A GRADIENT IN UNDERSTORY SHRUB COMPOSITION IN SOUTHERN WISCONSIN

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- - - - - - - - - - - - - - - - ABSTRACT - - - - - - - - - - - - - - - - -

This paper describes development of measures for shrub species importance values and a shrub gradient in the southern Wisconsin hardwood forests. A distributed sample of forest communities was obtained for the entire upland compositional gradient, including data on trees, saplings, seedlings and shrubs. Summary measures were developed to express the cover dominance of each shrub species, based on the area of the canopy as well as the number of stems. This approach allows computation of an "importance value" for each species in each size class. In addition, the gradient analysis, using shrub importance values, allows quantitative expression of species responses to environmental conditions. Analysis shows a relationship of shrub species composition and abundance to overstory forest structure and composition as well as to some aspects of the environment. Study of the competition between shrubs and tree seedlings along the vegetational gradient shows shrub dominance over intolerant tree seedlings midway along the gradient; however, the shade tolerant tree seedlings appear to exert dominance over most shrubs in the mesic hardwood forest.

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INTRODUCTION

The basic concept of a vegetational continuum in the central hardwood forest of southern Wisconsin was recognized very early by Curtis and McIntosh (1951). Their study investigated the overstory species using a quantitative measure of species importance, the sum of relative density, relative frequency and relative dominance. The objective of the work reported in this paper was to examine the relationships of shrub vegetation to the southern Wisconsin forest continuum and determine whether a similar approach aids in interpreting the sociology and autecology of the shrub species involved.

The method of Curtis and McIntosh involved the ranking of tree species numerically on a scale from 1 to 10, representing the degree of adaptation (CAV) of the species to conditions in the theoretical climax forest. Multiplication of the importance values for each species in the stand, by CAV for each species, resulted in cross-products whose sum is the compositional index (CI), a numerical ranking for the stand along a gradient from pioneer to climax (Curtis 1959). The range of values for a number of stands along the resulting gradient was termed the vegetational continuum.

These methods of evaluating importance of species and the position of individual stands along a continuum worked well for trees which possess a single canopy and tend toward full canopy occupancy. However, shrub species possess various canopy positions and largely lack the tendency of full canopy occupancy. Thus, quantitative evaluation of a shrub gradient presents unique problems.

Habeck (1959) made one of the first attempts at a gradient analysis of shrub composition. Using the quarter method to sample stands in the central Wisconsin sand plain area, he sought to determine absolute shrub cover. He was forced to conclude, however, that "an efficient method of measuring absolute shrub cover has not yet been devised."

The composition of shrubs along a small portion of the southern Wisconsin oak-hickory gradient was studied by Goff (1964), in stands selected from Noe and Grady woods in the University of Wisconsin Arboretum. Goff developed a "NDH index", which used the sum of number, diameter and height of shrubs to express shrub importance, instead of the relative density, dominance and frequency used for trees. While this system was a positive step forward, data collection was difficult, particularly when large numbers of stands were studied.

A study of shrubs across the entire range of a compositional gradient was done in northern New Jersey by Davidson and Buell (1966). However, their study was limited to conventional estimates of shrub importance, and the assignment of "climax adaptation values" to shrub species. Using the "method of leading dominants" of Curtis and McIntosh (1951), climax adaptation values from 1 to 10 were assigned to 45 shrub taxa. While this work constituted an affirmation of the suitability of the gradient analysis to shrubs, interpretation of species inter-relationships within the shrub community remained largely untouched.

Our present lack of knowledge of shrub autecology for even common species in the central hardwoods region indicates the great inadequacies of study approaches used to this time. This paper reports on an attempt to provide more adequate means of measurement and treatment of shrub data in these forests. In particular, it focuses on 1) development of suitable measures of shrub species importance; 2) characteristics of a shrub gradient across the southern Wisconsin forest gradient; 3) the relationship of shrub species composition to overstory structure and composition;

4) the relationship of shrub composition to environmental factors in southern Wisconsin; and 5) the competitive relationships of shrubs with tree seedlings along the vegetational gradient of southern Wisconsin.

DESCRIPTION OF THE STUDY AREA

Southern Wisconsin is part of the ecotone between the prairie to the west and southwest and the deciduous forest to the east and northeast. Prior to settlement and conversion to agriculture, the vegetation consisted mainly of scattered prairies and broad-leaved deciduous forests, as well as the intermediate "oak opening" with shrubs. Bur oak (*Quercus macrocarpa* Michx.) and black oak (*Q. velutina* Lam.) forest are representative on sandy soils, while on other sites where more moisture is available, the forests are dominated by white oak (*Q. alba* L.), red oak (*Q. rubra* L.) and finally sugar maple (*Acer saccharum* Marsh.).

The soils of the study area have been developed largely in a thin cover of wind-blown loess. In the western part, the lower portion of the soil profile is largely derived from residual parent material made up of Cambrian sandstones and Lower Magnesian, Ordovician and Silurian limestones (Curtis and McIntosh 1951). In the remainder of the study area, particularly Dane County and to the southeast, the lower portion of the profile is developed in glacial till. The loess cap reaches 7 to 8 feet thick on protected slopes at the western edge of the study area, and becomes progressively thinner until it is almost nonexistent in the eastern side of the state. The forest soils of the area generally belong to the gray-brown podzolic great soil group (largely Alfisols).

The climate of this southern Wisconsin study area is intermediate between the humid northeastern forest region with snowy winters and reliable summer rains, and the more arid prairie region with relatively dry winters and periodic summer droughts. All stands studied were located in this "prairie-forest province".

METHODS

Stand Selection

To obtain a distributed sample of forest communities across the entire compositional gradient of the southern Wisconsin upland forest, the upland compositional index of Curtis (1959) was divided into ten equal units. Since the CI ranges from 300 to 3000, each segment encompassed 270 units. Three stands were selected for each of the ten segments of the compositional gradient, giving a total of 30 stands.

Criteria for accepting stands for each segment were: 1) each stand had to represent upland forest communities free from any accumulation of seasonal runoff waters; 2) each stand had to be at least 3 acres,

surrounded by 15 acres of forest; 3) all stands had to be free from any major disturbance such as cutting, grazing or fire for at least 25 years; and 4) the stands had to possess internal homogeneity of overstory, soil texture and depth to impermeable substrates. Stands meeting these qualifications were entered into a pool (stratified by decimal segments of CI) from which the actual study sites were selected at random. Approximately two acres of each stand were utilized, chosen on the basis of homogeneity of overstory structure and substrate environment.

Sampling of Vegetation

Five sampling points were chosen at random within the boundaries of the selected stands. These points were used as the center of three nested circular plots which in turn were divided into quadrants. Trees were sampled on five 1/10 acre quadrats, giving a total sampled area of 1/2 acre in each stand.

Saplings were sampled on five 1/40 acre plots, also divided by quadrants, giving a total sample of 1/8 acre. The following size classes of saplings were distinguished by means of a template: 1) .5 to 1.5 inches at DBH; 2) 1.5 to 2.5 inches at DBH; and 3) 2.5 to 3.5 inches at DBH. All stems of species capable of reaching the tree canopy, and exceeding 3.5 inches were considered trees.

Seedlings were sampled on five 1/100 acre plots, giving a total sample area of 1/20 acre. The following size classes were recognized for seedlings: 1) less than 0.25 inches at 6 inches in height; 2) 0.25 to 0.5 inches at 6 inches; and 3) 0.5 inches at 6 inches to 0.5 inches at DBH.

Sampling of shrubs also employed the quadrat method, using four 1 milacre quadrats at each of the five points. Total area sampled was 20 milacres, or 1/50 acre, per stand. The four milacre plots were located at the outer edge of the 1/40 acre circular plots, between the cardinal directions. Size classes of shrubs distinguished were: 1) stems less than 6 inches in height; 2) taller than 6 inches, but less than .25 at 6 inches in height; 3) .25 to .5 inches at 6 inches; 4) .5 inches at 6 inches in height to .5 inches at DBH; 5) .5 to 1.5 inches at DBH; and 6) 1.5 to 2.5 inches at DBH. Table 1 lists the shrub species found in the southern Wisconsin forest.

Soil Studies

In a limited area of uniform climate, such as southern Wisconsin, soil fertility and related soil moisture factors appear to have a greater influence on determining stand composition than other environmental influences. To facilitate evaluation of soil characteristics, a major soil pit was dug in a portion of each stand that was considered representative. The pit was dug to bedrock or at least into the C horizon if bedrock was deeper than 5 feet. Depth of each soil horizon, determination of texture

Table 1. Shrub species encountered in the southern Wisconsin hardwood forests.

Family Name	Scientific name	Common Name
Anacardiaceae	Rhus radicans L.	poison ivy
"	Rhus typhina L.	staghorn sumac
Betulaceae	C. americana Walt	american hazel
"	C. cornuta Marsh.	beaked hazel
Caprifoliceae	Lonicera prolifera (Kirchn.) Rehd.	grape honeysuckle
"	Lonicera tartarica L.	tartarian honeysuckle
"	Viburnum acerifolium L.	maple leaf viburnum
"	Viburnum lentago L.	nannyberry
"	Sambucus canadensis L.	common elderberry
Celastraceae	Celastrus scandens L.	climbing bittersweet
Cornaceae	Cornus racemosa Lam.	gray dogwood
"	Cornus rugosa Lam.	round-leaved dogwood
Hamamelidaceae	Hamamelis virginiana L.	common witch hazel
Menispermaceae	Menispermum canadense L.	canada moonseed
Moraceae	Morus rubra L.	red mulberry
Rhamnaceae	Ceanothus americanus L.	new jersey tea
"	Rhamnus catharticia L.	common buckthorn
Rosaceae	Crataegus spp. L.	hawthorn
"	Prunus virginiana L.	choke cherry
"	Rosa spp. L.	rose
"	Rubus spp. mostly allegheniensis Porter	blackberry
"	Rubus idaeus L. var. strigosus	red raspberry
"	Rubus occidentalis L.	black raspberry
Rutaceae	Xanthoxylum americanum Mill.	northern prickly ash
Saxifragaceae	Ribes missouriense Nutt.	missouri gooseberry
Staphyleaceae	Staphylea trifolia L.	bladdernut
Vitaceae	Parthenocissus quinquefolia L. var. vitica	woodbine
"	Vitis aestivalis Michx.	summer grape
"	Vitis riparia Michx.	river bank grape

by finger test (also determined later in the laboratory), and soil color were recorded. A sample of each horizon was collected and air dried in the laboratory for later analysis following the procedures of Fralish and Loucks (1975). Other data included relief, slope position and aspect, exposure, parent material, and type of bedrock when encountered.

Tree Data Analysis

For analysis, the tree species data including saplings and seedlings were compiled using the computer programs SIZSUM and STRATSUM to give absolute and relative density, frequency and dominance on a per acre basis, by species, and for 14 size classes of stems in each stand. By summing the appropriate size classes, total importance value was determined by species for various grouping (e.g. trees, saplings, etc.) as desired. By summing the products of species importance value and adaptation value, a stand CI value was generated.

Shrub Importance Value

One of the most difficult problems in the ecological study of shrubs arises in the selection of suitable summarization techniques for shrub data. A system based on relative importance such as the one used by Curtis and McIntosh (1951) for overstory species does not satisfactorily express the importance of shrub species individuals. Density has been used as an indication of shrub cover (Habeck 1959), but because of the great variation in stem size and growth form, both between species and within the same species, some other means of evaluating shrub importance is needed.

Shrub data were tabulated for further analysis by computing the number of stems per milacre (density) for each size class of each species, in each of the 30 stands. However, evaluating shrub importance should take the canopy into account, since it is the portion of a woody plant which has the greatest influence on its surroundings. Thus, additional summary measures were developed to express the cover dominance of each species, based on the area of the canopy as well as the number of stems.

The original concept of importance value (Curtis and McIntosh 1951) was an expression that combined the size or "dominance" of an individual stem with the density of stems, to give an expression that more fully reflected the total influence of the species. In the context of shrubs, stem diameters are not measured for any standard height, because some may be only an inch or two in height (in the less than 6-inch class), while others may be several inches at breast height. These large stems have enough basal swelling to result in an over-estimation of size if measured close to the ground.

An alternative to measuring actual stem diameter in order to estimate "dominance" is to estimate average canopy cover of the individuals in each shrub size class. This area of cover, expressed as milacres of

canopy cover per individual, is presented in table 2. The cover term is based on canopy diameter measurements of representative individuals in each of the height classes, converted to areas, and rounded off. Field checks of canopy area for the shrubs in each size class indicated that variation within and between species was about equal, and therefore negligible for the purposes of this study.

When the cover term is multiplied by the shrub density in each size class, the result is an "importance value" for that species in units that are roughly equivalent to milacres of canopy cover per milacre of ground surface area. The importance value for each species in a stand can be obtained by adding the importance values of each species in all size classes.

To provide a generalized picture of shrub importance across the southern Wisconsin forest gradient, the original sets of three stands in each of ten units along the compositional gradient were combined into five segments with six samples in each. Data on available water capacity of the soils and overstory basal area for these five basic segments support this scale of grouping as proposed to the ten groups. Each of these five segments of the gradient comprises a numerical range of 540 units along the CI scale from 300 to 3000. Following the initiative of Curtis (1959) these divisions have been designated as follows: 1) dry forest, 300 to 840; 2) dry-mesic forest, 841 to 1380; 3) mesic oak forest, 1381 to 1920; 4) mesic medium-shade forest, 1921 to 2460; and 5) mesic deep-shade forest, 2461 to 3000.

Table 2. Shrub diameters and canopy cover terms for each shrub size class.

Shrub size class	Shrub diameter classes	Canopy cover term*
1	less than 6" in height	.008
2	0 to .25" at 6" in height	.025
3	.25 to .5" at 6" in height	.075
4	.5" at 6" to .5" at DBH	.210
5	.5 to 1.5" at DBH	.600
6	1.5 to 2.5" at DBH	1.500

*Equivalent to average milacres of canopy cover per individual shrub at that size class.

RESULTS

The Gradient in Total Importance of Shrubs

The sum of importance values of all species present in a stand gives a total dominance, or importance value, for shrubs in that particular stand (Figure 1). Shrub importance values increase initially with increasing CI, reaching a maximum in the dry-mesic forest (CI Decimal Segments 2 to 4). From this position, shrub importance decreases steadily with increasing CI. Throughout the entire range, however, individual stand values are highly variable, particularly at the xeric end of the gradient (CI Decimal Segments 0 to 2). Stands on sand or gravel with southwestern exposure and little available water seem to have low total shrub importance values, while the stands with less exposure, especially those on heavier textured soils, tend to have much higher shrub importance values. The increase in total shrub importance in the mesic deep-shade forest is due to the proliferation of one shrub species, woodbine (*Parthenocissus quinquefolia* L. var. *vitica*) which reaches its peak importance in this forest group.

Curtis (1959) considers available water capacity (AWC) of the soil, and microclimate, including available light, to be the dominant elements determining forest composition. To evaluate the role of the available water capacity on shrub importance, it is necessary to eliminate the effect of available light. When available water capacity is plotted against total shrub importance, for several levels of overstory basal area, a shift in the relationship of shrubs to AWC is found at a point where overstory basal area reaches about 100 square feet per acre. Stands with overstory basal area less than 100 square feet per acre, and without high CI species, show an increase in shrub importance with a corresponding increase in AWC. Two notable exceptions to this general trend occur where one species is capable of reaching high importance under extremely dry conditions. In one stand the species is woodbine, and in the other, hazel (*Corylus americana* Walt. and *C. cornuta* Marsh.).

When overstory basal area is greater than 100 square feet per acre, the general trend is toward reduction in shrub importance as available water increases. The increased tree cover on high AWC soils is a possible reason for this reduction (Auclair and Cottam 1971).

The basic stand characteristic affecting a change in available light is canopy leaf density, a factor closely related to overstory basal area and composition. To determine the effect of light intensity on shrub importance, the overstory basal area for each stand was plotted against total shrub importance for each stand. It was apparent that only stands on soil with available water capacity in excess of 7 inches showed a correlation between overstory cover and shrub importance. Shrub development on soils with less than 7 inches of AWC appears to be severely limited.

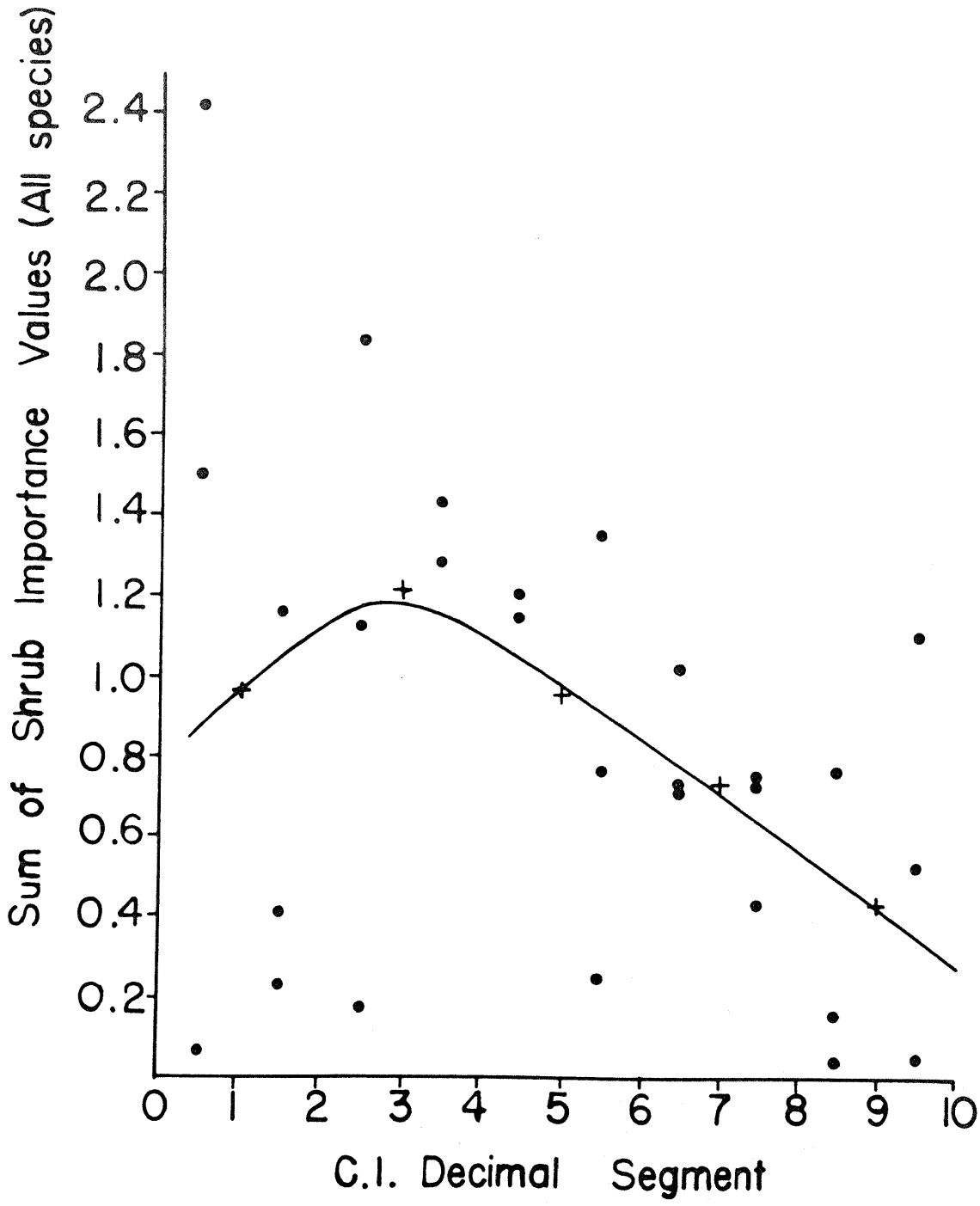

Figure 1. Stand shrub importance value totals across the compositional gradient: each locus represents the sum of total importance values for a stand; the average of six stands in each division of the CI range is shown by (+).

Figures 2A and 2B show the response of shrubs to changing overstory basal area for stands with available water in excess of 7 inches. Note that as overstory basal area increases from approximately 115 square feet per acre in the dry-mesic forest to a point where it reaches its peak in the mesic medium-shade forest at about 135 square feet per acre, there is a corresponding decrease in shrub importance (Figure 2A). A further reduction in light in the mesic deep-shade forest is due to change in overstory composition rather than increased basal area. Figure 2B, in fact, shows a slight decrease in overstory basal area under deep shade conditions, as well as a further decrease in shrub importance.

Investigation of the relationship between individual shrub species and environmental factors failed to show a correlation between available light or water, and the importance values of individual shrub species. The absence of a correlation suggests that while major environmental factors determine the conditions for shrub replacement, they do not determine which species will develop.

SHRUB AUTECOLOGY

In addition to understanding the gradient in total shrub cover, it is important to know the pattern of individual species distribution along this gradient. In order to examine these species relationships, therefore, absolute and normalized importance values of species were investigated, by forest segments. Modification of the absolute importance values by normalization provides for the equalization of peak importance for all species, and places them on an equivalent basis for comparison. In order to express graphically by normalization the importance values for each shrub, the forest group possessing the peak importance value for that shrub species is equated to 100. The four other importance values, one for each of the remaining forest groups, are proportionally determined.

Plotting these normalized importance values across the compositional gradient shows that most species have a minimum, optimum or mode, and maximum point of development along the gradient (Curtis and McIntosh, 1951). Two species which are exceptions are hazel and woodbine, because they reach an optimum at the ends of the gradient, xeric and mesic respectively. What results is a continuum consisting of overlapping

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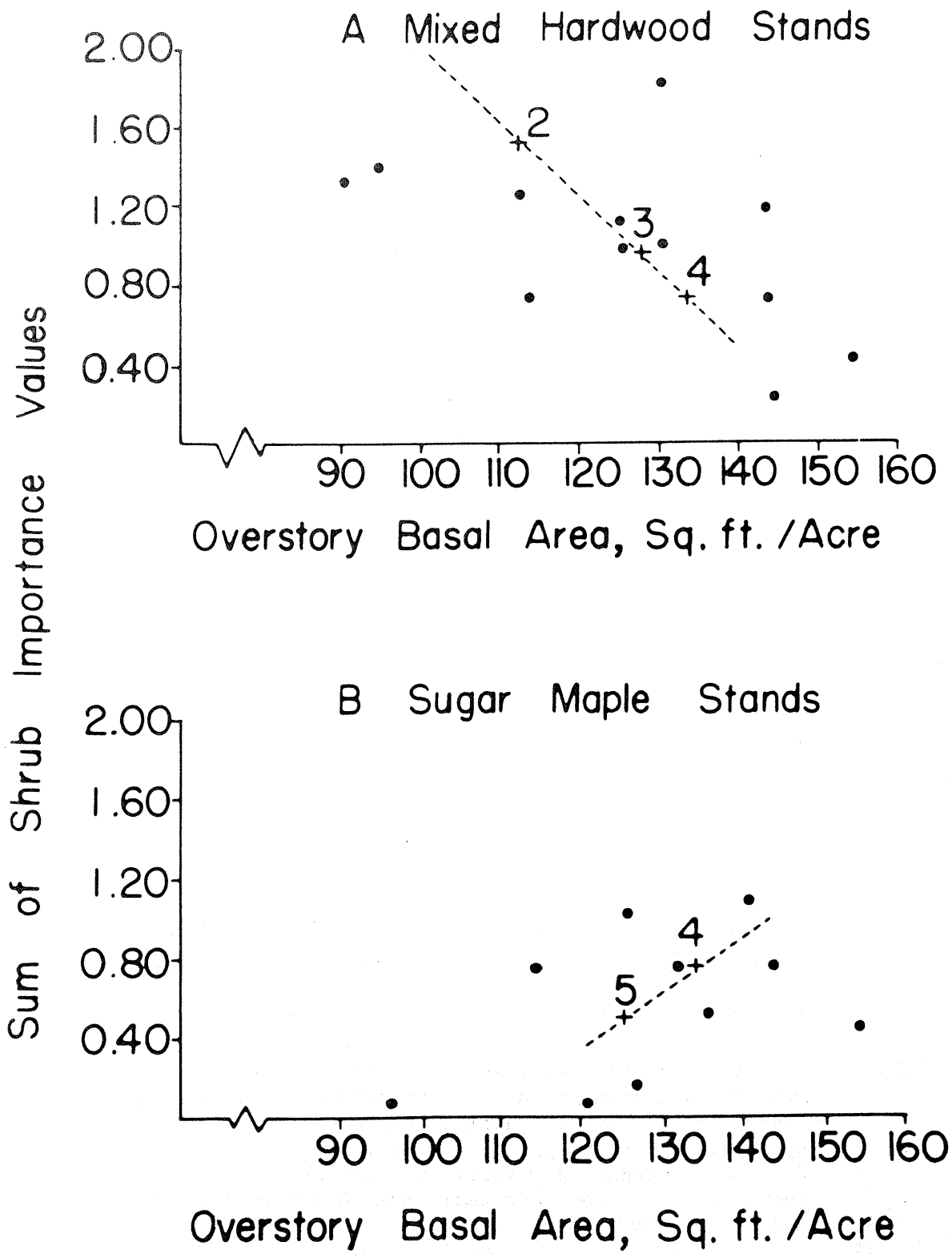
Figure 2. Response of shrubs to changing overstory basal area. Only those stands with available water capacity in excess of 7 inches are shown. Each locus represents the sum of total importance values for a stand; the average of the stands in each division of the CI range is shown by (+). The arabic numbers represent gradient groups as follows: Figure 2A, 2 - dry-mesic forest; 3 - mesic-oak forest; and 4 - mesic medium-shade forest. Figure 2B, 4 - mesic medium-shade forest; and 5 - mesic deep-shade forest.


A Mixed Hardwood Stands
2.00
1.60
1.20
0.80
0.40
2
3
4
90 100 110 120 130 140 150 160
Overstory Basal Area, Sq. ft. /Acre
Sum of Shrub Importance Values
B Sugar Maple Stands
2.00
1.60
1.20
0.80
0.40
4
5
90 100 110 120 130 140 150 160
Overstory Basal Area, Sq. ft. /Acre

ranges among the dominant species, with each species possessing its particular optimum point of development. A comparison of shrub importance in the 30 stands illustrates, for each species, the relative position of minimum, modal and maximum importance values along the gradient, and allows for a considerable improvement in evaluation of species autecology and habitat. The following sections summarize the autecology of these shrub species in different segments of the compositional gradient.

Species of the dry forest: Seven species reach their optimum importance in the dry forest (Figure 3A). Four of these, climbing bittersweet (Celastrus scandens L.), staghorn sumac (Rhus typhina L.), red mulberry (Morus rubra L.) and new jersey tea (Ceanothus americanus L.) are found only in this environment. Three other species, hazel, hawthorn (Crataegus spp. L.) and rose (Rosa spp. L.), range across most of the upland forest gradient. Hazel reaches maximum importance in the dry forest stands with an average cover of slightly more than 0.3 milacres of cover per milacre. Its importance decreases markedly in the intermediate dry-mesic forest, but it is prominent again in the mesic-oak group. From that point it decreases in importance and becomes practically

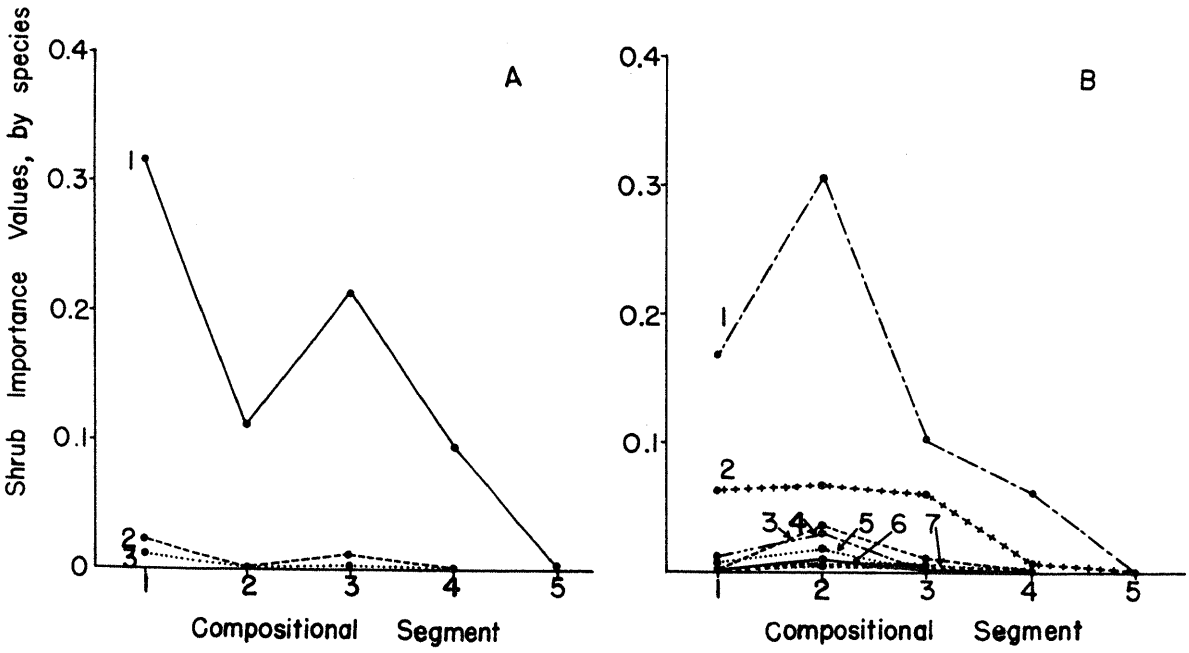


Figure 3. Importance of the major shrub species of the dry and dry-mesic forest segments across the compositional gradient: Figure 3A, 1 - Corylus americana and C. cornuta; 2 - Crataegus spp.; and 3 - Rosa spp. Figure 3B, 1 - Cornus racemosa; 2 - Rhus radicans; 3 - Viburnum acerifolium; 4 - Xanthoxylum americanum; 5 - Lonicera tartarica; 6 - Sambucus canadensis; and 7 - Cornus rugosa.

nonexistent under deep shade conditions. Hawthorn follows a similar pattern, although its average cover at optimum development in the dry forest is far less. Rose reaches its modal importance in the dry forest, but even here its importance is minimal.

Species of the dry-mesic forest: Nine species reach their optimum development in the dry-mesic forest. Of these, three reach significant importance in this group, and two of these possess a broad range of tolerance to environmental conditions (Figure 3B). Gray dogwood (Cornus racemosa Lam.) is the most important species in the dry-mesic forest, and is third in overall importance across the entire range of CI in southern Wisconsin.

Blackberry (Rubus spp., mostly R. allegheniensis Porter) and poison ivy (Rhus radicans L.) reach optimum development in the dry-mesic forest as well, rating second and third in overall importance in this environment (Figure 3B). The remaining 6 species of the dry-mesic forest are: red raspberry (Rubus idaeus L. var. strigosus), maple leaf viburnum (Viburnum acerifolium L.), northern prickly ash (Xanthoxylum americanum Mill.), tartarian honeysuckle (Lonicera tartarica L.), common elderberry (Sambucus canadensis L.) and round-leaved dogwood (Cornus rugosa Lam.).

Species of the mesic-oak forest: Choke cherry (Prunus virginiana L.) is the most important shrub in the mesic-oak forest, ranking with poison ivy in overall importance. The species maintains substantial importance across the entire range of the compositional gradient from the dry forest to the mesic deep-shade forest. The other seven species in this group reach importance values generally between .02 and .04 milacres per milacre (Figure 4A and 4B). The first five of these, although reaching maximum importance in the mesic-oak forest, have a range across most of the compositional gradient. They are: grape (Vitis spp. mostly V. riparia Michx. with small numbers of V. aestivalis Michx.), Missouri gooseberry (Ribes missouriense Nutt.), black raspberry (Rubus occidentatis L.), grape honeysuckle (Lonicera prolifera ((Kirchn.)) Redhd.) and witch hazel (Hamamelis virginiana L.). The remaining two species, moonseed (Menispermum canadense L.) and buckthorn (Rhamnus catharticia L.) are of minimal importance even in the mesic-oak forest, and appear only rarely in other parts of the gradient.

Species of the mesic medium-shade forest: Only two species of shrubs, bladdernut (Staphylea trifolia L.) and nannyberry (Viburnum lentago L.) reach their modal importance in the mesic medium-shade forest. Because these two species are very limited in importance, their distribution is not illustrated.

Species of the mesic deep-shade forest: One species, woodbine, reaches its optimum in this forest group. However, it exerts a profound influence on the mesic deep-shade forest, and indeed across the entire range of the southern Wisconsin compositional gradient. Its extremely high importance value is largely a reflection of sheer numbers of small

stems, rather than size, because woodbine rarely exceeds a 0.25 diameter at a 6 inch height. It reaches its peak importance under deep shade conditions with an average importance value of 0.45 milacres per milacre (Figure 4C).

Shrub Effects on Tree Seedlings

The previous sections have shown that the importance of shrubs is largely determined by the overstory forest structure and composition. The effect of the shrubs themselves on the structure and composition of the future overstory (tree seedlings), is largely unknown. Although it is difficult to distinguish between the effect of the overstory structure and composition and the effect of shrub structure and composition, the combined effect on the seedling population is quite pronounced.

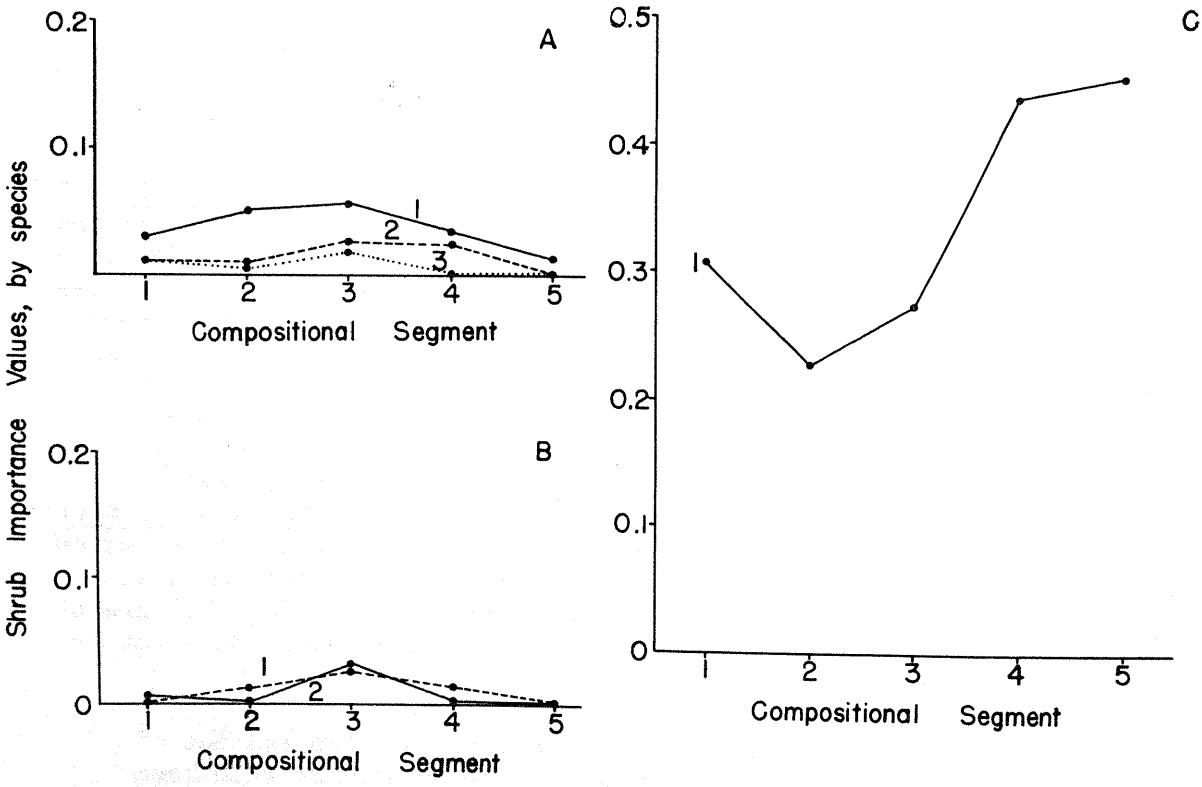


Figure 4. Importance values of major shrub species in the mesic-oak and mesic deep-shade forests of the compositional gradient: Figure 4A, 1 - Prunus virginiana; 2 - Vitis spp.; and 3 - Ribes missouriense. Figure 4B, 1 - Lonicera prolifera; and 2 - Hamamelis virginiana. Figure 4C, Importance Values of shrub species in the mesic deep-shade segment of the compositional gradient: 1 - woodbine.

Variations in density and composition across the gradient may be viewed as a result of several factors. Seedling species with high light requirements thrive in the dry forest where light intensities are high and shrub importance values are relatively low. As overstory basal area increases from 78 square feet per acre in the dry forest to 111 square feet per acre in the dry-mesic forest, and as shrub importance reaches its maximum, the seedling density is correspondingly reduced. This apparently is because of the reduction in light intensity, rainfall interception, and surface root competition (Anderson, Loucks, and Swain 1969).

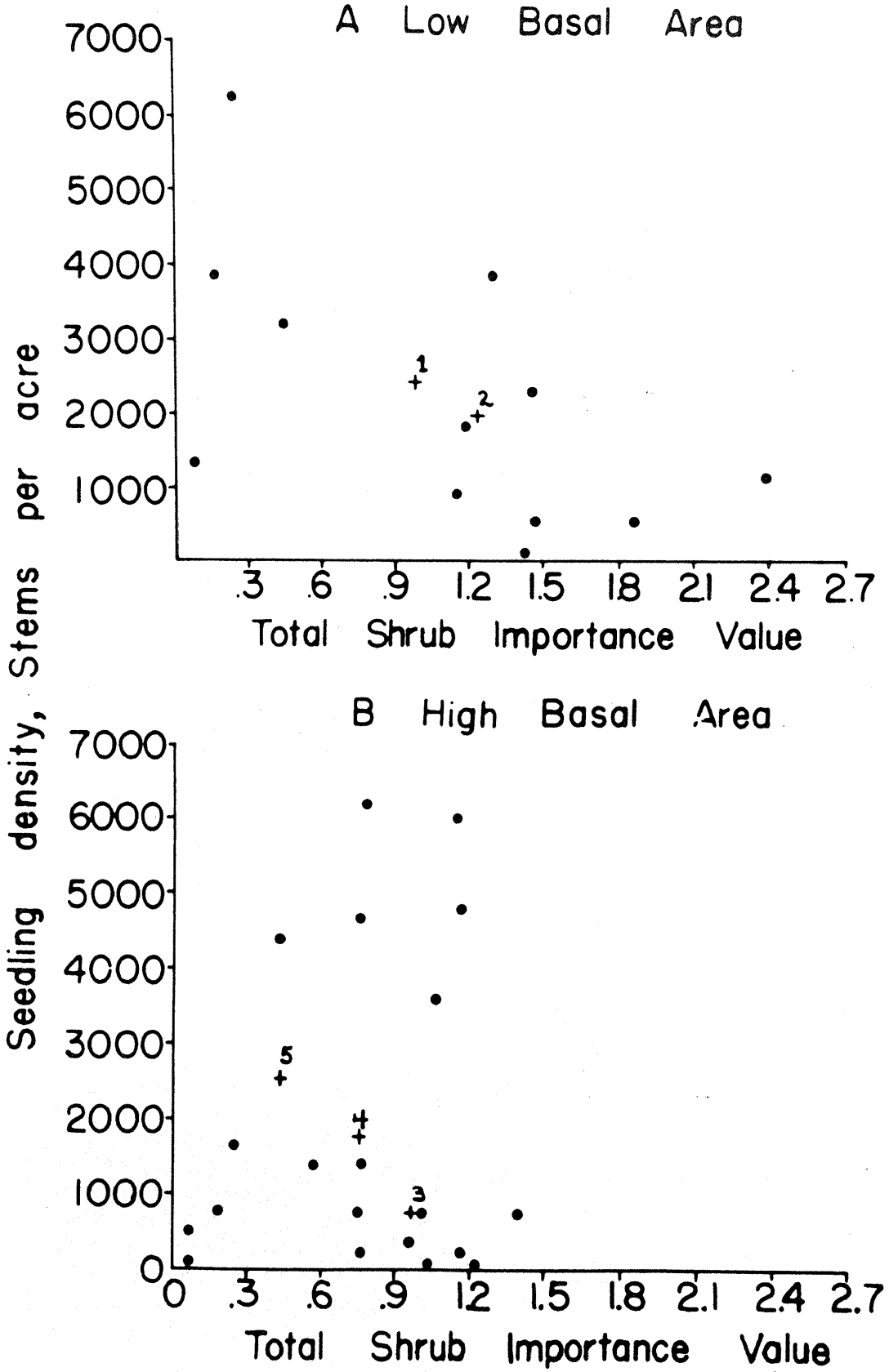
Seedling density in the mesic-oak forest reaches a minimum value, apparently due to further decreases in light from increased overstory basal area and relatively high shrub cover. On the other hand, the sharp rise in seedling density in the mesic medium-shade forest appears to be a result of the introduction of species which produce highly shade tolerant seedlings, especially sugar maple. It is possible that the lack of these overstory species, and the resultant lack of a seed source for them, caused some of the reduction in seedling density in the mesic-oak forest. In the mesic deep-shade forest, with its abundance of sugar maple in the overstory, the seedling density again increases.

Seedling density is plotted against total shrub importance values in figure 5. Under the xeric conditions of the dry and dry-mesic forests (Figure 5A), seedling density decreases as shrub importance increases, indicating a fairly strong negative relationship. On the other hand, shrub importance decreases from the dry-mesic forest (Figure 5A) to the mesic-oak forest (Figure 5B) along with seedling density. It is therefore apparent that some other factor, probably change in overstory structure and composition, is replacing shrub importance as the major influence on seedling density.

In the mesic medium-shade forest and the mesic deep-shade forest where shrub importance decreases, seedling densities increase (Figure 5B). This increase in seedlings is probably not a reflection of shrub influence because shrub cover here is minimal.

CONCLUSIONS

The lack of research on the shrub layer of the central hardwood forests, and the resultant lack of ecological knowledge concerning even the common species, is partly due to the wide variations in growth form in this group. The sampling and analysis method developed in this paper, which bases shrub importance on canopy cover as well as density, not only expresses shrub importance with a high level of ecological information, but is also easy to use in the field and in analysis. While there is no absolute by which to compare the method, the results appear to express quantitatively the ecological effects of shrub importance one perceives in the field.


A Low Basal Area
7000
6000
5000
4000
3000
2000
1000
1
2
.3 .6 .9 1.2 1.5 1.8 2.1 2.4 2.7
Total Shrub Importance Value
Seedling density, Stems per acre
B High Basal Area
7000
6000
5000
4000
3000
2000
1000
0
5
4
3
0 .3 .6 .9 1.2 1.5 1.8 2.1 2.4 2.7
Total Shrub Importance Value

Utilization of the continuum approach allows plotting of the minimum, modal and maximum development of each species across the broad range of environmental conditions of the southern Wisconsin hardwood forest. While the ranges of several shrub species overlap extensively, each reaches its peak development at a distinct point along the gradient. It is this point of peak development, as well as the amplitude of each species across the gradient, that leads to an expression of sociological interplay between the species.

In addition, the gradient analysis presented here provides a means of ascertaining much of the autecology of individual shrub species. The species' responses to environmental conditions illustrate the level and nature of its adaptation to these stresses and provides autecological information to interpret the role of each species in the community.

While use of the gradient approach as a means of investigating the sociology and autecology of constituent species is of appreciable importance, it is not without limitation. The southern Wisconsin forest continuum is not the only vegetational gradient in southern Wisconsin. The lowland forests (mostly river bottoms) were considered by Curtis (1959) and Swan (1961) as an extension of the upland forest gradient. Likewise, as moisture conditions are reduced, the gradient progresses from upland forest to a parallel sequence of prairie communities, including several shrub species. The relationships of shrub species in these communities are not yet fully understood.

The effect of forest overstory structure and composition on understory species has been recognized for many years. However, the influence of understory shrub species on overstory species, largely through their influence on seedling development, has been passed over. This study shows that the effect shrubs have on overstory species is seen most clearly in dry and dry-mesic forests. The increase in shade from the dry to dry-mesic forests, largely due to the increase in shrub importance, has the effect not only of reducing seedling density, but also of changing seedling composition. The degree of influence exerted on these xeric forests, and the speed at which the shrub layer may accelerate succession is beyond the scope of this study. However, the potential to measure such impacts has been established as a result of the techniques developed here.

Figure 5. The effect of total shrub importance on seedling density: Figure 5A, under low tree basal area; Figure 5B, under high tree basal area. Each locus represents the sum of total importance values for a stand; the average of six stands in each division of the CI range is shown by (+).

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ACKNOWLEDGMENTS

The authors are most grateful for financial support from the National Science Foundation (Grant GB-3548) and the capable editorial assistance of Alice D'Alessio.

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