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ABSTRACT

HERBACEOUS COMPOSITION AND PRODUCTIVITY AS INFLUENCED BY CANOPY REMOVAL IN AN OAK-MAPLE STAND

By

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Changes in the productivity and species composition of the herbaceous layer caused by timber harvesting of an oak-maple stand in southwestern Michigan were investigated. The stand was divided into 1.1 ha areas. Four cutting treatments, each replicated four times were applied: undisturbed control areas, clearcut areas, group selection areas, and shelterwood areas.

Five 3 m x 3 m plots were randomly established in each treatment area the year before cutting. After cutting, four of these plots were expanded to 20 x x 20 m and five m² subsamples were taken in each plot. Leaf area of the 37 most abundant species was estimated with the aid of a 0.01 m² template at each plot. These surveys were conducted during the mid-summer before cutting and the early and late summer after cutting.

Thirty two additional m² plots (8 in each of the 4 cutting treatment areas) were randomly established to

measure throughfall precipitation. Self-recording instruments were randomly placed in each treatment area to measure sunlight, relative humidity, and temperature.

Areas in which trees had been harvested had a significantly higher level of herbaceous net productivity as compared to control areas. However there were no significant differences among the clearcut, shelterwood, and group-selection harvest techniques. Slash distribution created very heterogeneous microenvironmental patterns in areas of harvesting. Throughfall precipitation was not significantly different among the four cutting treatments, and net herbaceous productivity was not significantly correlated with the amount of throughfall precipitation.

Species composition remained unchanged in control areas. In areas of harvesting, some shift in species composition did occur. Eight principle new invading species were observed. Parthenocissus quinquefolia, the dominant herbaceous species before harvesting, decreased in its proportion of total leaf area, but other resident species increased their proportions.

Species diversity increased in harvested areas, but remained unchanged in control areas. The relationship between diversity and net productivity is not clear. Plots with very low or very high net productivity had low diversity, while plots of intermediate net productivity

had high diversity. In comparison with the herbaceous layer in other forest ecosystems, the net productivity of the Russ Forest site is of an intermediate value.

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AS INFLUENCED BY CANOPY REMOVAL
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By

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CHAPTER I

INTRODUCTION

The study of the herbaceous layer's response to overstory removal in eastern deciduous forests has been largely neglected. While vegetative response to various cutting regimes has been examined, most studies have ignored the herbaceous species and concentrated on tree reproduction (Metzger and Tubbs 1967, Rudolph and Lamine, Minckler 1965, Ray 1932, Boivin 1971, Wendel and Trimble 1968, 1971, Church 1960). The usual procedure is to wait three to seven years and then tabulate the number of young trees that have become established since the cutting. The first few years after cutting are often described as being dominated by weedy invaders that are detrimental to tree reproduction.

The response of the herbaceous layer to overstory removal needs to be examined for several reasons. Marks and Bormann (1972) pointed out that the rapid growth of early successional species is important in preventing loss of nutrients from the site of disturbance. From a forest management point of view, the herbaceous response is

important since these species are competitors with the newly established tree species. Also, many of the herbaceous species growing in these forest openings have food value for wildlife (McCaffey and Creed 1968) and documentation of their abundance and distribution provides input for a wildlife management program.

The objective of this study is to document changes occurring in the herbaceous layer after varying degrees of canopy removal. There were two main hypotheses concerning changes in the herbaceous layer: (1) that there would be a significant increase in herbaceous productivity and a shift in species composition; (2) that environmental parameters of sunlight, relative humidity, temperature, and the amount of throughfall precipitation reaching the forest floor would be significantly changed.

CHAPTER II

LITERATURE REVIEW

Response of Tree Species to Canopy Removal

The effects of canopy removal on tree reproduction has been well documented. However, the response of herbaceous species has been neglected. This response is usually recorded as shifts in density and composition of species. For example, Tubbs (1968) found that the amount of canopy removal in Acer saccharum stands in Michigan was positively correlated with the number of seedlings. About one half of these seedlings germinated after cutting. On the other hand, Church (1960), studying a hardwood stand in upper Michigan, found that Acer saccharum seedlings developed in the same numbers regardless of what quantity of canopy was removed.

Most authors report a shift in tree species composition after cutting. Winget (1968) observed that clearcut and partially cut stands in Quebec were dominated by Acer saccharum, Fagus grandifolia, Abies balsamea, while Prunus serotina, Betula alleghaniensis, Tilia

americana, and Quercus rubra were eliminated. Leak and Wilson (1958) found that for old growth hardwoods in New Hampshire, selection cutting favored shade tolerant Acer saccharum; patch cuttings favored intermediate tolerant Acer rubra; and clearcutting favored intolerant Populus tremuloides. Trimble and Hart (1961) also found that the species composition measured five years after cutting was correlated with the amount of canopy removal. The exception to the above studies was the one by Tubbs (1968) in which he found that various amounts of canopy removal in an Acer saccharum stand did not significantly affect the tree species composition, Acer saccharum being predominant. The original stand was also dominated by Acer saccharum, and these results illustrate that the amount of change in species composition depends on the composition of the original stand.

Stump sprouts and advance reproduction (seedlings established before cutting) constitute a large percentage of the reproduction seen after cutting. Wendel and Trimble (1968) found 53 percent of the reproduction to be of sprout origin. Trees derived from this type of reproduction frequently outgrows seedlings and may dominate the stand for many years (Johnson 1971, Winget 1968). Trimble and Hart (1961) found that sprouting was positively correlated with the amount of canopy removal.

Herbaceous Productivity on Forest Sites

Productivity estimates of the herbaceous layer on forest sites have only recently been made. Early studies of the herbaceous layer were concerned with such structural parameters as density, composition, pattern, and frequency distributions under different amounts of canopy coverage (Gysel 1951, McIntosh 1962, Smith and Cottam 1957, Struik and Curtis 1962, Pace and Hurd 1957, Sanders 1969).

Much of the early work of estimating herbaceous productivity on forest sites was done by R. H. Whittaker (1966, 1968). Recently Siccama, Bormann and Likens (1970) reported on another important productivity study on the Hubbard Brook Experimental Forest. These authors estimated herbaceous productivity by destructive sampling techniques. Herbaceous material from field plots was clipped, dried, weighed, and converted into productivity estimates per unit area.

The level of herbaceous productivity varies within a forest site. Usually a negative correlation exists between percent canopy coverage and productivity (Siccama, Bormann, and Likens 1970, Hitherington 1969, Gainer et al. 1954). A study by Anderson et al. 1969 attempted to correlate productivity to light and soil moisture conditions as controlled by canopy coverage. Soil moisture was

found to have a greater influence on herbaceous production than light, and was highly dependent on canopy coverage.

Direct harvesting is a common method of estimating plant dry weight production. Such destructive sampling techniques for estimating productivity are both time consuming and unattractive since repeated measurements cannot be made on the same plots. A nondestructive technique such as recording plant volume or leaf area, with a subsequent conversion of these parameters into dry weight by the use of a regression equation, would be a better alternative if sufficient accuracy could be attained. This type of sampling technique has been applied for years by foresters in estimating merchantable timber, and lately by Whittaker (1966) and Whittaker and Woodwell (1969) to estimate total productivity of standing timber.

A number of workers have estimated dry production in forest understories by use of the harvest techniques (U.S. Forest Service, 1958). There have also been a number of indirect sampling techniques applied to estimate the coverage in forest understories (Tayle 1959, U.S. Forest Service 1958, Daubenmire 1959). However, only a few studies (Cristofoline 1970 and Anderson et al. 1969, Whittaker 1966, Siccama, Bormann, and Likens 1970, Whittaker and Woodwell 1968) were found that applied an indirect sampling technique to estimate the dry weight production by the herbaceous understory layer in a forest

community. Anderson et al. (1969) measured leaf width and converted these parameters into dry weight via a regression equation. Cristofoline (1970) visually estimated leaf area on 0.1m^2 plots and converted this parameter into dry weight in the same manner. The remaining authors converted percent plant cover into dry weight by the same regression technique. All the above studies found strong relationships (r .74 to .96) between the independent parameter and dry weight.

Succession in the Herbaceous Stratum

Studies documenting the course of herbaceous development after overstory removal have been well documented in the Pacific Northwest (Isaac 1940, Kienholz 1929, Mueller-Dombois 1965, Yerkes 1960, Steen 1966). Similar studies are reported for eastern deciduous forest communities (Gysel 1951, McCaffery and Creed 1969, McIntosh 1957, Rogers 1959, Kittredge 1934).

The above studies have described successional stages based on reconnaissance data. The investigators inventoried a number of sites ranging in age from recently logged to the oldest available rather than following vegetative changes on the same site over a period of years. In attempting to reconstruct successional stages from data on a wide range of sites, they were able to describe vegetative changes only in broad terms. This is because

vegetation on disturbed sites is influenced not only by age of disturbance, but also by differences in soil, microclimate, and severity of the disturbances.

No studies were found for the eastern deciduous forest similar to Dryness' (1973) in which vegetative development after logging in the Pacific Northwest was followed for seven years on permanent plots. Much of the data collected on old field succession (Odum 1960, Evans and Cain 1952, Evans and Dahl 1955) is probably non-applicable. Old field soils have been greatly altered by cultivation (Keever 1950, Booth 1941). Also, slash left on forest sites after cutting greatly alters the microclimate, resulting in a mosaic of different microsites.

Usually there is a great increase in herbaceous productivity the first few years after overstory removal, but as the remaining tree species begin to form a new canopy, herbaceous productivity declines. Dryness (1973) found average herbaceous coverage to increase from 26 percent to 45 percent by the fourth year after cutting. Studies like those of Ahlgren and Ahlgren (1960) and Lyon (1971) noted large increases of herbaceous coverage after forest fires. In some cases after intensive site preparations, productivity is greatly curtailed and re-population by herb and shrub species is delayed (Schultz, personal communication).¹

¹Robert Schultz, U.S.F.S., Olusee, Florida.

Factors Influencing Herbaceous Response

Removal of the canopy undoubtedly changes a plethora of biotic and abiotic factors to which the herbaceous layer responds. Few of these factors seem to have been studied directly in forest sites. Whipple (1968) found higher soil temperatures after clearcutting, and Larson (1970) noted that growth in Quercus rubra seedlings responds to total daily degree hours rather than to the differential between day and night temperature. After cutting, soil moisture decreases and has a higher rate of fluctuation than before cutting (Dixon 1969, Anderson et al. 1970, Whipple 1968).

After a clearcutting, slash will often cover 21-26 percent of the ground surface (Wendel and Trimble 1968). Microsites in and around this slash will undoubtedly have different environmental parameters than more exposed microsites. However, no references were found that discussed microclimate conditions.

There is some evidence that annual weed species have an inherently higher growth rate than tree species, and given optimum conditions, weeds have a higher net productivity. Coombe and Hadfield (1966) found dry matter production in fast growing woody species from secondary tropical rain forests to be significantly lower than herbaceous species. Growth and leaf area are highly

correlated, and the percent distribution of new growth to leaves is important (Newhouse 1968). Jarvis and Jarvis (1964) took published values of maximum assimilation rates for temperate species and found that woody plants lie in the range of $20-50 \text{ gm m}^{-2} \text{ wk}^{-1}$, while herbaceous plants lie in the range of $70-150 \text{ gm m}^{-2} \text{ wk}^{-1}$. They speculate the existence of some inherent corollary of wood formation which is incompatible with a high rate of net assimilation. Unfortunately none of the above authors considered the rapid growth of stump and root sprouts.

The role of allelochemics in regulating the herbaceous response is probably important, but at this point little is known of this subject. Allelochemic relationships among the various competing species have been studied, but unfortunately none of these species occurred in this study (Whittaker and Feeny 1971, Kohno 1969, del Moral and Muller 1970, Tubbs 1970).

CHAPTER III

THE STUDY AREA

Site Description

The study site is a 17.6 ha stand of oak and mixed hardwoods in the Fred Russ Experimental Forest, a property of Michigan State University. The study area is part of a 235 ha forest located in southwestern Michigan, Cass County, near Dowagiac.

Prior to 1930, the stand had been used for grazing cattle and a source of firewood, but during the last 40 years, it has remained essentially undisturbed. As a result of grazing and lack of forest management, stand structure was primarily of very large and very small trees. Basal area averaged $31.2 \text{ m}^2 \text{ ha}^{-1}$. Major species in the stand were Acer saccharum, Quercus rubra, Quercus alba, Quercus velutina, and Prunus serotina.

The stand is generally level to gently undulating in topography. One minor depression on the border of the stand leads to a swamp located outside the stand. Two major soil series are present in the area: the Kalamazoo

and Oshtemo. These are quite similar in soil properties, being well-drained typic hapludalf soils which have developed on gravelly loam, sandy loam, and loamy sand material. The Oshtemo soils differ from the Kalamazoo soils primarily in the thickness and the amount of clay in the B2t horizon. This horizon has a thickness of 20-31 cm in the Oshtemo and 25-56 cm in the Kalamazoo. The Kalamazoo series has the higher percentage of clay.

Annual precipitation over a 30 year period averages 1092 mm of which 16 mm is snow. Rainfall during the growing season of May 1 to September 15 is about 417 mm. During the two growing seasons of the study, rainfall was 317 mm (1971) and 376 mm (1972).

Spring vegetative growth begins between April 20 and May 1. However, trees are not in full leaf until about May 15, and much of the herbaceous growth does not appear before May 30. Growth measurements were arbitrarily terminated on September 15. The growing season does continue to the beginning of October, but few species show any gains of net productivity during these last few weeks.

Treatment Design

The present study was conducted within the framework of a larger experimental improvement cutting initiated by the Department of Forestry in 1970. The

stand was surveyed and divided into 16 rectangular treatment areas, each 1.1 ha in size (Fig. 1). There were four types of treatment areas: control, in which the trees were left undisturbed; clearcut, in which all trees were removed; shelterwood, in which 20 to 25 large trees (6.2 m^2 of basal area) were left undisturbed; and group selection, in which all trees were removed within the small areas (0.25 ha) indicated in Figure 1. These four types of treatment areas were arranged in a randomized block design, comprised of four blocks, four treatments per block.

The need for blocking was based on observed differences in the density, canopy coverage, and species composition of tree species within the whole stand. Herbaceous cover followed a similar pattern, being high in areas of low tree canopy coverage and low in areas of high tree canopy coverage. Thus the same randomized block design was used in studying the herbaceous stratum.

The stand was inventoried during the spring and summer of 1971. All trees larger than 1.27 cm diameter breast height (d.b.h.) were catalogued according to species, d.b.h., merchantable height, and form class. Cutting operations were carried out by a commercial logger from October to December, 1971.

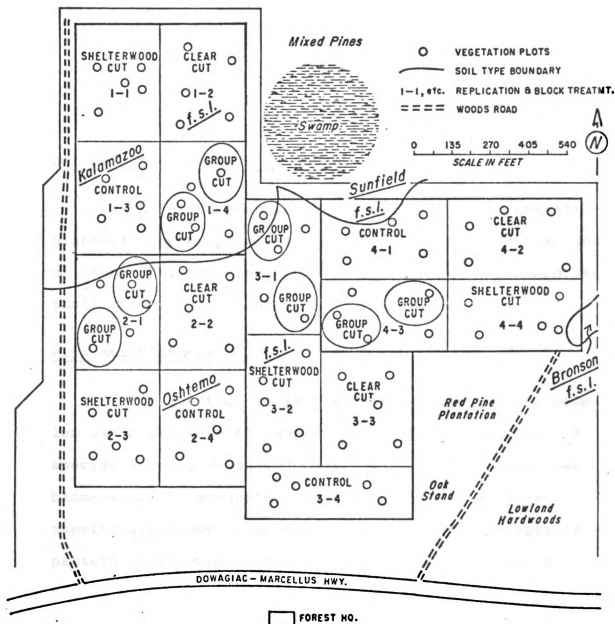


Figure 1. Arrangement of plots in the Fred Russ forest hardwood study area.

CHAPTER IV

FIELD METHODS

Definition of Herbaceous Layer

The herbaceous layer was defined as all annual-biannual species plus all perennial species less than 30 cm in height. The latter category included tree seedlings, small shrubs, and plants with a rhizomatous habit.

Plot Establishment

The question of initial sample size posed a problem as no estimate of sample variance was available. A species area curve showed that four 3 m x 3 m plots per block would be adequate. However, forest understory species are known to be distributed in a patchy type of pattern (Smith and Cottam 1967, McIntosh 1962) and a visual survey showed this to be the case on the study site. Thus 20 3 m x 3 m plots per block, 80 plots in total were used. To insure some uniformity in the arrangement of sample plots, one was randomly located in each quadrant of each treatment area, and one was located randomly in

respect to the whole treatment area (see Fig. 1). For statistical purposes, plots needed to be randomly located with an equal number in each treatment area.

Following the 1971 herbaceous layer survey, the data was analyzed for purposes of determining the inadequacies of the sample size. The graphical control method proposed by Grieg-Smith (1964) was applied for this (Fig. 2). The abscissa indicates progressive increases of plot numbers and the ordinate indicates mean leaf area or standard error expressed as a percentage of the mean. At first, the ordinate fluctuates widely, but later stabilizes as the number of samples is increased. Although this graphical technique is strictly empirical and only of suggestive value, it indicates that a sample size of 20 plots is a reasonable number for one block.

After cutting, microsite conditions became very heterogeneous due to slash deposits. To increase sample accuracy of productivity estimates, 64 of the original plots were expanded from 3 m x 3 m to 20 m x 20 m and then subsampled. A one meter square sample was taken at the original plot site, and four other meter square samples were randomly taken in the 20 m x 20 m area surrounding the original plot. Subsamples were then condensed into a one plot total. The remaining 16 3 m x 3 m plots were left unchanged. These plots, one in each treatment

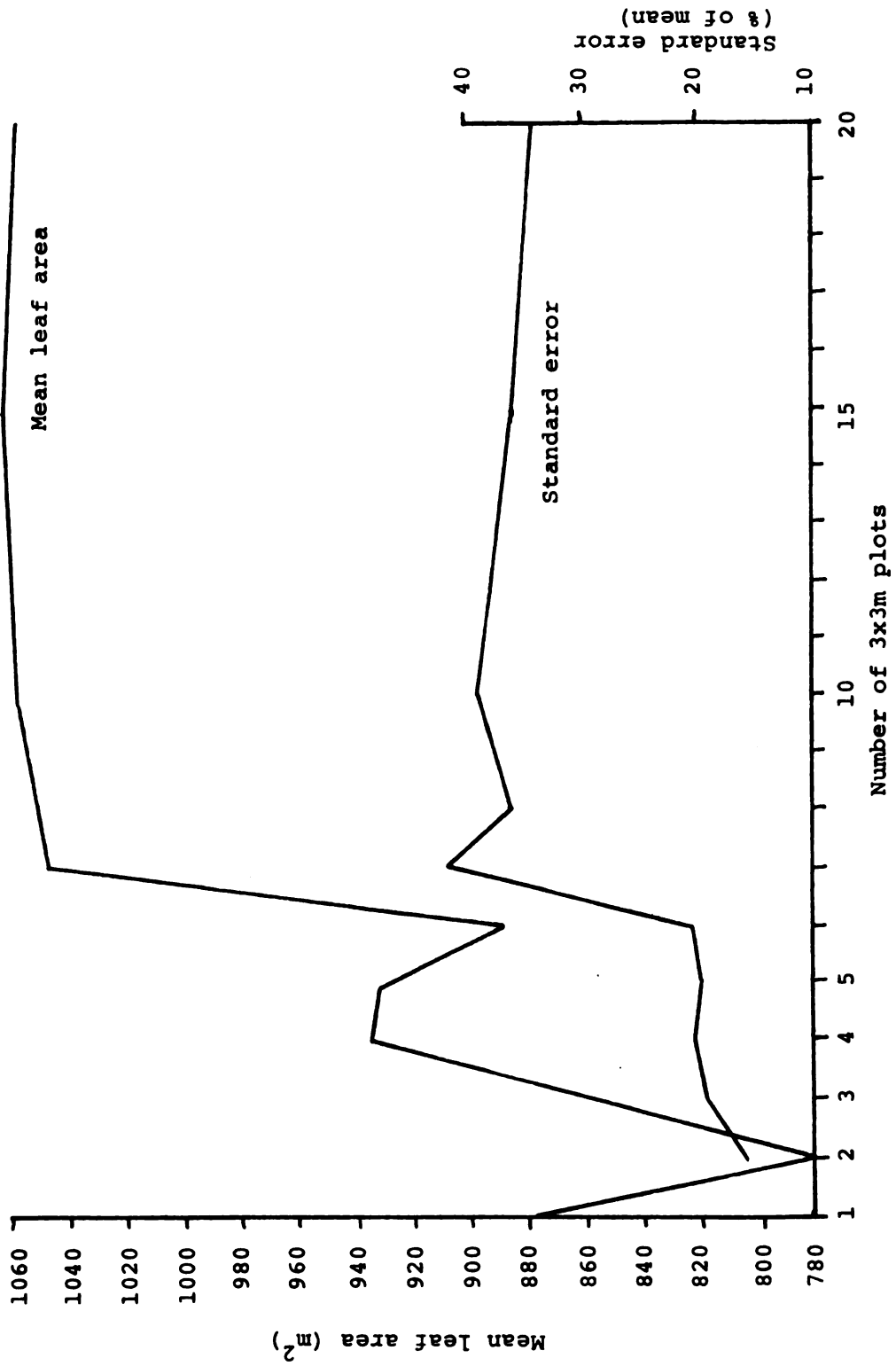


Figure 2. Determination of plot number in one block by graphical control method.

area, were used to estimate shifts in species composition and structure.

Productivity Measurement

This study employed an indirect, nondestructive sampling technique involving leaf area measurement and its subsequent conversion via regression analysis into dry weight. The most common means of determining leaf area is to measure maximum width and length of each leaf, and convert this to surface area. Such a tedious technique would be impossible for the number of samples involved in this study. To provide the needed speed with a reasonable level of accuracy, a visual method was adopted similar to one used by Cristofoline (1970) in a mixed hardwood understory community at Oak Ridge, Tennessee. Leaf area was estimated with the aid of the portable m^2 frame and templates shown in Figure 3. The borders of a plot were defined with the m^2 frame. Next, either a circular $.01 m^2$ template or a rectangular $.02 m^2$ template was placed on the plants to estimate leaf area of each of the major species. In cases where leaves were larger than or smaller than the templates the judgment of the author was important. An attempt was made to group small leaves or combine portions of large leaves in order to arrive at an estimate of total leaf area. The use of templates worked quite well in the case of multi-layer canopies since the

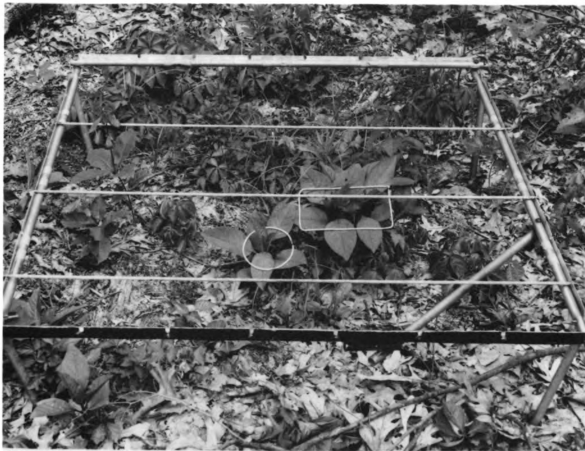


Figure 3. Portable m^2 sampling frame with $.01 m^2$ and $.02 m^2$ templates used in estimating leaf area. Templates were placed on each leaf of all plants within the plot.

templates could be repeatedly moved so as to measure all leaves in the canopy.

A series of samples was taken on 10 of the major species to determine the accuracy of the above technique. Leaf area, as measured by the templates, was compared to the value obtained by placing a grid of squared centimeters over the foliage and counting the number of squares occupied. The difference between the leaf area estimated by these two methods varied from species to species. Large broadleaf species were easier to measure and had more accurate estimates of leaf area than small multi-leaf species. For example, the percent error (the direct count minus the template estimate ÷ template estimate) was only +0.2 percent for Podophyllum peltatum. For Circaea quadriscata it was +9.3 percent and for Parthenocissus quinquefolia, it was +1.9 percent. Smaller leaf species had higher errors: Erigeron canadensis, +17.7 percent; Quercus rubra, -16.5 percent; Viola spp., -18.0 percent. The small multi-leaf species of Geranium robertianum had an error of +30.3 percent. Rubus spp. had an error of -29.1 percent. The greatest errors were found in the grasses, +122.9 percent, and in Galium circaeazans, +161.2 percent. The templates badly underestimated the leaf area of these species. This is probably due to their small laminar type foliage which greatly overlaps. Based

on these observed errors, corrections were made in the original field estimates of leaf area.

Table 1 shows the regression equations developed for the 29 most abundant species. This was done by repeated harvesting of the above-ground parts of a species after its leaf area had been recorded. The plant material was oven-dried at 85° C for 48 hours and dry weight determined. Leaf area was then regressed upon dry weight to give the equations. These species comprise 93 percent of the total leaf area measured over all plots. Development of a regression equation for each species present was not possible and although 7 percent of the total leaf area is ignored, the dry weight value calculated on the remaining leaf area should approximate annual productivity.

For each species, mean sample weight and standard error are given. Standard errors were, for the most part, less than 10 percent of the means. The standard error of a single measurement taken at mean sample weight is also shown. This standard error gives the maximum amount of deviation one would expect to find. In some cases, it is up to 60 percent of the mean, but this deviation would, of course, decrease with an increase in sample size.

The coefficient of variation shows the amount of variation in the dependent variable, weight, that is included in the regression equation. The coefficient of variation is analagous to a correlation coefficient and

Table 1. Regression equations converting leaf area ($\text{cm} \times 10^{-2}$) to dry weight (gm).

	Regression equation ($\bar{y} = \text{wt. (gm)}, x = \text{leaf area (cm} \times 10^{-2})$)	Coefficient of variation	Mean sample weight and standard errors	Standard error of single measurement at mean sample weight	Significance of the regression equation	Sample size
1 <i>Podophyllum peltatum</i> L. ¹	$Y = .01 + .78X$.59	3.8 (.37)	1.48	.01	15
2 <i>Eriogonum canadense</i> L. ¹	$Y = 6.84 + 3.56X$.84	19.0 (2.76)	11.07	.01	15
3 <i>Cirsium</i> spp.	$Y = -1.07 + 1.46X$.76	4.14 (0.4)	1.53	.01	14
4 <i>Phytolacca americana</i> L.	$Y = 3.07 + 1.35X$.75	41.0 (5.65)	26.23	.01	20
5 <i>Quercus alba</i> L.	$Y = .14 + .42X$.79	2.6 (.26)	.99	.01	12
6 <i>Quercus canadensis</i> Jacq. ²	$Y = 1.16 + .99X$.59	7.5 (.72)	1.11	.01	14
7 <i>Ulmus</i> spp.	$Y = .30 + .65X$.96	12.4 (.52)	2.46	.01	21
8 <i>Gallium circasense</i> (Michx.) C. B. Clarke	$Y = .40 + 1.58X$.69	10.5 (1.25)	3.56	.05	8
9 <i>Acer rubrum</i> L.	$Y = -.78 + .53X$.91	1.8 (.1)	.47	.01	24
10 <i>Oxalis stricta</i> L.	$Y = -2.05 + 1.47X$.95	10.3 (.76)	2.50	.01	10
11 <i>Prunus serotina</i> Ehrh. ³	$Y = .28 + .47X$.84	3.2 (.14)	.92	.01	27
12 <i>Hedeoma pulegioides</i> (L.) Pers.	$Y = -.50 + 2.36X$.96	11.8 (.71)	2.36	.01	10
13 <i>Cornus florida</i> L.	$Y = -1.70 + .66X$.87	7.2 (.56)	2.63	.01	21
14 <i>Poaceae</i> (species group)	$Y = -3.05 + 3.34X$.88	8.31 (.77)	2.56	.01	10
15 <i>Acer saccharum</i> Marsh.	$Y = -1.80 + .86X$.87	4.17 (.35)	1.53	.01	18
16 <i>Rubus</i> spp.	$Y = -2.00 + .93X$.95	5.26 (.28)	1.20	.01	18
17 <i>Osmorhiza claytonia</i> (Michx.) C. B. Clarke	$Y = .74 + .27X$.53	2.46 (.28)	1.30	.01	19
18 <i>Ribes</i> spp.	$Y = -1.45 + 1.26X$.72	11.52 (2.15)	7.73	.01	12
19 <i>Rhus radicans</i> L.	$Y = -.45 + .46X$.66	3.87 (.48)	2.10	.01	19
20 <i>Physalis subglabrata</i> Mackenz. and Bush	$Y = .49 + .69X$.95	8.70 (.79)	2.52	.01	9
21 <i>Parthenocissus quinquefolia</i> (L.) Planch.	$Y = .85 + .25X$.95	11.64 (.57)	3.09	.01	28
22 <i>Viola</i> spp.	$Y = -.46 + .52X$.76	2.54 (.24)	1.09	.01	24
23 <i>Phryma leptostachya</i> L.	$Y = -.99 + .67X$.83	3.51 (.95)	2.61	.01	14
24 <i>Polygónatum canaliculatum</i> (Muhl.) Pursh ⁴	$Y = -.77 + .66X$.64	3.52 (.55)	2.33	.01	17
25 <i>Circaea quadrifida</i> (Maxim.) Franch. and Sav.	$Y = 1.13 + .66X$.98	10.10 (.84)	3.99	.01	21
26 <i>Tovara virginiana</i> (L.) Raf.	$Y = -1.40 + .94X$.88	7.72 (.50)	2.28	.01	20
27 <i>Gernium robertianum</i> L.	$Y = -.78 + .65X$.93	13.46 (1.02)	4.79	.01	21
28 <i>Quercus rubra</i> L.	$Y = .14 + .42X$.79	2.6 (.26)	.99	.01	12
29 <i>Sassafras albidum</i> (Nutt.) Nees	$Y = -1.70 + .66X$.87	7.2 (.56)	2.63	.01	21

¹Include *Eriogonum annuum* L.²Includes *Sanicula canadensis* L.³Includes *Prunus virginiana* L.⁴Includes *Smilacina racemosa* (L.) Desf.

shows the strength of association between leaf area and dry weight. Most coefficient of variation values are high and only equations 1, 6, and 17 had low values.

During the period of June 12-July 7, 32 of the 20 m x 20 m plots were sampled, two in each treatment area. The remaining 32 plots (20 m x 20 m) were sampled during the period of September 5-September 24.

Measurement of Shifts in Composition and Structure

Estimates of leaf area for each species were made on the 16 3 m x 3 m permanent plots using the methods developed earlier for estimating herbaceous productivity.

Measurements were taken the year before and after cutting, but no attempt was made to record all species present. The year before cutting, the 29 most abundant species, as determined by frequency of occupied quadrants were tabulated. The year after cutting, 37 species were tabulated. Due to the difficulty of species identification, members of the family Poaceae were recorded as one multi-species group. Geum canadensis and Sanicula canadensis also were considered as one species group as was Polygonatum canaliculatum and Smilacina racemosa.

CHAPTER V

ESTIMATES OF PRODUCTIVITY

Results for Cutting Treatment and Control Areas

Net productivity is the amount of biomass produced, and is usually estimated by the standing crop of biomass that has accumulated over a growing season (Westlake 1963). The general formula for net productivity given by Newbould (1967) is $P_n = W_{\max} - W_{\min} + S + G + D$, where W equals biomass, S equals the accumulation of reserves, G equals the amount consumed by animals, and D equals the amount lost to mortality during an interval when standing crop is increasing to its peak level (W_{\min} to W_{\max}).

The factor S was ignored as was increases in root biomass since this study estimated only above-ground production. Large accumulations of root biomass or reserves could influence above-ground production but this factor was not considered here. The amount of net primary productivity of herbaceous species consumed by herbivores (G) is thought to be minor. Golley (1960) reported that *Microtus* consume .3 percent of net primary production while Wiegert and Evans (1967) reported that the combined consumption of all herbivores is approximately 1 percent. The latter authors

estimate that herbivorous consumption rarely exceeds 5 percent of net primary production and is usually lower. The factor D is also felt to be minor. This fact is based on the author's knowledge of the species involved in this study and daily observations during the growing season. Ignoring the factors S, G, and D reduces Newbould's expression to $P_n = W_{\text{max}} - W_{\text{min}}$. Assuming W_{min} equals zero for the above-ground parts of herbaceous species, all that is needed to estimate above-ground productivity is the value of peak biomass during the growing season.

By applying the regression equations developed in Table 1, leaf area was converted into dry weight (gm m^{-2}). Next, the average dry weight per square meter was calculated for each individual species surveyed during the first sampling period (June 12-July 7). The same was done for the second sampling period (September 5-September 24), and Table 2 lists the results. Peak biomass for each species was determined by selecting the larger value recorded in the two sampling periods. These peak biomass values were in turn summed to give the net productivity per square meter. More frequent sampling periods would have increased data accuracy, but the bulk of productivity occurred during the above two sampling periods.

During the 1972 growing season, net above-ground productivity of the herbaceous layer averaged 142.6 gm m^{-2} in the cutting treatment areas where the tree canopy had been removed and 34.4 gm m^{-2} in control areas where no

Table 2. Mean weight (gm m⁻²) of selected species for two sampling periods.

Species	Mean weight and standard error June 12-July 7	Mean weight and standard error Sept. 5-Sept. 24
Increasing Biomass		
*+ <i>Phytolacca americana</i> L.	6.00 (.93)	33.25 (3.75)
*+ Poaceae (species group)	18.71 (5.50)	26.10 (4.50)
*+ <i>Erigeron canadensis</i> L.	2.52 (.72)	12.74 (2.33)
*+ <i>Circaea quadrisulcata</i> (Maxim.) Franch. and Sav.	3.10 (.65)	8.17 (1.26)
+ <i>Geranium robertianum</i> L.	1.90 (.37)	5.95 (.74)
<i>Rubus</i> spp.	.97 (.57)	3.14 (.58)
+ <i>Cirsium</i> spp.	1.00 (.46)	3.87 (.83)
<i>Quercus rubra</i> L.	1.75 (.46)	3.14 (.53)
<i>Oxalis stricta</i> L.	.00 (.00)	3.13 (.73)
<i>Geum canadensis</i> Jacq. and <i>Sanicula canadensis</i> L.	.36 (.12)	2.79 (.68)
<i>Ulmus</i> spp.	1.13 (.30)	2.99 (.32)
<i>Sassifraga albidum</i> (Nutt.) Nees	.96 (.31)	1.92 (.54)
<i>Physalis subglabrata</i> Mackenz. and Bush	.20 (.08)	1.72 (.60)
<i>Hedeoma pulegioides</i> (L.) Pers.	.00 (.00)	1.73 (.73)
<i>Cornus florida</i> L.	.26 (.10)	.78 (.41)
<i>Acer rubrum</i> L.	.09 (.04)	.26 (.06)
<i>Polygonatum canaliculatum</i> (Muhl.) Pursh and <i>Prunus virginiana</i> L.	.12 (.06)	.38 (.14)
Decreasing Biomass		
*+ <i>Parthenocissus quinquefolia</i> (L.) Planch.	13.20 (1.38)	7.69 (.69)
* <i>Podophyllum peltatum</i> L.	2.88 (.55)	.48 (.25)
<i>Viola</i> spp.	1.84 (.28)	1.26 (.16)
* <i>Galium circaeazans</i> Michx. <i>Osmorrhiza claytonia</i> (Michx.) C. B. Clark	5.58 (1.33)	3.34 (1.27)
<i>Quercus alba</i> L.	1.57 (.17)	1.26 (.19)
<i>Amelanchier</i> spp.	.44 (.13)	.22 (.06)
<i>Phryma leptostachya</i> L.	.43 (.11)	.20 (.07)
	.19 (.06)	.43 (.16)
Constant Biomass		
<i>Ribes</i> spp.	1.23 (.34)	1.76 (.43)
<i>Rhus radicans</i> L.	.39 (.14)	.45 (.15)
<i>Acer saccharum</i> Marsh.	.42 (.17)	.67 (.17)
<i>Tovara virginiana</i> (L.) Raf.	.31 (.21)	.51 (.14)
<i>Prunus serotina</i> Ehrh. and <i>Prunus virginiana</i> L.	.73 (.11)	.52 (.10)
Total	68.30	130.84

*These species comprise 76% of the standing crop June 12-July 7.

+These species comprise 75% of the standing crop Sept. 5-Sept. 24.

canopy was removed. Both these values are probably underestimates of the true values since 7 percent of the leaf area was not converted to a dry weight basis (see page 21). By assuming that the species not accounted for in the regression equations had a leaf area-dry weight equal to the average leaf area-dry weight ratio for all other species, the original productivity values could be inflated by 7 percent. This would give an average of 152.6 gm m^{-2} in treatment areas and 36.8 gm m^{-2} in control areas. These values, although dependent on the above assumption, probably give a more accurate estimate of above-ground productivity.

Seasonal Patterns of Productivity

Using means and standard errors, species in Table 2 were grouped according to the period when maximum biomass was observed, i.e., early or late summer. It can be seen that these species can be categorized into three different groups. In the first group, biomass is continually increasing throughout the summer, reaching its maximum in the fall. The second group attains maximum biomass by early summer, and then slowly decreases. Species in the third group maintained a more or less constant biomass throughout the summer period.

Cristofolini (1970) found groups of species that had growth patterns similar to those above. He conducted an additional survey in late spring and consequently found a group of species, spring ephemerals, that had peak

biomass during spring and then decreased throughout the summer.

Both Cristofolini's (1970) study and this study emphasize the important point that in a natural assemblage of plants, a variety of growth patterns is present. This fact has great bearing on sampling techniques. In order to achieve optimum accuracy, each species group must be sampled during the period of its peak biomass. Compare, in Table 2, the dry weight for all species in the first sample period (68.3 gm m^{-2}) with the second sample period (130.8 gm m^{-2}) to that of the peak dry weight (142.6 gm m^{-2}) determined by summing the maximum values found for each species. The error inherent in a single sampling period is easily seen.

Cristofolini (1970) suggests four sampling periods: late winter, midspring, early summer and late summer. In this study, samples were not taken during late winter and midspring. However, based on the phenology of species encountered in this study, the bulk of productivity occurs during the summer sampling periods.

Effect of Cutting on Productivity

To determine if cutting treatments significantly affected herbaceous productivity, leaf area data from surveys of 1971 and 1972 was subjected to analysis of variance. Leaf area rather than dry weight was chosen to represent productivity because dry weight data ignored 7

percent of the total leaf area. Table 3 shows the analysis for the 1971 survey. Treatment areas had been laid out (Fig. 1) before the survey was taken, but no cutting had been done. That no significant differences existed among treatment areas indicates that the herbaceous productivity was essentially the same in all areas before cutting. A significant difference between blocks implies that blocking was done correctly.

Table 3. Analysis of variance of herbaceous productivity (leaf area) for all treatment areas before cutting--1971.

Source	Degrees of freedom	Mean square	F	Level of significance
Treatment	3	110485.245	1.0559	.373
Block	3	3282649.846	31.3714	.0005
Error	73	104638.474		

Table 4 shows the analysis of variance for the 1972 survey. As expected, cutting treatments significantly increased herbaceous productivity and treatment means (leaf area. m^{-2}) are shown in Table 5. These means were compared using Tukey's method, and none of the cutting treatments differed significantly from control areas. For 1971 and 1972; average leaf areas (m^{-2}) were 413, 445; 451, 665; 456, 586; 462, 601; for control, clearcut, shelterwood and group treatments, respectively.

Table 4. Analysis of variance for herbaceous productivity (leaf area) for all treatment areas after cutting--1972).

Source	Degrees of freedom	Mean square	F	Level of significance
Treatment	3	137937.307	3.368	.05
Block	3	205677.099	4.534	.01
Sample period	1	264507.797	6.459	.01
Treatment x time	3	176310.923	4.305	.01
Treatment x block	9	57431.918	1.250	.30
Error	44	38456.970		
additivity	1	781959.000	18.814	.0005
residual	43	7331.661		

Table 5. Significant differences among treatment means as determined by Tukey (leaf area expressed as m^2/m^2).

Group	Shelterwood	Clear cut	Control	Level of significance
1.330	1.204	<u>1.173</u> ¹	.890	.01 level

¹All figures not significantly different are connected by the underline.

Analysis of variance of the 1972 data provided an opportunity to test the effect of sampling at two time periods. As shown in Table 4, both time and the time x treatment interaction were significant sources of variation. This analysis of variance confirms the earlier results shown in Table 2 that the amount of standing crop varies greatly throughout the growing season.

It is notable that the F statistic for block in Table 4 is much lower than the same statistic in Table 3. Before cutting there were great differences of herbaceous productivity between blocks; block 2 being high and block 4 being very low. Cutting treatments eliminated much of this difference, all blocks being maintained at a high level of productivity. This effect is reflected in the lower F statistic seen in Table 4.

Productivity Differences Among Cutting Treatments

Why the various cutting treatment means did not differ among themselves is an interesting question. A partial explanation is offered by looking at the environmental data in Table 6. The parameters shown were monitored throughout the summer using self-recording pyroheliometers and hygrothermographs (Belfort instruments). Three hygrothermographs and four pyroheliometers were randomly placed in a control area. An equal number were placed in one treatment area. Each week the instruments in the

Table 6. Comparison among treatment means for various environmental parameters at the .01 level ^{1,2}

Parameter	Clearcut	Shelterwood	Group Selection	Control
Light (gm. cal./cm ²)	29.8 (12.95)	<u>25.1 (8.62)</u>	<u>17.1 (9.36)</u>	4.0 (3.02)
Temp. max. (c)	<u>31.00 (6.98)</u>	<u>32.7 (7.15)</u>	<u>31.6 (8.83)</u>	24.3 (4.73)
Rel. humidity max. (%)	94.4 (11.61)	<u>90.4 (12.62)</u>	92.6 (5.94)	<u>88.7 (5.37)</u>
Rel. humidity min. (%)	77.1 (35.62)	38.4 (21.75)	47.4 (24.2)	33.4 (13.35)

¹ means accompanied by standard errors

² all means not significantly different are connected by underlines

treatment area were moved to another treatment area. After three weeks, all instruments were moved to a new block. By concentrating instruments in one treatment area and control area, microsite variability could be better sampled.

There appears to be no clear cut differences between the environmental factors measured in the cutting treatments. However, all the environmental parameters, except maximum relative humidity, did show significant differences between controls and cutting treatments. Variability was extremely high in the environmental data, but it appears that the differential effect of the three cutting treatments on microsite conditions is negligible.

It is highly probable that slash distribution had the most profound effect on microsite conditions. Slash appeared to be distributed randomly across all treatment areas, and this may account for the lack of differences between cutting treatments in regard to both environmental parameters and productivity. Clearcut areas had larger amounts of slash than group-selection and shelterwood areas. However, the excessive slash in clearcut areas was concentrated in a few large piles with the remaining slash being distributed like that in the group-selection and shelterwood areas.

CHAPTER VI

THE INFLUENCE OF THROUGHFALL PRECIPITATION ON NET PRODUCTIVITY

Introduction

A study by Anderson et al. (1969) revealed that the understory herbaceous cover of a pine forest in northern Wisconsin was more responsive to differences in throughfall precipitation than to differences in light. Both light and throughfall precipitation were regulated by the amount of canopy opening. However, light was not found to be a limiting factor in herbaceous cover even in the dimmest sites.

Removal of the tree canopy and its capacity to intercept rain, will increase the amount of throughfall precipitation. It was hypothesized that results of the above study could be extended to this study where various proportions of the canopy had been removed. The increased amount of throughfall precipitation should be significantly associated with increases of herbaceous productivity.

Methods

The methods used in this chapter were adapted from the Anderson study. Eight meter square plots were assigned to the four treatment areas, giving a total of 32 plots. Plots were randomly located in the clearcut area. In the shelterwood and group selection areas, plots were located so each had at least a partial coverage of canopy. In the control area, with canopy intact, plots were chosen to include a wide range of herbaceous cover, from moderately dense to very sparse.

Canopy cover was estimated by use of photographs. Prints covering a canopy area of about 0.04 ha were enlarged to 18.4 cm square. A dot grid having 10 rows of 10 dots was placed over the photograph. The number of dots falling on undarkened portions of the photograph was divided by 100 to obtain percentage "open canopy" for each plot.

Rainfall reaching the forest floor as throughfall was measured with four rain gauges located 1 m from the center of the plot, one at each cardinal direction. The catchments of all gauges at each point were averaged to give an estimate of throughfall for each plot for a single rain period. Rainfall was measured within a few hours after storms during the daylight, or before 9:00 A.M. for precipitation having fallen during the night. Gross

precipitation measurements were made from a control gauge in a large opening near the plots.

The herbaceous response to changes in throughfall was measured by estimating net productivity. All above-ground plant material was clipped from each m² plot at the end of the 1972 growing season. The plant material was oven-dried at 85° C for 48 hours and weighed.

Results

The first set of correlation coefficients in Table 7 describes the relationship between percent throughfall precipitation and net herbaceous productivity. All coefficients were nonsignificant. Table 8 shows the mean of throughfall precipitation (mm) reaching the forest floor during the period of July 19-September 14. Although the amount of throughfall precipitation is slightly lower in the control area as compared to cutting areas, no significant differences exist between them.

These results indicate that throughfall precipitation had little influence upon the various levels of net herbaceous productivity. The amount of throughfall precipitation in the control area was approximately the same as in cutting areas. However, as stated earlier, herbaceous productivity was significantly higher in the latter areas.

Table 7. Correlation coefficients describing the relationship between percent open canopy, the percent of throughfall precipitation reaching the forest floor, and net herbaceous productivity.

Treatment	Correlation coefficient Russ 1972	Correlation coefficient Anderson et al. (1968)
Net productivity--percent throughfall		
Shelterwood	.43	
Groupcut	.08	
Control	-.22	.84
Clearcut	.30	
Net productivity--percent open canopy		
Shelterwood	-.23	
Groupcut	.43	
Control	-.02	.75
Percent throughfall--percent open canopy		
Shelterwood	.34	
Groupcut	.48	.81
Control	-.25	

Table 8. Mean throughfall precipitation (mm) reaching the forest floor during the period July 19-September 14, 1972.

	Control	Shelterwood	Groupcut	Clearcut
Ppt.	47	54	53	55

The remaining two sets of correlation coefficients in Table 7 describe the relationship between percent open canopy, percent throughfall precipitation, and net productivity. These coefficients also proved nonsignificant.

Since Anderson et al. (1969) found very strong correlation coefficients compared to the weak coefficients in this study, a careful re-examination of the Wisconsin study was done. It showed that several of the field conditions were similar to those in the present study area. Light intensities, 7-19 percent of full sunlight, were the same for both sites. Percent throughfall precipitation and the amount of herbaceous cover were also very similar.

There were also some differences between the two studies. A much greater range of percent open canopy was observed in Wisconsin, 15-50 percent, as compared to the control areas at Russ Forest at 7-18 percent. The Wisconsin study took place in a pine forest while Russ Forest is a deciduous hardwood stand. The recording of

the herbaceous response also differed. Total leaf area was measured in $\text{cm}^2 \text{ m}^{-2}$ in Wisconsin while net productivity was recorded in gm m^{-2} at the Russ study. However, these two sets of data should be comparable since leaf area can be converted to dry weight.

Soil on the Wisconsin site, is classified as Vilas sand, a soil of pitted outwash origin, overlying crystalline bed rock. Weathering and eluviation have improved the texture of the B horizon to a loamy sand. The Kalamazoo and Oshtemo soils at Russ Forest are well drained sandy loams. These soils have a much higher percentage of silt and clay than does the Vilas sand.

Differences in predominant overstory vegetation and soils, as well as greater variability in percent of open canopy coverage partially account for the lack of good comparisons between these two study sites. These site differences probably influence soil moisture greatly and whereas soil moisture was limiting in the Wisconsin study, it was not limiting in the Russ Forest study.

A basic tenet underlying the Anderson study is that the distribution of rhizomes and roots of herbaceous plants is mainly in the upper mineral or lower organic horizons where drying from the surface is minimal and recharge from showers is frequent. Since the roots of these herbaceous plants cannot draw on moisture from the water table, one would expect the productivity of these

plants to be very responsive to patterns of surface recharge in a soil where moisture in the upper horizons is frequently in critical amounts. The Wisconsin study never explicitly states whether soil moisture frequently reached limiting amounts, but the Vilas sand of the study site is a droughty soil, and soil moisture could indeed become limiting.

At Russ Forest, numerous gravimetric moisture samples of the upper 15 cm of soil were taken throughout the summer of 1972 (Table 9). The lowest percent moisture reading recorded in the control areas was about 8.3 percent by weight. This is approximately 4.0 atmospheres of tension (see Table 10). Fifteen atmospheres of tension is considered the wilting point. All other soil moisture values ranged from 14.5 to 21.7 percent by weight; 21.7 percent being field capacity. Thus it appears that during the study period, soil moisture in the upper 15 cm of the profile was rarely in limiting supply.

In addition, 1972 was a dry year, only 16.2 cm of rain recorded for June, July and August compared to the 30 year average of 27.2 cm. Therefore, the relative abundance of soil moisture cannot be attributed to an unusually wet season. Of course, gravimetric soil moisture data alone cannot conclusively prove whether soil moisture was or was not in limiting supply.

Table 9. A record of summer precipitation (inches) and percent soil moisture by weight taken simultaneously in various cutting treatment areas.

Date	Pot.	Control	Group Selection	Shelterwood	Clearcut
June 29	9.9				
30	1.0				
July 1		21.74			19.64
2					
3	2.5				
4					
5					
6					
7					
8	2.3				
9					14.44
10	.3				
11		14.15			
12	1.5	13.98			
13	3.6				
14	15.2				
15					
16					
17					19.12
18	22.0				
19			20.80		
20	2.3				
21					
22					
23					
24		20.40	14.94	18.32	22.68
25					
26		19.57	23.74		
27	10.9				
28	.3				
29					
30					
31		15.06	13.41	14.80	21.97
August 1					
2	4.6				
3	.8				
4	.3				
5					
6					
7	1.3				
8	3.0				
9	6.8				
10					
11					
12					
13					
14	6.8				
15					
16		14.50	14.87		13.94
17					
18		15.65	11.50	18.73	13.30
19	.3				
20					
21					
22		8.28	8.26	10.22	14.06

Table 10. Textural analysis and moisture content (% by weight) at several tension levels for a composite soil sample of all plots.

Sand	Texture % Silt	Clay	Soil Moisture Tension Atmospheres					
			1/3	1/2	2/3	1	5	10
63	26	11	21.7	18.1	16.5	13.3	7.9	6.5

If soil moisture was not limiting at Russ Forest, this would account for the weak correlation between canopy openings, throughfall precipitation and herbaceous productivity. It appears that the levels of herbaceous productivity are randomly distributed in relation to canopy openings. Therefore, it is very likely that the strong relationship Anderson et al. (1969) found between percent open canopy, percent throughfall precipitation, and herbaceous productivity cannot be routinely extrapolated to other areas.

CHAPTER VII

SHIFTS IN SPECIES COMPOSITION AND STRUCTURE

Species Dominance and Leaf Area in Cutting Treatment Areas

By taking successive measurements on the permanent 3 m x 3 m plots before and after cutting, two types of data are available: increases or decreases in leaf area for each species and the proportion of total leaf area occupied by that species. Table 11 shows the results of the 1971 and 1972 surveys for all treatments. Mean leaf areas, expressed as percent of one m² accompanied by their standard errors are given for each of the 37 species recorded. "T" tests of differences between the 1971 and 1972 means are also shown.

Parthenocissus quinquefolia dominated the herbaceous layer the year before cutting (1971). This species accounted for 63 percent of the total herbaceous leaf area. Four other predominant species: Ulmus rubra, Viola spp., Osmorrhiza claytonia, and Circaea quadrisulcata accounted for another 18 percent of the leaf area.

Table 11. Changes in mean leaf area (percent of 1 m^2) for each species in cutting treatment areas between the years 1971 and 1972.

		Mean leaf area and standard error 1971	Mean leaf area and standard error 1972	Difference 1971-1972	"T" sig. ¹	Changes in proportion 1971 to 1972
Herbs						
1	<i>Circaea quadrisulcata</i>	3.86 (.98)	10.81 (1.92)	6.95	**	+ 3.8
* 2	<i>Cirsium</i> spp.	.00 (.00)	.34 (.32)	.34		+ .2
* 3	<i>Erigeron canadensis</i>	.00 (.00)	2.05 (.68)	2.05	**	+ 1.7
4	<i>Galium circaeazans</i>	.51 (.20)	1.26 (.38)	.76		+ .4
5	<i>Geranium robertianum</i>	1.40 (.67)	2.51 (.46)	1.10		+ .3
6	<i>Geum canadensis</i> and <i>Sanicula canadensis</i>	.65 (.20)	2.61 (.57)	1.96	**	+ 1.5
* 7	<i>Hedeoma pulegioides</i>	.00 (.00)	.29 (.14)	.29		+ .2
8	<i>Hydrophyllum canadenses</i>	.00 (.00)	.01 (.01)	.01		
* 9	<i>Lactuca saligna</i>	.00 (.00)	.71 (.21)	.71	**	+ .6
10	<i>Osmorrhiza claytonia</i>	2.25 (.33)	3.61 (.91)	1.35		
*11	<i>Oxalis stricta</i>	.00 (.00)	1.25 (.33)	1.25	**	+ 1.1
12	<i>Parthenocissus quinquefolia</i>	46.51 (4.49)	37.94 (3.74)	8.57		-32.2
13	<i>Phryma leptostachya</i>	1.31 (.35)	.94 (.28)	.37		- 1.0
*14	<i>Physalis subglabriata</i>	.00 (.00)	.17 (.08)	.17	*	+ .1
*15	<i>Phytolacca americana</i>	.00 (.00)	12.55 (1.93)	12.55	**	+10.6
16	<i>Poaceae</i> (species group)	.62 (.30)	3.04 (.54)	2.42	**	+ 1.7
17	<i>Podophyllum peltatum</i>	.26 (.15)	3.57 (.99)	3.30	**	+ 2.6
*18	<i>Polygonatum canaliculatum</i> and <i>Smilacina racemosa</i>	.22 (.09)	1.09 (.45)	.87		+ .6
19	<i>Polygonatum sagittatum</i>	.00 (.00)	1.24 (.63)	1.24	**	+ 1.1
20	<i>Rhus radicans</i>	.85 (.25)	1.02 (.27)	.17		- .3
21	<i>Tovara virginiana</i>	1.76 (.80)	4.19 (1.23)	2.43		+ 1.2
22	<i>Viola</i> spp.	3.80 (.83)	3.38 (.47)	.41		- 2.4
Trees						
23	<i>Acer rubrum</i>	.33 (.11)	.56 (.16)	.23		+ .1
24	<i>Acer saccharum</i>	1.03 (.24)	3.28 (.63)	2.25	**	+ 1.4
25	<i>Carya cordiformis</i>	.23 (.13)	.00 (.00)	.23		- .3
26	<i>Cornus florida</i>	.66 (.33)	2.72 (.77)	.29		+ .2
27	<i>Ostrya virginiana</i>	.00 (.00)	.40 (.26)	.40		+ .3
28	<i>Prunus serotina</i>	.18 (.08)	1.10 (.19)	.92	**	+ .3
29	<i>Prunus virginiana</i>	.68 (.22)	1.05 (.38)	.37		
30	<i>Quercus alba</i>	.13 (.05)	.10 (.04)	.03		- .1
31	<i>Quercus rubra</i>	.13 (.06)	4.59 (.66)	4.46	**	+ 3.7
32	<i>Sassafras albidum</i>	.17 (.07)	1.73 (.68)	1.56	*	+ 1.2
33	<i>Ulmus rubra</i>	3.06 (.80)	3.82 (.63)	.76		- 1.0
Shrubs						
34	<i>Crataegus</i> spp.	.04 (.03)	.08 (.08)	.04		
35	<i>Ribes</i> spp.	.54 (.15)	1.19 (.50)	1.36	*	+ .9
36	<i>Rubus</i> spp.	.02 (.20)	1.94 (.56)	1.92	**	+ 1.6
37	<i>Viburnum lentago</i>	.71 (.22)	.00 (.00)	.71	**	- 1.0

*Invading species.

¹Test of significance between 1971 and 1972 means.

The remaining 28 percent was distributed among the other 33 species present. Although Parthenocissus quinquefolia dominated the herbaceous layer in terms of total leaf area, it was positively correlated at the 0.01 level, with all the major herbaceous species. Parthenocissus quinquefolia and all other herbaceous species were negatively correlated with woody species but not at a significant level. Judging from the correlation matrix for all species and knowledge of the area, it appears that the special distributions of all species are arranged in a generally random pattern. After cutting (1972), Parthenocissus quinquefolia still remained the largest component of the herbaceous leaf area, 32 percent. However, two other species: Phytolacca americana and Circae quadrisulcata were major codominants, collectively comprising 20 percent of the total leaf area. Four other major species: Osmorrhiza claytonia, Tovara virginiana, Ulmus rubra and Quercus rubra contributed another 14 percent. The above 7 species accounted for 56 percent of the total leaf area.

A comparison of the above data with the 1971 survey indicates that canopy removal caused a shift in the proportion of leaf area occupied by each species. This shift is shown in the right hand column of Table 11. Most resident species (those present before cutting) and invading species increased their proportion of total leaf

area at the expense of Parthenocissus quinquefolia which decreased 32 percent. These proportional shifts of leaf area resulted in a more equitable distribution of herbaceous leaf area among all species.

The three dominant species: Parthenocissus quinquefolia, Circaea quadrisulcata, and Phytolacca americana were negatively correlated with one another, but these correlations were not significant. The above three species were negatively correlated with all woody species and positively correlated with all herbaceous species, both correlations significant at the 0.01 level. Aside from these generalizations, there are no apparent groups of herbaceous or woody species associated with any of the dominant species. Plot size greatly influences correlations and a smaller plot than the 3 m x 3 m size used here would probably produce different results. The correlation matrix for the 1972 survey is similar to that of the 1971 survey.

Invading species (those not present before cutting) showed a significant increase in leaf area (Table 11). Hedeoma pulegioides is the only exception. Many of the resident species also had a significant increase in leaf area. Total leaf area increased from $0.72 \text{ m}^2 \cdot \text{m}^{-2}$ in 1971 to $1.18 \text{ m}^2 \cdot \text{m}^{-2}$ in 1972. It is interesting to note that of the total increase of $0.46 \text{ m}^2 \cdot \text{m}^{-2}$, 57 percent ($0.26 \text{ m}^2 \cdot \text{m}^{-2}$) can be attributed to invading species. The remaining 43 percent ($0.20 \text{ m}^2 \cdot \text{m}^{-2}$) came from resident species.

Those specific resident herbaceous species with significant increases of leaf area (numbers 1, 6, 16, 17) were examined further. They are all species described as occurring in open woods, thickets, borders, and small openings (Fernald 1950). The study area is a second growth stand and had been grazed up until 40 years ago. Therefore, it is not surprising that the above herbaceous species were present and that canopy removal did not present an unacceptable shock. Perhaps the herbaceous species were being slowly eliminated as the stand proceeded toward a climax state. Cutting treatments changed the environment to a more optimal state for these herbaceous species, and thus we observed a large increase in their leaf area.

Eight resident tree and shrub species also had significant increases in leaf area. All of these species except Prunus serotina are classified as high or intermediate in tolerance (Harlow and Harrar 1958). It is well known that these species respond to canopy removal and an increase in their leaf area was expected. The large increase in Quercus rubra leaf area (number 31) was due to the large acorn crop in the fall of 1971 rather than to an increase in growth of established seedlings.

Species Dominance and Leaf
Area in Control Areas

Table 12 shows the results of the 1971 and 1972 surveys for control areas. The format of data presentation is the same as in Table 11. Characteristics of the herbaceous layer in control areas were identical to those found in treatment areas for the 1971 pre-cutting survey. Parthenocissus quinquefolia was the single dominant species. Spatial distributions of all species are arranged in a random pattern.

Little change was observed in control areas between the 1971 and 1972 surveys. Parthenocissus quinquefolia was again the dominant species. Only three species (numbers 16, 21, 33) had significant shifts in leaf area, and all three were resident species. In fact, none of the invading species found in treatment areas were present in control areas.

The data on Podophyllum peltatum is somewhat misleading. The large increase of leaf area is due to a sample plot being located in the midst of a clone of these species. In the 1971 survey, this plot was not surveyed until late August, and most of the plant tops had already died. The 1972 survey was conducted in July, and the Podophyllum peltatum plant tops were still alive.

There were some shifts in the proportion of total coverage occupied by each species, possibly in the

Table 12. Changes in mean leaf area (percent of 1 m^2) for each species in control areas between the years 1971 and 1972.

	Species	Mean leaf area and standard error 1971	Mean leaf area and standard error 1972	Difference 1971-1972	"T" sig. ¹	Changes in proportion 1971 to 1972
Herbs						
1	Circaea quadrisulcata	10.89 (.235)	7.39 (.171)	3.50		- 1.2
* 2	Cirsium spp.					
* 3	Erigeron canadensis					
4	Galium circaeazans	.14 (.14)	.06 (.06)	.08		- .2
5	Geranium robertianum	2.33 (1.16)	.67 (.26)	1.66		- 1.5
6	Geum canadensis and Sanicula canadensis	1.67 (.48)	2.56 (.68)	.89		+ 1.9
* 7	Hedeoma pulegioides					
8	Hydrophyllum canadense	4.17 (1.96)	2.00 (.83)	2.17		- 1.6
* 9	Lactuca saligna					
10	Osmorrhiza claytonia	2.53 (.70)	1.58 (.32)	.95		- .5
*11	Oxalis stricta					
12	Parthenocissus quinquefolia	57.39(10.57)	43.56 (7.34)	13.83		+ .1
13	Phryma leptostachya	.42 (.31)	.64 (.26)	.22		+ .5
*14	Physalis subglabriata					
*15	Phytolacca americana					
16	Poaceae (species group)	.11 (.11)	.03 (.03)	.08		- .1
17	Podophyllum peltatum	.00 (.00)	2.06 (.72)	2.06	**	+ 3.0
18	Polygonatum canaliculatum and Smilacina racemosa	.91 (.14)	.22 (.15)	.04		+ .1
*19	Polygonatum sagittatum					
20	Rhus radicans	.14 (.14)	.00 (.00)	.14		- .2
21	Tovara virginiana	.69 (.69)	1.06 (.64)	.37		+ .7
22	Viola spp.	2.28 (.76)	1.55 (.41)	1.87	*	- .3
Trees						
23	Acer rubrum	.06 (.06)	.06 (.04)	.00		
24	Acer saccharum	.69 (.27)	1.00 (.31)	.31		+ .7
25	Carya cordiformis	.28 (.19)	.00 (.00)	.28		- .3
26	Cornus florida	1.69 (.94)	2.86 (1.30)	1.17		+ 2.3
27	Ostrya virginiana					
28	Prunus serotina	.97 (.37)	.11 (.09)	.86		- .9
29	Prunus virginiana	.75 (.45)	.14 (.09)	.61		- .6
30	Quercus alba	.28 (.17)	.17 (.12)	.11		- .1
31	Quercus rubra					
32	Sassafras albidum					
33	Ulmus rubra	1.56 (.48)	.92 (.36)	.64	*	- .4
Shrubs						
34	Crataegus spp.					
35	Ribes spp.	1.67 (.49)	1.06 (.44)	.61		- .3
36	Rubus spp.					
37	Viburnum lentago	.58 (.30)	.00 (.00)	.58		- .6

*Invading species.

¹Test of significance between 1971 and 1972 means.

direction of a climax community. However, shifts in herbaceous species similar to these have been found in a mature undisturbed Acer saccharum-Fagus grandifolis stand (Schneider 1966). Permanent plots had been observed in the previous stand for 30 years and it was concluded that the changes were non-directional.

Total leaf area in control areas dropped from about $0.92 \text{ m}^2 \cdot \text{m}^{-2}$ in 1971 to $0.70 \text{ m}^2 \cdot \text{m}^{-2}$ in 1972. There is no apparent explanation for this drop except to attribute it to annual variation.

These data from the control plots show that in the absence of canopy removal, a shift in species composition is slight. The lack of long term data, and the fact that grazing was excluded only 40 years ago, makes it difficult to characterize this herbaceous vegetation as approaching a climax state. The usefulness of data from these areas is in comparison with cutting treatment areas. From this comparison it can readily be seen that canopy removal definitely causes a shift in species composition and dominance.

Shift in Species Composition

Canopy removal had a very significant effect in increasing herbaceous productivity. One might expect this higher productivity to be associated with a collection of new invader species not present before cutting.

However, such a large shift in species composition did not take place. In a comparable old, second growth hardwood stand near East Lansing, Michigan, it was found that of the total of 144 species recorded over the whole stand, only 35 species were common to both clearcut and undisturbed areas (S. N. Stephenson, personal communication).²

A number of possible explanations exist as to why the species composition shift was only of moderate proportions in this particular study:

1. Much of the ground in the treatment cutting areas was not available for colonization. The 1971 survey showed that each plot contained a leaf area of about $0.92 \text{ m}^2 \cdot \text{m}^{-2}$. This is not to imply that $1.0 \text{ m}^2 \cdot \text{m}^{-2}$ is full site occupancy. Values as high as $3.2 \text{ m}^2 \cdot \text{m}^{-2}$ were recorded, but it does show that the forest floor is not comparable to the bare ground found in abandoned fields. Also, logging slash physically occupied much of the site. In many cases, this slash created microsites that appeared not too unlike the control areas in regard to shade, temperature, and relative humidity.
2. Time is an important factor. Dryness (1973), working in a clearcut area in the Cascade

²S. N. Stephenson, Dept. of Botany, Michigan State University.

Mountains of Oregon, found that invading herbaceous species dominated the site from the second through the fourth growing seasons. By the fifth year, residual herbaceous species had regained dominance. Perhaps a similar sequence will take place in this eastern deciduous forest.

3. McIntosh (1970) suggests that species do not grow exponentially and saturate a site. The occupancy of a species in any area is restricted by a combination of suppression and competition among all species having access to the site. As long as the resident species of a site can respond to changes in the microenvironment, they will surely be sufficiently competitive to prevent a large influx of invading species. Such seems to be the case in this study.
4. Advance reproduction, saplings and stump sprouts, quickly occupied large areas providing shade and competition for available resources.
5. Certainly, allelochemical reactions, internal regulation of germination, and seed availability all have an effect on what species will invade a site, but little is known of how these factors work.

Species Diversity

Diversity is property that can be used to measure changes in species composition and structure. Such changes are reflected in the number of species (the variety component) and how the individuals are distributed among the species (the equitability component). The two measures of diversity used here, the Shannon-Wiener function (H') and Simpson's index (D), combine both of these components into one value.

Canopy removal increased the mean diversity of herbs in treatment areas from $H'=2.48$ before cutting to $H'=3.88$ after cutting. These areas had a rather large increase in the number of species per plot; 4.46 m^{-2} in 1971 to 8.69 m^{-2} in 1972. Since only 8 new invading species were included in the 1972 survey, increasing the total number of species from 29 to 37, it seems likely that the large increase in number of species after a cutting is not entirely due to the new invaders. The spatial patterns of the resident species have also shifted, spreading these species more equally over all plots.

Figure 4 illustrates this spatial shift in species composition. Resident species, numbers 1, 5, 7, 16, 17, 22, 23, 24, 26, and 28 greatly increased in the number of quadrants occupied after cutting. These species are quite adaptable to successfully invading newly available sites created by canopy removal.

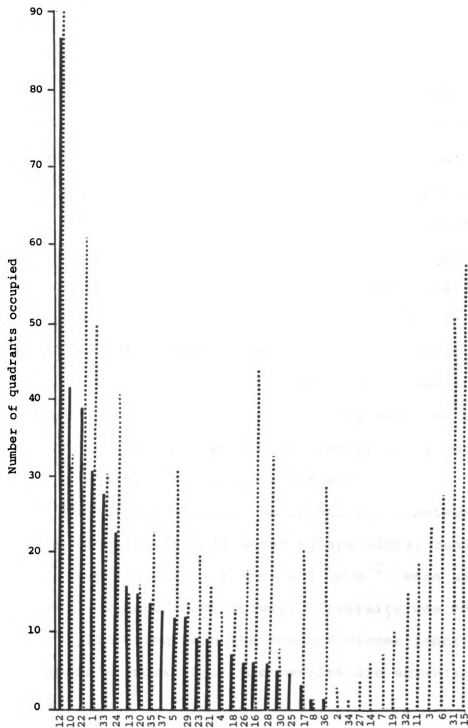


Figure 4. Number of quadrants occupied by species in cutting treatment areas during 1971 (black line) and 1972 (dash line).

Mean diversity in the undisturbed control areas remained very stable; $H'=2.27$ in 1971 and 2.26 in 1972. These areas did have a slight increase in number of species per plot; 4.11 m^{-2} in 1971 to 4.89 m^{-2} in 1972. This rather small shift is probably due to random new establishments of resident species. Figure 5 shows minor shifts in the number of quadrants occupied by each species. These shifts probably account for the increase in species number.

The increase in mean diversity and productivity in the same treatment areas indicates a positive relationship between diversity and productivity. However, Margalef (1969) suggests that these two parameters vary in an inverse logarithmic relationship. Odum (1971) feels that while productivity affects species diversity, the two are not related in any simple manner. He gives examples of very productive communities with high diversity: a coral reef, or low diversity: a temperate estuary.

To further examine the relationship between diversity and productivity, 14 meter square plots, ranging in productivity from 11 gm m^{-2} to 507 gm m^{-2} , were selected from the 1972 herbaceous survey. Diversity was calculated for each plot using both the Shannon-Wiener function (H') and Simpson's index (D). The results are shown in Table 13.

The number of species per plot first increases with increasing productivity, then levels off at a value

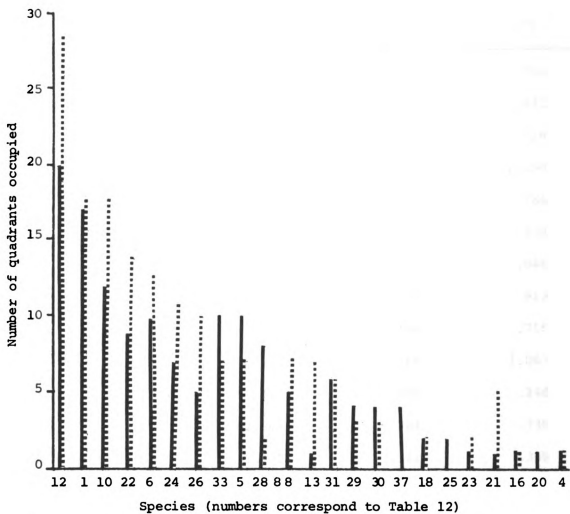


Figure 5. Number of quadrants occupied by various species in control areas during 1971 (black lines) and 1972 (dash lines).

Table 13. Changes in evenness and three measures of diversity; number of species, Shannon-Weiner function, and Simpson's index, in relation to changes in net productivity.

Dry Weight gm.m ⁻²	Number of Species	Shannon-Weiner function (H')	Simpson's index (D)	Evenness H'/H'max. (J)
11	5	1.827	.732	.786
19	5	1.901	.732	.822
40	6	1.339	.844	.518
50	6	2.973	.634	1.150
75	9	2.485	.749	.784
106	11	1.551	.548	.409
132	12	3.033	.435	.846
165	16	3.651	.915	.913
196	14	2.727	.786	.716
229	17	4.362	.918	1.067
292	11	1.458	.569	.348
303	12	2.641	.784	.736
425	10	1.192	.321	.359
507	12	1.538	.448	.429

of 17, and finally drops off slightly as productivity reaches its highest levels. The two diversity indices follow a similar pattern. The highest diversity is found in the intermediate plots, where productivity is between 132-229 gm m⁻². As productivity increases to its highest levels, diversity drops off sharply. Some of the lowest diversity values are found in the two most productive plots. These plots still contain a rather large number of species, but productivity is concentrated in one species, Phytolacca americana, as revealed by the low evenness values (J). This is why the diversity indices are so low in these same plots.

The two indices of diversity coincide rather closely (Figure 6). It is only in the three least productive plots that the two indices widely diverge. Both indices are rather insensitive to rarer species. Perhaps some inherent characteristic of each index causes them to diverge in such cases.

The decrease in diversity on the most productive of the 14 selected plots seems to contradict the general observation that mean diversity increases with productivity. Diversity, in this study, was calculated only for the 37 most abundant species. The data here only serves to emphasize Odum's generalization that the relationship between diversity and productivity is not clear.

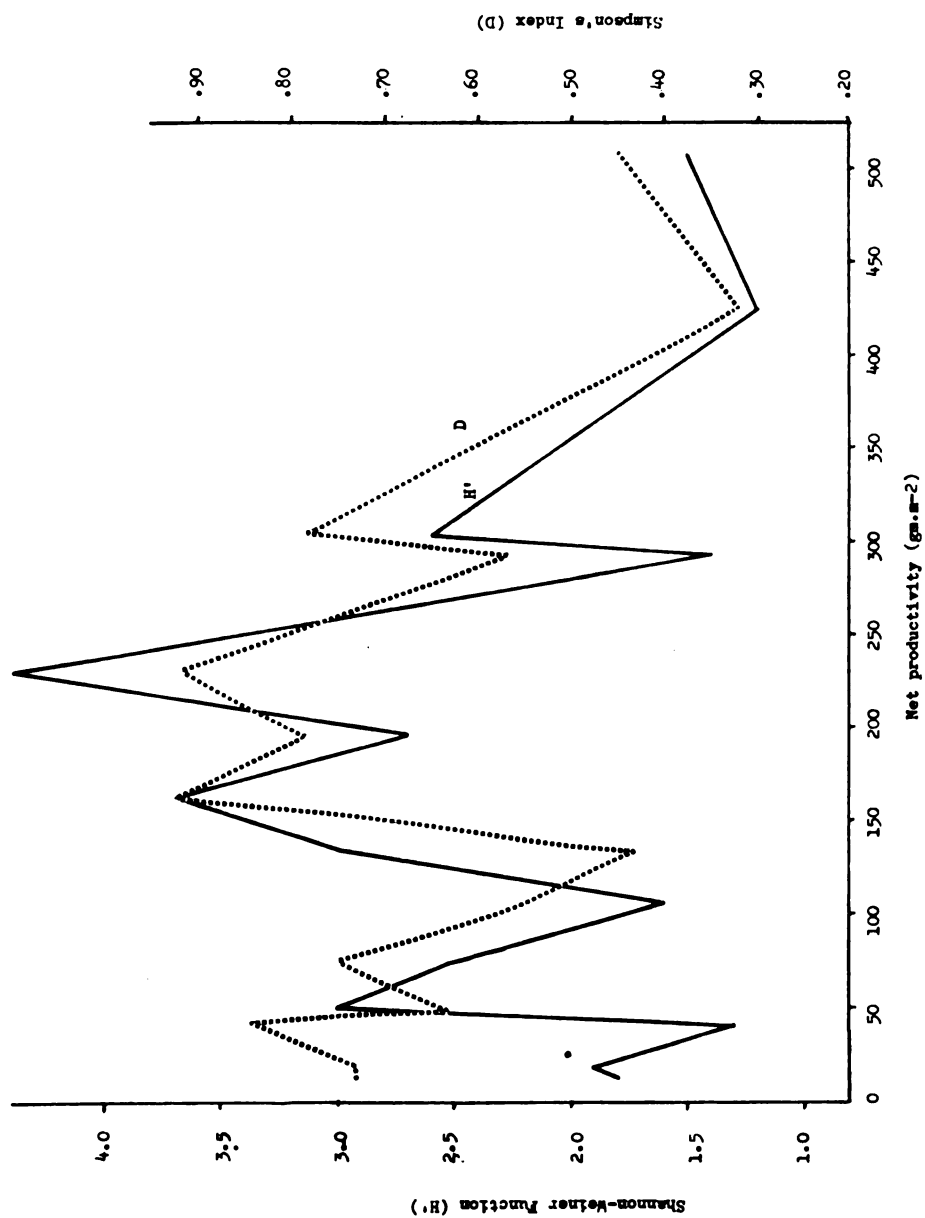


Figure 6. Variation in diversity, as measured by the Shannon-Weiner function and Simpson's index, with increasing above ground net productivity.

It should be noted that the data from these 14 selected plots again illustrates the large amount of spatial variability in productivity and diversity that can be encountered in cut-over areas. This variability was previously noted in regard to environmental parameters.

CHAPTER VIII

SUMMARY

Comparisons of above-ground net productivity of the herbaceous stratum at Russ Forest with other ecosystems of various ages, densities, and locations (Table 14). The uncut control areas of Russ Forest had a high-intermediate productivity value of $37 \text{ gm m}^{-2} \text{ yr}^{-1}$. This value is slightly lower than for other forest sites in Tennessee and Nova Scotia (numbers 2, 3, 4, 5, 6) and much higher than in forest sites at Brookhaven Hubbard Brook, Santa Catalina Mts., Louisiana, and Germany (numbers 7, 8, 9, 10, 11).

The cutting treatment areas at Russ Forest had an average productivity of $153 \text{ gm m}^{-2} \text{ yr}^{-1}$. This figure is high compared to partially cut stands in Louisiana (number 11), but low compared to an old field the first year after abandonment (number 14).

These comparisons, although general, do illustrate that the productivity of the herbaceous layer at Russ Forest was above average before cutting. It must still be determined if this high productivity had a direct influence upon the number of new invading species appearing the year

Table 14. Comparisons of above ground net herbaceous productivity ($\text{gm m}^{-2} \text{yr}^{-1}$) between Russ Forest and other ecosystems. All data concerns only the herbaceous strata.

Ecosystem	Aboveground productivity $\text{g m}^{-2} \text{yr}^{-1}$
1. Russ Forest (control areas), 80 yrs., 31 $\text{m}^2 \text{h}^{-1}$	37
2. Mixed hardwood forest (Oak Ridge, Tenn.), 4 yr. old opening	45(1)
3. Red-white oak forest (Smokey Mts., Tenn.), climax stand, 22 $\text{m}^2 \text{h}^{-1}$	35(2)
4. Red oak forest (Smokey Mts., Tenn.), climax stand, 24 $\text{m}^2 \text{h}^{-1}$	52(2)
5. Dense hardwood (N. Brunswick- Nova Scotia)	51(3)
6. Open mixed hardwood-conifer (Nova Scotia)	44(3)
7. Fagetum forest (West Germany), 120 yrs. dense	1(4)
8. Oak-pine woodland (Brookhaven, N.Y.), 56 yrs, 16 $\text{m}^2 \text{h}^{-1}$	2(5)
9. Pine-oak woodland (St. Catalina Mts., Calif.), climax stand, 26 $\text{m}^2 \text{h}^{-1}$	3(6)
10. Sugar maple, beech, birch forest (Hubbard Brook, N.H.), 67 yrs., 23 $\text{m}^2 \text{h}^{-1}$	10-16(max. 29) (7)
11. Pine-hardwood forest (Louisiana) evenage plantation, 17 $\text{m}^2 \text{h}^{-1}$	10(8)
12. Russ Forest (cutover areas)	153
13. Pine-hardwood forest after elimination of hardwoods (Louisiana)	62(8)
14. Oldfield first year after abandonment (Georgia)	494(9)

1. Cristofolini, 1970
2. Whittaker, 1966
3. Telfer, 1971
4. Eber, 1972
5. Whittaker and Woodwell, 1969

6. Ibid.
7. Siccama et al., 1970
8. Blair, 1971
9. Odum, 1960

after cutting. Do areas of high productivity have little species change after cutting, while areas of low productivity have a high species change after cutting?

Data reported by Dryness (1970) implies that areas of high productivity more fully occupy a site and there is less available space for invading species. In an unproductive site, 11 species were not present in both of the periods: one year before cutting and 7 years after cutting. In a highly productive site, only 5 species were not present in both the same two periods. At Russ Forest, 8 principle invading species were observed. These species constitute 22 percent of the total species observed. Although this data does not suggest that 8 new species is a high or low number, it can be seen that there was no large change of species. All 29 of the resident species were found after cutting.

Analysis of the correlation matrix for all species showed no distinct groupings of species in the herbaceous strata. This was true for both the precutting and post-cutting communities. Species composition remained very stable in the control area, while in cutting treatment areas, 8 invading species and a number of resident species increased their proportion of the total coverage at the expense of the dominant species, Parthenocissus quinquefolia.

It is difficult to project future shifts in species composition based only on two years' data. A visual survey in June, 1973, the second growing season after cutting, showed that grasses had greatly increased their coverage, especially in the more disturbed areas such as roads, skid trails and loading sites. Stump sprouts of Prunus serotina and Ulmus rubra have now attained heights of 2.5 m, and will soon begin to capture large portions of the solar nutrient and water resources. These sprouts can completely dominate a site as shown by Johnson (1971). In southern Wisconsin stump sprouts grew to a height of 5.8 m in four growing seasons.

At Russ Forest, stump sprouts may dominate portions of the cutting areas by the fourth or fifth growing season. What effect this will have on the herbaceous strata is difficult to say. On other areas, such as roads and loading sites which have no stump sprouts, herbaceous species should dominate longer.

It was emphasized that the cutting areas contained a mosaic of different microsites created by the distribution of slash. The conditions in these microsites range from hot and dry in exposed sites to cool and humid in very sheltered sites. This study did not specifically investigate the relationship between microsite conditions and herbaceous productivity. It was observed that under very large slash piles and in very exposed sites, the

level of herbaceous productivity was lower. It would be interesting to see the effect microsite conditions has on tree reproduction. Perhaps the manipulation of slash distribution could be a very useful tool in forest management creating microclimates to encourage desirable species and discourage undesirable ones.

The amount of basal area removed in each of the three treatments resulted in a similar herbaceous response. Herbaceous productivity was not significantly different between these treatments. Such a differential response of herbaceous productivity to canopy removal would probably have been observed had lesser amounts of basal area been removed as in single tree selection cuttings.

The dimension of time is a most important factor in a study of herbaceous response to canopy removal. It remains to be seen at just what time various herbaceous species will reach their peak abundance and then are replaced by other species. Results of this type will not be available until four to six years of data have been collected. Continuing annual surveys at Russ Forest are planned.

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