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THE ROLE OF BRANCH LENGTH AND ANGLE IN BRANCHING PATTERN OF FOREST SHRUBS ALONG A SUCCESSIONAL GRADIENT

BY JEFFREY S. KEMPF AND S. T. A. PICKETT

Botany Department, Rutgers College, Rutgers University, P.O. Box 1059,
Piscataway, NJ 08854, U.S.A.

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SUMMARY

We investigated the branching structure of shrubs to quantify architectural changes along a successional gradient and to compare these findings with the behaviour of trees. Although shrubs did not differ in bifurcation ratio, it was discovered that branch length, interbranch distance and branching angle are all important display characters. Later successional shrubs had longer whole branches or interbranch lengths than early successional shrubs. In addition, there is a tradeoff between interbranch length versus whole branch length and angle size as part of the overall strategy for minimizing leaf overlap in the later successional shrubs. Early successional shrubs allocate less to long branches as a component of multilayer display of numerous, small leaves. We conclude the existence of great flexibility in the shrub form which utilizes horizontal areas rather cheaply and exploits different successional positions by manipulating the same small-scale branching features that differ within single tree crowns.

INTRODUCTION

The stem system provides the structural support and leaf exposure framework of woody plants. Species which are found in different environments along a light intensity gradient would be expected to have adopted contrasting structural features, particularly in their branching patterns (Whitney, 1976). Species characteristic of closed, shady communities should be selected to minimize shading within the crown of an individual plant. Horn (1971) categorized this type of leaf display as a non-random, highly structured monolayer. Conversely, plants characteristic of open, sunny habitats should be selected to minimize energy expenditure on non-photosynthetic tissue. These species approach a multilayer state, having a number of small overlapping leaves randomly distributed throughout the crown (Horn, 1971).

One approach to the analysis of branching is the use of the bifurcation ratio. This ratio compares the number of terminal to proximal branches (Leopold, 1971). Lower bifuraction ratios are associated with the monolayer, while higher ratios are associated with multilayer leaf display (Whitney, 1976). The bifurcation ratios of early and late successional trees (Whitney, 1976) and of individuals of a given species in open *v.* closed habitats (Steingraeber, Kascht and Franck, 1979; Pickett and Kempf, 1980) do differ in the expected directions. However, bifurcation ratios of shrubs from different successional positions do not differ (Pickett and Kempf, 1980).

Fine scale features of leaf display have been found to differ in model and real plants. Branch length and angle are important determinants of model plant form (Honda, 1971; Barker, Cumming and Horsfield, 1973; Honda and Fisher, 1978),

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and these features differ significantly between shade and sun portions of the crown of a single forest grown *Quercus rubra* L. (Pickett and Kempf, 1980). Thus, such fine scale features may contribute to the contrasting leaf display patterns of shrubs from different successional positions.

The purpose of the present study is to extend branching analysis in early and late successional shrubs. It includes such fine scale parameters as branch length per order, branch angle per order, interbranch length per order and interleaf distance per order which may vary even though branching ratio does not differ. We would expect to find longer branch, interbranch, and interleaf lengths and wider angles in the later successional species. These features should enable shrubs found beneath closed canopies effectively to spread their leaves and so minimize overlap.

METHODS

The shrub species studied were *Viburnum dentatum* L. and *V. prunifolium* L. from early successional or open canopy environments and *V. acerifolium* L. and *Lindera benzoin* (L.) Blume of older forests and closed canopy environments. Samples were taken from old growth mixed-oak stands in the Rutgers University Ecological Preserve in Middlesex County, N.J. and the Hutcheson Memorial Forest, Somerset Co., N.J. The forests and species are described in detail elsewhere (Pickett and Kempf, 1980).

Six replicates were taken of each species from different individuals. In the case of large shrubs, only a sub-sample was taken; this consisted of a branch, and all its terminal branches which originated from the highest order shoot for that shrub. A sketch was made of each sample on which were recorded branch lengths, interbranch lengths, interleaf distances and branch angles. These data were evaluated by programs of the Statistical Analysis System (Helwig and Council, 1979). Analysis of variance and Duncan's Multiple range Test were used where appropriate.

The bifurcation ratio, R_b was determined by Motomura's formula (in Whitney, 1976):

$$R_b = \frac{\left(\sum_{1}^{t} N_0\right) - N_t}{\left(\sum_{1}^{t} N_0\right) - N_1}$$

where N_0 is the number of branches of order 0, N_t the number of branches of the highest order, t, and N_1 is the number of branches of the first order. The formula accounts for deviation of the ratio within the crown.

RESULTS

The branching ratios of *V. dentatum* and *V. prunifolium* tend to be higher than those of the other two species, but not significantly so. *V. prunifolium* showed the greatest range in branching ratio, from 4·18 to 11·00 (Table 1).

Lindera benzoin had the longest mean branch lengths for order 1. *V. acerifolium* and *V. dentatum's* branch lengths were significantly shorter than those of *Lindera*, but could not be statistically distinguished from each other. *V. prunifolium* had the shortest mean first order branch lengths, but they were not significantly different from those of *V. dentatum* (Table 2).

Lindera benzoin also had the longest branch lengths for order 2. *V. prunifolium*

Table 1. *Mean and range of bifurcation ratios of early and late successional shrubs from the New Jersey Piedmont*

Species	Mean	Range
Viburnum dentatum	5·0	4·08–6·54
V. prunifolium	6·6	4·18–11·00
V. acerifolium	4·0	3·16–5·65
Lindera benzoin	4·7	3·89–7·20

Table 2. *Mean length of whole branches of order one*

Species	Mean (cm)	N	Grouping	
Lindera benzoin	8·4	142	A	—
Viburnum acerifolium	3·2	409	B	—
V. dentatum	2·8	523	B	C
V. prunifolium	2·2	297	—	C

Means with the same letter are not significantly different. In this and the following tables, N = number of observations and $\alpha = 0{\cdot}05$.

Table 3. *Mean length of whole branches of order two*

Species	Mean (cm)	N	Grouping	
Lindera benzoin	24·5	21	A	—
Vibernum prunifolium	12·4	46	B	—
V. dentatum	10·2	97	B	C
V. acerifolium	9·5	103	—	C

Means with the same letter are not significantly different.

Table 4. *Mean length of whole branches of order three*

Species	Mean (cm)	N	Grouping
Lindera benzoin	23·0	5	A
Vibernum acerifolium	22·1	30	A
V. prunifolium	21·2	11	A
V. dentatum	17·0	24	A

Means with the same letter are not significantly different.

Table 5. *Mean angles of whole branches of order one*

Species	Mean (°)	N	Grouping
Lindera benzoin	61·2	142	A
Viburnum prunifolium	56·6	281	B
V. dentatum	49·5	525	C
V. acerifolium	40·9	409	D

Means with the same letter are not significantly different.

Table 6. *Mean angle of whole branches of order two*

Species	Mean (°)	*N*	Grouping
Lindera benzoin	58·3	21	A
Viburnum prunifolium	53·4	46	A
V. dentatum	51·9	97	A
V. acerifolium	43·7	103	B

Means with the same letter are not significantly different.

Table 7. *Mean angles of whole branches of order three*

Species	Mean (°)	*N*	Grouping
Lindera benzoin	57·0	5	A
Vibrunum prunifolium	48·6	11	A
V. acerifolium	40·8	30	A
V. dentatum	39·8	24	A

Means with the same letter are not significantly different.

Table 8. *Mean interbranch length of order two*

Species	Mean (cm)	*N*	Grouping
Virurnum acerifolium	6·3	93	A
V. dentatum	5·1	159	B
V. prunifolium	4·7	110	B
Lindera benzoin	4·3	93	B

Means with the same letter are not significantly different.

and *V. dentatum's* branch lengths were significantly shorter than those of *Lindera*, but they were not statistically different from each other. *V. acerifolium* had the shortest mean second order branch lengths, but they were not significantly different from those of *V. dentatum* (Table 3).

Lindera benzoin exhibited the longest mean lengths for third order branches, followed by *V. acerifolium*, *V. prunifolium* and *V. dentatum*. No significant differences were found between the four species (Table 4).

Lindera benzoin had the largest mean branching angles for order 1. It was followed in order by *V. prunifolium*, *V. dentatum* and *V. acerifolium*. Each species was statistically distinct (Table 5).

Lindera benzoin had the largest mean branching angles for order 2, followed by *V. prunifolium* and *V. dentatum*, but no significant differences were found between these three species. *V. acerifolium* had significantly smaller second order branching angles (Table 6).

Lindera benzoin had the largest branching angles for order 3, followed by *V. prunifolium*, *V. acerifolium*, and *V. dentatum*. No significant differences were found between the species (Table 7).

For interbranch lengths of order 2, *V. acerifolium* displayed the significantly greatest mean lengths, followed in order by *V. dentatum*, *V. prunifolium*, and

Table 9. *Mean interbranch length of order three*

Species	Mean (cm)	*N*	Grouping
Viburnum acerifolium	8·6	64	A
V. dentatum	6·6	52	B
V. prunifolium	4·9	44	C
Lindera benzoin	4·0	29	C

Means with the same letter are not significantly different.

Lindera benzoin. The latter three species showed no statistical differences (Table 8). The same order of species was found for mean interbranch lengths of order 3, but here *V. dentatum* fell into a statistically different class (Table 9).

No significant differences were found for interleaf distances over orders 1, 2 and 3. In addition, leaf internodes in *V. prunifolium* were confined to first order branches, as no leaves were found on higher order branches.

Discussion

The failure of shrubs which have optima in different successional environments to differ in branching ratio is contrary to the situation in canopy and understory trees. There are clear differences in branching ratio between early and late successional trees (Whitney, 1976) and differences have also been found in canopy and understory trees from field *v.* forest habitats (Steingraeber *et al.*, 1979; Pickett and Kempf, 1980). Thus, the data on trees support the theoretical expectations that a monolayer branching structure should appear in closed environments and a multilayer branching structure in open ones (Horn, 1971). However, in the case of the crown of a single *Quercus rubra*, although the branching ratio was constant, branches were longer and branch angles more obtuse deeper within the crown (Pickett and Kempf, 1980).

Discussion of the fine-scale branching parameters in relation to leaf display in shrubs will be confined to the lower order, distal branches. It is likely that higher order branches are more important in supporting lower order branches than in direct leaf display. This is supported by the lack of differentiation among the shrubs for third order branch lengths and branching angles.

The early successional species act as expected. *V. dentatum* and *V. prunifolium's* short branch lengths, short interbranch lengths and angles only slightly greater than 45°, all contribute towards a multilayer display of leaves. This correlates with their small leaf size and greater number of leaves per branch as compared to the later successional species.

Lindera benzoin consistently displayed the longest branches and largest branching angles for first and second order branches. These two habits are appropriate for growth in a closed environment as both contribute towards leaf spread and minimization of leaf overlap. Contrary to expectation, the interbranch length of *Lindera benzoin* was not significantly different from the early successional species; it appears that this is compensated by other features favouring leaf spread.

V. acerifolium's long interbranch lengths indicate that this species may be using branching as a means of dispersing its leaves. This habit compensates for the short whole branch lengths and small branching angles found in this species.

The overall goal of minimizing leaf overlap is achieved by both *Lindera benzoin* and *V. acerifolium*, but by different means. *V. acerifolium* has long interbranch lengths and short whole branch lengths with small angles, whereas *Lindera benzoin* has short interbranch lengths and long whole branch lengths with large angles. There is apparently a tradeoff here between interbranch lengths versus whole branch lengths and angle. One feature common to both species is their greater allocation to wood, in the form of long whole branches or interbranch lengths than in the early successional species.

The lack of differentiation of interleaf distances among shrubs seems to indicate a reliance on other parameters for leaf display. Perhaps it is too expensive for shrubs to increase the distance between leaf nodes by adding wood when changes in branching angle or petiole length may be accomplished more cheaply. This latter feature has been noted in forest grown *Acer rubrum* (Pickett and Kempf, 1980).

The larger range in *V. prunifolium's* bifurcation ratio is similar to the finding of high variation in open grown *Acer saccharum* saplings by Steingraeber *et al.* (1979). This presumably reflects the uncertainty of open environments. The failure of the shrub species to differ in their range of bifurcation ratio conforms to the suggestion that the clonal habit of shrubs is more flexible and requires less internal support than does the tree form (Pickett and Kempf, 1980).

In conclusion, it appears that shrubs are able to manipulate some of the same leaf display components that vary from treetop to crown base. The shrub form appears as a clonal system which can exploit a horizontal area rather cheaply, while simultaneously adjusting finer scale characters as seen in single tree crowns. Later successional shrubs seem to allocate more energy to wood in the form of longer whole branches or interbranch lengths, than do early successional shrubs. In addition, there appears to be a tradeoff between interbranch length versus whole branch length and angle. Thus, shrub species appear to alter fine scale leaf display characters in compensatory ways such that early and later successional species do conform to the multi- and monolayer leaf presentation patterns appropriate to their respective environments.

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