SPECIES DIVERSITY AND SITE POSITION AT SAVAGE GULF, CUMBERLAND PLATEAU, TENNESSEE

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Abstract.--Vegetation plots placed in virgin and secondary stands of the Savage Gulf Natural Area, Grundy County, Tennessee, were used to compare the effects of aspect and slope position on diversity, evenness, redundancy and richness of overstory and sapling layers.

South-facing virgin forests were oak-dominated, chestnut oak on upper slopes, northern red at mid-slope and white oak with hemlock on lower slopes. North-facing upper slope virgin forests were chestnut oak-hemlock dominated, middle and lower slopes were dominated by the mixed mesophytic forest with hemlock. Secondary south-facing slopes were also oak dominated; opposing slopes were sugar-maple dominated.

Sapling diversities averaged higher than those of the overstory but trends were similar. Redundancy varied widely; the calculated values declined toward south-facing low slope positions. Evenness varied only slightly by aspect, position and logging.

Overstory species richness was similar among aspects and treatments. Logging decreased richness slightly on the north but increased it on the south-facing slopes. Richness in the narrow upper gorge (all slopes) was less than half of that on either aspect at the greater gorge widths.

Keywords: Forest vegetation, diversity, richness, evenness, redundancy.

INTRODUCTION

This paper reports a study of the logged and non-logged (virgin) forests of Savage Gulf, a National Natural Landmark and Tennessee State Natural Area in Grundy County, in Middle Tennessee. The study area is comprised of a gorge cut in the Cumberland Plateau. The study was supported by funds from the Tennessee Heritage Program; field work was conducted, summer, 1977.

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The broad study had the objectives of, (1) quantifying and describing the forest community types and relating the characteristics to environmental parameters, (2) comparing the vegetation of the virgin area with that of adjacent logged slopes, and (3) testing hypotheses and assumptions, some derived from the literature, regarding the interrelationships of site, stand age, and stand diversity, richness, evenness and redundancy. More specifically most of this paper deals with the level of diversity here compared to such values calculated from other similar and non-similar vegetation, the consequences of logging on diversity and other attributes, the relationships of overstory and understory diversity and other attributes, the contribution of evenness and redundancy to our understanding of forest structure, and the contribution of evenness to diversity.

STUDY AREA

Savage Gulf is an east-west extending gorge cut into the bedrocks of the Plateau; it appears on the Collins U.S.G.S. 7.5 minete quadrangle. Elevation of the rolling upland surface here is about 549 m (1800 feet), in the study area the gorge has cut down to about 335 m (1100 feet) above msl. In the upper end of the gorge the bottom lies at about 430 m (1400 feet). The gorge is approximately 1600 ha (4000 acres) in area and 4.9 km (3.07 mi) long.

Bedrock is virtually horizontal and consists of the Pennsylvanian Gizzard and Crab Orchard Mountain Groups above and the Mississippian Pennington Formation and Bangor Limestone below. The Pennsylvanian consists of fine-grained to sandy shales and sandstones and conglomerates. These occupy half to most of the upper slopes of the gorge and the hardest beds form cliffs which line the gorge walls. Mississippian aged rocks underlie some middle and all lower slopes. The Pennington consists of interbedded sandstones, shales, dolimites and limestone; the Bangor is a fine to medium-grained limestone. The hard bed above furnish colluvium which cover most of the slopes (Stearns, 1954; Wilson, et al., 1956; Luther, 1975).

Gulf soils are classified as Ultisols and Alfisols: Typic and Humic Hapludults and Typic Paleudults. Named series include the deep cobbly soils of gentle slopes, the Welchland and Sequatchie. On bouldery, steep slopes the deep Boulding and Allen series occur and on a few footslopes, when the gorge is widest, the shallower, limestone derived Talbot series occurs. Beneath the sandstone cliffs, boulder fields occur. These are characterized by rocks a few to 75 cm diameter (USDA, 1974). The stony nature of the soils is somewhat negated by gorge depth which protects some slopes from direct insolation and by moisture seepage through the permeable bedrocks and soils.

Wofford, et al. (1978) reported that in a floristic study of an approximately 2600 ha (10 sq mi) area including this gorge and adjacent upland 678 vascular plant taxa occurred. North-facing slopes were about 40 percent richer than opposing slopes. Several taxa on the state's list of endangered, threatened and special concern taxa were found.

Studies of the vegetation of the Plateau in Tennessee are several. Although Braun (1950) designated much of the Appalachain (including the Cumberland) Plateau as part of the Mixed Mesophytic Forest Region, she recognized that southward (Tennessee and Alabama) the mixed mesophytic forest community was confined mainly to ravines (gorges, coves, gulfs). Hinkle (1978) and Wade (1977) have described the wide variety of oak and pine dominated communities and Hinkle (1978) and Smith (1977) the swamp to mesic commuunities on the flat to rolling surface of the Plateau. Ravines, although

they occupy much less land surface area are vegetated by 12 (Hinkle, 1978) or 14 (Schmalzer, 1978) forest communities. They vary in type from flood plain swamps to mixed mesophytic forests and oak forests. Caplenor (1965) described the gorges at Fall Creek Falls State Park, where he found several primary vegetation types which were generally similar to the ones to be described at Savage Gulf. Quarterman et al. (1972) described the results of transects across the Savage Gulf gorge. They report a north facing mixed mesophytic forest and a south facing oak - hickory - tulip tree forest which represent the average of the community mosaic seen in this study.

METHODS

In the upper narrow end, in the middle virgin area, and in the lower part-virgin, part-logged areas of the Gulf a total of 166 plots of 0.05 ha size were placed at random in four slope positions on the north and south aspects. Plot diameters were adjusted for slope angle (Bryan, 1956). On each plot saplings 2.5-10 cm dbh were counted by taxon. Trees 10 cm and greater dbh were placed in 5 cm classes by taxon. Canopy cover was estimated in 10 percent units. Evidence of disturbance (boulder movement, tree blowdown, fire, and erosion) was noted.

Relative gorge position of each plot was calculated based on its location relative to the total length of the gorge. Plot aspect was transformed using the method of Beers, et al., (1966) (southwest is 0, northeast is 2). Potential insolation from slope angle and actual aspect was recorded from the tables in Frank and Lee (1966). Relative basal area (RBA) and relative density (RD) were calculated for each overstory taxon by plot. Relative density of sapling taxa was also calculated. Importance (IV, 200) was calculated for each overstory species as the sum of RBA + RD.

Statistical and classification analysis was conducted using the computer facilities of the University of Tennessee Computing Center.

The Shannon-Wiener value of diversity (H') was developed using the program of Zar (1968). Species richness (S) or the number of species/unit area was determined and evenness (J') was calculated from the formula J'=H'/H' max where H' max is the maximum diversity possible when all species present contain an equal number of individuals. Redundancy or unevenness was calculated from the formula:

$$R = \frac{H'max - H'}{H'max - H'min}$$

Here H'min is the minimum diversity possible for the particular sample.

Species diversity was computed for both overstory (>10cm dbh) and sapling 2.5-10cm dbh) layers by slope position within aspect (north, south-facing slope) and forest condition (virgin, secondary). Diversity values were also calculated for the upper gorge area. Tree densities from seven sample plots (7/20 hectare) within each slope position were pooled to form each sample for subsequent calculations. All diversity values are based on a similar sampling area, advocated by Whittaker (1972) as the best measure of diversity within the community.

Pearson correlation coefficients were calculated to determine associations between richness, evenness, and diversity (H') as well as environmental factors (slope position, aspect), secondary vs. virgin forests.

RESULTS AND DISCUSSION

Communities

Using 30 tree taxa, 166 plots were classified using the method of Orloci (1967). At the 42 percent level of dispersion eight community types were defined for the central virgin area of the gorge and the upper narrow portion of Savage Gulf (the latter may have had a few selected trees removed in the past). The south-facing slope of the central area is occupied by white oak-hemlock, mockernut hickory-northern red oak and chestnut oak communities. The north-facing slope is dominated chiefly by the basswood-tulip poplar-sugar maple type; tulip poplar-hemlock occurs at lower slope positions. A beech-shagbark hickory type occurs on lower south-facing slope ridge positions and lower north-facing slope flats. The narrow portion of the gorge contains hemlock on lower slope positions and hemlock-chestnut oak on middle to upper slope positions. These communities extend westward into the central and lower portions of the gorge. The hemlock type is best developed along Savage Creek; the hemlock-chestnut oak type occurs on upper slope positions directly at the foot of the sandstone cliffs.

Mean overstory density ranges from 378 stems/hectare in the beech-shagbark hickory type to 484 stems/hectare in the tulip poplar-hemlock type. Mean basal area ranges from 39.4m^2/hectare in the hemlock-chestnut oak type to 51.4m^2/hectare in the basswood-tulip poplar-sugar maple type. Mean sapling density ranges from 706 stems/hectare in the basswood-tulip poplar-sugar maple type to 1400 stems/hectare in the mockernut hickory-northern red oak type.

Using the same level of dispersion, six community types have been defined for the selectively logged area. Communities of the south-facing slope are relatively distinct. White oak-tulip poplar occupies lower slope positions; white ash-northern red oak occupies middle slope positions and a mixed oak-hickory community occurs primarily on upper slopes. Community types of the north-facing slope are less distinct. The entire slope is dominated by sugar maple; upper slope sites are almost exclusively sugar maple. Draw positions are dominated by sugar maple and basswood; ridge positions contain a more uniform mixture of mesophytic taxa. Mean overstory density ranges from 295 to 440 stems/hectare and mean sapling density varies from 880 to 1757 stems/hectare. Mean basal area ranges from 17.9 to 25.4 m^2/hectare.

Full discussion of the relation of these forest communities to others on the Plateau may be found in Sherman (1978).

Species Richness and Diversity

Species diversity, evenness, redundancy and species richness of the Savage Gulf vegetation are shown in Table 1. Sapling diversity and richness are highest in the virgin area at each slope position. Sapling evenness varies by slope position, but the virgin arec has an overall higher evenness value. Trends in sapling diversity, evenness and redundancy are shown in Figure 1. Upper north-facing slopes and lower south-facing slopes support highest sapling diversities. Evenness and redundancy are inversely related. The lower diversity of the secondary area is due in part to the ability of several species, particularly sugar maple, to dominate the subsapling and sapling layers by the abundant production of seedlings and stump and root sprouts (Eyre and Zillgitt,

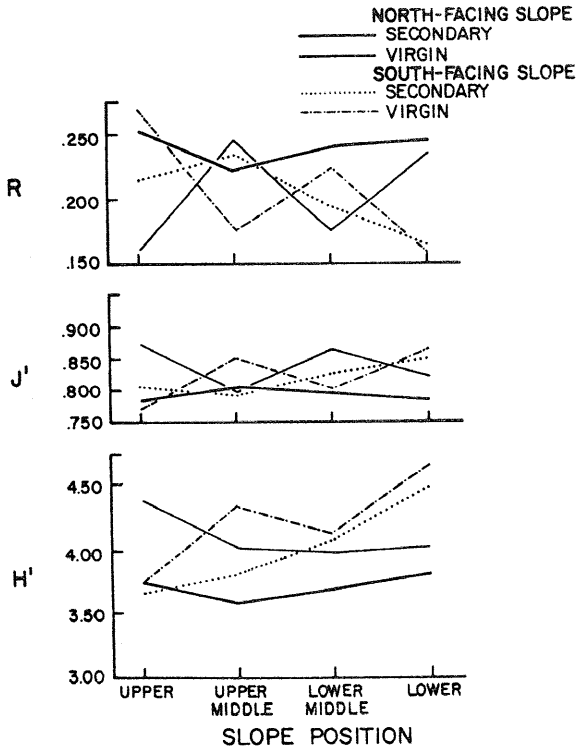

Figure 1.--Species diversity (H'), evenness (J'), and redundancy (R) of forest sapling species by slope position, aspect and forest condition.

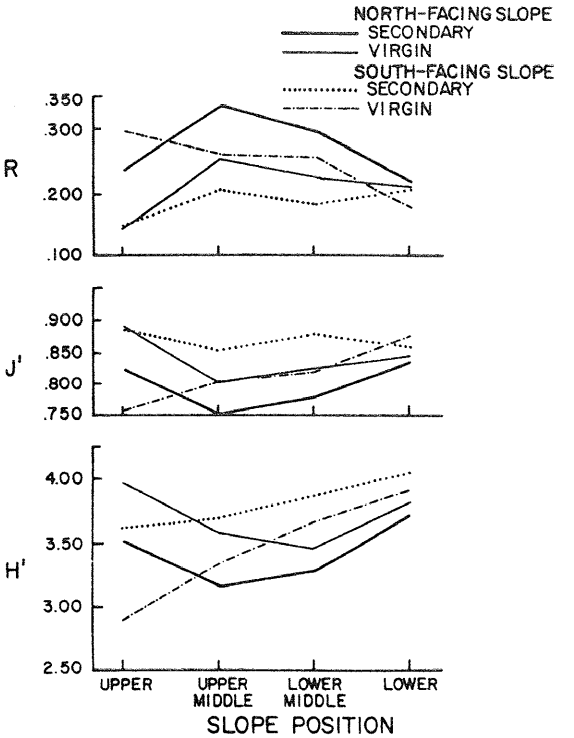

Figure 2.--Species diversity (H'), evenness (J'), and redundancy (R) of forest overstory species by slope position, aspect and forest condition.

Table 1.-- Vegetation diversity (H'), evenness (J'), species richness (S), and redundancy (R) for overstory (O) and sapling (U) layers by aspect, slope position and forest condition (virgin, secondary).

Area	Variable							
	UH'	OH'	UR	OR	UJ'	OJ'	US	OS
North-facing slope								
Upper slope virgin	4.40	3.96	.16	.14	.87	.89	33	22
Upper slope secondary	3.73	3.51	.25	.24	.78	.83	27	19
Upper middle slope virgin	4.04	3.58	.25	.26	.80	.80	33	22
Upper middle slope secondary	3.60	3.16	.22	.33	.81	.76	22	18
Lower middle slope virgin	4.01	3.45	.18	.27	.86	.83	25	18
Lower middle slope secondary	3.70	3.29	.24	.30	.80	.77	25	19
Lower slope virgin	4.04	3.83	.24	.21	.82	.85	30	23
Lower slope secondary	3.83	3.71	.24	.22	.79	.83	29	22
South-facing slope								
Upper slope virgin	3.75	2.89	.27	.29	.77	.76	29	14
Upper slope secondary	3.66	3.61	.22	.15	.81	.88	23	17
Upper middle slope virgin	4.34	3.35	.17	.26	.85	.80	34	18
Upper middle slope secondary	3.81	3.70	.24	.21	.79	.86	28	20
Lower middle slope virgin	4.14	3.67	.22	.25	.81	.82	35	22
Lower middle slope secondary	4.09	3.86	.20	.18	.83	.88	31	21
Lower slope virgin	4.67	3.90	.16	.17	.87	.88	42	22
Lower slope secondary	4.50	4.04	.16	.20	.86	.86	38	26
North-facing slope virgin	4.48	4.03	.22	.21	.80	.81	48	32
North-facing slope secondary	4.01	3.75	.24	.26	.77	.77	38	30
South-facing slope virgin	4.76	4.07	.17	.19	.84	.83	51	30
South-facing slope secondary	4.49	4.43	.18	.14	.82	.87	44	34
Upper gorge	3.32	3.10	.21	.21	.81	.84	17	13

1953). Loucks (1970) attributed the low diversity of northern hardwoods forests to the domination of seedling layers by sugar maple.

Trends in overstory diversity, evenness, redundancy and richness are shown in Table 1 and Figure 2. Diversity of the north-facing slope forest is higher in the virgin

Table 2.-- Species diversity (H') of selected community types.

Species Diversity (H')	Community Type	Reference
2.28	Mixed hardwoods-swamps	Monk (1967)
2.56	Climax southern mixed hardwoods	Monk (1967)
3.40	Deciduous mixed mesophytic	Monk (1967)
3.14	Chestnut-sugar maple-tulip	Monk (1967)
2.79	Sugar maple-basswood-buckeye	Monk (1967)
2.77	Beech-white oak	Monk (1967)
2.72	Hemlock-mixed mesophytic	Monk (1967)
2.23	Oak-chestnut	Monk (1967)
2.02	Beech ravines	Monk (1967)
2.66	Hemlock (Joyce Kilmer area)	Lorimer (1976)
3.08	Lower cove hardwoods	Lorimer (1976)
3.54	Upper cove hardwoods	Lorimer (1976)
3.12	Oak slope forest	Lorimer (1976)
.50 - 2.50	N Wisconsin forest	Auclair and Goff (1971)
2.20 - 3.40	Boreal forest transition	Shafi and Yarranton (1971)
2.39 - 2.59	Oak-hickory	Monk, Child and Nicholson (1969)

area; evenness and species richness are also slightly higher. Diversity on the south-facing slope is lower in the virgin area at each slope position; evenness and species richness are lower at three of four slope positions. The response of two species, sugar maple and chestnut oak, to logging contribute significantly to the overstory diversity trends. Sugar maple overstory density is low in the virgin area but is the overwhelming dominant in the secondary area on the north-facing slope. Chestnut oak dominates the south-facing slope of the virgin area resulting in low diversity, evenness and richness values there but is less abundant in the secondary area. Many successional species such as redbud, black locust, sassafras and others have invaded the young low canopy there. Growth of chestnut oak is slow (Bourdeau, 1954); it has not yet attained canopy dominance in the secondary area.

Overall overstory diversity and evenness are highest on the secondary south-facing slope followed by the south-facing virgin area, north-facing virgin area, north-facing secondary and upper gorge, respectively (Table 1). Species richness ranges from 51 taxa in the understory of the south-facing virgin area to 13 taxa in the overstory of the upper gorge. Differences in exposure,topography and soil conditions are obvious important factors. Lorimer (1976) found lowest diversity values in a hemlock forest which he related to microenvironmental characteristics such as cold air drainage and temperature extremes which favored taxa with a northerly distribution such as hemlock and yellow birch.

Higher evenness values in both the sapling and overstory layers of the virgin north-facing slope area differ from the low evenness values in mature northern stands observed by Loucks (1970), Auclair and Goff (1971) and Shafi and Yarranton (1973). The large number of species present which are characteristic of the mixed mesophytic forest and frequent small-scale disturbances which create a mosaic of habitats where both successional and climax specis coexist account for the higher richness and evenness values. Lower evenness in northern forests is due to dominance by one or two species similar here to the south-facing virgin area dominated by chestnut oak and the upper gorge which is dominated by hemlock.

Sapling diversity is higher than overstory diversity in all areas; the presence of many characteristic understory species such as dogwood, witch hazel, sassafras, hornbeam and paw-paw which seldom reach canopy stature accounts for the differences. Monk (1967) suggested that higher species diversity of the understory layer indicated unstable conditions but understory species may not have been considered. Lorimer (1976) reported highest diversities in the seedling layers due to the occurrence of taxa such as cucumber magnolia, tulip poplar and white ash which are shade tolerant in the seedling stage. As the seedlings develop and become shade intolerant, heavy mortality occurs and the diversity of the understory layer is reduced.

Diversity (H') values reported by other investigators are shown in Table 2. Monk (1967) computed diversity (H') using data for the Eastern Deciduous Forest from Braun (1950). Diversity of the Savage Gulf north-facing slope, south-facing slope and upper gorge are similar to the all-deciduous mixed mesophytic, chestnut-sugar maple-tulip and hemlock-mixed mesophytic types, respectively. Lorimer (1976) reported similar diversities for lower and upper cove hardwood forests from Joyce Kilmer Memorial Forest (Table 2). Savage Gulf diversities are in most cases higher than the literature values, due in part to the occurrence of both shade tolerant and intolerant taxa in the same stands. Frequent disturbances such as tip-ups and windthrow provide gap openings where shade tolerant taxa reproduce along the edge and intolerant taxa are abundant near the center (Lorimer, 1976).

Correlations of diversity and environmental variables suggest several important trends (Table 3). Slope position is positively correlated with overstory diversity and species richness indicating lower slopes support a more diverse canopy layer. Whittaker (1960) and Monk (1967) also found diversity highest at lower elevations and on mesic sites. Whittaker (1956) and Lorimer (1976) found highest species diversity in upper cove hardwood forests, located in the transition between cove forest and oak forest. Highest diversity values in this study are found on lower slope positions of the south-facing slope which contain both mesic and xeric taxa similar to the species mixture reported by Whittaker (1956) and Lorimer (1976). Sapling and overstory diversity are positively correlated, indicating a correspondence in diversity on both high and low diversity areas. Loucks (1970) reported an inverse relationship between understory and overstory layer diversity.

Table 3.--Correlation matrix between diversity and environmental variables.

Variables	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.
1. Aspect								.79[a]				-.45[b]
2. Slope position									.47[b]		.65[a]	
3. Forest condition				-.49[b]			-.45[b]					
4. Sapling H'					.82[a]	-.80[a]	.91[a]		.63[a]	.50[b]	.61[a]	
5. Sapling evenness							.51[b]		.53[b]	.51[b]		
6. Sapling redundancy							-.52[b]			-.55[a]		
7. Sap species richness								.47[b]	.56[a]		.62[a]	
8. Sapling density												-.51[b]
9. Overstory H'										.87[a]	.86[a]	
10. Overstory evenness											.51[b]	
11. Over species richness												
12. Overstory density												

[a]Significant correlation at P = .01.

[b]Significant correlation at P = .05.

Species richness and evenness of both sapling and overstory layers are highly correlated. Auclair and Goff (1971) reported a similar relationship. Species diversity (H') is highly correlated to both evenness and richness. Shafi and Yarranton (1973) found that changes in diversity were primarily a result of changes in richness; results of this study suggest both evenness and richness are equally important in this respect.

CONCLUSIONS

On the north-facing slope sapling and overstory species richness and diversity are lower in the secondary area, due primarily to the overwhelming dominance of sugar maple in both the overstory and reproductive layers. On the south-facing slope overstory diversity and richness are higher in the secondary area due to the replacement of chestnut oak by a variety of successional taxa such as redbud, black locust and sassafras. Sapling diversity and richness are higher in the virgin area. Species diversity and richness are low in the upper gorge due to dominance of hemlock in both the overstory and understory layers. Correlations indicate that species richness and diversity increase at lower slope positions, suggesting higher vegetation diversities occur in the mesic portion of the moisture gradient.

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