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THE ADAPTIVE ARCHITECTURE OF SHRUB CANOPIES: LEAF DISPLAY AND BIOMASS ALLOCATION IN RELATION TO LIGHT ENVIRONMENT

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SUMMARY

Leaf display features and biomass allocation were investigated in four dominant shrubs of forest and old-field habitats in central New Jersey, USA, to determine whether differences exist between species which reach optimum development in different successional environments. Late-successional shrubs were found to possess larger leaves, greater leaf area expansion (ratio of leaf area to leaf weight), and increased allocation of total energy to leaves versus wood, compared to early-successional shrubs. The shrubs appeared to deviate from patterns of biomass allocation expected in trees, possibly as a result of relative ease of horizontal exploitation of space through cloning. In addition, there appears to be a great deal of flexibility in features of leaf display which may play an important role in shrub adaptation to particular light regimes.

Introduction

The canopy structure of a plant, as determined by the vertical and horizontal distribution of leaves and branches, is the collective result of selection by a variety of environmental conditions. The amount and spatial arrangement of leaf area, the pattern of branching and leaf orientation, for example, interact to produce a micro-environment that is both a determinant and result of the processes of growth, development and interaction of plants. By modification and interception of the fluxes of heat, carbon dioxide, water vapour, and perhaps most importantly, light, canopy structure becomes a major determinant of the productivity of an individual plant, a population, or a community, and as such is of interest to plant ecologists, plant physiologists and evolutionary biologists alike.

Relating canopy structure to the competitive abilities and successional status of plants in nature is a complex task. It must include the spatial orientation of the woody components of plant canopies, the branches and all the resultant display parameters, such as branch angles, lengths of branches, size of leaves, etc. Horn (1971) proposed two extreme tree strategies, the monolayer and multilayer, each of which encompasses a syndrome of characters that collectively result in adaptation to particular habitats.

A method of quantifying the strategies of tree architecture is the bifurcation ratio, or the ratio of the number of terminal to proximal branches. Whitney (1976) proposed lower branching ratios for monolayered, late-successional trees, and associated high ratios with much-branched, early successional trees. The branching ratio was found to be useful in distinguishing between tree species of different

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successional status, but was later shown to vary between individuals of a given species in contrasting light habitats, as well as among crowns of individuals of a single tree species (Steingraeber, Kascht and Franck, 1979).

Honda (1971) extended research into the adptive architecture of trees with the aid of computer simulations, in which he varied the woody framework to maximize the 'effective leaf area' (the horizontal projection of leaf area) of the canopy. He found that theoretically optimal branch angles required to minimize leaf overlap are close to those actually observed in nature (Honda and Fisher, 1978; Fisher and Honda, 1977, 1979a, b). More recent work, however, has indicated limitations of the bifurcation ratio alone as a descriptive parameter of tree canopy architecture (Honda, Tomlinson and Fisher, 1981).

Applications of tree architectural theory to shrubs

The adaptive architecture of shrubs has been much less well investigated than that of trees. A few attempts have been made recently to apply the branching parameters discussed for trees to the shrub life form. Preliminary investigations have shown that the bifurcation ratio failed to distinguish between several shrubs of different light environments on the New Jersey Piedmont, suggesting alternative reliance of shrubs on fine-scale morphological features, including branching angle, branch length, and inter-branch distance in avoiding leaf overlap (Pickett and Kempf, 1980). In fact, these parameters proved to be of consequence in generating the particular leaf display of the shrub canopies. Late-successional, shade-tolerant shrubs were found to possess significantly longer whole branch or inter-branch lengths than shade-intolerant, early-successional shrubs. In addition possible trade-offs were suggested between inter-branch length versus whole branch length and angle size in the late successional species (Kempf and Pickett, 1981).

The present study

On the basis of recent studies, there is a great need for research in the area of shrub adaptive architecture. In particular, more work is needed to define the mechanisms of morphological adaptation to light conditions found in nature. Little or no knowledge exists of biomass allocation between woody and photosynthetic tissue within the canopy.

The present study aims to investigate the mechanisms of shrub structural adaptation to light in two ways. First, the light environment of the four most common forest shrubs in the New Jersey Piedmont are quantified and second, leaf display and biomass allocation of the shrubs are measured by harvest and application of plant growth analysis.

Methods

The species

The following four most predominant shrubs of the New Jersey Piedmont, present in various forest and old-field habitats, were selected: Nomenclature follows Gleason and Cronquist (1963).

Viburnum acerifolium L. A small shrub (to 2 m) of moist or dry forest habitats (Gleason and Cronquist, 1963). It is dominant in the shrub layer of mature, upland forest sites on the Piedmont (Monk, 1957), first appearing relatively late in the successional sequence (60-year-old field habitats) (Bard, 1952). On the basis of habitat requirements (Gill and Pogge, 1974) and controlled light regime studies

(Davidson, 1966), V. acerifolium has been classified as a highly shade-tolerant species, adapted to climax communities in New Jersey.

Viburnum dentatum L. A large shrub (to 5 m) of moist woods (Gill and Pogge, 1974). It may occur with low frequency and coverage in field habitats as early as 5 years from abandonment, increasing in coverage in older fields (Bard, 1952). Monk (1957) showed it to be predominant in poorly-drained and younger forest areas of the Hutcheson Memorial Forest on the New Jersey Piedmont. Partial shade may be a requirement for optimal growth and reproduction (Gill and Pogge, 1974).

Viburnum prunifolium L. A large (to 8 m), tree-like shrub of woods, thickets, and roadsides (Gleason and Cronquist, 1963). It colonizes recently abandoned field habitats, increasing in coverage in older fields (Bard, 1952). It is abundant in the younger forest habitats of the Hutcheson Memorial Forest, and may be particularly associated with windthrows (Monk, 1957). Optimal growth and reproduction has been demonstrated in open environments (Gill and Pogge, 1974).

Lindera benzoin L. Blume. A large shrub (to 5 m) of rich, moist forest habitats (Gleason and Cronquist, 1963). On the basis of controlled light regime studies, it has been classified as highly shade-tolerant and adapted to climax forest conditions (Davidson, 1966).

Viburnum dentatum and V. prunifolium may therefore be classified as largely shade intolerant, expected to show optimum growth in younger forest or old-field habitats. It is proposed that these two species are primarily early-successional in terms of light requirements. In contrast, V. acerifolium and L. benzoin have been classified as highly shade-tolerant species, and should show adaptation to late-successional forest habitats in which light intensity may be limiting.

Site selection

Sites were selected which appeared to support vigorous populations of one or more of the above species, based on factors such as amount of shrub canopy coverage, degree of flowering, and overall vigour.

All study sites were located on the New Jersey Piedmont, which has been described by Tedrow (1963) and Robichaud and Buell (1973). Four forest sites were chosen, all in old growth oak-hickory (mixed oak, Robichaud and Buell, 1973) forests. The canopy stratum was dominated by Quercus alba, Q. velutina, Q. rubra, Carya spp. and occasional individuals of Fagus grandifolia, Acer rubrum and Fraxinus americana. A distinct understory of Cornus florida was present. The shrub stratum consisted mainly of V. acerifolium, L. benzoin, V. dentatum and V. prunifolium. Dominant herbs include Podophyllum peltatum Circaea quadrisculcata and Impatiens capensis (Monk, 1961; Robichaud and Buell, 1973).

Site 1 (HW1) was in the well-drained portion of the William L. Hutcheson Memorial Forest, near East Millstone, (Somerset County) New Jersey. Site 2 (HW2) was located in the western portion of the forest, which is comparatively more poorly drained (Monk, 1961). Site 3 (CP) was in the Colonial Park Nature Preserve, East Millstone (Somerset County) New Jersey, about 1.6 km from the Hutcheson Forest sites. Site 4 (KW) was located in a pre-1840 forest tract on the Rutgers Ecological Preseve, or Kilmer Woods, Piscataway (Middlesex County) New Jersey.

Site 5 (Kilmer Field, KF) was a 50-year-old field located to the south of the Kilmer Woods tract. Rosa multiflora, Rubus spp., V. prunifolium, Rhus spp. and Myrica pennsylvanica were common members of the shrub community. Quercus

prinus and Juniperus virginiana formed localized canopies, while Lonicera japonica and Rhus radicans formed dense mats upon many of the shrubs and trees. Andropogon scoparius was a dominant herb.

Line transects were randomly located through portions of each site which were homogeneous in shrub cover, giving a total of 244 m at HW1, 137 m at HW2, 183 m at KW, 122 m at CP and 92 m at KF. The total transect length intercepted by the study species was recorded. The maximum height and number of basal stems per individual (here defined as a discrete clump of apparently related shoots) were measured for all transect shrubs. Viburnum acerifolium, V. prunifolium and L. benzoin were selected for study at the HW1 site, V. prunifolium and V. dentatum at the HW2 site, V. dentatum and L. benzoin at the CP site, V. acerifolium and L. benzoin at the KW site, and V. prunifolium at the KF site.

The light environment

Photosynthetically active radiation (μ E m⁻² s⁻¹ between 400 and 700 nm) was recorded at each site at approximately 3-week intervals from late April through late August, 1980 using a Lambda Quantum Sensor. Permanent light markers were set up at 3 m distances along the entire length of the transects at each site. Three readings were taken and averaged at each marker. All readings were made immediately above the shrub canopy level (approximately 2 m) between the hours of 11.00 and 14.00 on cloudless days. In addition, readings were taken in the open before and after each transect light survey, to allow the results to be expressed as percentage ambient quantum flux.

Structural and allocation parameters

Approximately ten individuals of each species per site (for a total of 100 shrubs) were selected for further study from the immediate vicinity of the transects, and from the entire transect area. Only readily definable individuals (discrete clumps of apparently related shoots) of relatively easy access were chosen covering a range of sizes up to a maximum height of c. 5 m. Care was taken to select vigorous shrubs without obvious structural damage, such as loss of branches and leaves from storms or herbivory.

All above-ground biomass was harvested for each individual and separated into woody and leafy components. Total leaf area was determined in the laboratory by a Lambda portable electronic area meter. Average leaf area was calculated on the basis of samples of 100 or more leaves. All biomass samples were bagged and dried at 80 °C to constant weight.

The following primary data were recorded for each individual: (1) mean leaf area (cm²); (2) total leaf area (cm²); (3) total leaf weight (g); (4) total wood weight (g).

The following secondary data were derived from the primary data: (1) specific leaf area = total leaf area (cm²)/total leaf biomass (g), a measure of leaf area expansion per unit leaf weight (Evans, 1972); (2) leaf weight ratio = total leaf biomass (g)/total leaf + wood biomass (g), a measure of partitioning of biomass to leaves versus wood (Evans, 1972).

Results were subjected to statistical analysis using an unbalanced ANOVA and Duncan's New Multiple Range Test, where appropriate (Zar, 1974; Barr et al., 1976).

Table 1. Mean photosynthetically active radiation per sampling period over the growing season. Sample size (N) and coefficient of variation (C.V.). Means followed by the same letter are not significantly different

Period	$\mu { m E} \ { m m}^{-2} \ { m s}^{-1}$	Site*	N	Grouping	$\mathbf{C}_{i}\mathbf{V}_{i}$
10 to 22 April	1340	KF	32	Α	37
•	1130	HW2	48	ΑВ	41
	1100	HW1	83	В	42
	1090	KW	63	В	39
2 to 23 May	1550	KF	32	A	30
•	390	KW	63	В	107
	230	HW1	83	В	140
	210	HW2	48	C	115
	88	CP	41	С	64
1 to 11 June	1000	KF	32	Α	90
-	270	KW	63	В	163
	230	HW1	83	В	189
	170	CP	41	В	228
	90	HW2	48	В	202
14 to 23 August	1460	KF	32	Α	67
ŭ	280	CP	41	В	149
	190	KW	63	В	156
	190	HW1	83	B	203
	160	HW2	48	В	202

^{*} KF = Kilmer Field, HW1 = Hutcheson Woods 1, CP = Colonial Park, KW = Kilmer Woods, HW2 = Hutcheson Woods 2.

Table 2. Mean leaf area

Species	Mean leaf area (cm²)	N	Grouping
Lindera benzoin	26:0	4900	A
Vihurnum acerifolium	19.0	1600	В
Viburnum dentatum	12· 4	2300	C
Viburnum prunifolium*	7.7	1900	\mathbf{D}

^{*} Forest individuals only.

Statistics and abbreviations are as in Table 1.

RESULTS

Light conditions

Absolute quanta received varied among sites and sampling intervals throughout the season (Table 1). From 19 to 22 April KF was significantly more 'open' than both KW and HW2. By 2 until 23 May all forest sites were significantly darker than the field site. From 1 to 11 June and from 14 to 23 August the field site remained the most open site. No forest site could be distinguished with respect to light availability on these dates.

Leaf display and allocation features

Mean leaf areas were statistically different for all species; L. benzoin had the largest leaves, followed by V. acerifolium, V. dentatum, and V. prunifolium in that order (Table 2).

	Mean specific leaf area (cm² g-1)						
				Site			
Species	HW1	HW2	CP	KW	KF	Overall	
indera benzoin	320a	_	303a	291a	_	305A	
Viburnum acerifolium	279a	_	_	214b	_	248B	
Viburnum dentatum	_	203a	196a	_	_	200C	
Viburnum prunifolium	195a	205a	_	_	161b	180C	

Table 3. Mean specific leaf areas for species grouped by site

Within species means belonging to the same population are indicated by the same lower-case letter. Differences among species over all sites are indicated by capital letters in the final column. Abbreviations as in Table 1.

Table 4. Mean leaf weight ratio for species grouped by site

Species	Mean specific leaf area (cm² g ⁻¹) Site					
	Lindera benzoin	0·21a	_	0·27a	0·38b	_
Viburnum acerifolium	0·17a	_		0·26a	_	0.21A
Viburnum dentatum	_	0·12a	0·16a	_	_	0·14B
Viburnum prunifolium	0·08a	0·10a			0·17b	0·15B

Statistical conventions as in Table 3.

Table 5. Allocation of biomass to leaves in 3rd order branching samples from red maple and flowering dogwood (From Pickett and Kempf, 1980)

Species	Sites	Percentage allocation to leaves	t	P
Acer rubrum	Forest Field	37 45 }	2.21	< 0.05
Cornus florida	Forest Field	²¹ }	5.70	< 0.001

Mean specific leaf area ratio, i.e. the amount of leaf area expansion per unit biomass, was greatest in L. benzoin and V. acerifolium, followed by V. dentatum and V. prunifolium (Table 3). The first two species were statistically different, but not the last two. There were no significant differences in specific leaf areas between sites for L. benzoin and V. dentatum. However, V. acerifolium showed larger leaf area expansion at HW1, while V. prunifolium showed significantly greater values in the forest habitats.

Lindera benzoin and V. acerifolium showed the greatest mean leaf weight ratios, i.e. the greatest allocation of total biomass to leaves versus wood, although they did not differ between themselves (Table 4). Viburnum prunifolium and V. dentatum do

not differ significantly. Lindera benzoin and V. prunifolium allocated more biomass to leaves at KW and KF, respectively. Viburnum acerifolium and V. dentatum showed no variation between sites (Table 4).

Discussion

Light conditions

In the present study, no significant differences in light availability could be established between the forest sites. This is not surprising in view of the large spatial variation found in all forest sites, due to canopy gaps of various sizes and frequencies in the otherwise dense, double-layered canopy. Coefficients of variation (Table 1) show an increase in variation within the forest sites with seasonal canopy closure. Maximum variation in light occurs in summer.

It appears that the KW area may be the most spatially homogeneous, and HW1 the most variable of the four forest sites. Davison and Forman (1982) report increasing light availability in the Hutcheson Memorial Forest over the last 30 years as a result of death and wind-throw of many very old canopy trees. As a consequence, HW1 and all the other forest sites to lesser extents, are mosaics of light micro-environments, the importance of which may be obscured by mean light availability values. It may be concluded that the shrubs are subject to great local variations in light availability. A knowledge of structural and physiological responses over the range of light conditions at a site would provide much information on the degree of phenotypic plasticity, and ultimately the level of adaptation of each species.

Leaf size

The large leaf areas of the later successional shrubs, L. benzoin and V. acerifolium, compared to V. dentatum and V. prunifolium, is in agreement with expectations for shade-adapted plants. It has been shown that shade-tolerant, late-successional tree species possess significantly larger leaves compared to early-successional, shade-intolerant species (White, 1983). These findings support the predictions of Horn (1971) for monolayer and multilayer tree forms. Small leaf size may also confer drought resistance to early successional trees since it may more effectively dissipate by convection, the larger heat loads associated with open environments. Conversely, the large leaf size of monolayer trees would represent an effective method of filling gaps between adjacent leaves within a single foliage layer, maximizing interception of radiation under limiting conditions (Horn, 1971).

Comparison of mean leaf sizes of each species among study sites was not studied here. However, Davidson (1966) showed an increased percentage of leaves in large size classes for *L. benzoin* when grown under low light intesities in greenhouse experiments. In contrast, *V. acerifolium* showed a greater proportion of large leaves in high light intensities. This suggests greater leaf display plasticity under shaded conditions and hence greater shade tolerance in general for *L. benzoin*.

Specific leaf area

The larger values exhibited by the late-successional species, L. benzoin and V. acerifolium, compared to the shade-intolerant species agree well with predictions generated by numerous controlled light experiments (Evans and Hughes, 1961; Jarvis, 1964; Evans, 1972).

There was a significantly greater leaf area expansion in V. prunifolium in the shady forest habitats compared to individuals in the open, as expected. Significant differences in specific leaf areas for V. acerifolium between KW and HW1 (Table 3) are more difficult to explain on the basis of contrasting light regimes, since no significant differences in light availability could be demonstrated between these sites. The observed differences in specific leaf areas may be real expressions of subtle variation in light regimes between the two sites (as discussed earlier), which have been obscured by averaging.

The increases in specific leaf areas for shade plants are well documented. In fact, the magnitude of increase in leaf area expansion of individuals transferred from high to low light regimes is a useful indication of shade adaptation, shade-tolerant species generally showing the largest increases (Evans and Hughes, 1961; Evans, 1972; Hutchings, 1976; Lewandowska and Jarvis, 1977). Contrary to these findings, Loach (1970) found difficulty in distinguishing between several sun and shade trees, including the shade-tolerant species Fagus grandifolia, on the basis of this parameter. He suggested that large specific leaf areas may be disadvantageous to some shade plants due to increased transpiration rates of large, thin leaves. This may be of some consequence in the water relations of V. acerifolium, since it is commonly found in the drier forest sites of the New Jersey Piedmont (Monk, 1957). It is possible that the contrast between optimal leaf characteristics for shade versus drought adaptation has resulted in evolutionary trade-offs between leaf area expansion and leaf thickness.

Leaf weight ratios

Late successional shrubs showed greater allocation to leafy tissue compared to wood. These findings are contrary to the proposals by Horn (1971) and Whitney (1976) of decreased allocation to leaves in shade-adapted trees based on the selective advantage in distributing leaf area in monolayered canopies without mutual shading. Evidence to support the prediction of greater allocation to wood was reported for shaded Sitka spruce (Lewandowska and Jarvis, 1977) and for shade-adapted, late-successional deciduous trees (Loach, 1970). Individuals of red maple (Acer rubrum) and flowering dogwood (Cornus florida), in forests had higher allocation to wood than those from open fields (cf. Pickett and Kempf, 1980; Table 5).

The variations exhibited by V. prunifolium in contrasting light habitats support the theory for trees, while opposing the trends in the other shrub species, in that the allocation to wood increased with shade. It is significant that V. prunifolium is most 'tree-like' in its tall stature and limited multi-stemmed nature. It appears that resource allocation in this shrub may be governed by the same constraints which operate in true trees.

Increased allocation of biomass to leaves demonstrated by *L. benzoin* at KW is difficult to explain on the basis of the light data, but again may suggest a particular sensitivity to subtle differences in light availability. Previous studies with *Lindera* have shown similar increases in the proportion of leafy tissue in shaded individuals compared to those growing in canopy gaps (Veres and Pickett, 1982). These trends suggest that decreased light availability may be a factor associated with the increased leaf weight ratios of *Lindera* at Kilmer Woods as well.

Overall strategies of leaf display

The divergence of responses between these shrubs and trees in relation to

patterns of resource allocation suggest fundamental differences in mechanisms between the two life forms. Apparently, shrubs may not be limited by the same structural constraints as the primarily vertical tree life form, as evidenced by the relative flexibility of increase in leafy components with shade. Perhaps the shade tolerant shrubs capitalize on greater flexibility in horizontal expansion by cloning, with much of the support cost borne by the ground, to minimize leaf overlap, instead of the massive, vertical expansion of a monolayered tree.

Kempf and Pickett (1981) demonstrated that L. benzoin and V. acerifolium may use large branch angles and later inter-branch or whole branch lengths to avoid leaf overlap. The larger leaf size and greater area expansion per unit leaf biomass demonstrated in the present study support their conclusions on shade-adaptation in these species. The late-successional shrubs, however, allocate a greater proportion of total biomass to leaves than the early-successional species, contrary to expectations. It may be that the shrubs avoid costly increases in allocation to wood by manipulating fine-scale features of leaf display in preventing mutual shading. L. benzoin, for example, may utilize 'cantilever' shoot structure, spiral leaf insertion and leaf variation along branches (with larger leaves at the distal ends) as mechanisms for reducing overlap between neighbouring leaves (Veres and Pickett, 1982). It has been suggested that Lindera has fundamentally a multilayer strategy, which is able to adapt plastically through structural modification to closed or open forest canopy environments (Veres and Pickett, 1982). In support of this idea, a significant increase in Lindera coverage has been demonstrated at the Hutcheson Memorial Forest over the last 30 years, probably in response to increasing light availability (Davison and Forman, 1982).

Viburnum dentatum and V. prunfolium exhibit features of multilayered strategies in their comparatively small leaf size and limited leaf area expansion per unit leaf biomass. Viburnum prunifolium, in particular, differed from the late-successional species in allocating more biomass to wood versus leaves in shady environments, following the pattern for trees. In addition, evidence of self-pruning of lower canopy leaves (in forest habitats) seems to suggest the limited shade adaptation of this species.

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