CHANGES IN UPLAND OAK-HICKORY FORESTS OF CENTRAL MISSOURI: 1968-1982[1,2]

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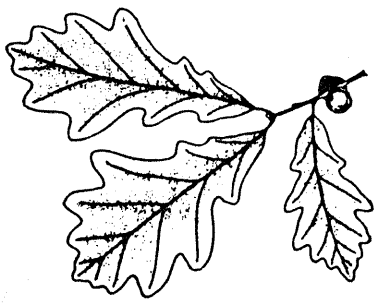

ABSTRACT.--Remeasurement of permanent plots in eighteen upland oak-hickory stands on the Ashland Wildlife Area in central Missouri indicated significant changes in species importance over a 14-year period (1968-1982). While tree density decreased in most stands--except in those which were relatively young(40-50 yr)--basal area of trees was maintained or increased. Density of the dominant tree species, white oak (Quercus alba L.), decreased while basal area remained constant through growth on surviving stems. Whereas white oak sapling density was reduced throughout these forests, sugar maple (Acer saccharum Marsh.) importance in both sapling and tree classes increased. Direct gradient analysis of changes in sugar maple and white oak sapling density indicated that density of small sugar maple saplings decreased in mesic stands and increased slightly in intermediate and xeric stands. The loss of small saplings in mesic stands was associated with large increases in density of larger saplings, indicating substantial growth of sugar maple saplings in mesic forests. White oak saplings were not found on mesic sites in 1968 and were numerous only on xeric sites. Between 1968 and 1982 white oak sapling density decreased dramatically in intermediate and xeric stands, resulting in near elimination of saplings of this important species except on the driest sites.

Forest succession in the Midwest has received some attention from plant ecologists, but the potential the region offers for study of vegetational dynamics in an environment characterized by steep gradients in climate, diverse microenvironments, and man's influence on the landscape has not been well developed. Some studies, most notably those summarized by Curtis (1959), have shown that species composition of northern forests of the region shift from xeric oak (Quercus) species to more mesic sugar maple (Acer saccharum Marsh.)-basswood (Tilia americana L.) forests if fire is excluded or drastically reduced in frequency. However, there are few data from other forests of the region.

Because of the relatively xeric climate, it was thought that the more drought-tolerant oaks would form relatively stable, self-perpetuating forests on the western edge of the eastern deciduous forest (Braun 1950, Kuchler 1964). However, several studies in the past two decades have indirectly suggested, through analysis of reproduction patterns, that oak species are regenerating poorly in many stands in this region and that sugar maple is increasing in importance (Wuenscher and Valiunas 1967, Rochow, 1972). Presettlement survey records indicate the presence of sugar maple in Missouri forests (Howell and Kucera 1956), but until recently it has been largely confined to relatively isolated mesic sites (Howell and Kucera 1956, Kucera and

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McDermott 1955). The pattern of decline in the oaks, and sugar maple success, is of particular interest and concern to foresters because oak forests are economically more important.

The only direct means of documenting succession is by repeated sampling of permanent plots. Because of the long-term nature of such research, only a small number of studies in the region have progressed to the point of repeated samples. Miceli et al. (1977) conducted a complete resampling of Brownfield Woods, a 24 ha tract of upland forest in east central Illinois. The fifty-year record indicated that oak species are declining in importance and sugar maple is becoming more important in this stand. Schlesinger (1976) also noted an increase in hard maples, [sugar maple, black maple (A. nigrum Michx)., A. barbatum Michx.] in upland forests of southern Illinois over a 35-year period.

The presence of permanent plots established in 1968 on the Ashland Wildlife Research Area (AWA) in central Missouri (Rochow 1972) allowed resampling and examination of short-term successional trends in the upland, white oak-dominated forests near the western margin of the eastern deciduous forest. In addition, environmental data relating to site microenvironment were available to conduct direct gradient analysis (Gauch 1982) of the vegetation patterns and successional trends in these forests.

METHODS

Plot centers, marked by iron reinforcing bars, were relocated in eighteen stands. These stands represented "upland oak" and "mesic slope" forest types defined by Rochow (1972). Original placement of the plots was designed to sample the range of variation present in topographical and stand age structure in these types. Stands selected for analysis ranged from those dominated by white oak mixed with other oak species [black (Quercus velutina Lam.), chinkapin (Q. muehlenbergii Engelm.), northern red (Q. rubra L.) and post (Q. stellata Wangenh.)] and hickories [shagbark (Carya ovata (Mill.) K. Koch.), mockernut (C. tomentosa (Poir.) Nutt.) and black (C. texana Buckl.)] to more mesic stands dominated by northern red oak and containing red and American elm (Ulmus rubra Muhl., U. americana L.), bitternut hickory (Carya cordiformis (Wangenh.) K. Koch) and black walnut (Juglans nigra L.). Mesic sugar maple-basswood stands (Kucera and McDermott 1956) that are occasionally encountered in the region were not sampled.

Vegetation sampling was conducted as in 1968 by establishing nested circular plots (0.08 and 0.04 ha) about the plot centers. All trees greater than 8.75 cm dbh were recorded by species in the larger plot. From these data, density and basal area per ha were calculated. Saplings were sampled on the smaller plot and recorded in one of four size classes (0-1.25 cm dbh; 1.25-3.75 cm dbh; 3.75-6.25 cm dbh; 6.25-8.75 cm dbh).

Environmental data taken in 1968 were used after checking for accuracy. These measurements included slope aspect, position and percent. These data were used in a direct gradient analysis of density for selected species versus an index of microenvironmental stress. Direct gradient analysis (Gauch 1982), which involves the plotting of stand vegetation parameters versus an environmental factor, permits simple visual interpretation of vegetation response to dominant influencing factors of the environment. The index of environmental stress used in this study was a modification of the Potential Annual Solar Radiation (PSR) index described by Frank and Lee (1966). Frank and Lee's index varies with slope and aspect, being more xeric on south-facing slopes and more mesic on north-facing slopes. However, a problem arises in that values of PSR are equivalent for east- and west-facing aspects (i. e., SE=SW, etc.), despite recognized microenvironmental differences between such sites. To more closely approximate actual stress on these sites Rochow (1972) developed an index, "Solar Radiation Stress" (SRS), that adjusted PSR by a factor proportional to the average July temperature corresponding to the time when the sun's rays were perpendicular to a particular aspect. As a result, southwest-facing aspects (which receive perpendicular radiation in the afternoon when summer air temperatures are much higher than in the morning) have higher values of SRS than southeast-facing aspects.

This index showed a reasonably good correlation with vegetation, but on slopes with equivalent slope percentage and aspect (and SRS), stands in lower slope positions tended to have more mesic character than those in upper positions. This effect of slope position is likely attributable to the following: 1) lower slopes tend to be shaded by opposite slopes during certain portions of the day, 2) drainage and overland water flow results in more abundant soil moisture on lower slopes and 3) protection from desiccating winds and cool air drainage tend to reduce stress on lower slopes. To account for these influences, a modified SRS (SRS^*) was calculated by multiplying SRS by a factor ranging from four for lower slope stands to nine for upper slope stands and ten for stands on ridgetops. This new index was then used in direct gradient analysis.

RESULTS AND DISCUSSION

Changes in stand tree density and basal area

Total tree density decreased significantly between 1968 and 1982 in the 18 study plots (Table 1). Data from two stands (14 and 24), which were among a group of four stands (33, 36 and the above) that were established after heavy logging 40-50 years ago, showed an increase in density over the period. These two stands had low tree density in 1968, containing few large trees and a majority of

TABLE 1.--Stand tree density and basal area data and results of paired t-tests for mean 1968-1982 changes in 18 resampled plots at the AWA. Stand numbers were originally assigned by Rochow (1972).

	Stand number																		STAND SUMMARY	
	6	7	5	10	37	18	22	8	12	9	33	36	14	24	60	23	19	13	Mean of 18 stands	Mean of 14 stands (less young stands)
Tree Density (#/ha)																				
All species																				
1968	728	654	469	543	444	519	420	469	457	543	704	1062	383	383	407	333	395	407	527.4** [1]	497.4**
1982	481	593	420	444	333	395	358	383	284	444	617	642	556	469	370	309	259	346	439.5	395.0
White oak																				
1968	407	519	74	531	370	481	383	272	333	296	185	395	198	346	37	39	196	148	288.9*	291.8**
1982	259	457	49	432	272	383	321	198	185	272	198	370	321	420	12	86	74	111	244.4	222.2
Sugar maple																				
1968	0	0	37	37	12	0	0	25	25	0	0	12	0	0	0	0	0	74	10.9*	15.0*
1982	0	25	86	25	12	0	12	37	25	0	0	37	0	0	62	12	0	111	25.4	29.1
Tree basal area (m^2/ha)																				
All species																				
1968	21.9	25.7	17.7	18.3	21.1	22.4	21.8	23.7	27.7	18.3	16.7	19.9	16.1	13.5	25.7	30.1	26.6	26.4	21.9	23.4
1982	22.8	30.0	18.5	17.6	21.5	22.3	25.5	23.1	22.4	17.6	18.5	15.0	21.3	17.3	26.5	23.5	23.1	21.0	21.6	22.6
White oak																				
1968	11.1	19.5	2.1	23.6	17.5	20.4	19.4	13.0	22.3	9.2	4.3	6.5	5.5	13.0	0.6	12.9	9.2	10.8	12.3	13.7
1982	12.4	22.0	2.4	24.6	16.6	22.2	25.1	13.0	17.6	10.4	7.0	8.1	8.9	16.5	0.3	8.6	8.6	10.7	13.1	14.2
Sugar maple																				
1968	0	0	1.1	0.5	0.4	0	0	0.9	0.3	0	0.1	0	0	0	0	0	0	1.0	0.2	0.3
1982	0	0.2	2.1	0.2	0.2	0	0.1	0.9	0.5	0	0.4	0	0	0	0.6	0	0	1.7	0.5	0.5

[1] *=difference between 1968 and 1982 significant at the 5 percent level.
**=difference between 1968 and 1982 significant at the 1 percent level.

TABLE 2.--Summary of sapling density changes between 1968 and 1982 and results of paired t-test for 18 resampled stands at the Ashland Wildlife Area. For total sapling density, data are also presented for 14 stands (young stands deleted).

Sapling density	Diameter class (dbh) 0-1.25 cm		1.25-3.75 cm		3.75-6.25 cm		6.25-8.75 cm		Sum of all classes	
(#/ha)	18 stands	14 stands	18 stands	14 stands	18 stands	14 stands	18 stands	14 stands	18 stands	14 stands
All species										
1968	1430	1718* [1]	1447*	1551*	415	262**	168	94	3460*	3625*
1982	1049	1121	1128	1242	467	491	193	148	2837	3002
White oak										
1968	52		109**		143*		77**		381**	
1982	23		20		44		57		144	
Sugar maple										
1968	489		647		64**		17		1217	
1982	454		632		249		62**		1397	

[1] *=difference between 1968 and 1982 significant at the 5 percent level.
**=difference between 1968 and 1982 significant at the 1 percent level.

small oak and scattered hickory stems. In other stands, which were 80-110 years old, tree density had declined dramatically. Changes in basal area in study plots were not as consistent, and there was no significant difference in plot basal area between sampling years. In most stands, decreasing density was offset by basal area growth of surviving stems, resulting in sustained basal area despite decreased density. In other stands (e.g., 7) plot basal area increased because of the growth of very large trees. Losses in basal area occurred in certain stands (23, 19, 13) because of the death of large northern red and black oak trees.

Changes in stand sapling density

There was a significant decline in total sapling density between 1968 and 1982 in the 18 plots (Table 2). Numerically, most of this decline occurred in saplings less than 3.75 cm in diameter. An exception to this trend was observed in three of four young stands which showed a dramatic increase in very small saplings. When data from these stands were eliminated from the analysis, sapling density decreased significantly in both of the smaller sapling classes. Density of saplings between 3.75 and 8.75 cm dbh increased between 1968 and 1982, although this change was not significant. This lack of significance was attributable again to the four young stands which had a tendency to have relatively few large saplings. When these stands were removed, significant increases in 3.75-6.25 cm-class saplings were observed and increases in the largest sapling class approached significance (P=0.06).

Changes in white oak and sugar maple

In 1968, white oak made up 55 percent of the total basal area and more than 60 percent of oak basal area present in the sampled stands; however, Rochow (1972) observed that at this same time sugar maple was the dominant understory species in upland oak forests of the AWA, and predicted that most stands were in transition toward a more mesic condition. Because of this distinct difference in overstory and understory composition, white oak and sugar maple were chosen for more thorough analysis of successional trends.

White oak tree density decreased in most sample plots, although increases in density were observed in data from young stands (14 and 24) (Table 1). Changes in white oak basal area varied among plots, but in general basal area was maintained through growth on fewer surviving stems. Total white oak sapling density showed a significant decrease during the 14-year period, with most of the decrease occurring in the intermediate and smaller sapling classes. Sample plots of five stands had no white oak saplings in 1968. Four of these (60, 23, 19 and 13) were mesic stands largely dominated by northern red oak, with a few canopy trees of white oak, bitternut hickory, black walnut and black maple. By 1982, half of all sample plots had no white oak saplings, a result attributable largely to mortality, but also to growth of some of the larger saplings into tree-sized individuals.

Density of sugar maple trees was low compared to that of white oak (Table 1). However, tree density of sugar maple increased significantly between 1968 and 1982. Because of the small size of the new trees in the 1982 sample, there was relatively little change in sugar maple basal area during the period.

In 1982, sugar maple saplings accounted for nearly half of all saplings in sampled stands (Table 2), emphasizing the dominance of this species in the understory of upland oak forests at the AWA. The total number of sugar maple saplings increased between 1968 and 1982, but this trend only approached statistical significance (P=0.06). The higher density of sugar maple saplings in 1982 was not a result of increases in small saplings (the density of which remained relatively constant), but was instead attributable to significant increases in the two larger sapling classes. There was a definite trend toward increased sapling size and greater representation of sugar maple in the tree stratum of upland forests of the AWA.

Direct gradient analysis of successional trends in white oak and sugar maple

Direct gradient analysis (Whittaker 1975, Gauch 1982) was performed by plotting the calculated index of stand microenvironmental stress SRS* versus selected density data for white oak and sugar maple tree and sapling classes. The moving average of plot density (using three stand density values) was utilized to minimize stand-to-stand variations that tend to mask environmental relations (Brown and Curtis, 1952; Curtis 1959). Additionally, to minimize the influences of differences in stand successional stage, which can also obscure environmental relationships (Peet and Loucks 1977), data of the four young stands were eliminated.

Total density of white oak trees tended to increase from mesic to xeric stands (Fig. 1), although at the xeric extreme density began to decline, probably in response to environmental conditions exceeding those optimal for white oak. On extremely mesic sites, such as those encountered on lower north- and east-facing slopes, stands were dominated by northern red oak instead of white oak. Over the 14-year period, white oak tree density declined across the environmental gradient, but mortality was noticeably lower on mesic sites.

There were no white oak saplings in mesic stands in 1968 or 1982 (Fig. 2). During this time period reductions in sapling density in stands in the middle of the gradient were very great, leading to complete elimination in many cases. Only on extremely xeric sites was white oak sapling density maintained at significant levels in 1982, but even in these stands density had decreased substantially over the 14-year period.

As sugar maple tree density was still very low

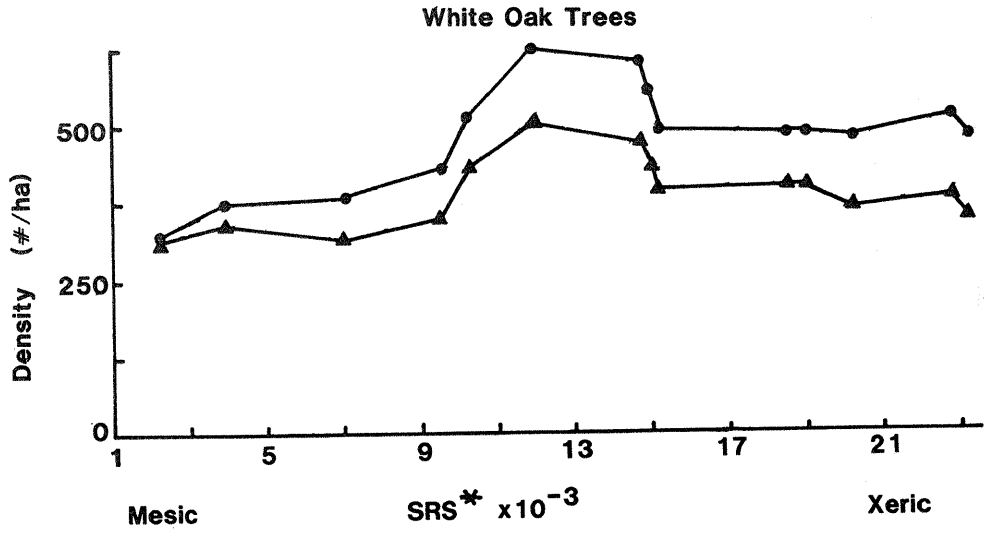

FIGURE 1.--Direct gradient analysis of modified solar radiation stress index (SRS*) and density of white oak trees. Four young stands were excluded from the analysis (see text). (● -1968; ▲ -1982).

in 1982 (Table 1), these data were not plotted. Sapling densities for sugar maple showed definite environmental relationships, the particular relationship varying with sapling size. In 1968, total plot sapling density (Fig. 3) was higher in more mesic stands. However, by 1982 the density of saplings had decreased in mesic stands, indicating a substantial loss of saplings over the 14-year period. In intermediate and xeric stands, some increases in sapling density occurred between 1968 and 1982. Density of smaller saplings exhibited trends similar to that of the entire sapling population (Fig. 4), with a decrease between 1968 and 1982 in the initially more abundant population in mesic stands and a slight increase in plot sapling density in intermediate and xeric stands.

Trends in density of large sapling classes were quite different from those of smaller classes (Fig. 5). In general, large saplings were found only in intermediate and mesic stands in 1968, but by 1982 they were present in sample plots of all stands. Significantly, the density of large saplings increased in mesic stands, whereas the density of smaller saplings had decreased. At least some increase in the density of large saplings occurred in all stands. These data strongly suggest that at least some of the reduction of small sapling densities in mesic stands was attributable to growth into larger classes. A slower, but noticeable increase in large saplings was also evident even on xeric sites. Ingrowth cannot account for all of the decline in sugar maple sapling density on mesic sites. Hence other factors such as sapling mortality and/or reduced seedling recruitment into the smallest sapling class may also have occurred.

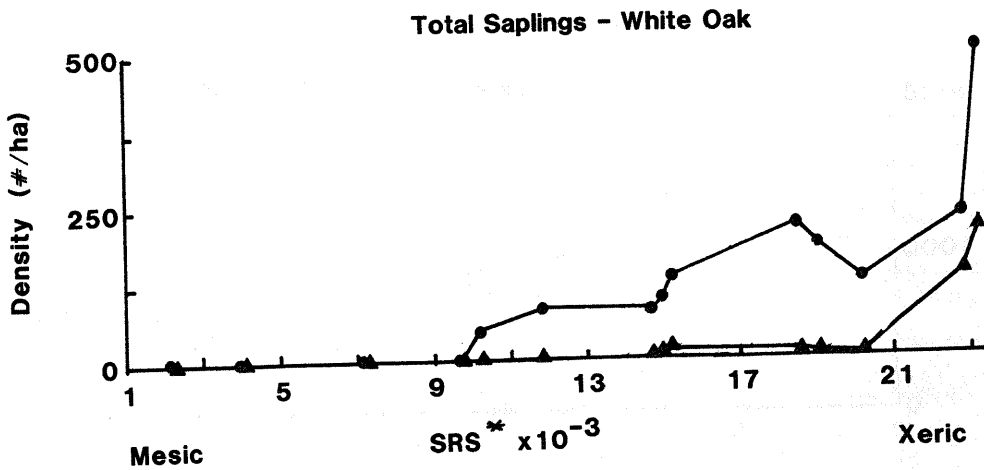

FIGURE 2.--Direct gradient analysis of modified solar radiation stress index (SRS*) and total density of white oak saplings. Four young stands were excluded from the analysis (see text). (● -1968; ▲ -1982).

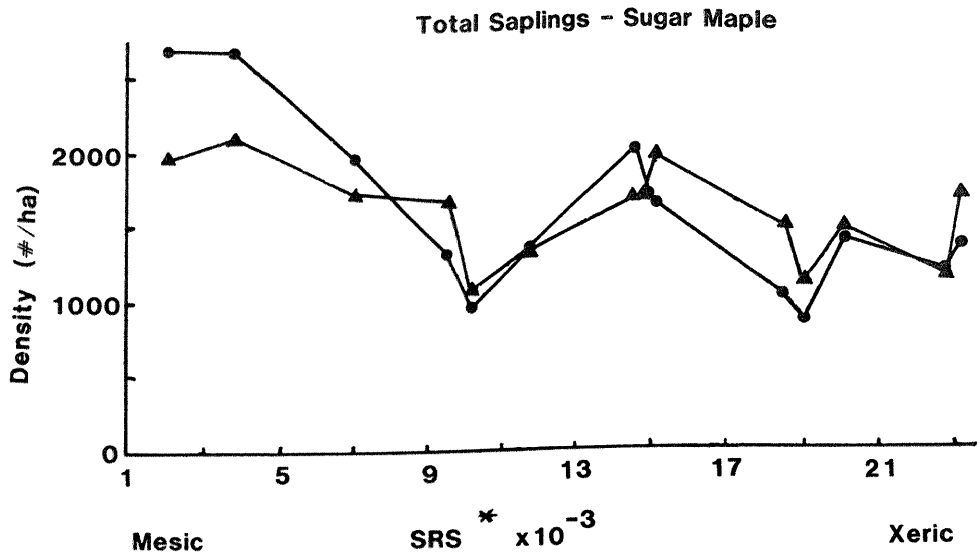

FIGURE 3.--Direct gradient analysis of modified solar radiation stress index (SRS*) and total density of sugar maple saplings. Four young stands were excluded from the analysis (see text). (● -1968; ▲-1982).

SUMMARY AND CONCLUSIONS

In 1968, sugar maple dominated the understory of much of the upland oak forest at the AWA, with little representation in tree-sized individuals. Most saplings were small, the greatest densities occurring in more mesic stands. Since 1968, sugar maple has continued to increase in overall density in the sapling and tree classes. Moreover, mesic stands with very dense understories of small sugar maple saplings in 1968 now show vigorous sapling growth; such growth from the small to the large sapling class has apparently contributed to the depletion of the population of smaller saplings. In more xeric stands, sugar maple was present in the understory in 1968, but to a lesser degree than in mesic stands. In the interval 1968-1982, an increase in sugar maple total sapling density has occurred. Given the generally recognized mesic preference of sugar maple, it is not clear why there was an increase in sapling density in xeric stands and a decrease in more mesic stands.

In contrast to sugar maple, white oak has shown a decrease in sapling and tree density since 1968. White oak saplings were not present in mesic stands in 1968 and had been essentially eliminated from all but the most xeric stands by 1982. This decrease in white oak sapling density has been accompanied by a corresponding increase in sugar maple saplings (especially large saplings).

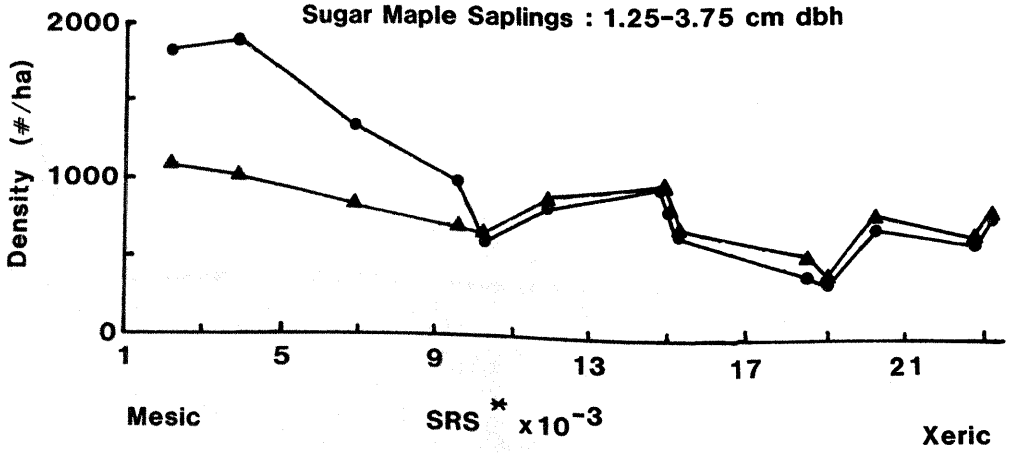

FIGURE 4.--Direct gradient analysis of modified solar radiation stress index (SRS*) and density of sugar maple saplings between 1.25 and 3.75 cm dbh. Four young stands were excluded from the analysis (see text). (● -1968; ▲-1982).

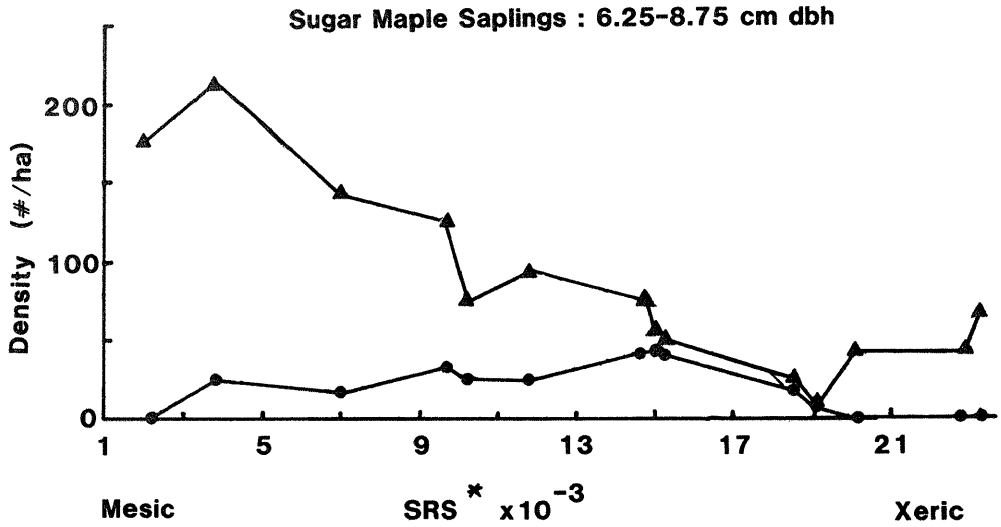

FIGURE 5.--Direct gradient analysis of modified solar radiation stress index (SRS*) and density of sugar maple saplings between 6.25 and 8.75 cm dbh. Four young stands were excluded from the analysis (see text). (● -1968; ▲ -1982).

Because of sustained basal area growth in white oak canopy trees, the decline in density of white oak at the AWA has not resulted in large changes in forest dominance by this species. However, with further passage of time, it is likely that sugar maple will be a more important component of the tree stratum. Hence, the results of this study support the prediction of Rochow (1972) that the forests of the AWA are moving toward a more mesic state. It is unclear whether sugar maple will ever dominate the canopy, as this species, when it no longer has the moderating influence of a canopy above, may not have the capacity to withstand the frequent severe droughts characteristic of the region (Hinckley et al. 1979). However, it is clear that composition of future forests of the region will be fundamentally different from those existing now.

LITERATURE CITED

BRAUN, L. E. 1950. Deciduous forests of eastern North America. Hafner Publ.Co., New York. 596 p.

BROWN, R. T., and J. T. CURTIS. 1952. The upland conifer-hardwood forests of northern Wisconsin. Ecol. Monogr. 22: 271-287.

CURTIS, J. T. 1959. The vegetation of Wisconsin. University of Wisconsin Press, Madison. 655 p.

FRANK, E. C., and R. LEE. 1966. Potential solar beam irradiation on slopes for 30 to 50 degrees latitude. USDA For. Serv. Res. Rep. RM-18.

GAUCH, H. G. 1982. Multivariate analysis in community ecology. Cambridge Univ. Press, New York. 298 p.

HINCKLEY, T. M., P. M. DOUGHERTY, J. P. LASSOIE, J. E. ROBERTS, and R. O. TESKEY. 1979. A severe drought: impact on tree growth, phenology, net photosynthetic rate and water relations. Amer. Midl. Nat. 102: 307-316.

HOWELL, D. L., and C. L. KUCERA. 1956. Composition of presettlement forests in three counties of Missouri. Bull. Torrey Bot. Club 83: 207-217.

KUCERA, C. L., and R. E. MCDERMOTT. 1955. Sugar maple-basswood studies in the forest-prairie transition of central Missouri. Amer. Midl. Nat. 54: 496-503.

KUCHLER, A. W. 1964. Potential natural vegetation of the counterminous United States. Amer. Geog. Soc. Spec. Publ. 36. 155 p.

MICELI, J. C., G. L. ROLFE, D. R. PELZ, and J. M. EDGINGTON. 1977. Brownfield Woods, Illinois: woody vegetation changes since 1960. Amer. Midl. Nat. 98: 469-476.

PEET, R. K., and O. L. LOUCKS. 1977. A gradient analysis of southern Wisconsin forests. Ecology 58: 485-499.

ROCHOW, J. J. 1972. A vegetational description of a mid-Missouri forest using gradient analysis techniques. Amer. Midl. Nat. 87: 377-396.

SCHLESINGER, R. C. 1976. Hard maples increasing in upland hardwood stand. P. 177-185 in Proc. First Central Hdwd. Conf., Southern Illinois University, Carbondale, IL.

WHITTAKER, R. H. 1975. Communities and ecosystems. Second edition. Macmillan Publ. Co., New York. 385 p.

WUENSCHER, J. E., AND A. J. VALIUNAS. 1967. Presettlement forest composition of the river hills region of Missouri. Amer. Midl. Nat. 78: 487-495.