# Branching Patterns in Forest Shrubs and Understory Trees in Relation to Habitat

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# BRANCHING PATTERNS IN FOREST SHRUBS AND UNDERSTORY TREES IN RELATION TO HABITAT

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## SUMMARY

We investigated the branching and leaf display of dominant forest shrubs and understory trees in central New Jersey to determine (1) whether branching differentiation occurs in shrubs which reach optimum development in different successional environments, (2) the contrast in branching of small trees between field and forest and (3) the nature of within-crown branching plasticity in a mature canopy tree. We discovered that shrubs do not differ in gross branching structure (ratio of terminal to supporting branches) and propose that branch angle, length and alteration of leaf orientation may be significant display characters. Small trees exhibit markedly variable response to open *v.* closed habitats, confirming the expected increase in branching ratio in open environments. Within, but not outside, the forest, earlier successional species were more variable in branching. A single canopy tree crown also demonstrated alteration of leaf display components, including increased length and wider angle of branches, but not branch ratio in the shaded, lower crown. We suggest some of the fine-scale morphological traits of shrub branching which may be important in determining their leaf display. Finally, we discuss differences in shrub and tree habit, such as cloning and the presumably reduced costs of support in shrubs, which may explain the failure of shrubs to exploit the same component of branching strategy as trees.

## INTRODUCTION

Branching pattern is one of the most conspicuous features of woody plants, yet, although little investigated, it is clear that its adaptive significance is great. Efficaceous leaf display, minimization of non-photosynthetic tissue (Horn, 1971; Whitney, 1976; Honda and Fisher, 1978), structural strength (McMahon and Kronhauer, 1976) and optimization of translocation (Leopold, 1971; Leigh, 1975) are among these potential adaptive functions. The antagonism of some of these functions suggests that plastic or evolutionary trade-offs (cf. Levins, 1968) may be involved in determining branching of a species within particular habitats.

Whitney (1976) proposed that the branching pattern of species characteristic of closed, shady communities should be selected to favour the minimization of shading within the crown of an individual plant. Conversely, plants characteristic of open, bright habitats should be selected to minimize energy expenditure on non-photosynthetic tissue. These expectations are related to the slower growth (Marks, 1975) of late- *v.* early-successional species and ultimately, to the generally lower resource demand of the former (Grime, 1979; Bazzaz, 1979).

Differences in branching in trees are denoted by the bifurcation or branching ratio, which is the ratio of numbers of distal to proximal branches. This type of ratio was first used to quantify the drainage patterns of stream basins (Horton, 1945). Whitney's

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(1976) expectations of branching in relation to light translate into low branching ratios for shade-adapted and high ratios for sun-adapted species (Fig. 1). His expectations were borne out in a survey of saplings of tree species of eastern deciduous forest of North America. Additionally, an examination of several individuals of *Fraxinus americana* led him to conclude that the ratio was constant for a species. Thus, we expect that the branching ratio will vary among other woody plants adapted to contrasting light environments.

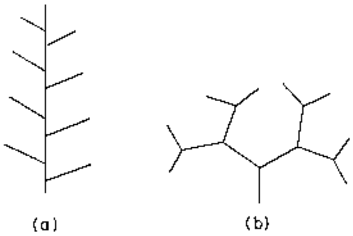

Fig. 1. Schematic representation of contrasting branching patterns. (a) branch segment of a sun-adapted plant with a high branching ratio (9 distal/1 proximal), corresponding to the early-successional or multilayer model of Horn (1971). (b) Branch segment of a shade-adapted plant with the minimum branching ratio (2 distal/1 proximal), corresponding to the late-successional or monolayer model of Horn (1971).

It appears however, that habitat can influence the branching structure in individuals of a given species growing in different light environemtns, contrary to Whitney's (1976) conclusion. Steingraeber, Kascht and Franck (1979) examined individuals of *Acer saccharum* in forest and oldfield habitats and found significant differences in branching ratio between habitats. More exposed individuals had higher branching ratios and in addition, possessed longer terminal branches than those beneath the canopy.

In this paper, we pose three primary questions, and an additional correlative one, concerning the branching structure of woody plants in different light environments. (1) Do shrub species differ in branching pattern ? While there is not a great deal of data on tree branching, shrubs are even less well known. Additionally, we wish to relate branching in shrubs to other features of their ecologies. (2) What is the nature of structural differentiation of understory trees between forest and field ? Here we can contrast the structures of early- and late-successional species and may expect earlier-successional species to be more variable in branching. (3) Does leaf display vary within the crown of a single dominant canopy tree ? Prior work on branching structure in trees has been restricted to saplings, but there is reason to expect (Whitney, 1976; Braham, 1977) that the crown of a single tree might respond plastically to different light environments. Finally, we may ask, in a preliminary way, what branching characteristics recur in equivalent light environments in the three life-forms, shrub, understory tree and canopy tree ? This study is limited to a subset of all possible leaf display parameters and further, is confined to structural rather than physiological characters.

## METHODS

Samples were taken in the Rutgers University Ecological Preserve in Middlesex County, New Jersey and in the Hutcheson Memorial Forest, Somerset County, New Jersey. The forest samples came from old growth stands on red shale dominated by

*Quercus alba*, *Q. velutina* and *Q. rubra*, along with *Carya ovata*, *C. ovalis*, *Fraxinus americana* and small amounts of *Fagus grandifolia* (Buell, 1957). The forest understory was dominated by *Viburnum acerifolium*, *V. dentatum*, *V. prunifolium* and *Lindera benzoin* (Monk, 1961). The oldfields were a variety of ages, ranging from 11 to 34 years since abandonment. All are similar in light environment, being dominated by perennial herbs, *Solidago* spp., *Andropogon scoparius* (Bard, 1952), interspersed with patches of woody species including *Rubus allegheniensis*, *R. flagellaris*, *Rosa multiflora*, *Rhus* spp. and individuals of *Cornus florida*, *C. ammomum*, *Acer rubrum*, *A. negundo*, *Fraxinus americana*, *Juniperus virginiana* and *V. prunifolium* scattered throughout.

The shrub species studied were *Viburnum acerifolium* L., a small shrub of old-growth forests, which is particularly common on well drained sites, *V. dentatum* L., a large shrub of younger forests and streamsides, *V. prunifolium* L., a large shrub which may reach tree size, of oldfields and poorly drained sites and *Lindera benzoin* (L.) Blume, a large shrub of moist old-growth forests. There is much variability in distribution of these species, but individuals found in other habitats in central New Jersey are not vigorous.

*Viburnum acerifolium* and *V. dentatum* clone by means of sucker shoots, root sprouts and rooting of decumbent aerial shoots, often forming large patches. *Lindera benzoin* clones by means of suckers, forming discrete clusters of shoots. *Viburnum prunifolium* may form dense clumps in oldfields by means of root sprouts.

The small trees studied were *Cornus florida* L., the dominant understory species in central New Jersey old-growth forests, although it also invades oldfields, *Acer rubrum* L., which invades oldfields and persists in forests as an understory tree and *Fraxinus americana* L., a tree of young forests and light-gaps in old-growth forests.

Quantification of branching structure requires that the branches be classified according to position in the crown using branch orders (Horton, 1945). First order branches are terminal branches. The juncture of two first order branches defines a second order branch; the juncture of two second order branches, a third, and so on. The juncture of branches of unlike order does not affect the classification of either. The branching or bifuraction ratio is calculated after Motomura (in Whitney, 1976):

$$R_b = \frac{\left(\sum_{1}^{t} N_o\right) - N_t}{\left(\sum_{1}^{t} N_o\right) - N_1}.$$

Where $R_b$ is the branching ratio, $N_o$ is the number of branches of order $o$, $N_t$ the number of branches of the highest order, $t$ and $N_1$ the number of branches of the first order. The formula allows for deviation of the ratio within the crown. Branching ratio may also be derived as the antilog of the slope of the line relating log number of branches with order.

Branching was determined in 10 individuals of each shrub species in old-growth forest, in 10 individuals of *V. prunifolium* in a 35-year oldfield, in 10 individuals of the small tree species in old-growth forest and 10 in an 11-year oldfield. Branching ratio was also determined at the top (27 m) and base (16 m) of a recently fallen *Quercus rubra* L.

Allocation of biomass to leaves versus branches in the shrub species was determined by collecting first through third order branch samples, separating the two components and weighing them after drying at 75 °C. The proportion of leaves is expressed as percent weight of branches and leaves (cf. Harper and Ogden, 1970).

Leaf display angle of *Acer rubrum*, as deviation from horizontal, was measured using a protractor equipped with a plumb bob; the protractor was aligned with the midrib of the leaf and the angle read. Leaf length was measured on the same specimens. Internodes of these individuals were also measured. All measurements were made on randomly chosen sample branches.

Sample branches were chosen from the base and top of the crown of a 27 m fallen *Q. rubra*. At sampling, the leaves maintained the same orientation as when the tree was still standing. Sample branches were clipped and returned to the laboratory for measurement of branching angles, branch length and petiole length.

Series of samples were compared using a balanced ANOVA, and where appropriate, Duncan's New Multiple Range Test (Barr *et al.*, 1976). Pairs of populations were compared by *t*-tests (Zar, 1974).

## RESULTS

### *Shrubs*

Samples of shoots defined by complete third order branches (i.e. a branch spray which terminates at a fourth order branch) represent the branching ratio of the entire shrub remarkably well.

$$Rb_{(1-3)} = 0{\cdot}03 + 1{\cdot}05\,(Rb_{(1-\infty)}).$$

Where $Rb_{(1-3)}$ is the branching ratio of the third order sample and $Rb_{(1-\infty)}$ is the ratio for the entire above-ground shoot from which the sample was taken. The equation is based on five individuals of each shrub species for a total of 20 points. The relationship is highly significant ($r^2 = 0{\cdot}98$) and the calculated branching ratios correspond well with those determined graphically (Table 1).

Table 1. *Structural characteristics of forest shrubs*

| Species | *Rb* (graphic) | *Rb* (calculated) | Percentage leaf |
|---|---|---|---|
| *Viburnum prunifolium* | 6·92 | 6·82 ± 1·32 a | 66 ± 7 |
| *Lindera benzoin* | 3·80 | 4·83 ± 1·95 b | 76 ± 4 |
| *Viburnum dentatum* | 3·80 | 4·57 ± 1·06 b | 81 ± 4 |
| *Viburnum acerifolium* | 3·98 | 3·73 ± 0·90 b | 78 ± 6 |

Branching ratios (Rb) were determined from the slopes of plots of log number of branches against order (graphic) and from the formula of Motomura (calculated). Leaf weight is expressed as percentage total sample biomass. S.D.s followed by the same letter are not significantly different at the 0·05 level.

The biomass of leaves as a percentage of leaf plus first order branch tissue (Table 1) differed significantly only in *Viburnum prunifolium*, and was lower than that of the other shrubs. The proportion based on all branches in each third order sample showed the same statistical relationship.

### *Small trees*

The branching ratios of *Cornus florida* and *Acer rubrum* were significantly higher in open fields than in closed-canopy forest (Table 2). Branching ratios of *V. pruni-*

*folium* were higher in oldfields but not significantly so (Table 2). None of the other shrub species occurred in the oldfield habitats studied. *Fraxinus americana*, a compound-leaved tree, did not differ between forest and field habitats. Whether or not the rachis is counted as a first order branch or considerad a part of the leaf makes no significant difference in branching ratio.

Finer scale leaf display characters, including leaf angle, leaf size and internode length, were examined in *Acer rubrum*. Leaves in the oldfield were displayed at angles significantly further from horizontal than were forest leaves (Table 3). The leaves in the field were significantly smaller and the internodes longer than in the forest (Table 3).

Table 2. *Branching ratios of field and forest understory trees*

| Species | Field | Forest | $t$-test |
|---|---|---|---|
| *Cornus florida* | 4·8 ± 0·9 | 3·6 ± 0·3 | $P$ < 0·001 |
| *Acer rubrum* | 8·8 ± 2·4 | 5·0 ± 1·1 | $P$ < 0·001 |
| *Viburnum prunifolium* | 8·3 ± 2·2 | 6·8 ± 1·3 | $P$ < 0·10 |
| *Fraxinus americana* (with rachis) | 4·1 ± 2·3 | 4·7 ± 2·3 | $P$ > 0·50 |
| *Fraxinus americana* (without rachis) | 4·4 ± 1·0 | 2·4 ± 0·9 | $P$ > 0·50 |

Means ± s.d. are based on samples of 10 individuals in each habitat.

Table 3. *Leaf display parameters of* Acer rubrum

| Characteristic | Field | Forest | $P$ |
|---|---|---|---|
| Leaf display angle (°) | 127 ± 20 (76) | 103 ± 7 (49) | ≪ 0·001 |
| Leaf length (cm) | 8·2 ± 1·1 (76) | 8·8 ± 1·4 (50) | < 0·01 |
| Internode length (cm) | 5·4 ± 1·7 (44) | 1·5 ± 0·8 (27) | ≪ 0·001 |

Means ± s.d. with numbers in parentheses. $P$ level is based on $t$-test.

Table 4. *Structural characteristics of different portions of a* Quercus rubra

| Crown position | $Rb$ | 1st order length | Branch angle | Petiole length |
|---|---|---|---|---|
| Sun | 3·7 ± 0·9 | 5·1 ± 2·8* | 46 ± 15** | 2·4 ± 0·4** |
| Shade | 3·8 ± 0·9 | 7·4 ± 5·1 | 77 ± 18 | 2·6 ± 0·6 |

Branch length is given in cm, angle in degrees. Means ± s.d.
* 0·01 > $P$ > 0·005. ** $P$ ≪ 0·001.

### *Tree crown*

The branching ratio did not differ significantly in samples taken from 16 and 27 m height in the *Q. rubra* crown (Table 4), but other components of leaf display did so. Both first order branches and petioles were significantly longer within the crown than at its top (Table 4). The angles between first order branches joining first or higher order branches were significantly more acute at the top of the crown than in the shade.

## DISCUSSION

### *Shrubs*

Our finding that shrubs which have optima in different successional environments do not differ in branching ratio is contrary to the situation in large and small trees (Whitney, 1976). Thus, the data on trees support the theoretical expectation that the monolayer structure should appear in late successional and the multilayer structure in early-successional species (Horn 1971, 1975).

Perhaps the failure of shrubs to differ in the expected directions indicates important differences from the architecture of trees, upon which branching theory is largely built (Horn, 1971; Leopold, 1971; Honda, 1971; Honda and Fisher, 1978; MacMahon and Kronauer, 1976). One mitigating factor for the shrubs studied here is that they do not exploit as broad a range of light environments as do the various trees sampled by Whitney (1976). In the New Jersey Piedmont, only *V. prunifolium* can be found in field habitats. Many of Whitney's (1976) early-successional trees are typically found in open fields. In an open field habitat, *V. prunifolium* tends to have a higher branching ratio, indicating some plastic or genetic variation of shrub architecture in response to the light environment.

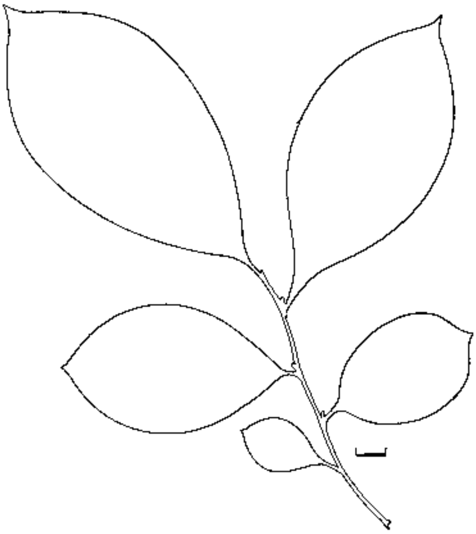

Fig. 2. Tracing of a representative branch tip of *Lindera benzoin*. The leaves increase in size toward the branch tips. All blades are naturally presented in the same plane. The scale bar represents 1 cm.

Alternatively, the failure of shrub species to differ in branching ratio may indicate a reliance on other parameters. These shrub species are characterized by a capacity for extensive clonal growth by suckers or root sprouts permitting a single genetic individul to explore an area but without the costly support requirement of single-stemmed trees. Trees represent a primarily vertically oriented strategy while shrubs represent a horizontally oriented strategy for reduction of mutual shading. Thus, much of the broad leaf dispersion in shrubs may be accommodated relatively cheaply in terms of wood and shading. The ability of many *Viburnum* spp. to root from decumbent shoots is a well known mechanism of clonal spread (Gill and Helay, 1974). *Viburnum prunifolium,* while apparently not cloning from above-ground parts, was observed to have root connections about 15 cm deep. *Lindera benzoin* does not spread as extensively as the *Vibrunum* spp. but develops a more compact spray of shoots over time.

The gross morphology of shoots within a clump may also increase the flexibility of the shrub life form relative to trees. For example, the shoots of *Lindera benzion* form a cantilever, so that a broad plane is exploited from a single rooting point, but without the need for extensive offshoots. Within the cantilever of *Lindera*, the leaves are arranged so as to utilize the plane effectively. A representative leaf spray of *L. benzoin* is shown in Figure 2. All leaves lie naturally in the same plane, and distal leaves are larger than proximal leaves on a given branch. The change in leaf size along a branch allows more complete in-filling of interleaf spaces towards branch tips and simultaneously, reduces overlap within the plane. The distal increase in leaf size followed a significant parabolic relationship in six randomly chosen first order branches. The branch with the largest number of leaves (8) gave the equation $Y = -9{\cdot}33 + 13{\cdot}73x - 1{\cdot}25x^2$ ($r^2 = 0{\cdot}94$, $P < 0{\cdot}01$), where $y$ is leaf area in cm and $x$ is leaf rank, beginning proximally.

The planar leaf arrangement of *Lindera* is accomplished in spite of the spiral insertion of the petioles by twisting of the petioles (cf. also Leigh, 1975). A spiral leaf arrangement, as a mechanism to effectively display the leaves on a shoot, is expected in bright environments (Leigh, 1972, 1975).

Other fine-scale structural features can be effective in determining shrub architecture. The branching ratio is, of course, a relatively crude index of plant architecture. Branching angle and branch length have been found, in both real and model trees, to have a major effect on the architecture (Honda, 1971; Honda and Fisher, 1978; Barker, Cumming and Horsfield, 1973; Steingraeber *et al.*, 1979). In addition, the length of internodes may be an important architectural character. These characters are currently under investigation in the shrubs.

The proportion of leaves per total tissue weight did not conform to expectations. Only *V. prunifolium* differed in either leaf weight or leaf area per unit branch. The other species could not be differentiated. This may indicate that the more upright, tree-like form of *V. prunifolium*, though cloning by root sprouts, requires larger amounts of wood than other species which branch beneath the ground. This conforms to the suggestion above that the clonal habit of shrubs is more flexible and requires less internal support than does the tree habit. *Viburnum prunifolium* may be considered to behave intermediately between strictly single-trunked small trees and profusely clonal, multiple-stemmed shrubs. The rank of allocation was the same whether based on a first order sample or on the whole third order sample, which included many non-leafy, supporting branches. Studies on small trees may shed light on these ideas.

### *Trees in Contrasting Environments*

On the basis of a sample of seven *Fraxinus americana* saplings, Whitney (1976) concluded that branching ratio was a constant species character. Horn (1971) had noted previously, however, that the leaf display pattern of some species, including *F. americana*, changed as they matured. This would suggest that branching ratio might vary among different habitats. Steingraeber *et al.* (1979) recently described branching differences in *Acer saccharum* between different habitats; forest-grown specimens had the expected low branching ratio. Here, we found that both *Cornus florida* and *Acer rubrum* exhibit significantly lower branching ratios in forest than in field. Thus we concur with Stringraeber *et al.* (1979) that tree species vary considerably in branching between habitats. *Fraxinus americana* specimens however, did not differ between the two habitats; this apparent lack of significant plasticity correlates with the poor condition of most forest grown specimens. Except in light gaps, *Fraxinus* had massive die-back and an etiolated, weak 'whip' form. *Fraxinus* saplings, which led Whitney (1976) to conclude absence of plasticity, may be unusual.

Strictly speaking, we do not know whether the variation discovered in this survey represents phenotypic plasticity or selective discrimination among different branching genotypes. Because of the modular nature of plant shoots (Harper, 1977) it may be relatively easy to alter the branching structure of most plants through the manipulation of module number and size. Consequently, at this stage, we can only suggest phenotypic and developmental plasticity as the causes of differences in branching patterns between habitats in the same species, although experimental evidence is unavailable. We use the word plasticity with this in mind.

There are trade-offs in the components of leaf display in forest and field habitats. An example is the shortening of nodes coupled with the lenghtening of petioles in the forest *Acer rubrum*. Shorter nodes would seem to increase mutual shading within a leaf spray, but this is circumvented by the longer petioles (data not presented). Other characters participate in the syndromes of field and forest leaf display. Planar configuration of leaf sprays and increased spacing between layers in the forest specimens are characteristics which we observed (cf. also Steingraeber *et al.*, 1979).

The variation of branching, indicated by the standard deviation S.D., differs among species and between habitats. First, all species studied here, as well as *Acer saccharum* studied by Steingraeber *et al.* (1979), are more variable in field than in forest, having both greater S.D.s and range in the field (Table 1), perhaps reflecting the presumed unpredictability of open environments. Furthermore, within the forest the S.D. is lower for later- than for earlier-successional species. In the field, however, *A. saccharum* violates this trend and has very high plasticity (S.D. = 2·79 field, 0·33 forest, Steingraeber *et al.* 1979; Table 1). Thus we find very high plasticity for one of the late-successional species in some situations. We do not include *F. americana* in this analysis because all specimens that were not beneath canopy light gaps were moribund. Hence, we do not know how much of the variation in this species is strategic and how much is accidental. It appears, as noted earlier, that *F. americana* may be unusually inflexible in branching.

Significant, and in this case, true plasticity exists within the crown of a single canopy dominant *Q. ruba* as well. This plasticity is not however, expressed as a change in branching ratio, but rather as an alteration of other components of leaf display. The well known increase in leaf size and reduction of lobing from crown top to base (Hanson, 1917; Horn, 1971; Braham, 1977) was noted here but not quantified. The differences in branch and petiole length, and in branch angle (Table 4) are the basis of the contrast. Additionally, we noted that leaves near the top of the crown were inclined at generally steeper angles than leaves lower in the crown. This is apparently the first demonstration of leaf display variation within the crown of a single mature tree.

### *Congruences among life forms*

The problem of congruence of branching and leaf display among life forms can only be discussed here in a preliminary way. There are still very few data available to allow for a comparison of branching characteristics. First, it appears that shrubs may be rather different from sapling trees in their branching pattern. Rather than exploiting differences in degree of bifurcation as do trees, shrubs employ mechanisms which may not be available to trees. Cantilever, or inclined shoots as parts of clonal systems seem to be an important adaptation. The clonal form of shrubs may itself be a significant difference between the two life forms, one which may permit shrubs to exploit a single plane for mutually non-overlapping leaf display with a fraction of the structural investiment required of trees. Within this broad strategy, a number of additional components can be evolutionarily or plastically manipulated to display leaves efficaceously. Shrubs appear, but have not been demonstrated, to vary in some of the same features that vary from tree-top to crown base. Branch angle, length and petiole characters are a few of those which also vary in shrubs. Such congruence may lend support to the idea of shrubs as clonal systems which can exploit a broad horizontal area relatively cheaply, but the architecture of these and other plants is still in need of much study.

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