	126.5	79.1	—
All Tolerant SPP	32.6	.02	4.1	135.9	84.2	6419.3
Standard Deviation	20.7	.01	.7	53.4	38.0	1818.8
ALL SPECIES	179.6	.12	7.05	1507.9	45.1	2816.9
Standard Deviation	232.9	.15	3.95	2242.2	49.1	2956.6

was also confirmed. If trees of equal diameter are compared, trees with thick twigs and large leaves bore fewer twigs than trees with thin twigs and small leaves (Table 3). Because of the difficulty of counting twigs in tree crowns (particularly for thin-twigged, densely branched species), only one individual of each species was sampled. However, differences between species again spanned several orders of magnitude, from 42 (*Aralia spinosa*) to 7590 first-year shoots (*Carpinus caroliniana*) (Table 3).

Mean number of leaves per twig varied from 3.6 (*Cornus florida*) to 18.8 (*Salix nigra*) (Table 3). Shade intolerant trees (mean = 10.2) bore more leaves per shoot than shade tolerant trees (mean = 4.1). The number of leaves needed to bear 10^4 cm^2 leaf area varied from 1.2 (*Magnolia ma-*

crophylla) to 169.8 (*Ulmus alata*) (Table 3). Leaf size and branching density were negatively correlated (Table 4 and Fig. 2). A stronger relationship was evident for branching density based on twigs borne at 10 cm dbh than for branching density based on the number of twigs needed to bear 10^4 cm^2 leaf area.

There was no significant (p > .05) correlation between leaf size and leaf number per twig, nor between twig thickness and leaf number per twig (Table 4). However, mean leaf area per first-year shoot (mean leaf size times leaf number) was strongly correlated with twig thickness.

Compound-leaved trees bore fewer branches than simple-leaved trees. The mean number of twigs needed to bear 10^4 cm^2 leaf area for five compound-leaved trees

Table 4. Correlation coefficients for the data in Table 3. (LA = leaf area per leaf; TA = twig cross-sectional area. Significance levels: * = p < .05; ** = p < .01; *** = p < .001; **** = p < .0001. Blank areas represent correlations not significant at the .05 level.)

	LA	TA	No. Leaves/ Twig	Total LA/ Twig	No. Twigs Bearing 10^4 cm^2 Total LA	No. Twigs at 10 cm dbh
LA	—	.93****		.98****	−.58***	−.75**
TA		—		.96***	−.54**	−.63*
No. Leaves/Twig			—			
Total LA/Twig				—	−.55**	−.72*
Twigs Bearing 10^4 cm^2 total LA					—	.90***

was 3.9 (SD 1.8) (Table 3). For thirteen simple-leaved trees (excluding the two *Magnolia* species in Table 3) this value was 67.6 (SD 47.5). The two *Magnolia* species had large simple leaves and similar branching densities to compound-leaved trees (mean = 2.7 twigs/10^4 cm^2 leaf area).

In general, shade intolerant trees bore smaller leaves at a given twig size than more shade tolerant trees (Fig. 1) but, as noted above, had more leaves per shoot. Because they gained more by higher leaf numbers than they lost by smaller leaves, shade intolerant trees had greater total leaf area per first-year shoot (mean = 2000.9 cm^2/shoot) and bore a given leaf area with fewer first-year shoots (mean = 19.6) than more shade tolerant trees (135.9 cm^2 LA/shoot, 84.2 twigs/10^4 cm^2 total LA; see Table 3). For example, *Acer saccharum* and *Liquidambar styraciflua* had similar leaf sizes, but the more intolerant *Liquidambar* had thicker twigs, more leaves per first-year shoot, and a lower branching density. Other species pairs with similar leaf sizes which showed a similar contrast in branching density were *Carpinus caroliniana* (shade tolerant) versus *Salix nigra* (shade intolerant) and *Aesculus octandra* (intermediate) versus *Rhus typhina* (shade intolerant).

Discussion. There are fundamental implications for tree strategy in the allometric relationships reported here: they describe alternative ways tree biomass is divided into photosynthetic and supportive tissue. Several possible biological constraints underlie this allometry. Optimum leaf arrangement and spacing are stressed here, but other explanations may be important.

Dimensional limits on twig diameter are influenced by the need for support—large leaves need stronger stems to resist weight and stress in wind. The amount of xylem needed to supply a leaf is related to leaf size. This may set a lower limit on twig diameter for given sized leaves (and a given number of leaves per twig). As trees taper from trunk to crown, the amount of branching (and the resulting distribution of xylem) may set limits on the diameter of the ultimate branches: fewer branching junctions result in thicker ultimate branches (see also Leonardo da Vinci's observation reported in Stevens 1974, p. 119).

In view of the explanations of the leaf size/twig area relationship that are based on support and transport, it is interesting to note that thick twigs are often hollow (e.g., the tropical tree, *Cecropia*), chambered (e.g., *Juglans*), or filled with lightweight pith (e.g., *Sambucus, Rhus, Aralia*). This pith functions neither in support nor transport. In the case I am most familiar with (*Aralia spinosa*, White 1981), the large pith seems to result in a kind of hollow beam construction for the thick twigs—weight and strength are concentrated in a peripheral cylinder of wood.

The relation between leaf size, twig thickness, and crown branching can also be explained by optimum placement of leaves within a continuous tree crown. If a tree bears large leaves, its twigs can be spaced more widely to achieve a given degree of overlap between the leaves of neighboring shoots (or, conversely, branch spacing sets the leaf size needed to bridge the gap between branches). A complicating factor is that not all trees have the same leaf overlap (Horn 1971). Different leaf densities
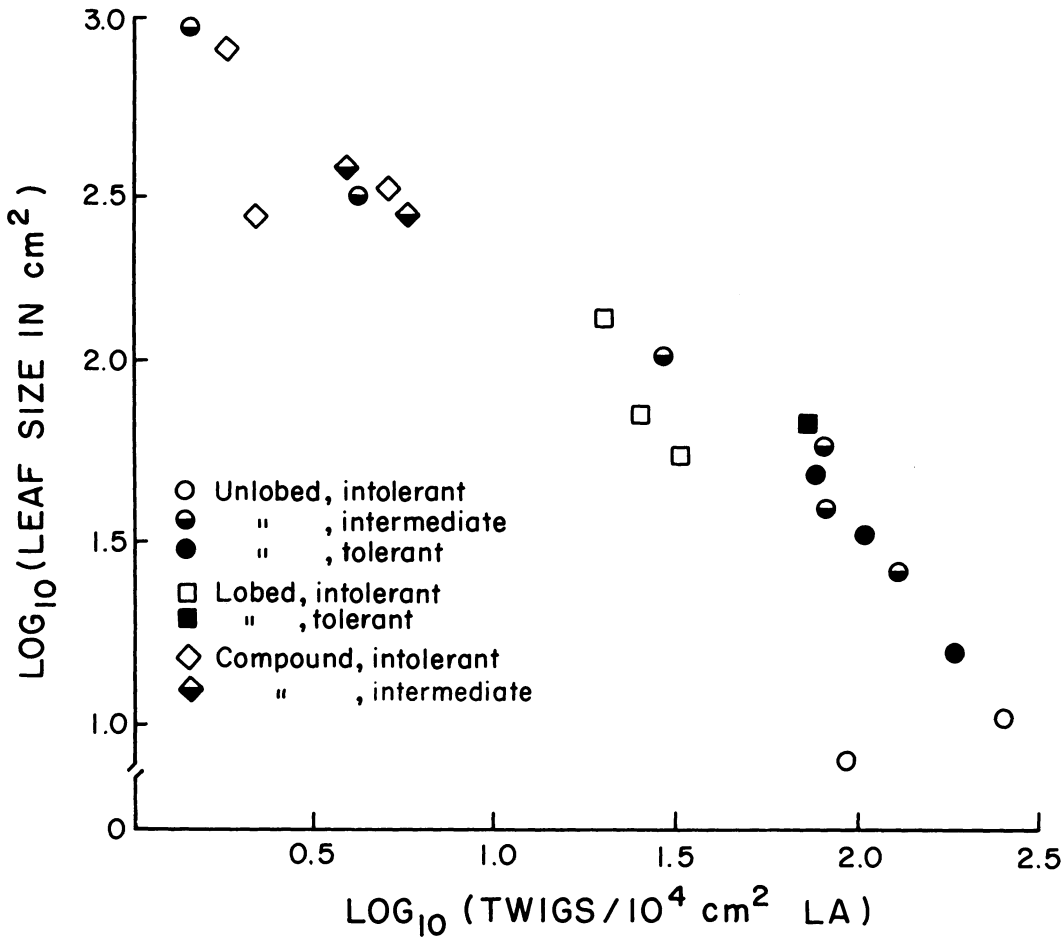
Fig. 2. The relationship between leaf size (leaf area for individual leaves) and branching density for 20 deciduous trees. Data are taken from Table 3. Note log scales.

in crowns can be produced by the overlap of leaves on one first-year shoot (regulated by the number and spacing of leaves on that shoot) or by the overlap of leaves on different first-year shoots (regulated by the number and spacing of branches).

Horn (1971) predicted that mono-layered tree canopies would predominate in shady environments and multi-layered canopies in full sunlight. For multi-layers, leaves are arranged in space such that the distance between layers of leaves is a function of leaf size. The smaller the leaf, the smaller the vertical separation between leaves needed to achieve optimum multi-layers. Early successional trees should have smaller leaves than late successional trees.

In the data reported here, a wide range of leaf sizes occurs for both shade tolerant,

mono-layered trees and intolerant multi-layered trees. At first, this seems to contradict Horn's predictions. However, further inspection of the data reveals that at a given twig size (and, presumably, at a given branching density), shade intolerant trees bore smaller leaves than forest species. This suggests that successional role is embedded within the allometric series—shade intolerant trees bear small leaves if all other factors (tree branching density) are equal. Early successional trees with large simple leaves must possess vigorous yearly extension growth and high bifurcations ratios (Whitney 1976) to separate their large leaves in a multi-layered crown. Some of the largest leaves in our flora are those of early successional, fast-growing, short-lived trees, (e.g.) *Rhus typhina* and *Aralia spi-*

nosa. However, even these trees bear smaller leaf sizes than trees of relatively shady environments with the same twig diameter. Also, the leaf area is broken up into relatively small leaflets, each year's growth producing a fairly dense multi-layer structure made up, not of branch layers, but of sets of compound leaves. Horn's predictions, then, ought to apply to the separation and orientation of compound leaflets in these trees.

The spectrum of leaf and twig sizes gives additional insight on the role of the compound leaf. As leaf size increased and branching density decreased, the percent of trees with compound leaves increased. This might be expected, based on the need to dissipate heat (compound leaves being more efficient at this than simple leaves with the same total leaf area; Givnish 1978a, Parkhurst and Loucks 1972). The very largest simple leaves are usually found on trees of moist, at least partially shaded habitats (e.g., *Magnolia macrophylla*), but there are exceptions—*Paulownia tomentosa* and *Magnolia fraseri* are tolerant of xeric situations with full sunlight in the Great Smoky Mountains.

Another line of reasoning takes into consideration branching density—compound-leaved trees bear fewer branches than simple-leaved trees with the same leaf area. The compound leaf may be a means of dispersing photosynthetic tissue away from the shoot without investment in a woody support frame (although there is a yearly investment in the deciduous leaf rachis and stiff petiole). The compound leaf may function as a deciduous branch system (Givnish 1978a, Whitney 1976). Because compound-leaved trees invest in fewer branches, they may have longer extension growth on each first-year shoot (Givnish 1978a). Hence, a given crown size may be constructed with less perennial woody tissue. It is interesting to note that the rachis of compound leaves approximates the twig thickness of simple-leaved trees (1-6 mm^2) and the leaflet size resembles the leaf size of simple-leaved trees (e.g., the 40 to 80 leaflets of *Aralia spinosa* range from the size of *Carpinus caroliniana* leaves to the size of *Cornus florida* leaves). In sum, these arguments lend support to Givnish's (1978a) and Dolph's (1977) treatment of leaflets as functional equivalents of simple leaves. Leaflet sizes can be smaller in some compound-leaved trees than the smallest simple leaves (e.g., the leaflets of *Gleditsia triacanthos* range from 30 to 300 mm^2/leaf). To support crowns of very small simple leaves would require a large number of slender twigs. Such a situation occurs in the conifer *Tsuga canadensis* (132.4 mm^2/leaf), but it does not occur in moist, temperate, deciduous Angiosperm taxa.

Differentiation of branch role occurs in many tree crowns (Whitney 1976, Leopold 1971)—some branches grow primarily by extension and create the overall shape of the crown ("long shoots"), while others are short and bear clusters of leaves within the crown ("short shoots" or spur branches). A compound leaf can be held horizontally from a crown-constructing shoot. In this sense it is the ultimate leaf-bearing spur and can disperse photosynthetic tissue away from the stem. It is not surprising, then, that compound-leaved trees have low bifurcation ratios (Rb = 3, Whitney 1976) nor that early successional compound-leaved trees have bifurcation ratios similar to late successional simple-leaved trees. By contrast, early successional trees with simple leaves usually have a division of role between long shoots and short shoots and high bifurcation ratios (Rb = 5-8, Whitney 1976) in generating multi-layered crowns.

Two trees with very different architectures and successional roles, *Acer saccharum* and *Aralia spinosa*, have similar bifurcation ratios (Rb = 3). *Acer* has moderate-sized, simple leaves borne in a much-branched woody frame. *Aralia* achieves the same bifurcation ratio with large compound leaves, borne in a few-branched woody frame. *Aralia* has high leaf numbers per shoot and long first-year shoots. Branching density is better than two orders of magnitude different despite the similar bifurcation ratios.

Bifurcation ratios describe only the average number of branches borne on each branch of the next highest order (Whitney 1976) and are thus independent of absolute measures of tree form. The morphological approach of Hallé et al. (1978) to describing tree architecture is also based on relative characters. The allometric series reported

here suggests that true insight into the ecological significance of tree form can only be gained from architectural analyses that take into account absolute measures of tree size, leaf area, and shoot growth. This requires a broader definition of tree architecture (to avoid the relative approach) than is present in the literature. Borchert and Slade (1981) reach a similar conclusion based on models of tree branching.

One of the most striking of the tree forms is that of the large-leaved, thick-twigged, few-branched, early successional trees, like that of *Aralia spinosa*. This form also occurs in tropical mesic forests—e.g., *Cecropia* (which has hollow stems) and members of the Bombacaceae (*Ochroma*) come to mind (see Givnish 1978a, 1978b). Two Asian trees established in the United States, *Paulownia tomentosa* (with simple leaves) and *Ailanthus altissima* (with compound leaves) are immediately recognizable from their form and growth rates as early successional species. Both have large leaves, high leaf numbers per shoot, thick twigs, sparse branching, and fast growth rates. Despite the fact that compound-leaved trees seem able to economize on their woody frames by bearing deciduous branch systems, not all of them are successional. None treated here can be regarded as deeply shade tolerant, but there are marked contrasts in growth rates and ability to exploit disturbances in such compound-leaved trees as *Aralia spinosa* and *Rhus typhina* on one hand and *Aesculus octandra* and *Carya cordiformis* on the other. It remains to be seen if compound leaves in the latter species allow greater yearly extension growth and perhaps exploitation of small-scale disturbance openings within forest stands. It is likely also that there are no successional implications for small, simple-leaved trees as well. While small-leaved, much-branched trees have a higher twig production, they have lower yearly extension growth and lower survivorship since only a few twigs survive to be major crown banches.

Finally, allometry can only be directly interpreted within one environmental context. Leaf size, leaf thickness, and potential tree biomass vary as a function of overall climate (Dolph and Dilcher 1980) as well as local environmental gradients (Hamann 1979). Within temperate and tropical mesic environments, however, there seems to be a differentiation of tree form which can be summarized in Corner's allometry.

Summary and Conclusions. Angiosperm deciduous trees in continental temperate climates are rich in leaf shapes, leaf sizes, and architectural forms. Leaf size is positively correlated with twig area and negatively correlated with branching density. As leaf size increases, representations of lobed and then compound leaves increases. This seems to have resulted from adaptation based on allocation of total leaf area to individual leaves, the allocation of woody tissue to branches, and the arrangement of leaves within the tree crown. Leaf size is predictable from twig thickness and branching pattern when trees are leafless; successional role may be deduced from leaf number per twig and leaf area per twig. Intra-family and intra-generic differences in tree architecture follow the same patterns as those for the full data set, suggesting that differences in tree architecture and allometry may evolve independently as aspects of niche differentiation.

Although a large variety of leaf sizes and architectural forms can be seen in early successional trees, they tend to have smaller leaves than late successional trees at the same twig diameter, more leaves per twig, and larger total area per twig. They have longer extension growth per year in first-year shoots and have either compound leaves or high bifurcation ratios. Early successional trees seem to economize on branches in that they bear a given leaf area with fewer twigs than do late successional trees. Compound-leaved trees, in general, also economize on the woody frame, in that compound leaves can be viewed as deciduous branch systems. Trade-offs between leaf size, leaf number/shoot, and branching density mean that overall tree form and not single attributes (e.g., leaf size) are correlated with successional roles.

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