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The paper was published in US Forest Service General Technical Report SRS-74, pp. 198-204.

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Ouachita and Ozark Mountains Symposium:
Ecosystem Management Research

Hot Springs, Arkansas
October 26–28, 1999

James M. Guldin, Technical Compiler

Bibliographic citation:

Guldin, James M., tech. comp. 2004. Ouachita and Ozark Mountains symposium: ecosystem management research. Gen. Tech. Rep. SRS–74. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 321 p.

Symposium objectives:

- to present an overview of ecosystem management research in the Ouachita and Ozark Mountains
- to present results from 5 years of postharvest measurements from the phase II stand-level studies including silviculture, understory vegetation, wildlife, soils and water quality; logging and economics; visual quality; and arthropods and microbial diversity
- to present results from 5 years of baseline data collection from the phase III landscape-scale studies including vegetation, wildlife, aquatic ecology, hydrology, and social sciences.
- to present an overview of other ecosystem-based projects in the Interior Highlands.

Symposium sponsors:

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ORDINATION OF WOODY VEGETATION IN A OUACHITA NATIONAL FOREST WATERSHED

Denise Marion and George Malanson[1]

Abstract—Species response to competition and other environmental gradients has important implications for forest ecosystem managers who desire to both maintain diversity and provide a sustained flow of forest goods and services. Woody species on a 140-acre watershed in the Ouachita National Forest are ordinated with detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA) to identify the important influences on species distribution at this scale. Species composition is found to respond primarily to a moisture gradient, and secondarily to competition with shortleaf pine (*Pinus echinata* Mill.). Centrifugal organization of species along gradients is suggested by the relative locations of species in the ordination diagrams.

INTRODUCTION

The objective of ecosystem management is to sustain the structure, function, and diversity of the ecosystem while still providing goods and services to the public. Meeting these goals requires a fuller understanding how environmental factors such as disturbance, soil moisture, and interspecific competition affect the distribution of plant species across the landscape. This study uses multivariate ordination to examine the influence of competition on the pattern of distribution of woody species. The resulting pattern is compared with the centrifugal model of plant community organization proposed by Keddy and MacLellan (1990) (fig. 1).

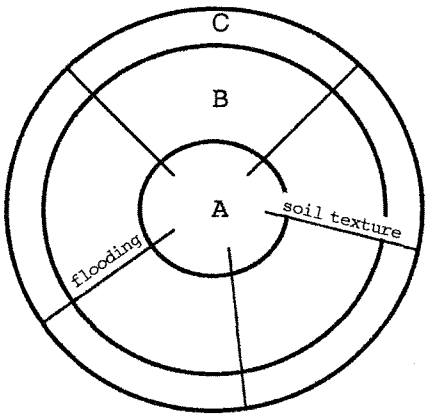

Figure 1—Centrifugal model of plant community organization. Environmental gradients represented by lines radiating out from core; e.g. flooding and soil texture, (A) mesic fertile sites, gap dynamics, one or two dominant species; (B) competitive hierarchy, shade tolerance increases toward core; (C) extreme site conditions, large-scale disturbance, greatest beta diversity (adapted from Keddy and MacLellan 1990).

Keddy and MacLellan's model describes the pattern of species distribution along biomass gradients[2] which radiate out from a central core which is characterized by fertile, mesic, and low disturbance environments. The underlying mechanism in this model is competition for light; consequently the largest species dominate the most productive habitat. Although all species could thrive in the core habitat, most species are prevented from doing so by virtue of being shaded by the large dominant. Species distribution within the core is primarily a result of gap dynamics. At their core ends the biomass gradients have similar species composition:

At the less fertile and/or high disturbance end of the gradients species compositions vary as the environmental stresses change. Less successful competitors for light in the optimal habitat achieve greater importance in more stressful environments where adaptations to specific conditions give them a competitive advantage. A greater beta diversity, or turnover of species, is thus predicted in the extreme environments represented at the periphery of the model.

DOMINANCE OF SHORTLEAF PINE

Shortleaf pine (*Pinus echinata* Mill.) density and volume is highest in the Ouachita Mountains, where it has regenerated naturally from seedlings on cut-over, burned, or abandoned land to dominate natural stands. It dominates the Ouachita pine-oak forest where the colder and drier conditions are not suitable for loblolly, and where the moisture, nutrient, and disturbance regimes discourage the growth of hardwood species (Guldin 1986).

Shortleaf pine is an example of a species which has its greatest abundance outside of its optimal habitat. It is most productive in well drained, sandy loam soils with a low pH and calcium content, on low gradient north aspects, at lower elevation and latitude. In these sites, however, it is outcompeted by faster growing pines or overtaken by longer-lived

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[2] Organization is based on biomass, with the greatest biomass in the optimal habitat. Because the model was originally developed for herbaceous vegetation, biomass was used as a surrogate measure of productivity. This interpretation of biomass does not transfer to woody species, however, where biomass is the accumulation of productivity of years past. Therefore, no conclusions regarding productivity can be inferred from this study.

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hardwoods. Its ecological importance increases in drier, less fertile upland sites where its large root system, lower demand for nutrients, and tolerance of fire and cold give it a competitive advantage. The success of the shortleaf pine in the Ouachitas can be attributed to the location of the uplands relative to the neighboring loblolly-oak forest to the south, and the oak-hickory forest to the north (Burns and Honkala 1990, Guldin 1986).

STUDY SITE

The study site is the north-facing, 56.7 ha (140 acres) watershed located in the shortleaf pine and oak forest of the Ouachita National Forest, northwest of Hot Springs, AR. The watershed was surveyed and sampled by foresters in 1994 as part of a fluvial geomorphology research project (Personal communication. Daniel A. Marion. 1996. Research Hydrologist, USDA Forest Service, Southern Research Station, 1000 Front St., Oxford, MS 38655). Average annual precipitation is 51 inches. Elevation ranges from 160 to 396 m (560 to 1,300 feet), with slope gradients up to 30 percent.

Three soil units occur in the watershed, classified according to the USDA Forest Service, Southern Region Soil Resource Guide and the Natural Resources Conservation Service (NRCS) (Luckow and Lee 1995). The majority of the watershed falls in one soil map unit which is identified as a Pirum-Clebit-Carnasaw complex. These are characteristic of moderately steep mountain side slopes. Soils at the upper elevations on the western divide are moderately deep clayey and loamy soils characteristic of mountain tops. The major component of this unit is a Carnasaw soil. The third soil unit occurs on the highest elevations in the watershed, which form the southeastern divide. It is a Clebit-Carnasaw-Pirum complex characteristic of upper side slopes and mountain tops. About 3 inches of very stony, fine sandy loam overlay a gravelly loam subsoil layer.

Three vegetation patches represent the pattern of disturbance in the watershed: approximately 75 acres are shortleaf pine-hardwood forest, 56 acres are plantation, and 8 acres are riparian. The forest to the west of the creek and in the southern end of the watershed is roughly 70 years old. It has been relatively undisturbed since logging in the early part of this century. Flooding in the riparian zone establishes a 1- to 5-year disturbance regime adjacent to the channel, and a 30- to 50-year regime near the break in the slope. The eastern side of the watershed is a plantation < 10 years free of disturbance. A seed-tree harvest was completed sometime between 1979 and 1982. When the seed trees were removed in 1986 natural reseeding was judged unsuccessful. In 1988 the plantation site was prepared for planting with herbicide suppression of hardwoods and mechanized exposure of bare soil. In 1989 the area was planted uniformly with 1 year-old shortleaf pine seedlings, grown from seeds obtained in the Forest Service's seed orchard in the Ouachita National Forest.

METHODS

All stems >1 m in height are identified, tallied, and measured. Stems < 4 inches in diameter are grouped into one size-class. Sample sites are located by stratified random sampling: 50 percent of the plots are located in the forested area; 30 percent of the plots are located in the clear-cut area; 20 percent of the plots are in the riparian zone. The riparian zone is defined as the land adjacent to the stream channel between the slope breaks; a distance of 5 to 30 feet on either side.

Environmental variables used in the analysis are elevation, percent slope, aspect, height above stream, Natural Resources Conservation Service (NRCS) soil factor T, litter cover, and shortleaf pine importance. Elevation, slope, height above stream, and aspect are taken from the U.S. Geological Survey 7.5 minute Nimrod SE topographic map, revised in 1985. An insolation value for aspect was read from a table calculated by Beers (1966). NRCS factor T is an estimate of the maximum average annual rate of soil erosion by wind or water that can occur without affecting crop productivity over a sustained period. Litter cover is the percentage of ground with no bare mineral exposed, estimated visually. Importance values are computed as each species' percent basal area plus its percent of individuals. In order to evaluate the effect of competition with shortleaf pine its importance value is removed from the dependent (species) variables and used as an environmental variable.

ORDINATION

Ordination is the ordering of species characteristics, such as abundance or productivity, along an environmental gradient, or a transect thought to represent a change in environmental conditions. The goal of ordination is to identify important environmental influences on plant community composition. An ordination diagram displays compositionally similar sites near each other; dissimilar sites are located farther apart. Multivariate ordination represents species or site data in two or more dimensions where axes represent complex gradients. The first axis explains the greatest proportion of variance in the data, the second axis explains the next greatest proportion, and so forth for additional axes.

Indirect ordination techniques, such as detrended correspondence analysis (DCA) order only species and sample plots without direct information regarding habitat conditions. Environmental variables are then correlated with the ordination in a second step. In direct ordination, such as canonical correspondence analysis (CCA), axes represent a linear combination of environmental variables that optimize the separation of the species response curves. In a CCA graph, environmental gradients are indicated by arrows pointing in the direction of the greatest rate of change. Arrows pointing in a similar direction are highly correlated; arrows pointing in opposite directions indicate a high negative correlation (ter Braak and Prentice 1988). The length of the arrow is proportional to the strength of the correlation with the ordination axes. The length is, therefore, an indicator of the strength of the relationship of the environmental variable to the pattern of community variation shown in the graph (ter Braak 1987).

In both DCA and CCA ordination graphs, points that represent sample sites are located at the center of gravity of the species that occur there. Species points at the edges of a DCA ordination are often rare species occupying extreme environmental conditions (ter Braak and Prentice 1988).

Data are ordinated with PC-ORD (McCune and Mefford 1995). DCA ordination is run with all species. CCA ordinations are run with all species, without shortleaf pine, and with shortleaf pine as an environmental (independent) variable. Shortleaf pine is removed from the species variables to allow evaluation of the effect of shortleaf pine competition as an environmental variable. Rare species are not downweighted. DCA and CCA ordination scores are correlated with environmental variables in PC-ORD with both Pearson's and Kendall's correlation coefficients.

RESULTS

Importance Values

Table 1 lists the woody species identified in the watershed. Shortleaf pine dominates the watershed as a whole at with an importance value of 48 percent. Only five sample plots in the watershed are dominated by species other than shortleaf pine: two are plantation sites where snowbell and red maple (*Acer rubrum* L.) reach high importance; the others are riparian sites where ironwood (*Ostrya virginiana* Scop.), and sometimes sweetgum (*Liquidambar styraciflua* L.) and/or blackgum (*Nyssa sylvatica* Marsh.) are more important than pine. Shortleaf pine dominance is greatest in the forest patch where its importance reaches 48 percent, and its closest competitor, white oak, achieves only 12 percent (fig. 2). In the plantation patch, the importance of shortleaf pine is 28 percent, whereas both snowbell and hickory (*Carya* spp.) achieve 15 percent importance. In the riparian patch

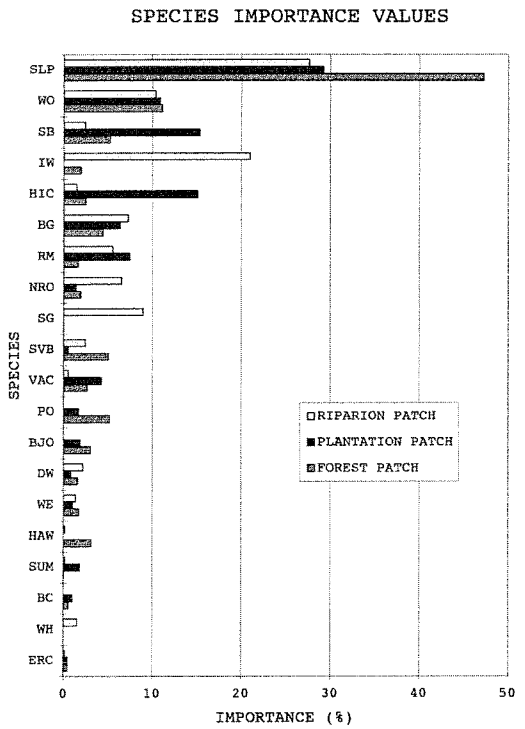

Figure 2—Species importance values by patch type. Species with importance values <1 percent are omitted.

Table 1—Species and code names in Toots Creek watershed survey

Code	Scientific name	Common name
BC	*Prunus serotina* Ehrh.	Black cherry
BG	*Nyssa sylvatica* Marsh	Blackgum
BH	*Viburnum rufidulum* Raf.	Rusty blackhaw
BJO	*Quercus marilandica* Muenchh.	Blackjack oak
BO	*Quercus velutina* Lam.	Black oak
ERC	*Juniperus virginiana* Alt	Eastern red cedar
DW	*Cornus florida* L.	Flowering dogwood
FM	*Acer barbatum* Michx.	Florida maple
HAW	*Crataegus* spp.	Hawthorn
HBM	*Carpinus caroliniana* Walt.	Hornbeam, blue beech
HIC	*Carya* spp.	Hickory
IW	*Ostrya virginiana* Scop.	Ironwood, eastern hophornbeam
NRO	*Quercus rubra* Michx. f.	Northern red oak
PL	*Prunus* spp.	Plum
PO	*Quercus stellata* Wangenh.	Post oak
RM	*Acer rubrum* L.	Red maple
SB	*Styrax grandifolius* Ait.	Bigleaf snowbell
SG	*Liquidambar styraciflua* L.	Sweetgum
SLP	*Pinus echinata* Mill.	Shortleaf pine
SUM	*Rhus* spp.	Sumac smooth, shining
SVB	*Amelanchier* spp.	Service berry
VAC	*Vaccinium* spp.	Farkleberry, huckleberry
WA	*Fraxinus americana* L.	White ash
WE	*Ulmus alata* Michx.	Winged elm
WH	*Hamamelis virginiana* L.	Witch-hazel
WIO	*Quercus phellos* L.	Willow oak
WO	*Quercus alba* L.	White oak
WTO	*Quercus nigra* L.	Water oak

shortleaf pine's importance value, 28 percent, is only slightly greater than that of ironwood at 22 percent. White oak also reaches 10 percent importance in the riparian patch.

CCA

Figure 3 shows the results of CCA ordination in three different sets: shortleaf pine as a species variable but not an environmental variable; shortleaf pine omitted from both the species variables and environmental variables; and shortleaf pine employed as an environmental variable rather than a species variable. Table 2 lists correlation coefficients between the axes and the environmental variables.

In the all-species ordination (fig. 3A) forest sites are in the center, and riparian and plantation sites are distributed on either end of the first axis. The first CCA axis is most strongly correlated with height above the stream (r = .786), which represents a moisture gradient. The second axis is correlated most strongly with soils (r = -.782). The pattern of distribution of the sites in ordination space is altered radically when pine is removed from the environmental variables (fig. 3B). All sites except three, four, and six are tightly clustered in the middle of axis two, stretched in a slightly negative trend along axis one. Species composition appears to be influenced primarily by moisture and soil gradients. Patch types remain in the same relative locations as in the all-species analysis.

When shortleaf pine is used in the analysis as an environmental variable (fig. 3C) the central cluster is scattered vertically by the second axis, which is now most strongly correlated with importance value of shortleaf pine (r = -.652). The spread of the plantation group is nearly parallel to the shortleaf pine vector, indicating a strong association with this environmental variable. The limited change in the riparian group indicates that shortleaf pine has less effect on species composition in the riparian sites than in the forest and plantation sites.

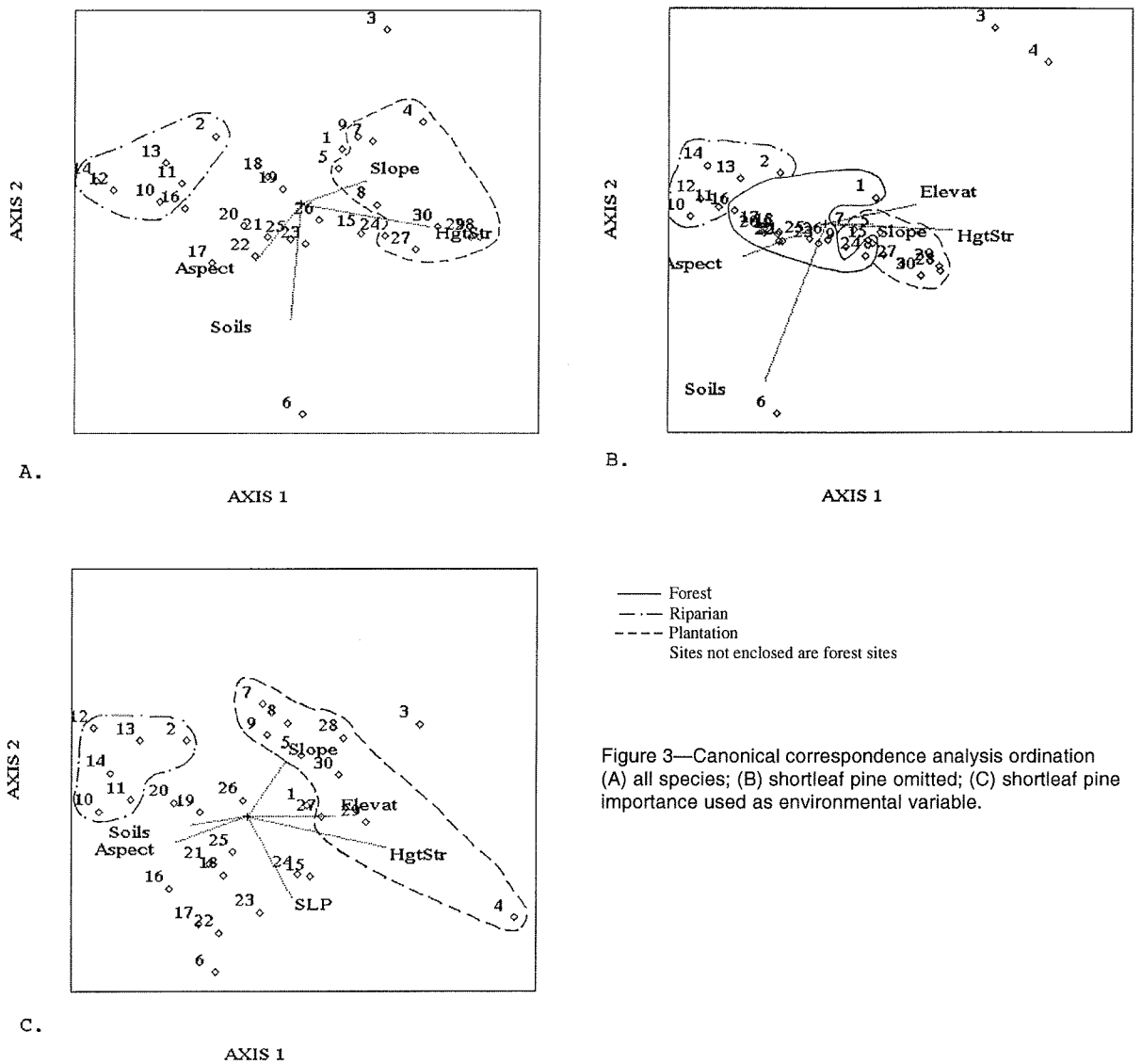

Figure 3—Canonical correspondence analysis ordination (A) all species; (B) shortleaf pine omitted; (C) shortleaf pine importance used as environmental variable.

Table 2—Correlation of environmental variables with CCA axes (Pearson's r)

	All species			No pine			Pine as environmental variable		
	Axis1	Axis2	Axis3	Axis1	Axis2	Axis3	Axis1	Axis2	Axis3
Height above stream	.786	-.344	.437	.777	-.166	.558	.809	-.402	.096
Soils	-.214	-.782	-.486	-.534	-.904	-.173	-.527	-.214	-.841
Aspect	-.461	-.551	-.055	-.627	-.411	.118	-.588	-.364	-.275
Slope	.556	.344	-.563	.476	-.047	-.656	.417	.538	-.334
Elevation	.410	.208	.367	.655	.321	.343	.646	.027	.388
Litter	-.205	-.235	.627	-.233	.034	.572	-.201	-.372	.268
SLP IV							.455	-.652	.299

CCA = canonical correspondence analysis.
SLP = Shortleaf pine.

Table 3—CCA percent of variance in species data explained by axes

	CCA percent of variance explained			
	Axis 1	Axis 2	Axis 3	Cumulative
All species	15.9	7.5	5.7	29.1
Without SLP	15.7	9.2	8.1	33.1
SLP as environmental variance	15.4	11.1	8.7	35.2

CCA = canonical correspondence analysis.
SLP = shortleaf pine.

The percentage of variance in the data explained by the first three axes increases from 29.1 percent for the all-species ordination to 35.2 percent when pine is an environmental variable (table 3). This increase is largely due to the contribution of the second axis, which is most closely correlated with shortleaf pine importance. The proportion of variance explained by soils is displaced to the third axis.

DCA

DCA ordination of sample sites using all species is shown in figure 4. Patch types are again separated along the first axis. (Note that the orientation of the first axis is reversed from the CCA graph.) Riparian plots are grouped at the right end of first axis and in the middle range of the second axis; plantation plots form a group in the lower left quadrant. Forest plots are clustered in the center of the ordination space, except for outlier sites 3, 17, and 6, indicating unusual species compositions for these 3 sites.

Table 4 lists the correlation coefficients for the environmental variables and the distribution of sites in the ordination space. Height above the stream correlates most closely with the first axis (r = -.649). Consequently, the riparian sites (sites 10-15) and the upper sites on southwest facing slopes (sites 3, 4) occupy opposite ends of axis one. The second axis for the all-species ordination is most strongly correlated with slope (r = -.486) and organic litter (r-.411).

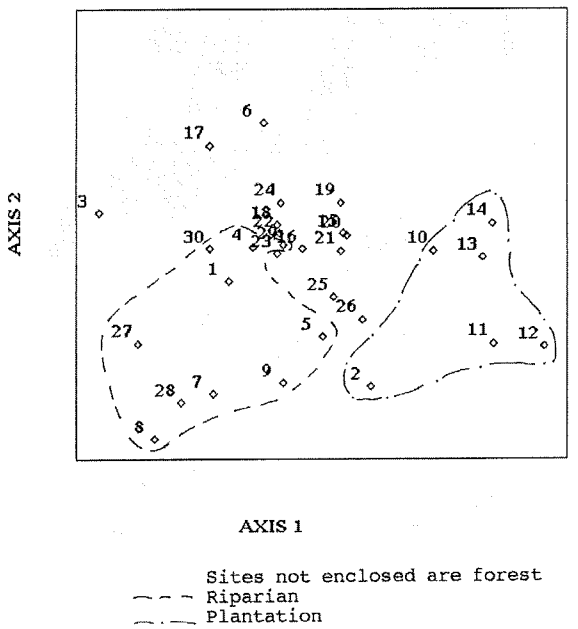

Figure 4—Detrended correspondence analysis ordination.

Table 4—Correlation of environmental variables with DCA axes (Pearson's r)

	Axis 1	Axis 2	Axis 3
Height above stream	-.649	.185	.058
Soils	.217	.084	-.251
Aspect	.356	.247	-.062
Slope	-.382	-.486	-.137
Elevation	-.353	.036	-.075
Litter	.094	.411	.009

DCA = detrended correspondence analysis.

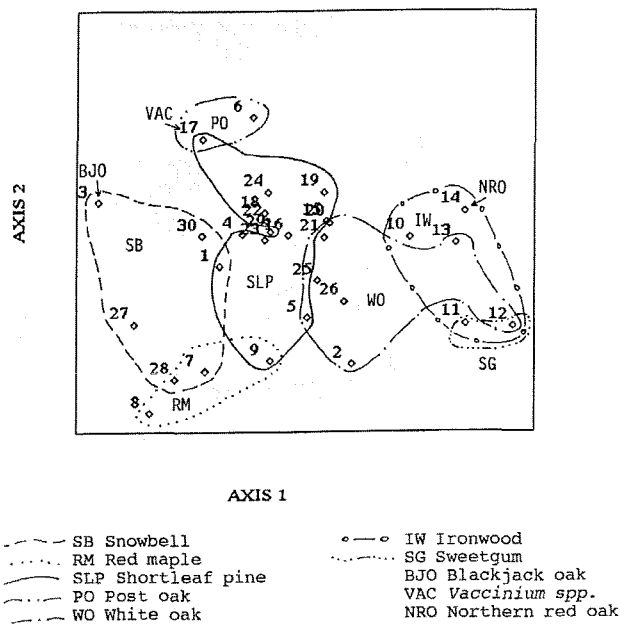

Figure 5—Detrended correspondence analysis ordination. Grouping of sites which exceed importance value of 15 percent for given species, or importance value of 50 percent for shortleaf pine.

Following the example of Ware and others (1992), sites with importance values ≥15 percent for given species are grouped in the ordination graph in figure 5. Since shortleaf pine exceeds 15 percent on all sites except riparian plot 12, sites with ≥ 50 percent pine are grouped. Five species other than shortleaf pine reach importance values ≥15 percent in two or more sites: Post oak (*Quercus Stellata* Wangenh.), snowbell (*Styrax grandifolius* Ait.), red maple, white oak (*Quercus alba* L.), and ironwood. There is little overlap of these groups. Only four sites have importance values ≥15 percent for other species when importance values for shortleaf pine are ≥ 50 percent: forest sites 17 and 1; and plantation sites 9 and 5. Only three of the sites with shortleaf pine importance value ≥ 50 percent are not forest; these are all plantation sites. The groups of secondary competitors are located at the periphery of the cluster of sites, with the shortleaf pine cluster in the center of the ordination space.

DISCUSSION AND CONCLUSION

The anomalous positions of site three in the DCA ordinations, and sites three, four, and six in the CCA ordinations deserve fuller discussion. Plots located at extreme positions in the ordination space frequently represent rare species occupying extreme sites (ter Braak 1987). Plot six is the only site located within the soil unit with the highest T factor. It has other unusual characteristics as well: it has the highest importance values for post oak (17 percent) and hickory (9 percent), and it is on a ridge top at 900 feet elevation. Only three sample plots are higher in elevation, and the two highest of these plots, three and four, are also outliers. Sites three and four are the two sites on the soil factor with the lowest T factor, and the only two on exposed southwest slopes. Plot three has an unusually high importance value (31 percent) for blackjack oak (*Q. marilandica* Muench.). Site four has an extremely high importance value for shortleaf pine (84 percent). CCA puts these unusual species compositions and unusual environmental conditions in extreme locations in ordination space.

Gradients

The most important gradient influencing species composition in this watershed is a moisture gradient, represented by height above the stream. As competition for light represented by shortleaf pine importance value is associated with the second CCA axis when it is used as an environmental variable, it is concluded that competition is the second greatest influence on the pattern of species distribution. Improved proportion of variance explained and improved correlation coefficients when pine is removed from the list of species variables or added to the environmental variables also support that conclusion.

The effect of competition on the pattern of species distribution is reflected in a comparison of the three CCA ordination diagrams (fig. 4). There is a marked separation of species response curves when a shortleaf pine importance gradient is introduced. The shift in site scores in the plantation patch (fig. 4C), where the planting of pines was fairly uniform is interesting. The orientation of the spread nearly parallel to the shortleaf pine importance vector may be explained by management practices, including uniform planting, that have been designed to foster the growth of shortleaf pine and suppress competition by other woody species. It indicates the relative success of early successional species. It must be noted, however, that the patch's elongation is largely due to the location of site 4, one of the sites with extreme environmental conditions. High shortleaf pine dominance at this site may be more directly the result of environmental stress that limits the success of other species rather than the effect of shading.

Centrifugal Organization

The pattern displayed in ordination space when species are grouped by importance values is consistent with centrifugal organization as proposed by Keddy and MacLellan (1990) (figs. 1 and 5). The dominant species, shortleaf pine, is in the center of the ordination space, while competitor species are grouped in specific locations around the periphery. In interpreting this distribution in can be inferred that the more peripheral sites represent sites with more extreme environmental conditions. The limited overlap among sites with ≥ 50 percent importance value of shortleaf pine and sites with ≥ 15 percent importance value of other species is evidence that shortleaf pine dominance inhibits the productivity of other species where competition with the dominant species is great. The clustering of the most successful species other than pine in specific locations around the periphery of the ordination space indicates that these species can achieve greater productivity in more extreme environmental conditions where adaptations to the specific conditions may give them a competitive edge.

Time

The Toots Creek ordination diagrams represent species distribution at one point in time—1996. The pattern is expected to change with time. The effects of disturbance or lack of it, human intervention, and time must be taken into account when interpreting the meaning of the pattern shown in these ordination diagrams.

Ordinations of this watershed in 30 years may show white oak displacing shortleaf pine from the center of ordination space. In forest ecology the dominant species in the optimal habitats are generally shade-tolerant. That is, they are the best competitors for other plant resources, soil moisture and nutrients, in low light conditions. In disturbance-free sites these species are expected to eventually overtop pioneer or intermediate sequential species. The central location of white oak in the ordination space suggests that white oak has this competitive strategy. When the shortleaf pine reaches the end of its relatively short life span, the white oak will be in a position in the shared optimal habitat to respond to increases in plant resources.

Keddy and MacLellan's centrifugal organization model assumes a natural species distribution in response to natural gradients. If management to maximize the productivity of the commercial species is successful, in 30 years one would expect an ordination of the plantation patch to show uniformity of composition, few species other than shortleaf pine, and little or no response to environmental gradients. This pattern represents the artificially induced species composition which is the objective of human intervention. As this pattern is not a result of naturally occurring variation, application of the centrifugal model is inappropriate.

Management Implications

One might feel justified in concluding that managed stands on all optimal sites do not reduce diversity, since beta diversity is greater in poorer site conditions. However, species richness is greatest ($p = .05$) in this watershed in the 80-year-old natural forest patch, currently occupying the optimal habitat. Furthermore, in these low stress environments, where all species could thrive were it not for competition, it is reasonable to conclude that periodic natural disturbance such as fire may result in the greatest species diversity. Forest ecosystem management that uses all optimal environments for plantations may then forfeit the greatest potential for increasing and sustaining biodiversity.

ACKNOWLEDGMENTS

Data for this study were collected by Gordon McWhirter, Hydrologic Technician; Clifford Harwell, Hydrologic Technician; and Dennis Carlson, Forester; put in usable form by Gail Henderson, Computer Specialist; and made available to me by Dan Marion, Research Hydrologist, USDA Forest Service, Southern Research Station, Oxford, MS. Hunter Speed, Silviculturalist, USDA Forest Service, Ouachita National Forest, Jessieville, AR, researched the management history of the Toots Creek watershed and Steve Brewer, Assistant Professor, Department of Biology, University of Mississippi, gave valuable criticism and insight.

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