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Changes in tree species diversity after successive clearcuts in the Southern Appalachians

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Abstract

A 16 ha watershed in the Coweeta Basin was clearcut in 1939 and 1962. Vegetation was inventoried in 1934 and at about 7-year intervals to 1991. After the first clearcut, tree diversity remained high until after the second cut. Diversity based on density and basal area decreased significantly 14 years after the second clearcut and remained low through 1991. Diversity was highest in the early establishment stage of stand development, then declined at the intermediate stage with canopy closure. Evenness based on basal area declined more than evenness based on density because basal area of *Liriodendron tulipifera* increased substantially from 1977 to 1991. Trends in diversity were due to changes in evenness rather than changes in species richness.

Introduction

Clearcutting temperate deciduous forests, can change species composition (Parker & Swank 1982), thus influencing species diversity (Huston 1979; 1985) and other community and ecosystem properties (Pastor & Post 1986; Huston & Smith 1987). Diversity reflects the structural dynamics of a site relative to evolutionary history and patterns of disturbance. The maintenance of a diverse landscape, rich in community types and species, requires knowledge of the dynamics of ecosystems as well as the ecology of individual species. Conflicting hypotheses have been provided relating vegetation diversity to successional status: diversity fluctuates with successional sequence, being reported both as highest at intermediate stages (Huston & Smith 1987), or highest at the establishment and later phases where gaps are created by canopy mortality (Peet & Christensen 1988).

In this paper, we describe the effects of two successive clearcuts on overstory diversity and species richness. We also examine relationships between species diversity and basal area growth. The study area, Watershed 13 (WS13), is a 16.1 ha catchment at the Coweeta Hydrologic Laboratory in southwestern North Carolina, USA.

Methods

Site description

Leopold *et al.* (1985) described Watershed 13 in the Coweeta Basin in detail. It is a northeast-facing catchment in southwestern North Carolina, 35° 04′ 30″ N latitude, 83° 26′ W longitude. Elevation within the drainage ranges from 724 to 853 m, mean land slope is 49 percent, and mean annual precipitation is 1829 mm. Mean annual temperature is 12.6 °C, and average temperature is 6.7 °C in the dormant season and 18.5 °C in the growing season (Swift *et al.* 1988). Four soil types are present on the watershed: (1) Cullasaja-Tuckasegee (cove bottoms), a loamy-skeletal/coarse-loamy, mixed, mesic Typic Haplumbrepts; (2) Edneyville-Chestnut (lower slopes), a coarse loamy, mixed, mesic Typic Dystrochrepts; (3) Plott (middle slopes), a coarse loamy, mixed, mesic Typic Haplumbrepts; and (4) Evard-

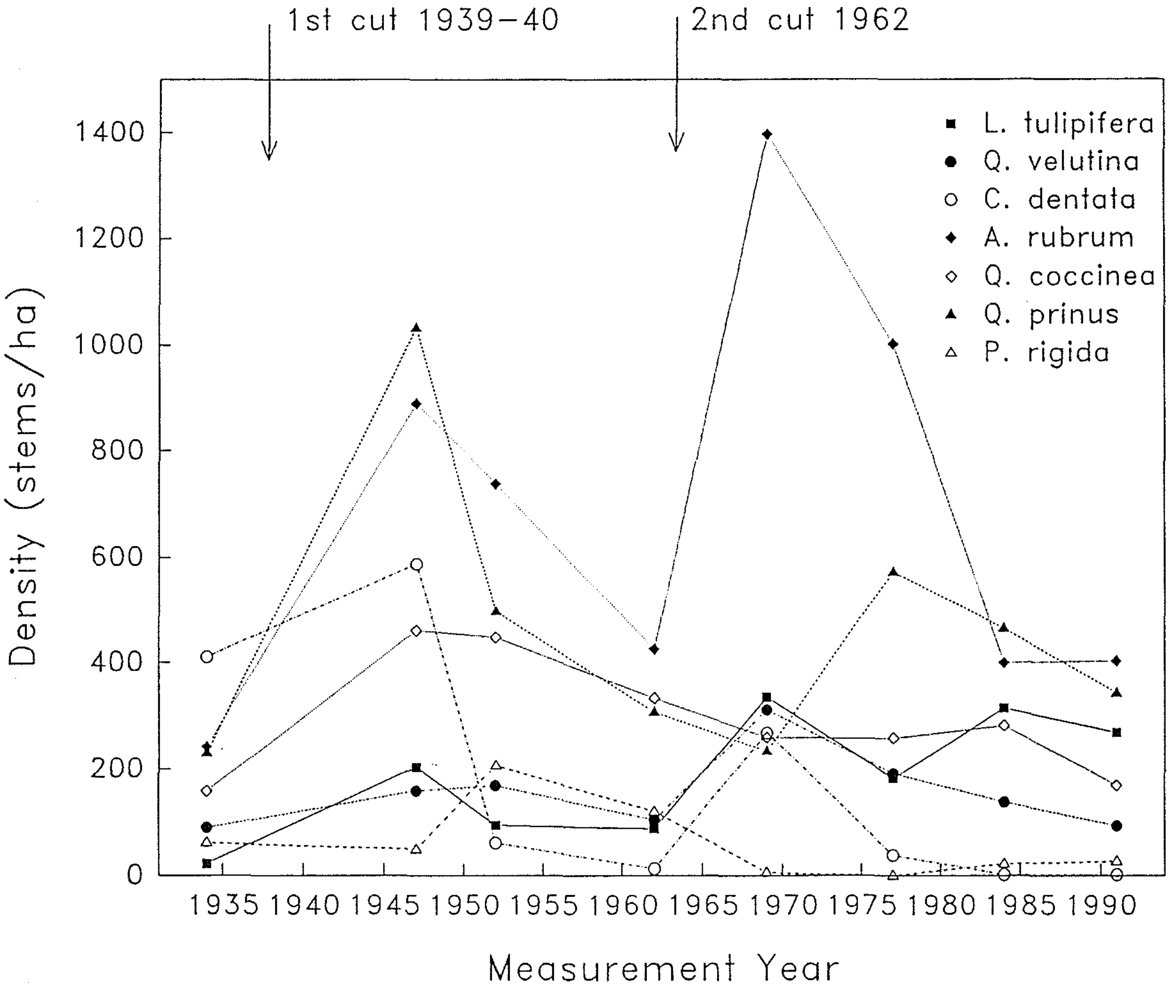

Fig. 1. Density of selected tree species in Watershed 13, Coweeta Basin from 1934 to 1991.

Cowee (upper slopes), fine-loamy, mixed, mesic Typic Hapludults.

Prior to 1923 when the US Forest Service purchased the land, the forest was heavily disturbed. Timber larger than 38 cm dbh was logged in 1919 throughout the Coweeta Basin (see Douglas & Hoover 1988 for a complete description of the history of the Coweeta Basin). All trees and shrubs on the entire drainage were cut in 1939–40 and again in late 1962. No trees or shrubs were removed after either clearcut and soil disturbance was minimal. No other treatments have occurred since 1934. Cuts were made primarily to study the effect of forest clearing on hydrologic processes (Swank & Helvey 1970; Swift & Swank 1981). After the second clearcut, vegetation was inventoried in 1962, 1969, 1977, 1984, and 1991.

Plot measurements

Leopold *et al.* (1985) described previous forest inventories in 1934, 1948, 1952, 1962, 1969, and 1977. A minimum of 19 sample plots (a range from 19 to 43) were taken for each inventory date and plot size ranged from 0.01 ha to 0.08 ha. The least intensive inventory occurred in 1948 with twenty 0.01 ha (10× 10 m) size plots. In the summer of 1981, twenty-six 0.02 ha (10× 20 m) permanent plots were systematically located over WS13 to sample the vegetation in three community types: Cove Hardwoods, Mixed Oak, and Oak-Pine (Leopold & Parker 1985). In 1984, 17 additional plots were added to the original 26 located in 1981. Diameters at breast height (dbh, 1.37 m aboveground) of all trees >5.0 cm dbh were measured in all 43 plots (Leopold *et al.* 1985). In 1991, 26 of the original 43

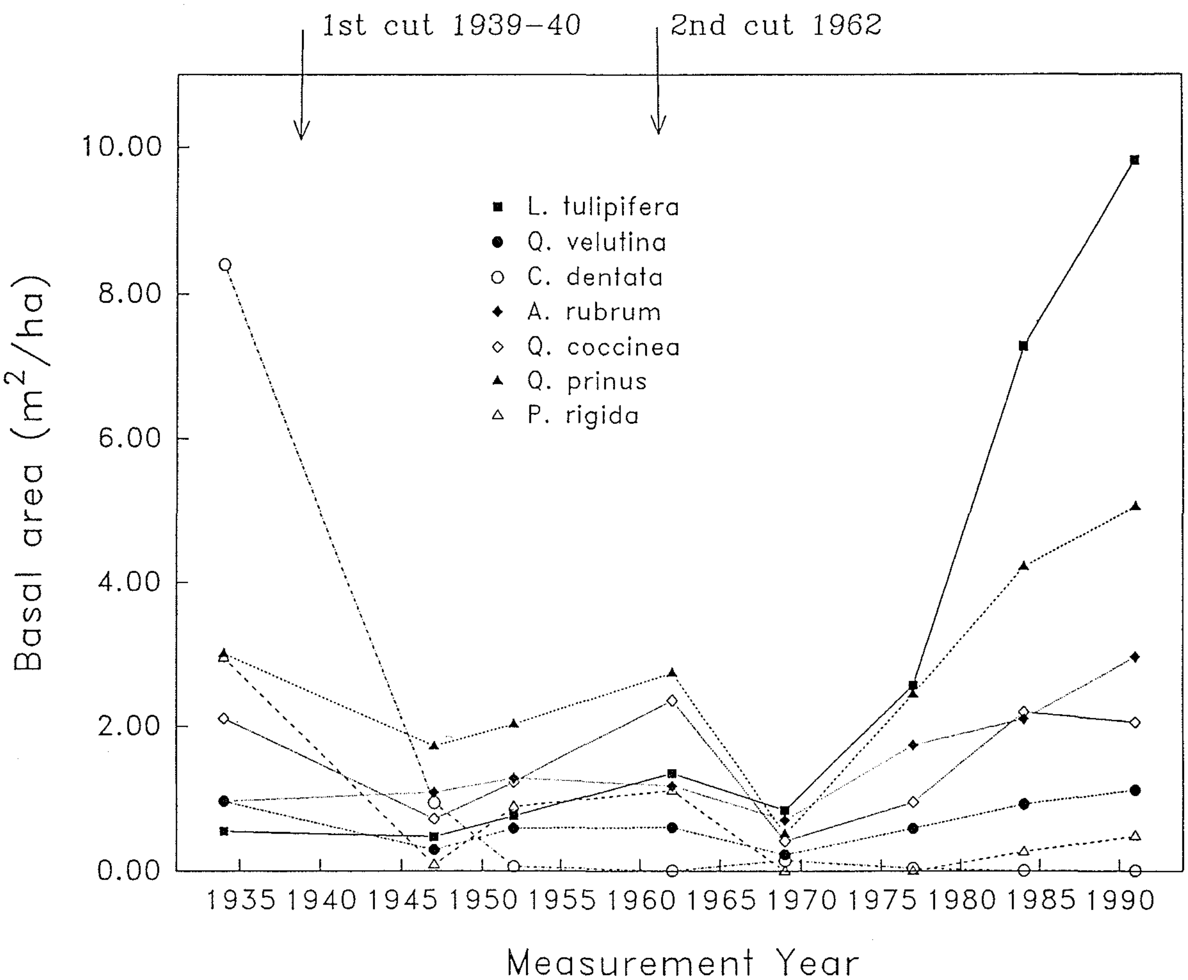

Fig. 2. Basal area of selected tree species in Watershed 13, Coweeta Basin from 1934 to 1991.

plots that were permanently marked were relocated and remeasured. Tree diameters were recorded in 2.5 cm interval classes during all inventories except 1984 and 1991 when trees were measured to the nearest 0.1 cm. The inventory data from 1934 included dead and dying *Castanea dentata* Marsh. infected by chestnut blight because those trees were still merchantable. Although inventories were not made on the same plots over the 57 year interval, all inventories included a reasonable sample size to estimate average density and basal area of tree species for this small watershed.

Data analysis

To evaluate species diversity, we computed Shannon-Weiner's index of diversity (H′), Pielou's (1966) evenness index (J′), and dominance-diversity curves (Magurran 1988). Shannon-Weiner's index was selected because it is a simple quantitative expression that incorporates both species richness and the evenness of species abundance. Because the calculated value of H′ alone does not show the degree to which each factor contributes to diversity, we calculated a separate measure of evenness (J′). Many of the *C. dentata* stems were dead at the time of the 1934 inventory and thus we calculated H′ and J′ with and without *C. dentata* in the species list for 1934 to evaluate the contribution of *C. dentata* in tree diversity for 1934.

Diversity index was calculated for both density (number of stems) and stem basal area at breast height per hectare: $H' = -\Sigma\, p_i \ln p_i$, where p_i = proportion of total density or of total basal area of species i. Species evenness based on density or basal area was calculated as: $J' = H'/H'_{max}$, where H'_{max} = maximum level of

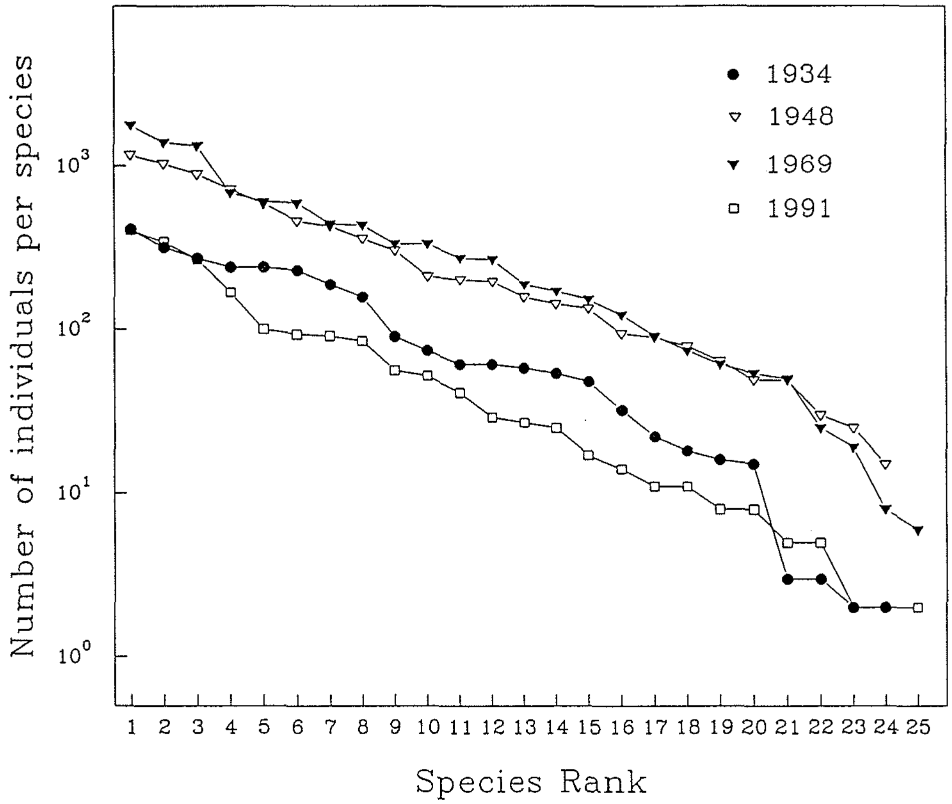

Fig. 3. Dominance-diversity curves for Watershed 13 based on density (number of individuals per species) for 1934, precut condition; 1947, 8 years after the first clearcut; 1969, 7 years after the second clearcut; and 1991, 29 years after the second clearcut.

diversity possible within a given population = ln (number of species). We compared diversity, basal area, and density of all trees >5.0 cm dbh for inventories from previously published data (Kovner 1955; Parker & Swank 1982; Leopold *et al.* 1985) and the present inventory (1991). We used pairwise t-tests (Magurran 1988) to examine the differences in tree diversity between inventories from 1934 to 1991.

In addition, we constructed dominance-diversity curves based on density and basal area (Whittaker 1965; Patil & Tallie 1982) to represent four of the inventory dates: 1934 (prior to clearcutting including *C. dentata*); 1947 (8 years after the first clearcut); 1969 (7 years after the second clearcut); and 1991 (29 years after the second clearcut). For communities with high species diversity or a high degree of evenness (low degree of dominance) curves are almost horizontal. For communities with low species diversity or a low degree of evenness (high degree of dominance) curves are nearly vertical (Whittaker 1965). To test for equality of slopes for the dominance-diversity curves, we ranked values for species with 1 being most dominant and the highest number being least dominant for each inventory date. The ranked value was considered the independent variable and log (basal area) or log (density) the dependent variable in PROC GLM/analysis of homogeneity-of-slopes model (SAS Institute 1987).

Results and discussion

Both anthropogenic and natural disturbances have shaped forest composition in Watershed 13. In addition to successive clearcutting, fire suppression and high-grade logging prior to 1934 influenced the vegetative community. The function and composition of southern Appalachian forests have also been significantly altered by the loss of American chestnut (Woods & Shanks 1957; Arends 1981; Day *et al.* 1988; Busing 1989). Simulation models suggest that leaf area and biomass of stands would be higher if chestnut had maintained its position in the forest (Shugart & West 1977).

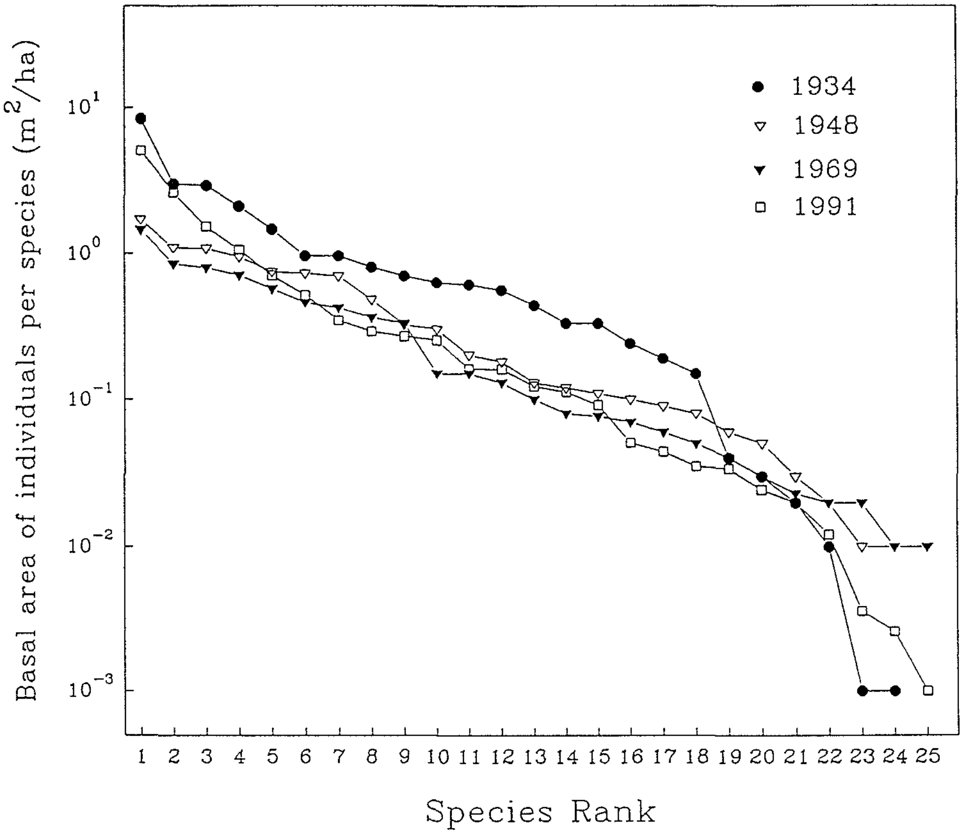

Fig. 4. Dominance-diversity curves for Watershed 13 based on basal area of individuals for 1934, precut condition; 1947, 8 years after the first clearcut; 1969, 7 years after the second clearcut; and 1991, 29 years after the second clearcut.

Prior to the clearcutting in 1934, *C. dentata* accounted for 16% of the stems and 34% of the basal area on WS13. It was the most common species. After the first clearcut, *C. dentata* density increased from 400 to about 600 stems/ha due to sprouting. It then decreased to near zero by 1952 due to the impacts of the chestnut blight, which was first noted in the Coweeta Basin in the early 1920's. *C. dentata* currently makes up about 0.1% of the basal area on WS13.

Density of *Acer rubrum* L. increased from about 400 stems/ha in 1962 to 1400 stems/ha 7 years after the second cut (1969), and *Liriodendron tulipifera* L. increased from 100 to 350 stems/ha (Fig. 1). Basal area of the four dominant species (*L. tulipifera*, *Quercus prinus* L., *Quercus coccinea* Muenchh., and *A. rubrum*) were similar to each other in 1969 (Fig. 2). By 1984, *L. tulipifera* basal area had increased dramatically; it now makes up 35% of total basal area on the watershed. Total basal area of WS13 has recovered to precutting levels, whereas density is below the precut condition (Table 1).

After the first clearcut, H′ and J′ based on density remained high until after the second clearcut and the removal of *C. dentata* from the species list in 1934 did not significantly change H′ based on density (Table 1). H′ and J′ based on basal area significantly increased after the first clearcut and remained high until 14 years after the second clearcut whereas H′ based on basal area without *C. dentata* in the species list in 1934 was not significant higher after the first clearcut. Although separating the effects of the first clearcut from the effects of *C. dentata* mortality due to the chestnut blight would be impossible due to the probable interactions of these two simultaneous disturbances, comparing H′ with and without *C. dentata* in the species list in 1934 demonstrates the importance of this species in WS13 prior to the chestnut blight. H′ based on density and basal area significantly decreased 14 years after the second clearcut (Table 1). J′ based on basal area declined more than J′ based on density because basal area of *L. tulipifera* increased substantially from 1977 to 1991 (Fig. 2).

Table 1. Density, basal area (BA), diversity (H′) and evenness (J′) based on density or basal area of tree species on Watershed 13 at Coweeta Hydrologic Laboratory from 1934 to 1991 (29 years after second clearcut).

	1934*	1948	1952	1962	1969	1977	1984	1991
	Precut	Years after first clearcut			Years after second clearcut			
		8	13	23	7	14	21	29
No. of plots	20	20	19	36	36	35	43	26
Plot size (ha)	0.08	0.01	0.08	0.08	0 .010	.050	.020	.02
Density (stems/ha)	2632 (2222)	7499	5068	3390	9518	4697	2330	1874
Species	25	24	25	27	24	21	27	25
Basal area (m^2/ha)	25.01 (16.52)	9.33	11.04	14.39	6.99	11.80	20.83	26.14
$H'_{Density}$	2.649a (2.625)	2.691a	2.613a	2.717a	2.676a	2.335b	2.462b	2.450b
$J'_{Density}$	0.823 (0.816)	0.847	0.812	0.824	0.842	0.779	0.756	0.752
H'_{BA}	2.313b (2.525)	2.590a	2.613a	2.612a	2.555a	2.338b	2.101bc	2.058c
J'_{BA}	0.719 (0.784)	0.815	0.812	0.792	0.804	0.780	0.645	0.632

* 1934 inventory included dead stems of *Castenea dentata* to represent the forest structure and composition prior to the chestnut blight.
H′ = Shannon-Wiener index of diversity ($\Sigma p_i \ln p_i$) based on density or basal area (BA). $J'=H'/H_{MAX}$=estimate of evenness of species distribution based on density or BA. Values in parentheses for 1934 represent density, basal area, H′, and J′ of trees without *Castanea dentata*. Values in rows followed by different letters are significantly different at the $p<0.05$ level.

Total number of woody species in Watershed 13 declined from 27 in 1962 to 21 in 1977 but rose to 27 again in 1984 (Table 1). Rare species such as *Castanea pumila* Miller, *Diospyros virginiana* L., *Fraxinus americana* L., *Symplocos tinctoria* (L.) L′Her, and *Quercus falcata* Michaux were not recorded in the 1977 inventory, 14 years after the second clearcut, but were occasionally observed outside inventory plots. Thus, the differences in H′ and J′ among the inventory dates was primarily due to different species proportions, rather than to the small differences in number of species. For example, *A. rubrum* density increased dramatically after the second clearcut, whereas *Pinus rigida* Miller declined from 3.0 m^2/ha in 1934 to nearly zero after the first clearcut and remained low.

The slopes of the dominance-diversity curves based on density for 1934, 1969, and 1991 were significantly steeper ($p<0.005$) than the slope of the curve for 1948, 8 years after the first cut (Fig. 3). However, the slope of the curve for the precut forest in 1934 was not significantly steeper than curves for 1969 ($p = 0.164$) and 1991 ($p = 0.426$), 7 and 29 years after the second clearcut, respectively (Fig. 3). The dominance-diversity curves using density as the measure of abundance suggest that diversity increased only in the early successional stage of stand development 7 years after the first clearcut.

Dominance-diversity curves based on basal area show that diversity was higher and species were significantly more evenly distributed ($p<0.001$) in the early stages of stand development (i.e., 1948 and 1969) than after the canopy closed, 1934 and 1991 (Fig. 4). The curves for 1934 and 1991 have a steeper profile than those for 1948 and 1969 suggesting lower diversity. In Fig. 4, the right-hand tails of the curve drop off less rapidly for 1948 and 1969 than for 1934 and 1991.

The decreases in H′ and J′ for tree species from 1934 to 1991 after successive clearcuts contrast with changes in diversity found in undisturbed successional deciduous forests. For example, Parker & Ward

(1988) found that H′ and J′ increased after 55 years of forest development in a central hardwood forest primarily due to mortality of *Quercus rubra* L. and *Fraxinus americana*, which created significant gaps in the canopy. The composition of tree species on WS13 is largely attributable to differential sprouting ability and growth among species after clearcutting. In general, H′ declined as basal area increased. Basal area in 1934 was comparable to that in 1984 or 1991, but H′ was significantly higher ($p<0.001$) in 1934 than in 1984 suggesting that the decline in H′ was attributable to additional factors than simply an increase in basal area growth.

Conclusions

After clearcutting, trees for a new stand can come from seeds, existing understory plants, or sprouts. After the initial clearcut, all three types of regeneration were present (Kovner 1955). Twenty-one years after that clearcut the new stand was more diverse than the original one. After the second clearcut, which removed a relatively young forest, stump sprouts were dominant (Leopold *et al.* 1985) because younger, more vigorous trees tend to sprout more than older trees (Kays *et al.* 1988). Also, young trees produce relatively few seeds. Thus, successive clearcuts with a short time interval between them decreased tree diversity and evenness. As the forest matures in WS13, additional mortality may create canopy gaps (Clinton *et al.* in press), allowing diversity of all vegetative layers to increase (Barden 1980; Runkle 1982).

In our study, the estimates of change in diversity and evenness depended on the measure of abundance. Estimates of change were higher for diversity based on density than for diversity based on basal area. Basal area is a better reflection than density of the degree to which each species occupies a site (McMinn 1992).

We found that tree diversity was negatively related to basal area growth and dominance. As basal area of dominant species, such as *L. tulipifera* and *Q. prinus*, increased in the watershed, diversity and evenness declined. Diversity was highest in the early establishment stage of stand development, rather than in the intermediate stage as suggested by Huston & Smith (1987). Diversity also was higher prior to clearcutting (1934) than it was at the intermediate stage after canopy closure (from 1984 through 1991). The observed pattern is the one suggested by Peet & Christensen (1988): diversity is highest at early stages of stand development and lowest at intermediate stages soon after canopy closure.

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