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Follow Corner's Rules**

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EVIDENCE THAT TEMPERATE EAST NORTH AMERICAN EVERGREEN WOODY PLANTS FOLLOW CORNER'S RULES

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SUMMARY

Corner's rules, first developed for tropical trees, predict a spectrum of woody plant forms, from ones with small leaves, thin twigs (first-year shoots) and many branches, to ones with larger leaves, thick twigs and few branches. These rules were confirmed for nine broad-leaved and 12 needle-leaved evergreen woody plants of temperate eastern North America: for each of these groups, leaf size was positively correlated with twig cross-sectional area and both of these were negatively correlated with the number of twigs needed to bear 10^4 cm² total leaf area. When compared to deciduous trees, characterized in a previous study, broad-leaved evergreens had leaves that were 85% smaller at a given twig thickness and needed 750% more twigs to bear a given total leaf area (at least when leaves older than 1 year were ignored). Needle-leaved evergreens bore relatively small leaves but large numbers of leaves per first-year shoot; they bore fewer twigs per 10^4 cm² total leaf area than broad-leaved evergreens, but more than broad-leaved deciduous species. Broad-leaved deciduous trees were characterized by relatively large leaf sizes as a function of twig cross-sectional area and low numbers of twigs per 10^4 cm² total leaf area. Although Corner's rules are a significant index of plant form, a full resolution of the differences between deciduous and evergreen species awaits further study.

INTRODUCTION

E. J. H. Corner (Hallé, Oldeman and Tomlinson, 1978, p. 82) proposed the following empirical rules for tropical tree form (Corner's Rules): (1) the thicker the plant axis (i.e. the stem), the larger the appendage (i.e. the leaf); (2) the greater the ramification (i.e. the number of branches), the thinner the ultimate axes and their appendages. Corner's Rules predict a spectrum of trees from ones with small leaves, thin twigs and many branches, to ones with large leaves, thick twigs and few branches. A previous investigation (White, 1983) showed that east North American deciduous trees follow this allometric pattern, but Corner's Rules have not, for the most part, been tested. Corner's Rules have, however, implications for adaptive aspects of tree form (Hallé *et al.*, 1978; White, 1983), in that they are a potential index of alternative ways that biomass is divided into photosynthetic and supportive tissues.

These data were developed to test Corner's Rules for broad-leaved and needle-leaved evergreen species of temperate eastern North America. Specific hypotheses were (1) that leaf area per individual leaf (leaf size) is positively correlated with first-year shoot cross-sectional area (twig thickness) and (2) that

leaf size and twig thickness are negatively correlated with the number of twigs borne within plant crowns. Leaf size, twig thickness and branching are all notoriously variable among individuals of one species, within a single individual, and among developmental stages of individuals (Critchfield, 1960; Jackson, 1967; Borchert and Slade, 1981). Nonetheless, interspecific contrast can be extreme; the sampling was carried out, not to model the variability or development of any one species, but rather to test interspecific trends as predicted in Corner's Rules.

METHODS

Nineteen evergreen woody plant species, native or cultivated species in the vicinity of the Great Smoky Mountains, Sevier County, TN (the study area used by White, 1983), were used in this investigation. Nine broad-leaved, angiosperm, evergreens (*Ilex opaca*, *Kalmia latifolia*, *Leiophyllum buxifolium*, *Leucothoe fontanesiana*, *Pieris floribunda*, *Rhododendron catawbiense*, *Rhododendron maximum* and *Rhododendron minus* as native plants; *Magnolia grandiflora*, as a cultivated plant) and ten needle-leaved, gymnosperm, evergreens (*Abies fraseri*, *Picea rubens*, *Pinus echinata*, *Pinus pungens*, *Pinus rigida*, *Pinus strobus*, *Pinus virginiana* and *Tsuga canadensis* as native plants; *Pinus palustris* and *Pinus taeda* as cultivated plants) made up the initial species pool. *Pinus banksiana* and *Pinus resinosa*, two northern species, were added from herbarium sheets. Nomenclature follows Kartesz and Kartesz (1980).

Fifteen first-year shoots were randomly selected from separate, open grown, 10 cm or more diameter, individuals of each species sampled (or from herbarium sheets for the two northern species). One leaf was then selected randomly from each first-year shoot. Leaf length and width were measured, and leaf size (leaf area per individual leaf) was calculated as (from Dolph, 1977):

$$LA = L \times W \times C$$

where LA is leaf area, L is leaf length, W is leaf width, C is a correction factor based on leaf shape. The total number of leaves on each twig was counted (in *Pinus*, each needle was a separate leaf). Twig diameter was measured on the internode below the measured leaf, and was used to calculate twig cross-sectional area. The mean number of leaves per twig was multiplied by the mean leaf area per individual leaf to get the mean total leaf area per first-year shoot. This number was then divided into 10^4 cm^2 (near the maximum leaf area observed for broad-leaved deciduous trees – White, 1983) to arrive at an index of the number of twigs needed to bear this standard leaf area. Correlations were performed between leaf size, twig thickness and number of shoots per 10^4 cm^2 total leaf area, using statistical programmes available in SAS (SAS Institute, 1979). Since only first-year shoots were sampled, total leaf area borne does not reflect any contribution of 2- to 3-or more-year-old leaves in these evergreen species.

RESULTS

There is much variation in the measured variables; coefficients of variation were often above 50% (Table 1). Hence, the spectrum of characteristics is stressed here, and not precise values with regard to any one species. Mean leaf size spanned two orders in magnitude in broad-leaved evergreens, from 0.03 cm^2 (*Leiophyllum buxifolium*) to 84.4 cm^2 (*Magnolia grandiflora*) (Table 1). Twig thickness ranged from 0.006 cm^2 (*Leiophyllum*) to 0.23 cm^2 (*Rhododendron maximum*) and number

Table 1. Mean leaf size (leaf area per individual leaf), twig thickness (cross-sectional area), number of leaves per shoot and number of shoots per 10^4 cm² total leaf area, for broad-leaved and needle-leaved evergreen woody plants

	Leaf size (cm ²)	Twig thickness (cm ²)	No. leaves per shoot	No. shoots to bear 10^4 cm ² LA new leaves
a. Broad-leaved evergreens				
<i>Ilex opaca</i>	19.4 (4.8)	0.03 (0.02)	4.4 (1.7)	116.0
<i>Kalmia latifolia</i>	10.9 (6.3)	0.04 (0.02)	5.7 (1.0)	161.0
<i>Leiophyllum buxifolium</i>	0.3 (0.7)	0.006 (0.002)	16.1 (4.8)	2070.4
<i>Leucothoe fontanesiana</i>	20.5 (8.3)	0.10 (0.03)	13.8 (1.2)	35.3
<i>Magnolia grandiflora</i>	84.4 (3.1)	0.17 (0.08)	7.1 (1.8)	16.7
<i>Pieris floribunda</i>	4.8 (1.5)	0.02 (0.01)	6.7 (1.8)	306.7
<i>Rhododendron catawbiense</i>	31.8 (17.6)	0.20 (0.03)	5.7 (1.5)	55.2
<i>Rhododendron maximum</i>	47.9 (11.9)	0.23 (0.06)	5.1 (1.2)	40.9
<i>Rhododendron minus</i>	9.9 (4.4)	0.03 (0.01)	4.0 (1.2)	252.5
b. Needle-leaved evergreens				
<i>Abies fraseri</i>	0.24 (0.08)	0.02 (0.01)	210.8 (79.8)	197.6
<i>Picea rubens</i>	0.16 (0.02)	0.02 (0.01)	152.6 (70.8)	409.8
<i>Pinus banksiana</i>	0.22 (0.07)	0.04 (0.008)	117.5 (48.0)	386.1
<i>Pinus echinata</i>	0.43 (0.13)	0.06 (0.02)	119.2 (34.4)	194.9
<i>Pinus palustris</i>	2.95 (0.05)	0.69 (0.12)	700.8 (254.6)	5.0
<i>Pinus pungens</i>	0.70 (0.13)	0.15 (0.04)	136.7 (96.2)	104.5
<i>Pinus resinosa</i>	1.27 (0.25)	0.26 (0.20)	97.8 (38.9)	80.5
<i>Pinus rigida</i>	0.74 (0.14)	0.11 (0.05)	120.5 (67.3)	112.4
<i>Pinus strobus</i>	0.53 (0.12)	0.10 (0.05)	176.7 (96.9)	106.7
<i>Pinus taeda</i>	1.71 (0.42)	0.13 (0.05)	189.6 (116.3)	30.9
<i>Pinus virginiana</i>	0.44 (0.10)	0.05 (0.02)	139.5 (155.0)	162.9
<i>Tsuga canadensis</i>	0.13 (0.03)	0.004 (0.001)	56.0 (23.1)	1373.6

The values in parentheses are standard deviations.

of leaves per twig ranged from 4.0 (*Rhododendron minus*) to 16.1 (*Leiophyllum*). The mean number of shoots bearing 10^4 cm² total leaf area ranged from 16.7 (*Magnolia grandiflora*) to 2070.8 (*Leiophyllum*).

Needle-leaved evergreens bore leaves that were one or two orders of magnitude smaller than broad-leaved species (Table 1). Needle-shaped leaves ranged from 0.13 cm² (*Tsuga canadensis*) to 2.85 cm² (*Pinus palustris*). The range in twig thickness was similar to that of broad-leaved evergreens (0.004 cm in *Tsuga* to 0.69 cm² in *Pinus palustris*). An obvious distinguishing feature of the needle-leaved species is the very large numbers of small leaves per shoot; leaves per shoot ranged from 97.8 (*Pinus resinosa*) to 700.8 (*Pinus palustris*). The range in number of shoots per 10^4 cm² total leaf area, because of these large numbers of leaves per shoot, was lower than that for broad-leaved evergreens: it varied from 5.0 (*Pinus palustris*) to 1373.6 (*Tsuga canadensis*).

Corner's Rules were supported by these data: plants with large leaves have thick twigs and few branches (Table 2a). The strongest correlations were between leaf size and twig thickness (0.77 for broad-leaved species, 0.92 for needle-leaved species). The number of leaves per shoot was weakly and negatively correlated with leaf size (-0.24, not significant) and twig thickness (-0.23, not significant) in broad-leaved evergreens, but is more strongly and positively correlated with these values in needle-leaved evergreens (0.81 and 0.89). Number of shoots per 10^4 cm²

Table 2. *Correlations between variables of Table 1*

	<i>LA</i>	<i>TA</i>	No. leaves per shoot	No. shoots per 10 ⁴ cm ² <i>LA</i>
a. Broad-leaved/needle-leaved:				
Leaf size (<i>LA</i>) (leaf area per individual leaf)	—	0.77/0.92	-/0.81	-0.46/-0.49
Twig cross-sectional area (<i>TA</i>)	—	—	-/0.89	-0.48/-
No. leaves per shoot			—	0.69/-
No. shoots per 10 ⁴ cm ² total leaf area				—
b. <i>Rhododendron/Pinus</i>				
<i>LA</i>	—	0.96/0.91	0.70/0.86	-0.93/-0.73
<i>TA</i>		—	0.88/0.92	-0.99/-0.57
No. leaves per shoot			—	-0.91/-0.48
No. shoots per 10 ⁴ cm ² <i>LA</i>				—

All correlations are significant at the 0.05 level (for broad-leaved evergreens, $n = 135$; needle-leaved evergreens, $n = 180$; *Rhododendron*, $n = 45$; *Pinus*, $n = 135$).

leaf area was negatively correlated with leaf size and twig thickness. This value was positively correlated with the number of leaves per shoot in broad-leaved evergreens (0.69) but was weakly and negatively correlated with leaves per shoot in needle-leaved evergreens (-0.36, not significant).

All of these correlations were stronger within the two genera with multiple species sampled (*Pinus* and *Rhododendron*; Table 2b). The positive correlation between leaves per shoot and shoots per 10⁴ cm² leaf area for all broad-leaved evergreens was reversed for *Rhododendron* species (-0.91). This was because in *Rhododendron*, unlike the other broad-leaved evergreens, the number of leaves per shoot was positively and strongly correlated with leaf size.

Like eastern deciduous trees (White, 1983), the evergreen woody plants considered here followed Corner's Rules. However, there are important differences among broad-leaved deciduous, broad-leaved evergreen and needle-leaved evergreen woody plants in these patterns. Evergreens bear smaller leaves than deciduous plants (Table 3), when the whole data set is considered. Since Corner's allometry holds within all groups, leaf size is best compared for species with similar twig thicknesses. Needle-leaved evergreens average about 0.4% and broad-leaved evergreens averaged about 15% the leaf size of broad-leaved deciduous trees at a given twig thickness (Table 3).

Mean twig thickness was comparable in needle-leaved evergreens (0.14 cm²) and broad-leaved deciduous trees (0.12 cm²). Broad-leaved evergreens had thinner twigs (0.09 cm²) when the whole data set was considered, but thicker twigs when only the smallest leaf size class was used (Table 3). Since evergreen species all fall in this small-leaf-size class (0 to 50 cm²), eliminating the larger-leaved, thicker twigged deciduous species allows a more direct comparison among the groups. Correcting for Corner's allometry in this way, needle-leaved evergreens have relatively thick first-year stems compared to the other two groups (0.14 cm² in the smallest leaf size class, Table 3).

Needle-leaved evergreens are architecturally distinguished by very small leaves and by high numbers of leaves per shoot (184.8, 25 times greater than in broad-leaved species, Table 3). The higher leaf numbers partially compensate for the smaller leaf sizes so that needle-leaved evergreens have comparable numbers of shoots per 10⁴ cm² total leaf area to the other two groups. Even when the whole

Table 3. Comparisons of broad-leaved deciduous species (data from White, 1983), broad-leaved evergreens, and needle-leaved evergreens in mean leaf size (LA), twig cross-sectional area (TA), number of leaves per first-year shoot and number of first-year shoots per 10^4 cm^2 total leaf area

	LS (cm^2) whole data set	By twig thickness classes (cm^2)		TA (cm^2) whole data set	Smallest leaf size class 0 to $50\ cm^2$	No. shoots per $10^4\ cm^2$ total leaf area		
		0 to $0.09\ TA$	0.1 to $0.3\ TA$			No. leaves per twig	Smallest leaf size class 0 to $50\ cm^2$	
							Whole data set	
Broad-leaved deciduous ($n = 720$)	179.6	62.6 ($n = 555$)	305.7 ($n = 120$)	0.12	0.02 ($n = 120$)	7.1	45.1	91.9 ($n = 120$)
Broad-leaved, evergreen ($n = 125$)	25.6	9.1 ($n = 75$)	54.7 ($n = 45$)	0.09	0.08 ($n = 120$)	7.6	339.4	379.8 ($n = 120$)
Needle-leaved, evergreen ($n = 180$)	0.8	0.3 ($n = 75$)	1.2 ($n = 45$)	0.14	0.14 ($n = 180$)	184.8	263.7	263.7 ($n = 180$)

data set is considered (and ignoring the leaf area borne in leaves older than 1 year), needle-leaved evergreens averaged about 30 % fewer first-year shoots per $10^4\ cm^2$ total leaf area than broad-leaved evergreen species (Table 3).

For broad-leaved species, evergreens (7.6) were similar to deciduous species (7.1) in numbers of leaves per shoot. The result is that evergreen woody plants needed more first-year shoots to bear a given superficial leaf area. For the whole data set, evergreen species needed 7.5 times more first-year shoots than deciduous species (Table 3). In the smallest leaf size class (holding leaf size to comparable magnitude for the groups), this was about four times more first-year shoots than deciduous species.

DISCUSSION

There are several possible interpretations of the correlations known as Corner's Rules (White, 1983). Two concern vascular supply and mechanical support: larger leaves would seem to require a larger cross-sectional area of vascular supply and need greater mechanical support. Fewer branches might then be an outcome of larger leaves – branches would be spaced farther apart to reduce (or optimize) leaf overlap and self-shading.

A third argument, advanced first for compound-leaved trees but holding also for trees with large simple leaves (Givnish, 1979), consists of the following points. If photosynthetic spread is partly accomplished with large leaves, then fewer branches are required, large-leaved plants could expend more energy in extension growth, rather than branched growth. In other words, large-leaved trees should be able to overtop smaller-leaved plants in successional time, all other factors being equal, because smaller-leaved plants must branch more to spread the same total photosynthetic surface (Givnish, 1979). Indeed, it is clear that early successional plants after disturbance in mesic productive environments have longer yearly extension growth than later successional trees, even when both are open-grown

(Marks, 1975; Grime, 1979). Others, however, have argued that early successional plants in full sunlight ought to have small leaves to minimize (1) heat load problems (Parkhurst and Loucks, 1976) and (2) self-shading (Horn, 1971). In fact, Horn's prediction was that early successional tree crowns would be multi-layered, small-leaved and not as efficient in light extinction as later successional trees.

Studies of Corner's Rules have several bearings on these points. Leaf size is not the only variable affecting total leaf area borne by a shoot and hence relative investment in photosynthetic and supportive tissues; leaf number per shoot is important. Leaf number per shoot was uncorrelated with leaf size and twig thickness, in deciduous trees, but was significantly higher in intolerant species than in tolerant species (White, 1983). Thus, in deciduous trees, leaves per shoot was the best index of successional role. In broad-leaved evergreens, leaf number was not significantly correlated with leaf size or twig thickness for the whole data set, but was positively correlated with these measures for *Rhododendron* species, all conifers and *Pinus* species. Thus leaf size and leaf numbers per shoot reinforce one another in the last three groups, and their separate effects are more difficult to discern.

High leaf numbers per shoot are less predictive of successional role in evergreens than in deciduous trees. A full-sunlight, multi-layered, much-branched shrub, *Leiophyllum buxifolium*, and a shade-adapted, mono-layered, few branched shrub, *Leucothoe fontanesiana*, have the two highest leaf numbers in the broad-leaved data set. Among the conifers, only *Tsuga canadensis* survives long periods in the shade; it has, indeed, the lowest numbers of leaves per shoot of any of the needle-leaved species. However, *Abies* and *Picea*, which both reproduce in shade, have high leaf numbers per shoot, and there is a wide range of leaf numbers per shoot in the pines, which are all intolerant.

There are problems with analysing the evergreens in the study area not encountered in the deciduous trees. There are relatively few species of evergreens, and they are often found in other than mesic environments. Leaf size varies as a function of Corner's allometry within one environment, but it also varies regionally as a function of overall climate (Dolph and Dilcher, 1980) and within one landscape as a function of environmental gradients (Hamman, 1979), primarily as a function of humidity, moisture availability and nutrient supply (Givnish, 1979). In deciduous trees, co-occurring, mesic site, species could be selected for study; in the evergreens, the sample crosses landscape and regional environmental gradients and cannot be easily interpreted in terms of successional differentiation within any one environment.

Another difficulty in comparing broad-leaved evergreen species with deciduous species is that evergreens bear thicker leaves (which cause higher light extinction than deciduous leaves). Pine needles are several-sided and leaf size is difficult to define. Thus, superficial leaf size does not address the underlying question of light-gathering ability (in particular the relation of this ability to support investment) in the three groups of plants. The suggestion from the data presented here was that broad-leaved evergreen species need more branches to bear a given superficial leaf area than deciduous species. At a given twig thickness, broad-leaved evergreens had smaller leaves than deciduous species. Since evergreen leaves are heavier, the relatively thicker twigs makes sense; the hypothesis that they are less efficient (as a function of number of branches or woody biomass) in bearing a given photosynthetic area, awaits further study. However, increasing evergreenness along temperate to tropical gradients in humid regions might indeed reflect the

fact that longer growing seasons compensate for the greater woody investment that is potentially needed to support evergreen leaves. Thick, evergreen, leaves also serve to more tightly control water loss and greater leaf longevity serves to retain nutrients (Givnish, 1979). Thus, there are other physiological properties involved, in addition to light-gathering ability.

Another source of leaf area in evergreen species, not considered to this point, is that of the leaves on older than first-year shoots. Two factors influence this contribution: (1) leaf longevity (generally 2 to 4 years) and (2) branching pattern. These factors work in opposite ways. The longer leaves survive, the higher their contribution relative to first-year leaves (for example, if leaves live 4 years and a plant never branches, older leaves increase total leaf area by four times).

The more branches a plant produces per year (the more new shoots), the lower the relative contribution of these older leaves (if leaves survive 4 years and the plant branches dichotomously every year, the old leaves increase total leaf area by 1.9 times). This reasoning assumes that leaf size and leaf numbers per shoot do not vary with age. Since leaves generally live less than 4 years and plants branch, when the whole crown is considered, less than strictly dichotomously (White, 1980), we can take 1.9 to four times as an upper bound on the relative contribution of older leaves in evergreen crowns. This contribution is at most half the difference between the superficial leaf area of first-year shoots of broad-leaved deciduous *vs* evergreen woody plants studied here: broad-leaved evergreens averaged seven times the number of first-year shoots to bear a standard leaf area when compared to broad-leaved deciduous species. Thus, although Corner's allometry is followed in these plants, a full understanding of the spread of photosynthetic area as a function of investment in non-photosynthetic structures awaits further analysis.

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