ENVIRONMENTAL DETERMINISM AND FOREST STRUCTURE AND COMPOSITION: A NATURALLY REPLICATED EXPERIMENT

by

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(ABSTRACT)

Ecological theory states that forest succession is largely environmentally determined. Many investigators have suggested, however, that stochastic processes can frequently alter successional pathways. In particular, the colonization phase is thought to be very stochastic. This study utilizes a unique series of 6 naturally replicated sites on Brush Mountain (Montgomery Co., VA) to determine whether forest structure and species composition is primarily deterministic or stochastic in nature. Although the canopy stratum of the mature forest at these environmentally similar sites was very similar in structure and species composition ($p>0.05$), the composition of the subcanopy strata vegetation differed significantly among sites ($p<0.05$). This indicated that stochastic events (e.g. low intensity ground fires, deer browsing, cattle grazing) were were important factors during the development of understory and groundlayer vegetation.

Site-to-site differences in subcanopy species composition remained apparent during the first 2 years following disturbance (removal of canopy cover) of 4 sites. Brush Mountain lacked a significant seed bank (< 1 seed/m^2),

and the dominant subcanopy species reproduced largely by vegetative sprouting. Postdisturbance colonization of the sites was very stochastic, but had relatively little immediate effect on vegetation structure and composition. In the future, however, as colonist species reproduce and increase in density, stochastic colonization events may become an important aspect of forest development at some of the sites.

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Lastly, and most of all, I would like to thank my parents, Sam and Peggy Schiffman, for the continual support that they provided throughout my graduate student career. I would not have been able to achieve this goal without their strong encouragement and financial aid. I dedicate this dissertation to them.

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I. INTRODUCTION

Ecological theory states that succession is largely a deterministic process, strongly dependent upon environmental factors such as climate, topography, soils, and disturbance (Clements 1916, Gleason 1927, Drury and Nisbet 1973, Mueller-Dombois and Ellenberg 1974, Pickett et al. 1988). Therefore, when sites have similar environments, they should support similar biotic communities (Clements 1916, Daubenmire 1966, Drury and Nisbet 1973, Boerner 1985, McCune and Allen 1985a, Halpern 1989). This concept is basic to our understanding of community ecology. Field studies frequently view vegetation with similar environments as statistical replicates (Austin 1977, Hurlbert 1984, Abrams et al. 1985, Boerner 1985, Inouye and Tilman 1988) or in temporal sequences (Billings 1938, Stearns 1958, Olson 1958, Christensen and Peet 1984, Christensen 1989). In addition the assumption that similar vegetation develops at environmentally similar sites is the basis for some simulation models of succession (Shugart et al. 1973, Johnson and Sharpe 1976, Johnson 1977). Management of natural areas is also typically based on this assumption (White 1988).

Some investigators, however, argue that succession is not a predictable process and that vastly different communities can become established on environmentally similar sites (Gleason 1927, 1939, Horn 1974, 1981, Connell and Slatyer 1977, May 1977, Matthews 1979, White 1979, Glenn-Lewin 1980 Noble and Slatyer 1980, Malanson 1980, Grimm 1984, Abrams et al. 1985, McCune and Allen 1985a, Peterken and Jones 1987, Walker and Chapin 1987). Apparent causes of divergence of successional pathways vary, ranging from small differences in sensitive abiotic environmental variables to differential biotic responses to past disturbances.

Abiotic factors affecting vegetation development are typically those associated with climate and topography. Connell and Sousa (1983) state that "when alternate or multiple stable states are postulated to exist, it is essential to establish that any relevent conditions of the abiotic environment are similar (in average and in variance)." Since these parameters can often be measured accurately, studies of relationships between vegetation and the physical environment dominate the literature (Daubenmire 1966, Whittaker 1967, White 1979, McEvoy et al. 1980, Stephenson 1982, Adams and Stephenson 1983, Meiners et al. 1983, Leopold and Parker 1985, Harrison et al. 1989, Lipscomb 1986).

In contrast, identification of specific cause and effect relationships between biotic environmental factors (e.g. soil processes, herbivory, seed flux, human disturbance) and vegetation composition can be more difficult. Biotic processes are diverse, complex and can be hard to detect and control in field studies (Quinn and Dunham 1983, Strong 1983, Weatherhead 1986). Still, if the mix of past and present abiotic factors affecting forest development on several sites is similar, then the theory suggests that processes affecting these sites should also be similar.

When community composition varies among otherwise similar sites, the variability is frequently attributed to stochasticity (= chance) (Palmgren 1929, Gleason 1939, Whittaker 1953, Terborgh 1973, Strong 1983, Christensen and Peet 1984, Grimm 1984, Abrams et al. 1985, Schafale and Christensen 1986, Walker et al. 1986, Ricklefs 1987, Walker and Chapin 1987, Robinson and Edgemon 1988, Wildi 1988, Halpern 1989). In this context a stochastic event is any occurrence for which there is no apparent ecological cause or explanation. Differential low frequency seed inputs or undetectable localized past disturbances are biotic processes that can result in measurable site-to-site differences in forest composition and may, therefore, be termed stochastic. Since identification and quantification of many biotic parameters can be difficult and expensive, the concept of stochasticity "can be made a 'rubbish heap' on which any phenomenon of distribution that is difficult to explain may easily be thrown" (Palmgren 1929).

To isolate and estimate the effects of stochastic processes on forest vegetation patterns and development, all other factors that may influence forest species composition must be as strictly controlled as possible, and replication of sites is necessary (Poole 1974, Austin 1977, Rahel et al. 1984, Hurlbert 1984, Walker and Chapin 1987, Robinson and Edgemon 1988). Given the great temporal and spatial heterogeneity of biotic and abiotic processes, adequate replication in community-level experiments in natural environments is particularly difficult (Quinn and Dunham 1983, Strong 1983).

This study utilizes a series of naturally replicated sites in the southern Appalachian Mountains to test an important tenet of ecological theory: Forest vegetation of similar community structure and composition develops at environmentally similar sites. The unusual degree of environmental similarity of these replicate sites provides an ideal framework for separating the effects of environment from stochasticity in the development of forest communities. Failure to reject the hypothesis would support this long-held ecological tenet by suggesting that environmental factors, rather than stochastic processes, dominate forest structure and community composition. If the hypothesis is rejected, however, and the replicate sites support differing vegetations, then this divergence should be directly attributable to stochastic processes. In addition, replication allows for quantitative estimation of the effects of stochasticity on forest vegetation.

Since some biotic factors affecting the development of vegetation are only loosely coupled to the physical environment, identification of causes of site-to-site differences in community structure and composition can still be difficult. For example, postdisturbance regeneration is frequently dependent upon seed dispersal and recruitment from the buried seed bank. Yet, dispersal of propagules in a landscape is patchy (Gadgil 1971, Smith 1975, Johnson et al. 1981, McDonnell and Stiles 1983, McClanahan 1986, Walker et al. 1986), and viable seeds hidden in the soil frequently have heterogeneous distributions (Keever 1983, Bigwood and Inouye 1988). Therefore, seed availability can be highly variable, and these differences are often not readily detectable. Variation in community structure and composition among environmentally similar sites are frequently attributed to chance colonizations (Palmgren 1929, Gleason 1939, Whittaker 1953, Drury and Nisbet 1973, Tergborgh 1973, Conner and Simberloff 1979, Christensen and Peet 1979, Grieg-Smith 1979, Schafale and Christensen 1986, Wood and del Moral 1987, Robinson and Edgemon 1988, Halpern 1989).

Early stages of community development may be the most sensitive to stochastic processes (Egler 1954, Connell and

Slatyer 1977, Boerner 1985, McCune and Allen 1985, Walker and Chapin 1987, Halpern 1989). After decades of growth and change, however, initial causes of variability among sites may no longer be apparent in mature forests. To estimate the importance of stochastic processes early in succession, this project included an analysis of plant recruitment during the first 2 years of regrowth following a disturbance (killing of canopy trees). If postdisturbance regeneration is largely driven by environmental processes, then community structure and composition at the recently disturbed, environmentally replicated sites should be similar. If, however, stochastic colonization events are important determinants of vegetation early in its development, then significant differences in the composition and structure of the regenerating vegetation should be apparent among sites.

II. METHODS

A. Study Area

Brush Mountain is a 40 km long ridge in southwestern Virginia. Part of the Ridge and Valley physiographic province, Brush Mountain is mostly contained within Jefferson National Forest. Along its crest, elevation ranges from 855 to 915 m a.s.l. A parallel-running array of spur-ridges extends perpendicularly and to the northwest from the main ridge (Figure 1). The parallel spur-ridges, each with nearly identical environments, were the units of study. They provide environmental replication necessary for community-level experimentation.

The spur-ridges have steep northeast and west-facing slopes. The soils, which are rocky and formed from Devonian and Mississippian shale and sandstone residuum, are classified as loamy-skeletal, mesic Typic Dystrochrepts and loamy-skeletal mixed, mesic Lithic Dystrochrepts (Creggar et al. 1985). Precipitation averages 103 cm annually (Creggar et al. 1985). Summers are warm and and winters relatively cool. The average daily temperature is 10.8° C (Creggar et al. 1985).

Oak forest (_Quercus prinus_, _Q. coccinea_; all nomenclature follows Radford et al. 1968) dominates the northeast-facing slopes of the spur-ridges. The more xeric

Figure 1. View of the northwest slope of Brush Mountain (Montgomery Co., VA). Note the parallel spur-ridges extending perpendicularly from the main ridge.

west-facing slopes support pines (*Pinus pungens*, *P. rigida*). Ericaceous understory shrubs (*Vaccinium vacillans*, *Gaylussacia baccata*, *Kalmia latifolia*) occur beneath both canopy types (Lipscomb 1986). Although a detailed account of the disturbance history of Brush Mountain is not available, it is known that logging and forest fires early in the 20th century were the last major disturbances in the area (E. Leonard, personal communication). Because of the steep slopes, low site quality and poor form of the trees, these spur-ridge forests are not managed for commercial timber production.

B. Environmental Sampling and Site Selection

The goal of site selection was to identify the most environmentally similar subset of spur-ridge sites at which experiments could later be conducted. By examining a variety of environmental parameters at each potential research site, the vegetation survey could be restricted to only those sites with measurably similar topography, soil, and disturbance history. Furthermore, to avoid biasing the vegetation survey, only environmental variables thought to affect vegetation composition and structure were measured during site selection. Direct analysis of forest species composition was purposely excluded from the selection process.

The initial step in site selection involved an examination of topographic maps, soil maps, and aerial photographs (1953, 1962, 1971, 1975, 1979) of Brush Mountain. Eight adjacent spur-ridges ("A, B, C, D, E, F, G, H") in Montgomery County, Virginia (37° 18´N, 80° 24´W) were chosen for detailed on-site environmental sampling. These spur-ridges spanned a distance of 3.2 km.

In the summer of 1986, single 30 X 30 m (0.09 ha) quadrats were established at midslope (elevation 730 m) on the northeast-facing slopes of the 8 spur-ridges (Figure 2). Each quadrat was subdivided into five 6 X 30 m belts, and a stratified random design was used to collect topographic data and surface soil samples. Slope and aspect (degrees) measurements were made at 2 random points along each belt with a hand-held clinometer and compass, respectively. Samples of the surface 10 cm of soil (approximately 275 cm^3) were also collected at these points.

Concentration (ppm) of nitrogen (ammonium) was determined for 10 g subsamples of each soil sample using an Orion ammonia ionization electrode (model 95-10) and Orion digital pH/millivolt meter (model 811). Available phosphorus, potassium, calcium and magnesium concentrations and pH were determined by the Virginia Cooperative Extension Soil Testing Laboratory (Blacksburg, Virginia) using methods descibed by Donohue and Friedericks (1984).

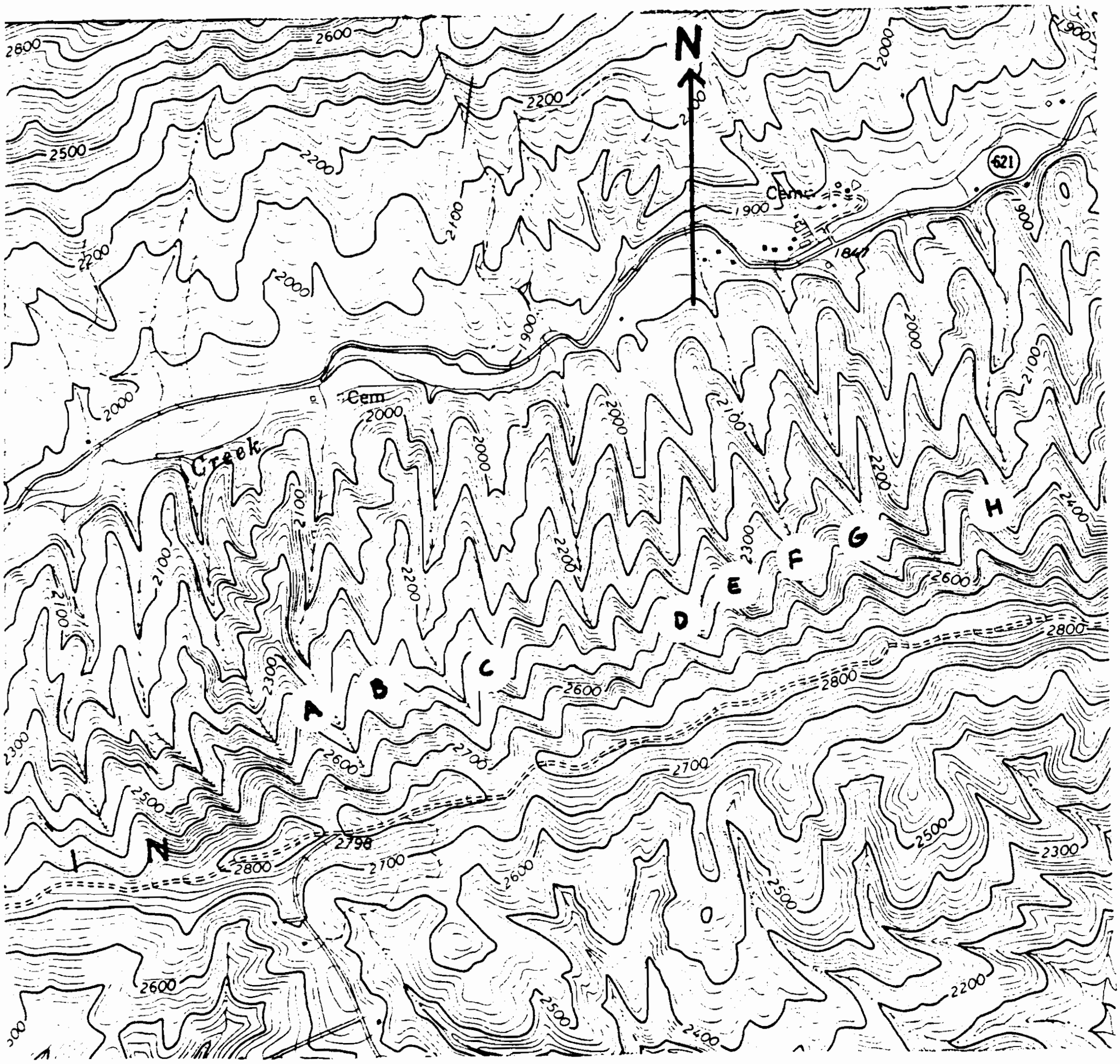


Figure 2. Locations of the 8 spur-ridge sites on Brush Mountain (A, B, C, D, E, F, G, H) which were selected for detailed on-site environmental sampling.
SCALE: 4.1 cm = 1 km.

Although the disturbance histories of the spur-ridge sites was not well known, the sites are located very near one another, so it is likely that all experienced the same large-scale disturbances in the past. Charcoal on the forest floor and in the surface soil, and the presence of fire-scarred trees were evidence that each site had burned. The absence of open-grown trees also suggested that these sites had experienced similar canopy disturbances. No evidence of agricultural use or recent tree cutting was found at any of the spur-ridge sites.

Because detailed information about site history was unavailable, canopy tree age structure distributions were developed to assist in determining whether time since disturbance was similar among sites. To compile these distributions, DBH measurements of 50 randomly selected canopy trees (> 5 cm DBH) were collected from each spur-ridge quadrat. These data were tabulated without regard to species.

The most similar spur-ridge sites were identified by comparing topographic, soil, and canopy DBH data collected at each spur-ridge. A variety of univariate and multivariate statistical tests and analyses (Ray 1982) were used for this purpose. Only sites exhibiting consistent similarity for all measured environmental parameters were selected for later vegetation study.

Because of clear environmental differences, sites F and G were excluded from the vegetation study. Analysis of variance indicated that the pH and the concentrations of calcium and magnesium in the soil at site F were significantly greater than at the other sites ($p<0.001$). In addition, site G had a significantly more east-facing aspect than the other sites ($p<0.001$). These and other findings associated with site selection are detailed in the following results section. Because of the clear environmental differences at sites F and G, they were excluded from the vegetation study.

C. Predisturbance Vegetation Survey

The vegetation of the most similar sites (A, B, C, D, E, and H) was divided into 3 relatively distinct vertical strata: canopy (> 5 cm DBH), understory (≤ 5 cm DBH and > 30 cm high), and groundlayer (≤ 30 cm high). Since plants in different forest strata differ in size and vary in abundance at different spatial scales (Mueller-Dombois and Ellenberg 1974), the composition and structure of vegetation in each stratum was quantified and analyzed separately. To sample canopy trees, each 0.09 ha spur-ridge research quadrat was sectioned into 4 square 225 m^2 plots, and DBH for all canopy trees in the plots was measured. Average density and basal area by species was calculated for each quadrat. Understory and groundlayer vegetation was sampled within circular, permanently marked 7.1 m^2 and 1.0 m^2 plots, respectively. Three understory plots and 12 groundlayer plots were positioned at random in each of three 6 X 30 m belts in the spur-ridge quadrats. Species density and percent cover (cover classes: 0-10, 11-25, 26-50, 51-75, 76-100%; cover was estimated visually) were determined for the plots. From these data, average understory and groundlayer species density and cover were estimated.

Analysis of variance was used to determine whether these environmentally similar sites supported similar vegetation. In addition, Sorensen's index of similarity (IS) was used to make pairwise comparisons of vegetation density among sites (IS=2w/a+b, where a=total relative density for the species at one site, b=total relative density for the species at another site, and w=sum of lower relative densities for the species found at both sites; Sorensen 1948 as cited in Curtis 1959). Comparisons of species composition and richness were also made among sites.

D. Seed Bank Sampling

To characterize the potential flora stored in the buried seed banks of the sites, separate samples of leaf litter (L and F layers), humus layer (H), and surface soil (to 5 cm) were collected within circular 28.2 cm^2 plots. Twelve seed bank plots were located at random points within each of 3 sampling belts. Seed bank sampling points were different from vegetation sampling points. A total of 108 samples were collected at each site. Three-fourths of the leaf litter, humus layer and surface soil samples (81 samples per site) were planted in the greenhouse in 420 cm^2 flats on a 2 cm deep substrate of sterilized potting soil. The flats were watered daily and remained in the heated greenhouse for 1 year. Seedlings were identified as they germinated. Only plants derived from seeds were tallied. Because sampling was done early in the spring of 1987, prior to the production of seeds that season, all seeds should been winter stratified. The remaining seedbank samples (not planted in the greenhouse; 27 samples per site) were dried, sieved, and examined visually for seeds with a binocular dissecting microscope (total magnification = 40x) (Poiani and Johnson 1988). Seeds were identified to species where possible.

E. Disturbance

In the winter of 1986, all canopy trees in the 0.09 ha quadrats on spur-ridges B, C, D, and E were girdled. A 25% solution of the biodegradable systemic herbicide, glyphosate ("Roundup" - Monsanto), was applied to the fresh wounds with a hand-held spray bottle (Wendel and Kochenderfer 1982, Campbell 1985, McLemore and Yeiser 1987). This treatment killed the leafless trees (including the roots), creating replicate 30 X 30 m canopy openings on each of the 4 treated spur-ridges. Because of inclement weather and time constraints, canopy openings at spur-ridges A and H were not created.

Killing tree roots precluded rapid resprouting of canopy trees, which is the common mode of postdisturbance oak regeneration in this region (Whitney and Johnson 1984, Ross et al. 1986). Prevention of sprouting increased the potential for successful colonizations by plants derived from recently dispersed seeds or the buried seed bank, thereby increasing the potential for stochastic biotic processes to alter postdisturbance forest structure and composition. Because sprouting by canopy trees was prevented, this disturbance did not simulate the effects of fire or clear-cutting, the 2 most common forest disturbances in this region. Still, death of oak tree roots can be caused by severe drought (L. R. Boring, personal communication) or gypsy moth herbivory (Ehrenfeld 1980). To further stimulate postdisturbance plant recruitment, leaf litter was removed from half of the groundlayer plots at the 4 treated spur-ridges.

F. Postdisturbance Vegetation Survey

Vegetation within the permanently marked understory and groundlayer plots at sites B, C, D, and E was monitored for 2 growing seasons following canopy disturbance (1987 and 1988). Plant density, cover, and species richness were estimated each year at the 4 disturbed sites. When possible, origin of plant recruitment (seed germination or vegetative reproduction from existing plants) was determined.

Analysis of variance was used to determine whether the regenerating vegetation was similar among sites. Because each species did not occur in all sampling sampling plots of a particular vegetation stratum, the data contained many zeros. All canopy, understory and groundlayer data collected for this study were transformed ($\log_{10}$+1) prior to statistical analysis.

To estimate seed inputs, nine 0.25 m^2 seed traps were placed at random positions in each spur-ridge quadrat. The traps were elevated 15 cm off the ground and consisted of square wood frames covered on top by 1.2 cm mesh galvinized hardware cloth and on the bottom by 1.0 mm mesh aluminum window screen. The traps were monitored monthly throughout the seed dispersal season.

III. RESULTS

A. Site Selection

The goal of the site selection process was to identify a group of northeast-facing spur-ridge sites that could be treated as environmental replicates. Six of the 8 sites were selected for study. Clear edaphic and topographic differences at 2 sites (F and G) resulted in their exclusion from the study. One-way analysis of variance and Duncan's multiple range test (alpha=0.05) indicated that mean pH (5.09, S.E.=0.1), and concentrations of calcium (652.8 ppm, S.E.=111.7) and magnesium (90.8 ppm, S.E.=9.5) ~~of~~ in soil samples collected at spur-ridge F were significantly greater than those of samples collected from the other 7 sites ($p<0.001$; Figure 3). These differences were probably linked to greater proportions of limestone and dolomite in the soil at this site. In addition, site G had a significantly more east-facing topographic aspect (42.5°, S.E.=1.7) than the other sites (24.6°, S.E.=0.6, $p<0.001$; Figure 3). Multivariate analysis of variance and Mahalanobis tests (Ray 1982) also indicated that the environmental data collected at sites F and G were statistically different from data collected at A, B, C, D, E, and H ($p<0.001$).

Ordination of the spur-ridges in reduced environmental space using canonical discriminant analysis corroborated

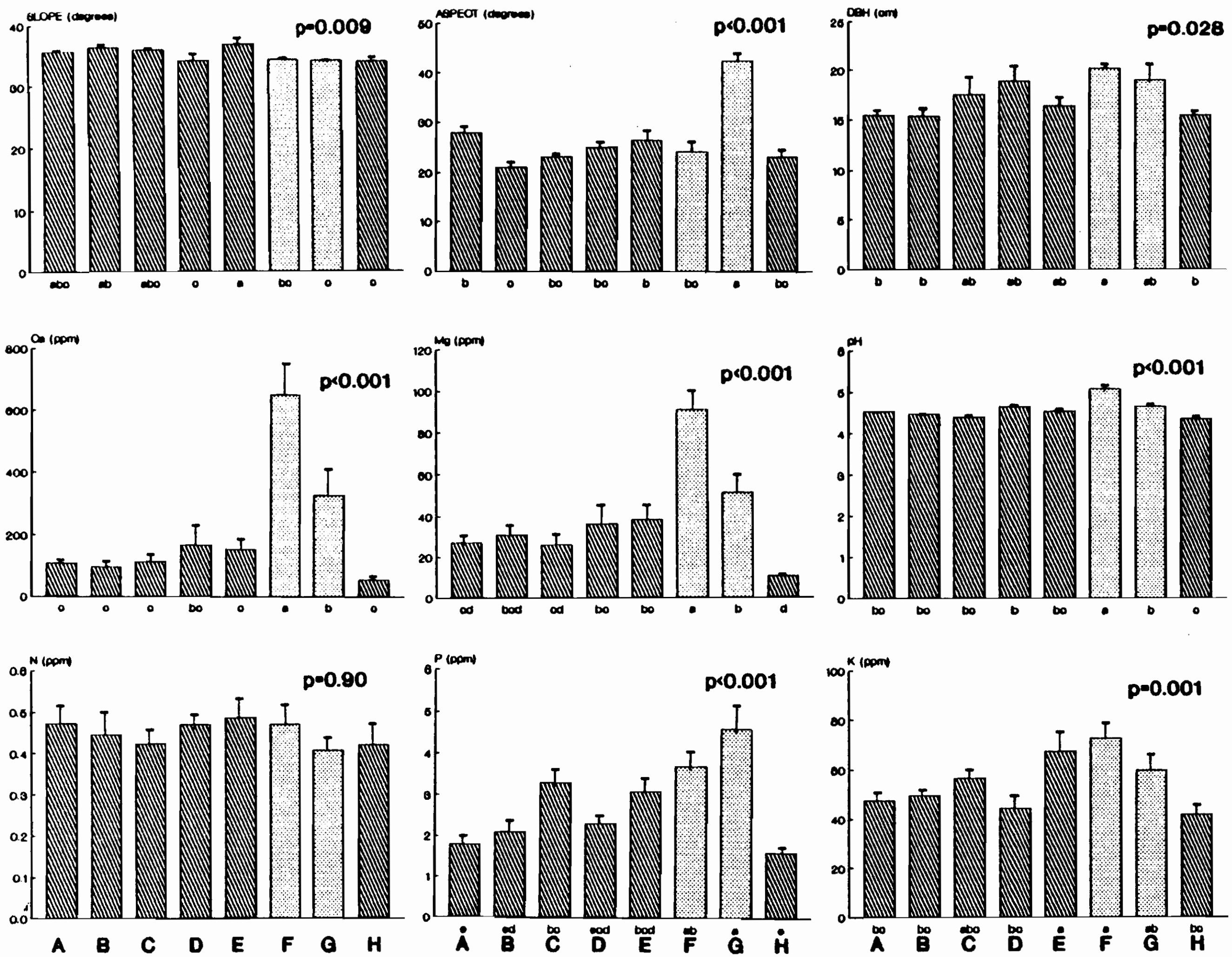


Figure 3. Environmental variables (slope and aspect [degrees], surface soil pH, Ca, Mg, P, K, and ammonium [ppm], canopy DBH [cm]) measured at each of 8 Brush Mountain spur-ridge sites (mean ± S.E.). Note: y-axis scales differ. Lower-case letters along x-axis indicate groupings produced by Duncan's multiple range test (alpha=0.05).

these findings. This multivariate technique summarizes between-class variability and, therefore, was sensitive to environmental differences among the spur-ridges. The first canonical component (the linear combination of environmental variables with the highest multiple correlation) accounted for 59.2% of the variability between spur-ridges (eigenvalue=3.35). Differences in topographic aspect among sites dominated this canonical component. Spur-ridge G was segregated from the other sites along this axis (Figure 4). The second canonical component was primarily associated with variability in soil pH, calcium, and magnesium among sites. It contributed an additional 24.3% to the canonical structure (eigenvalue=1.37), and site F separated from sites A, B, C, D, E, and H along this axis (Figure 4).

Soil moisture availability often affects forest growth and composition in the mountains of southwestern Virginia (McEvoy et al. 1980, Meiners et al. 1983, Stephenson 1983, Lipscomb 1986). The 6 remaining sites had virtually identical slope inclination, aspect, and topographic position. Therefore, moisture availability levels and site quality, should also have been virtually identical (Meiners et al. 1983, Callaway et al. 1987).

Between-site variation for the environmental parameters measured was very low (Figure 3). In particular, differences in available soil nutrients were small. Since differences in

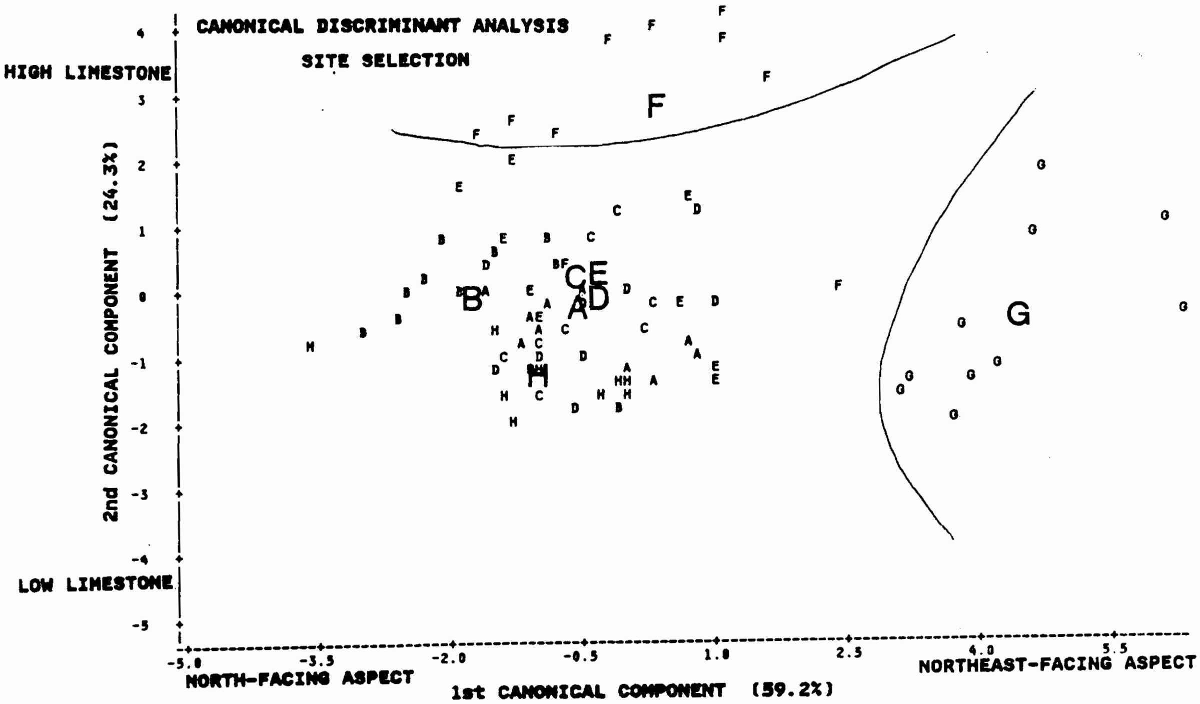


Figure 4. Ordination of the 8 spur-ridge sites by canonical discriminant analysis. Large letters indicate group means for each site.

soil nutrient status can be a cause of spatial heterogeneity of vegetation (Tilman 1984, 1987), this was an important finding. It is unlikely that the small differences in nutrient concentrations observed among some of the sites could cause detectable differences in vegetation at these sites (Christensen and Peet 1984, Schafale and Christensen 1986 Collins and Good 1987).

Not only did environmental parameters measured at the 6 spur-ridges exhibit little variability among sites, variability within each site was also quite low. Because variance both within and among sites was small, analysis of variance indicated that topographic aspect, canopy tree DBH, and soil phosphorus and potassium concentrations differed statistically among sites ($p<0.05$; Figure 3). Overlap of standard error bars and ranges produced by Duncan's multiple range test, however, suggested that these apparent differences were not distinctive, and were statistically ambiguous. Moreover, the very small differences among sites were not great enough to have measurably affected vegetation structure or composition. The overall concentration of points in the ordination and their high degree of overlap (Figure 4) also indicated that sites A, B, C, D, E, and H were highly similar.

Although this series of 6 sites certainly provided environmental replication that was better than most natural systems where relationships between the environment, vegetation, and stochastic processes have been examined (Malanson 1980, Christensen and Peet 1984, Abrams et al. 1985, Boerner 1985, McCune and Allen 1985a, Shafale and Christensen 1986, Walker et al. 1986, Halpern 1989), the existence of small measureable differences in environmental parameters indicated that the Brush Mountain spur-ridges are not, in the strictest sense, true replicates. Since true replication is a condition that probably does not exist anywhere in nature, particularly at the scale required for community-level experimentation (Gleason 1939, Gauch 1982, Strong 1983, Hurlbert 1984), the approximate site replication produced by naturally repeating topographic formations, like Brush Mountain's spur-ridges, provide the next best systems for examining the causes of community development patterns (McCune and Allen 1985, Ricklefs 1987, Walker and Chapin 1987).

B. Framework for Vegetation Analysis

This study addressed vegetation structure and composition, and their relationships with the environment and stochastic processes. Forest structure can be divided into vertical and horizontal components (McEvoy et al. 1980). Densities of plants in 3 vertical strata (groundlayer, understory, and canopy) were determined at each of the 6 spur-ridge sites. Estimates of groundlayer and understory plant cover and canopy tree basal area served as measures of the horizontal component of the vegetation. The species composition of vegetation at each site was characterized by stem density and species richness. These structural and compositional variables are frequently used to characterize forest vegetation because they are easy to measure and provide detailed quantitative information (Mueller-Dombois and Ellenberg 1974). Furthermore, studies that specifically examine environmental and biotic processes that affect forest communities typically utilize measures of plant density, cover, and richness to characterize vegetation structure and species composition. Therefore, the findings of this study can be directly compared with other studies of forest vegetation.

In this study, the 5% statistical probability level was used as the criterion for significance. If analysis of variance showed that differences in vegetation density among these environmentally similar sites were significant ($p<0.05$), then it was concluded that the dissimilarities may be attributable to stochastic processes. Although the 5% probability level is arbitrary, it is a generally accepted and widely used statistical criterion. Because this study of forest vegetation on Brush Mountain was replicated, error due to spatial or temporal environmental variability among sites was largely controlled for. Therefore, the use of this strict criterion was appropriate here.

C. Predisturbance Vegetation

1a. Canopy Structure

The canopy vegetation at the 6 sites exhibited a high degree of structural similarity. Tree density-diameter distributions were virtually identical in shape (Figure 5). Each site supported several hundred small trees (< 10 cm DBH) and only a few individuals with large diameters (>30 cm DBH). Although the average densities of trees in the 10 - 20 cm DBH range were somewhat lower at sites C and D, these differences were not statistically significant ($p>0.05$).

Canopy basal area was also similar among sites, averaging 23.6 m^2/ha (S.E.=1.28). On these spur-ridges, total basal area was clearly linked to tree density. Basal areas were somewhat higher (though not significantly so; $p>0.05$) at sites B and E, where average tree densities were highest, and lower at C and D where tree densities were lower.

1b. Canopy Composition

Quercus prinus, *Quercus coccinea*, *Acer rubrum*, and *Amelanchier arborea* occurred in the canopies of all 6 spur-ridges (Figure 6). These 4 species comprised over 90% of the

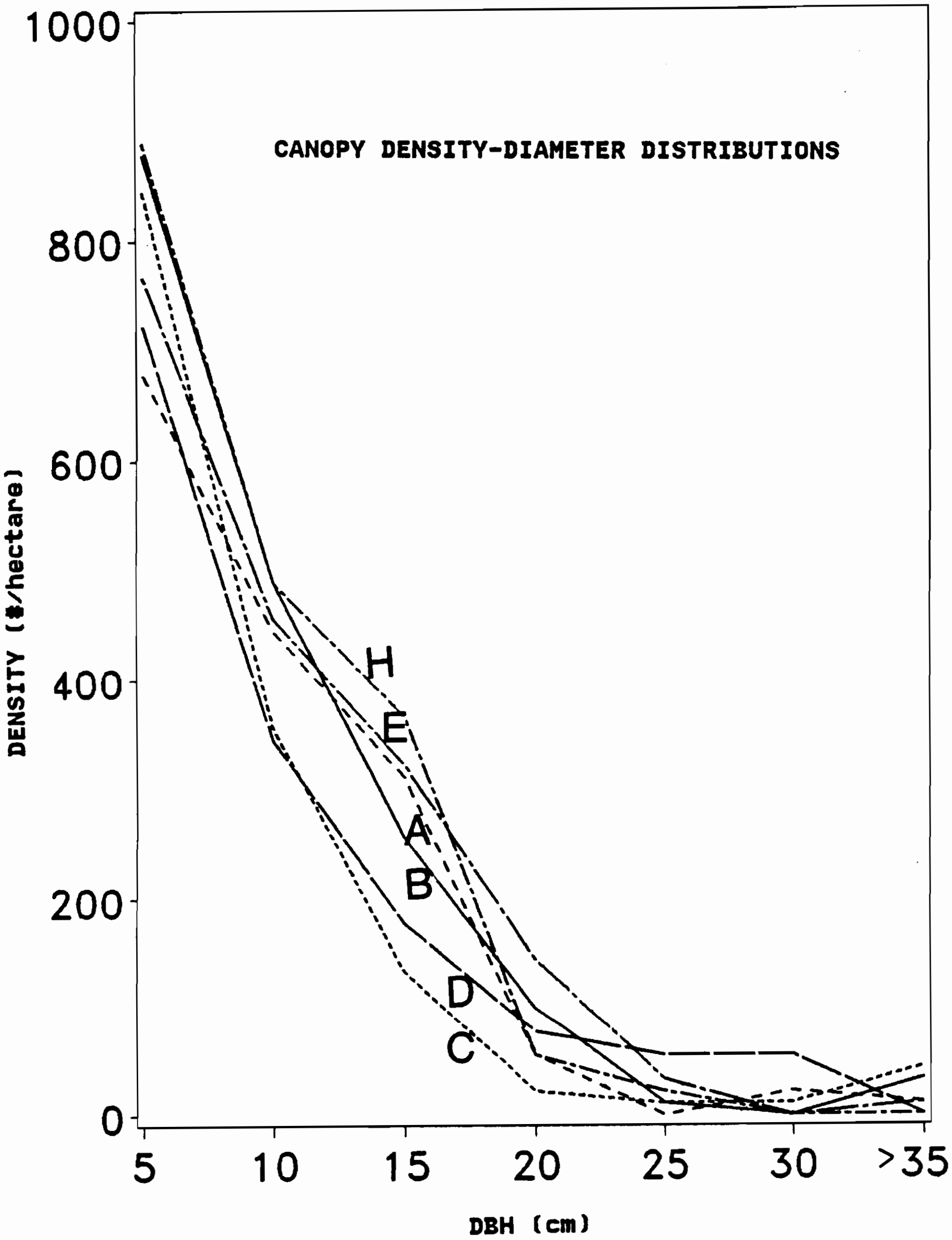


Figure 5. Density-diameter distributions for canopy trees at each of the 6 spur-ridge sites.

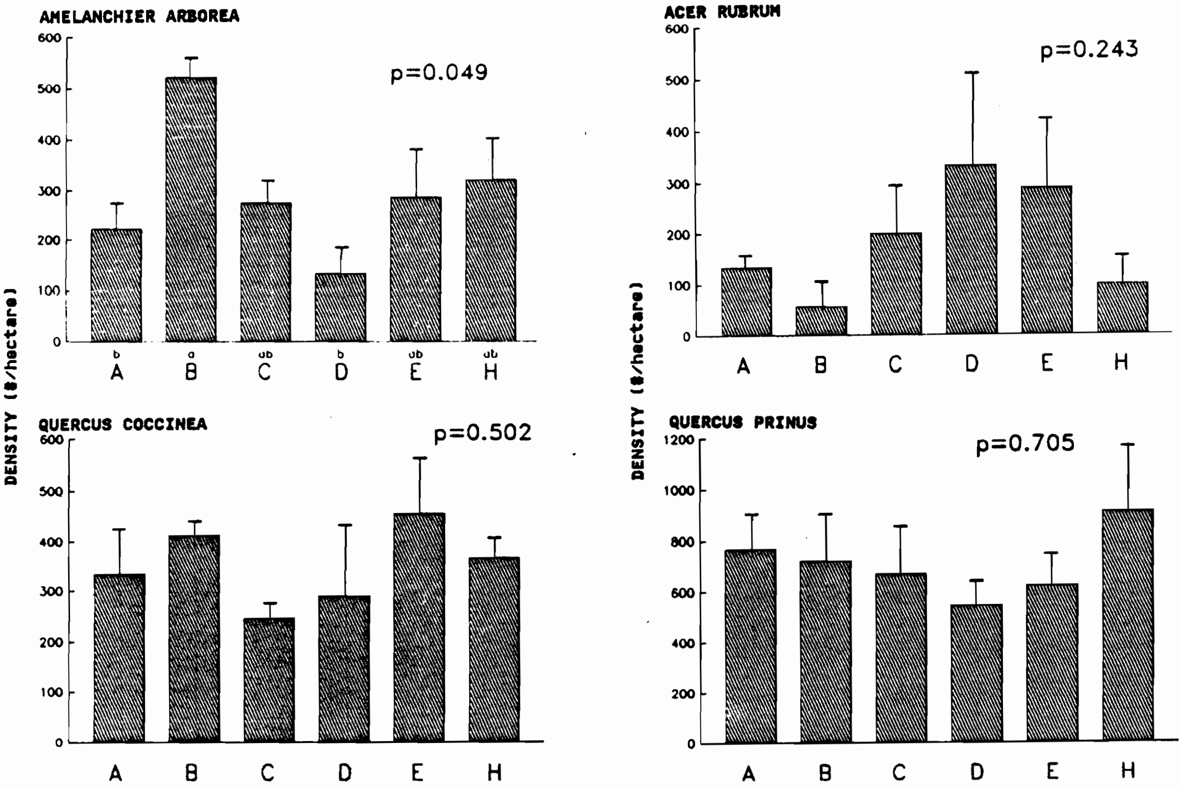


Figure 6. Density (mean ± S.E.) of the 4 species found in the canopy of all 6 spur-ridge sites. Note: y-axis scales differ. Lower-case letters along x-axis indicate groupings produced by Duncan's multiple range test (alpha=0.05).

total density and basal area at each site, having an average cumulative density of 1540 trees/ha and average cumulative basal area of 23.2 m^2/ha. *Quercus prinus* was clearly the dominant species at each site with a mean basal area of 15.8 m^2/ha. As with *Q. coccinea* (mean basal area = 5.7 m^2/ha), it occurred primarily in the upper forest canopy. Both species were relatively evenly distributed in the canopy with many individuals occurring within all 4 sampling plots of each 0.09 ha spur-ridge quadrat. *Acer rubrum* and *Amelanchier arborea* were considerably less important and smaller in size (mean basal areas = 0.7 m^2/ha and 1.0 m^2/ha, respectively). These 2 species were more patchily distributed within sites. *Acer rubrum* occurred in all but 1 sampling plot at H and 2 sampling plots at B. *Amelanchier arborea* was absent only from 1 plot at E.

The densities (trees/ha) of *Q. prinus*, *Q. coccinea*, and *Acer rubrum* did not differ significantly among sites ($p>0.05$; Figure 6). Since they comprised the bulk of the canopy this indicated highly similar canopy vegetation at all sites. An exception was *Amelanchier arborea*, however, its density was only marginally significant ($p=0.049$) among sites.

A few individuals of 5 less common species (*Acer pensylvanicum*, *Carya glabra*, *Cornus florida*, *Ostrya virginiana*, *Pinus pungens*) were found in varying combinations on the spur-ridges. For example, *O. virginiana*, was observed only at sites D, E, and H, while *Carya glabra* was found at A, C, and E (Table 1). The total density of these less common species on each spur-ridge was very low, averaging only 71.8 trees/ha and making them only minor constituents of the spur-ridge canopies.

Even though the mixture of uncommon species differed among sites, species richness was virtually identical. Seven canopy species were found at site E and 6 species at all of the others. Furthermore, Sorensen's coefficients of similarity (pairwise comparisons of species proportions at these sites) consistently showed moderately high levels of canopy similarity among sites (mean similarity coefficient = 0.82, S.E.=0.01; Table 2).

2a. Understory Structure

Two distinct growth form groups (shrubs and trees) occurred in the understory of each spur-ridge site. The shrub group consisted of ericaceous species (*Gaylussacia baccata*, *Kalmia latifolia*, *Rhododendron* sp., *Vaccinium vacillans*, *Vaccinium stamineum*) and other species of relatively low stature that are naturally confined to subcanopy strata (*Castanea dentata*, *Hamamelis virginiana*, *Sassafras albidum*, *Viburnum acerifolium*). In contrast, species in the tree group (*Amelanchier arborea*, *Acer pensylvanicum*, *Carya glabra*, *Ostrya virginiana*, *Quercus*

Table 1. Density (trees/ha) of canopy species that occurred at fewer than all 6 spur-ridge sites in 1986.

	SPUR-RIDGE					
SPECIES	A	B	C	D	E	H
Acer pensylvanicum	-	-	-	22	-	-
Carya glabra	44	-	11	-	33	-
Cornus florida	22	44	-	-	-	44
Ostrya virginiana	-	-	-	89	11	78
Pinus pungens	-	11	11	-	11	-
TOTALS:	66	55	22	111	55	122

Table 2. Matrix of Sorensen´s coefficients of similarity. Scores indicate the degree of similarity of canopy species density between each pair of spur-ridge sites (1986).

SPUR-RIDGE

	A	B	C	D	E	H
A	1.00	0.80	0.88	0.77	0.83	0.92
B		1.00	0.80	0.72	0.79	0.83
C			1.00	0.79	0.86	0.87
D				1.00	0.84	0.81
E					1.00	0.81
H						1.00

coccinea, *Quercus prinus*) had the potential to grow out of this stratum into the canopy.

The structure of understory vegetation varied considerably among spur-ridges. This was in sharp contrast to the structurally uniform canopy stratum. Understory plants occurred at A, C, and H in densities exceeding 30000 stems/ha, while fewer than 20000 stems/ha were found at B, D, and E (Figure 7). Plants in the shrub group comprised a particularly large proportion of the understory stratum vegetation at the 3 high density sites (Figure 7). An average of 72.5% of the understory stratum density at A, C, and H was made up of shrubs, while this subgroup averaged only 48.9% at B, D, and E.

In addition, there was a strong positive correlation between the density and cover of vegetation in the understory stratum ($r=0.894$, $0.01<p<0.02$). Sites with the highest density vegetation also had the greatest amount of cover. Average percent cover at A and C were very high, 110.2% and 88.1% respectively. The distributions of cover at these sites were also high. Four of the 9 understory plots at site A and 2 plots at site C exceeded 100% cover (Figure 8). Percent cover values of over 100 were possible because leaves of different plant species frequently overlapped. In contrast, cover at B and E was low, averaging 30.7% and 29.6%, respectively. More than half of the understory plots

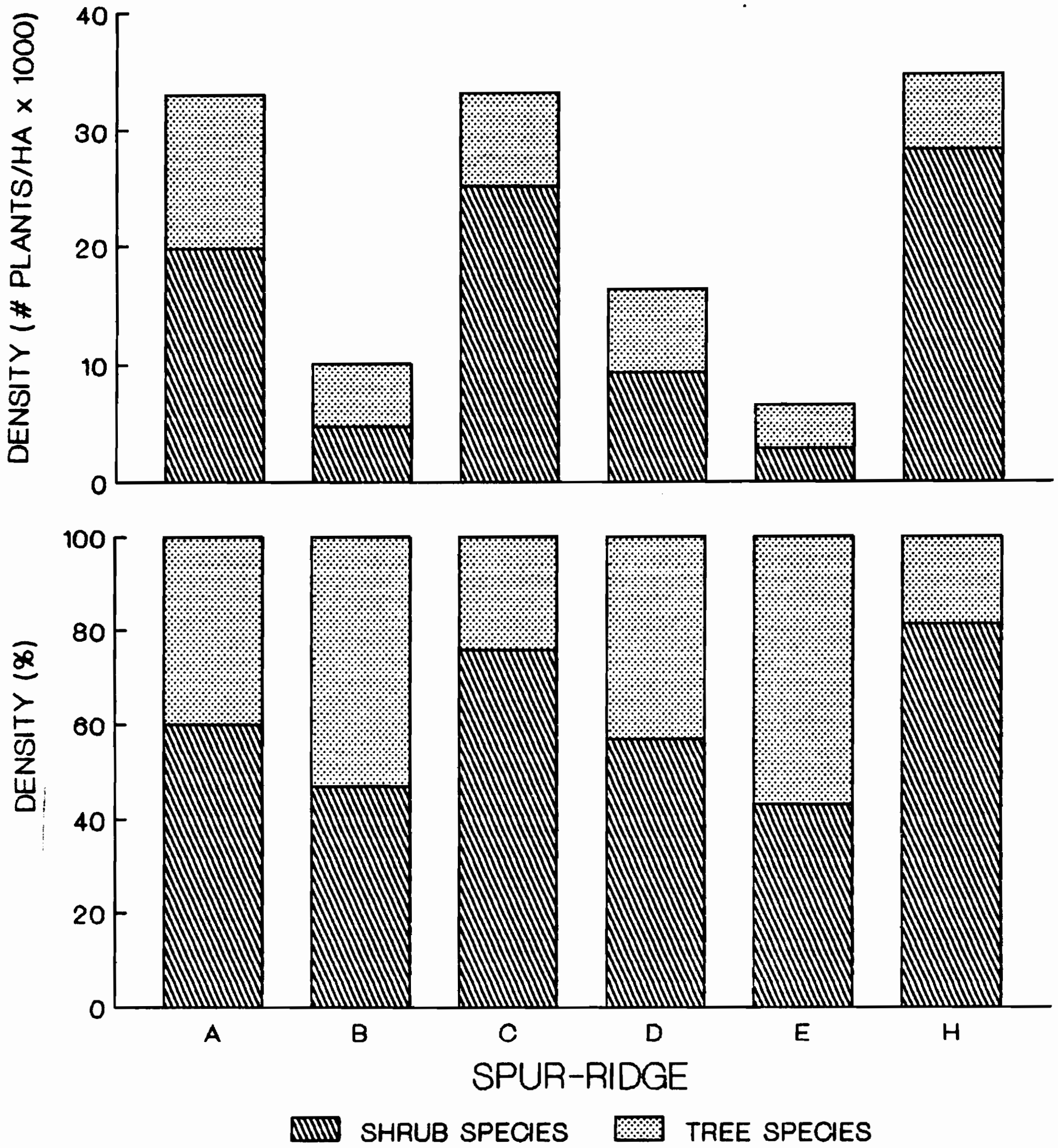


Figure 7. Density (actual stems/ha [upper graph] and percentages [lower graph]) of tree and shrub species found in the understory stratum of the 6 spur-ridge sites.

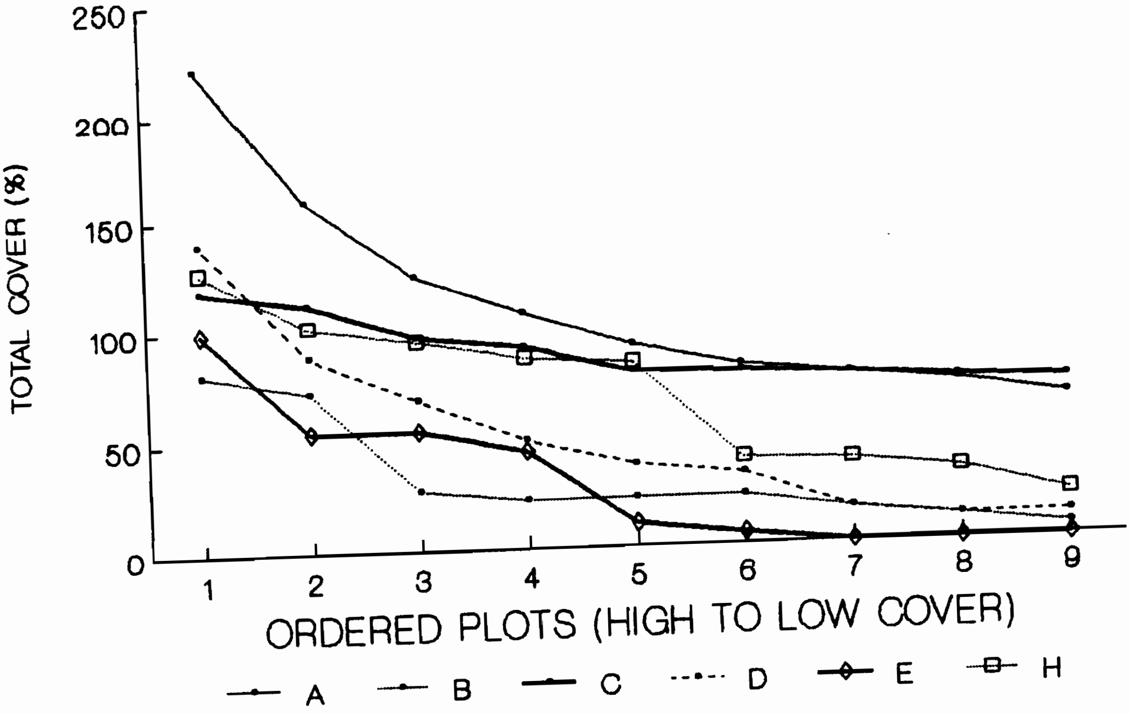


Figure 8. Cover distributions of understory stratum vegetation at the 6 spur-ridge sites. Distributions were produced by ordering the 9 understory sampling plots at each site from highest to lowest percent cover.

at these 2 sites contained vegetation with less than 50% total cover. Moreover, 3 sampling plots at site E contained no understory stratum vegetation at all (Figure 7).

2b. Understory Composition

Quercus prinus, Acer pensylvanicum, Acer rubrum, and Vaccinium vacillans occurred in the understories of all 6 spur-ridge sites. Although the densities of these species varied within and among sites, differences among sites exhibited by the 3 tree species were not statistically significant ($p>0.05$; Figure 9). The density of Vaccinium vacillans, a shrub, did differ significantly among sites ($p=0.033$; Figure 9). There was an eight-fold difference in density between sites C and E.

Approximately half of the total density of each spur-ridge understory was made up of locally abundant species (Figure 10). Hence, tree and shrub species with patchy distributions constituted a major component of this stratum. This group consisted of 13 species (Table 3). Like the locally abundant species in the canopy stratum, these less frequent species occurred in different combinations at each site. For instance, Amelanchier arborea and Gaylussacia baccata were found at all sites except E, while Carya glabra occurred only in the understory of D. The uniformly low coefficients of similarity (mean=0.43, S.E.=0.03; Table 4)

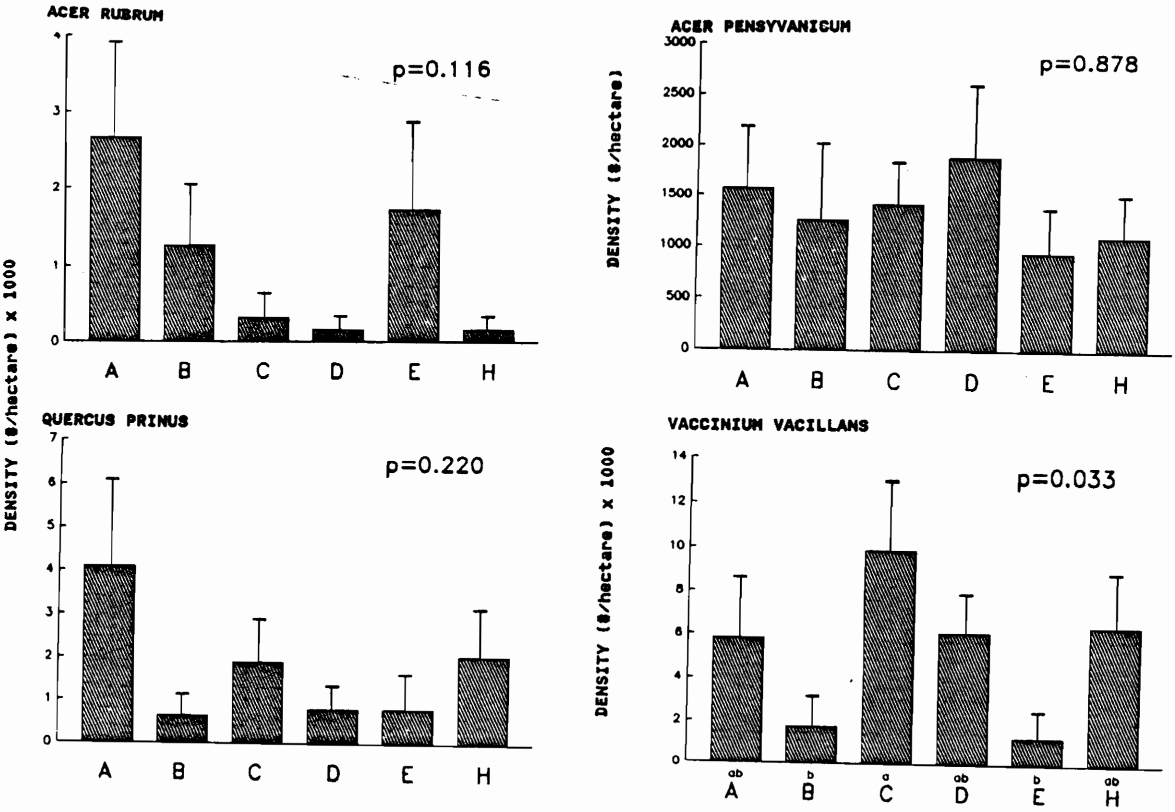


Figure 9. Density (mean ± S.E.) of the 4 species found in the understory stratum of all 6 spur-ridge sites. Note: y-axis scales differ. Lower-case letters along x-axis indicate groupings produced by Duncan's multiple range test (alpha=0.05).

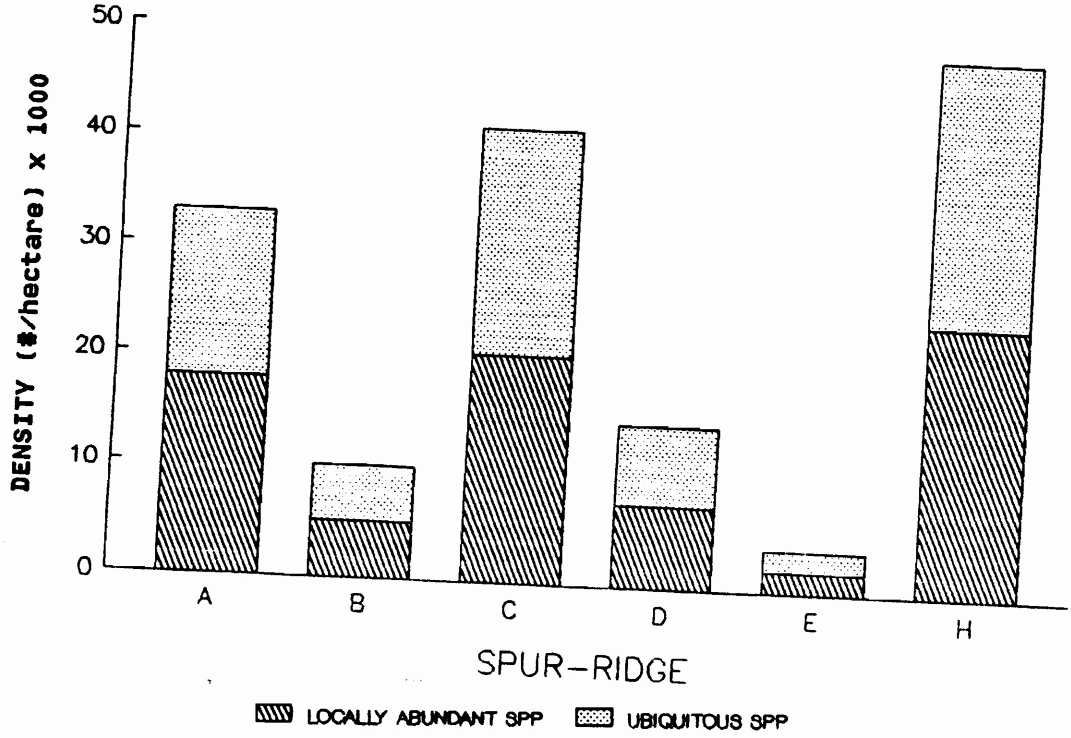


Figure 10. Total density of species found in the understory stratum that occurred ubiquitously on the Brush Mountain spur-ridges ($p>0.05$) or were only locally abundant ($p<0.05$).

Table 3. Density (stems/ha) of understory species that occurred at fewer than all 6 spur-ridge sites in 1986.

	SPUR-RIDGE					
SPECIES	A	B	C	D	E	H
Trees species:						
Amelanchier arborea	2515	1729	2043	472	-	629
Carya glabra	-	-	-	157	-	-
Cornus florida	-	-	2200	-	-	2043
Ostrya virginiana	1100	-	-	2515	314	157
Quercus coccinea	786	470	1100	1060	-	629
Shrub species:						
Castanea dentata	-	-	-	157	-	943
Gaylussacia baccata	1572	629	8331	1257	-	17133
Hamamelis virginiana	1415	1570	2986	-	1257	1886
Kalmia latifolia	157	-	471	-	314	-
Rhododendron sp.	157	-	-	472	-	472
Sassafras albidum	-	-	1414	472	-	-
Vaccinium stamineum	10217	628	-	-	-	-
Viburnum acerifolium	629	-	2043	786	-	472
TOTALS:	18548	5026	20588	7348	1885	24364

Table 4. Matrix of Sorensen's coefficients of similarity. Scores indicate the degree of similarity of understory species density between each pair of spur-ridge sites (1986).

SPUR-RIDGE

	A	B	C	D	E	H
A	1.00	0.53	0.39	0.33	0.40	0.44
B		1.00	0.58	0.46	0.66	0.33
C			1.00	0.58	0.38	0.38
D				1.00	0.42	0.32
E					1.00	0.30
H						1.00

reflected the presence of patchily distributed species at each spur-ridge site.

The species richness of the understory stratum also varied among sites. A total of 12 species occurred at A, D, and H. Eleven different species were found at C. Sites B and E had only 8 and 7 species, respectively. There were marginally significant positive correlations between species richness and vegetation density ($r=0.81$, $p=0.05$) and cover ($r=0.74$, $0.05<p<0.10$) at these spur-ridges.

3a. Groundlayer Structure

The groundlayer stratum vegetation on Brush Mountain can be divided into 4 growth form groups (trees, shrubs, forest herbs, and ruderals; Appendix 1). As in the understory, tree and shrub species comprised fairly large proportions of the total groundlayer density at each site (Figure 11). The density of shrub species in this stratum varied a great deal among sites, however. At site C, the total density of shrub species was high (51120 stems/ha [35.6%]), while at E the few shrub species present in the groundlayer had relatively low densities (10000 stems/ha [12.6%]). Annual and perennial forest herbs dominated the groundlayer at C, D, and E, averaging over 61000 stems/ha. Since ruderal plant species typically favor marginal and disturbed habitats, it is not surprising that their densities in the groundlayer of the mature forests on Brush Mountain were very low (Figure 11). Site C was the only site at which ruderal species were completely absent from the groundlayer. Interestingly, C had the greatest density and diversity of forest herbs, shrubs, and trees.

The similar form of groundlayer cover distributions among the 6 spur-ridge sites (Figure 12) indicated similar distributions in space. Cover distributions at A, B, E, and H especially resembled one another, and estimates of mean cover at these sites were very close (A=22.3%, B=23.8%, E=20.8%, and H=24.0%). Sites C and D had somewhat greater cover, averaging 38.6% and 32.3%, respectively. The groundlayer stratum at E was the sparsest with 3 sampling plots containing no vegetation at all.

Like the upper strata vegetation at these spur-ridges, the extent of groundlayer cover was very closely linked to plant density ($r=0.989$, $p<0.001$). Sites C and D had greater cover and greater plant density (143640 and 126390 stems/ha, respectively) than the other 4 sites. Densities at A, B, E, and H were considerably lower and comparable to one another in magnitude (A=76400, B=87790, E=79190, and H=83510 stems/ha).

3b. Groundlayer Composition

A total of 42 species was observed in the groundlayer stratum on Brush Mountain. Of these, 30 species (64%) were

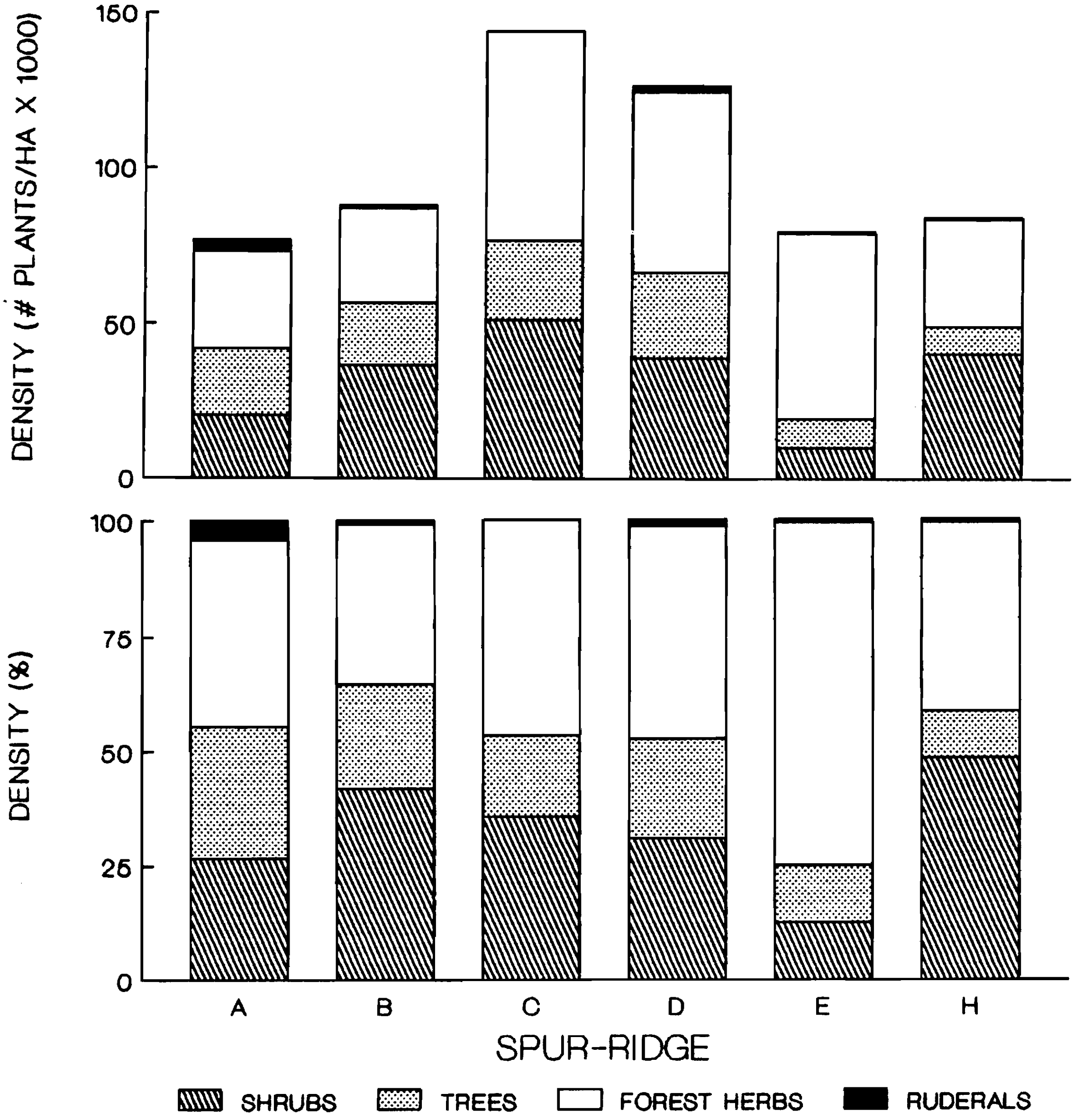


Figure 11. Density (actual stems/ha [upper graph] and percentages [lower graph]) of tree, shrub, forest herb, and ruderal species in the groundlayer stratum of the 6 spur-ridge sites.

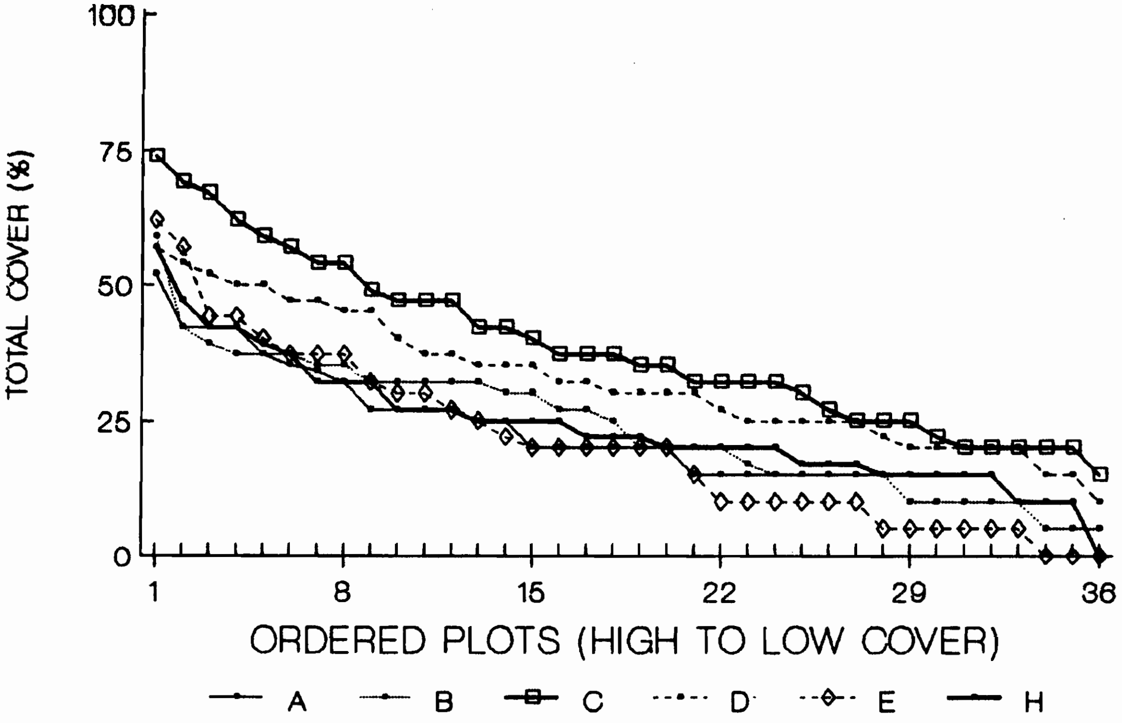


Figure 12. Cover distributions of groundlayer stratum vegetation at the 6 spur-ridge sites. Distributions were produced by ordering the 36 groundlayer sampling plots at each site from highest to lowest percent cover

restricted to fewer than 6 spur-ridges. Only 5 of the species that occurred at all 6 sites (Dryopteris marginalis, Galax aphylla, Houstonia purpurea, Quercus coccinea, Quercus prinus) were found in densities that did not differ significantly among sites (p>0.05). Locally abundant species were clearly very important groundlayer constituents.

Each site had a unique combination of groundlayer species (Table 5). Like the understory stratum, the groundlayer species composition at E was particularly unusual. For example, nearly 37000 Convallaria majalis stems/ha were found there. This forest herb species also occurred at B and D, but in much lower densities. The presence of C. majalis in such high density at E accounts for the unusually high relative density of forest herbs observed at that site (Figure 11).

Twelve groundlayer species were ubiquitous: Amelanchier arborea, Acer rubrum, Carex digitalis, Dioscorea villosa, Dryopteris marginalis, Hieracium venosum, Heuchera americana, Houstonia purpurea, Galax aphylla, Quercus coccinea, Quercus prinus, Vaccinium vacillans (Figure 13). These species accounted for varied proportions of the total density at each site (Figure 14). The density of Vaccinium vacillans was especially variable (Figure 13). While densities exceeding 32000 stems/ha were found at C and H, only 3300 stems/ha occurred at E.

Table 5. Density (stems/ha) of groundlayer species that occurred at fewer than all 6 spur-ridge sites in 1986.

	SPUR-RIDGE					
SPECIES	A	B	C	D	E	H
Tree species:						
Acer pensylvanicum	-	1667	556	278	556	556
Cornus florida	-	-	556	-	-	-
Ostrya virginiana	833	556	278	2222	556	-
Shrub species:						
Gaylussacia baccata	-	-	6390	278	-	278
Hamamelis virginiana	556	278	1667	-	833	-
Kalmia latifolia	-	-	278	-	-	-
Rhododendron sp.	-	-	1389	556	278	-
Sassafras albidum	-	-	2778	-	-	-
Smilax rotundifolia	1111	4722	-	278	2500	-
Viburnum acerifolium	2500	8333	4722	3333	3333	-
Vaccinium stamineum	5556	3333	1667	3333	-	-
Forest Herb species:						
Antennaria plantag.[1]	833	-	278	833	-	-
Asplenium platyneuron	3056	5556	833	278	-	3056
Convallaria majalis	-	4167	-	278	36666	-
Cunila oreganoides	-	-	-	556	-	1389
Carex platyphylla	-	278	278	3333	-	7222
Danthonia spicata	-	1111	5000	2778	-	2222
Epigaea repens	833	-	-	-	-	278
Geranium maculatum	-	-	-	556	-	-
Gaultheria procumbens	-	-	-	-	-	1389
Gillenia trifoliata	-	-	1389	-	-	-
Houstonia longifolia	8056	-	2222	2500	-	1111
Potentilla canadensis	-	-	1111	1667	-	556
Polygala pauciflora	-	833	5556	-	-	-
Polypodium virginianum	278	-	14167	278	-	-
Solidago sp.	-	-	1667	833	-	-
Thaspium trifoliatum	-	1944	1389	4722	2778	-
Ruderal species:						
Erechtites hieracif.[2]	833	-	-	-	-	-
Rosa carolina	2222	-	-	1944	556	278
Rubus sp.	-	833	-	-	-	278
TOTALS:	26667	33611	54171	30834	48056	18613

[1] Antennaria plantaginifolia
[2] Erechtites hieracifolia

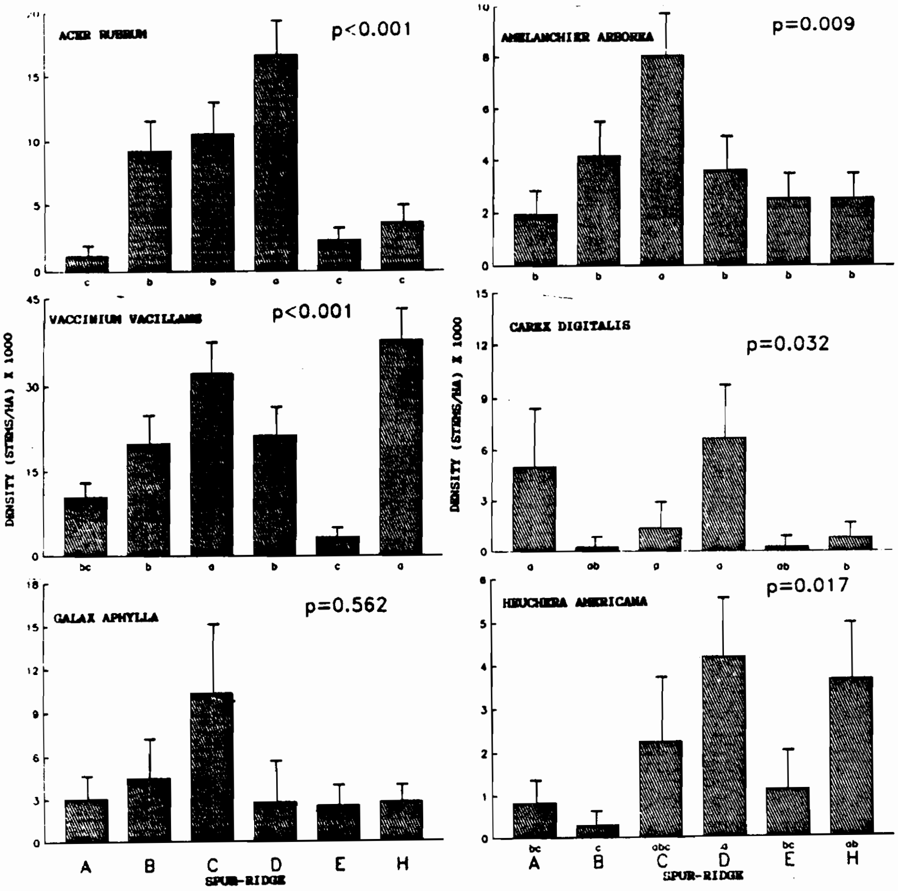


Figure 13. Density (mean ± S.E.) of the 12 species found in the groundlayer stratum of all 6 spur-ridge sites. Note: y-axis scales differ. Lower-case letters along x-axis indicate groupings produced by Duncan's multiple range test (alpha=0.05).

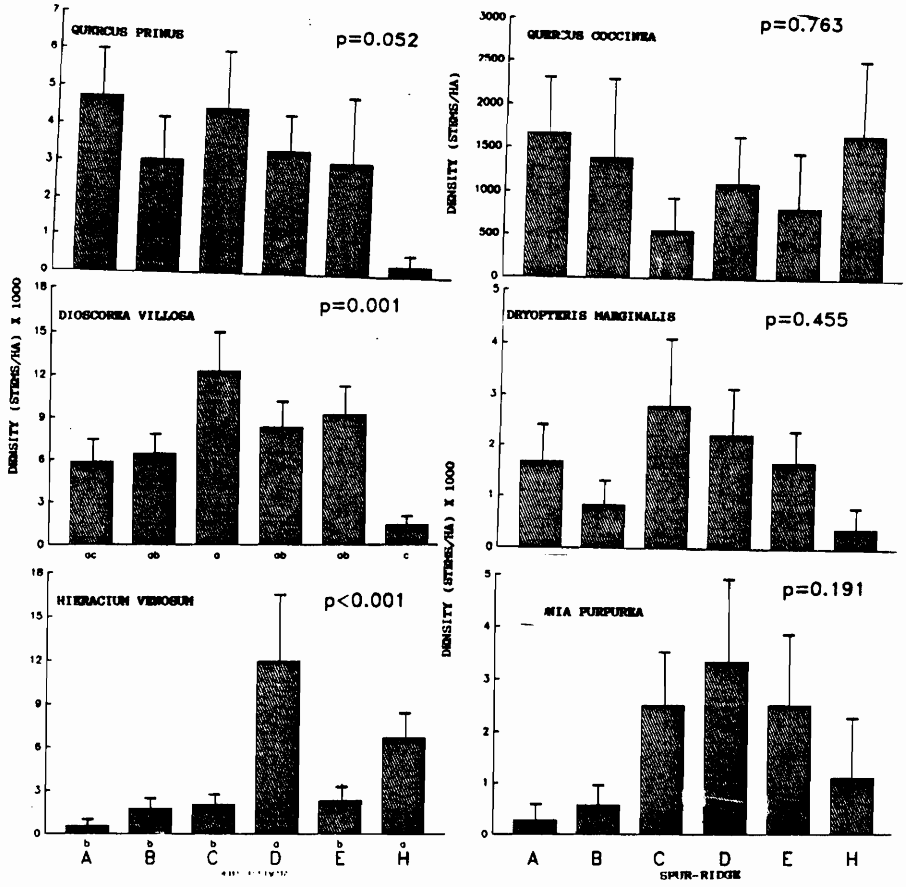


Figure 13 (CONTINUED)

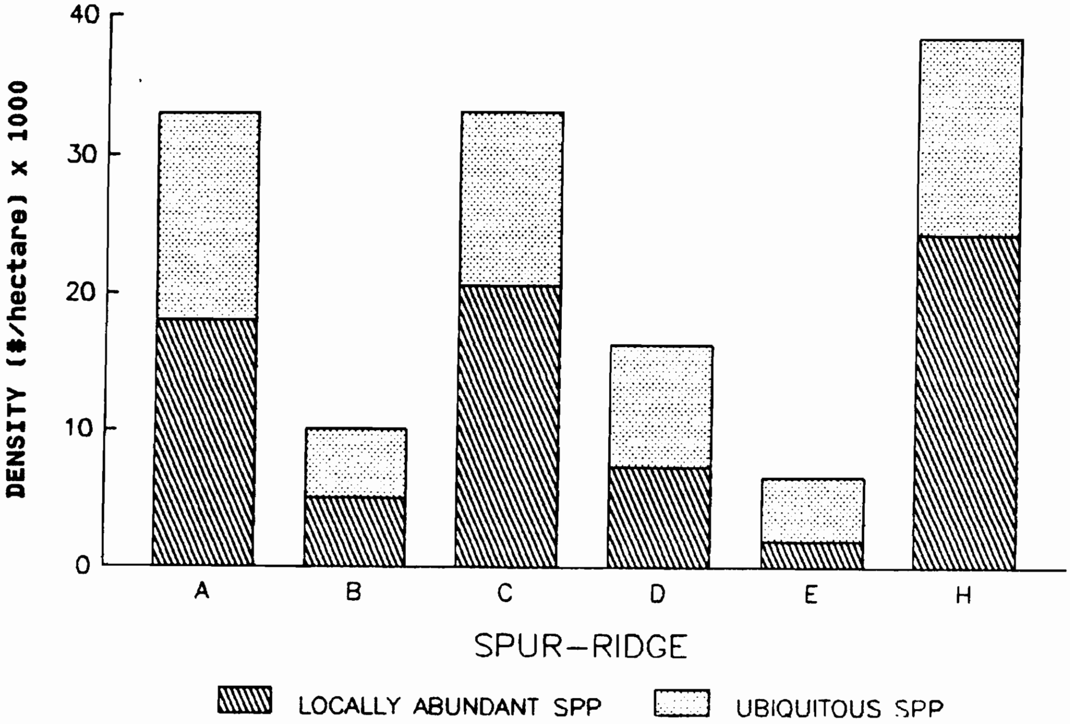


Figure 14. Total density of species found in the groundlayer stratum that occurred ubiquitously on the Brush Mountain spur-ridges (p>0.05) or were only locally abundant (p<0.05).

Sorensen's coefficients of similarity for the groundlayer stratum were low (mean=0.44 S.E.=0.03; Table 6). These low scores reflect the high degree of compositional variability among sites, and the particular importance of locally abundant species to the overall groundlayer composition at each site.

Total species richness also varied considerably among the spur-ridges. There were strong positive correlations between species richness and vegetation cover (r=0.96, p=0.002), and species richness and vegetation density (r=0.96, p=0.002). Not only did C and D have groundlayer vegetation of higher density and cover, these sites also had much greater species richness. Thirty-three species were observed in the groundlayer at C and 32 at D. Sites A, B, and H had 24, 25, and 24 species, respectively. The fewest groundlayer species (21) were found at E, a site with vegetation of very low density and cover.

D. Buried Seed Bank

1. Seed Bank Composition

Seed banks were surveyed to estimate density and composition of the potential flora. The Brush Mountain spur-ridge seed banks were extremely sparse. Both the greenhouse study and the visual search for seeds showed that an average of less than 1 seed/m^2 was present in the soil and forest

Table 6. Matrix of Sorensen's coefficients of similarity. Scores indicate the degree of similarity of groundlayer species density between each pair of spur-ridge sites (1986).

SPUR-RIDGE

	A	B	C	D	E	H
A	1.00	0.46	0.42	0.49	0.27	0.40
B		1.00	0.64	0.66	0.41	0.43
C			1.00	0.60	0.40	0.46
D				1.00	0.41	0.38
E					1.00	0.19
H						1.00

floor detritus (range = 0.23 to 0.69 seeds/m^2; Table 7). An average of only 10.3% of the greenhouse samples and 9.3% of the visual search samples was found to contain any seeds at all. The data were log-transformed ($\log_{10}$+1) prior to statistical analysis.

Analysis of variance on the pooled greenhouse and visual search data indicated that significantly more seeds were stored in the humus layer (mean density=0.64 seeds/m^2) than in the leaf litter (mean density=0.29 seeds/m^2) or surface 5 cm of soil (mean density=0.36 seeds/m^2, p=0.003; Figure 15). This indicated that most seeds deposited on the forest floor sift through the leaf litter and accumulated in the dense humus mat, where many probably decayed.

There were statistically significant differences in seed densities among the spur-ridge sites (p=0.025; Figure 16). Because of the patchy distribution of seeds at each site, however, standard error bars and ranges produced by Duncan´s multiple range test overlapped considerably. Despite this variability, density of buried seeds at the 6 spur-ridges was positively correlated with density of groundlayer vegetation (r=0.91, 0.01<p<0.02). Seed density was highest at C (mean = 0.69 seeds/m^2; Figure 16), the site which supported the greatest density of extant groundlayer vegetation.

Like the extant vegetation on these spur-ridges, the composition of the seed banks differed from site to site

Table 7. Density of species (seeds/m^2) found in seed bank samples collected at each spur-ridge. Asterisk indicates seeds found in visually searched samples. All others were identified from greenhouse germination samples.

			SPUR-RIDGE			
SPECIES	A	B	C	D	E	H
Tree species:						
Acer rubrum	-	-	-	-	0.03	-
Betula lenta	-	-	0.07	-	-	-
Ostrya virginiana	0.03*	0.03*	0.03* 0.30	0.07*	-	0.03
Shrub species:						
Vaccinium vacillans	-	-	-	0.03*	-	-
Viburnum acerifolium	0.03	-	-	-	0.07	-
Forest Herb species:						
Antennaria plantag.[1]	-	-	-	0.03	-	-
Danthonia spicata	0.07	-	0.03	-	-	-
Geranium maculatum	-	-	-	-	0.03	-
Houstonia purpurea	-	0.03	-	-	-	0.07
Heuchera americana	-	0.20	0.16	0.36	0.26	0.16
Potentilla canadensis	-	-	0.07	-	0.03*	-
Thaspium trifoliatum	-	-	-	0.03	-	-
Ruderal species:						
Erechtites hieracif.[2]	-	0.03	0.03	0.03	-	-
Phytolacca americana	-	0.03	-	-	-	-
Rhus typhina	0.03* 0.07	-	-	-	-	-
Robinia pseudo-acacia	-	-	-	-	0.03	-
Taraxacum officinale	-	-	-	0.03*	-	-
Verbascum thapsus	-	0.03	-	-	-	-
Unknown species	-	-	-	0.03	-	-
TOTALS:	0.23	0.35	0.69	0.61	0.45	0.26

[1] Antennaria plantaginifolia

[2] Erechtites hieracifolia

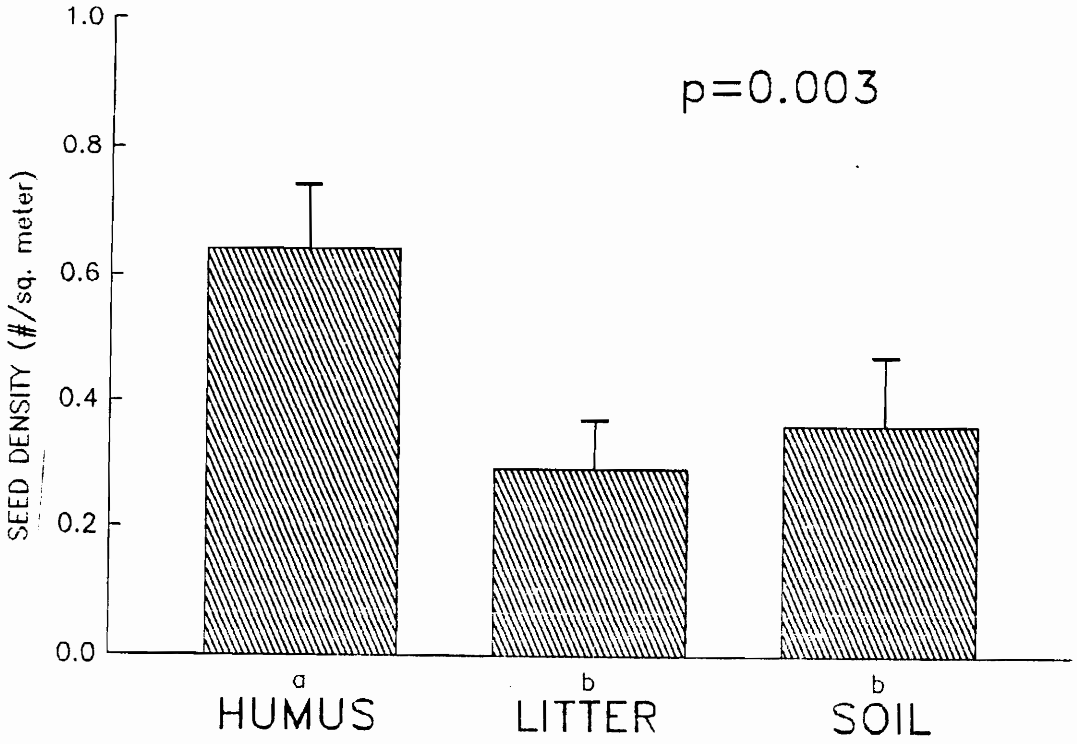


Figure 15. Density of seeds (mean ± S.E.) found in the leaf litter, humus, and surface 5 cm of soil. The greenhouse germination and visual search data were pooled to produce these values. Lower-case letters along x-axis indicate groupings produced by Duncan's multiple range test (alpha=0.05).

(Table 7). No species was detected at all 6 sites. Seeds of *Ostrya virginiana* and *Heuchera americana* were each found at 5 sites. All 4 groundlayer plant growth form groups (trees, shrubs, forest herbs, and ruderals) were represented in the seed bank, although not necessarily at each site. Overall, seeds of forest herbs were found in highest abundance, especially those of *Heuchera americana*. Interestingly, *Betula lenta* occurred in the seed bank yet was not observed growing on or near the sites. Seeds of several ruderal species (*Erechtites hieracifolia*, *Phytolacca americana*, *Rhus typhina*, *Robinia pseudo-acacia*, *Taraxacum officinale*, *Verbascum thapsus*) also were found in the seed bank samples, but only *E. hieracifolia* was observed in the extant groundlayer vegetation (site A).

The existence of extremely low seed bank densities (mean for the 6 sites = 0.43 seeds/m^2) was surprising, given the high densities of seeds found in most studies. For example, Olmstead and Curtis (1947) examined 7 different forests in Maine and found an average of 50 viable seeds/m^2. Livingston and Allessio (1968) found 1200 - 5000 seeds/m^2 buried in the soil of Massachusetts old field forests, and Fyles (1989) estimated the seed bank density of *Pinus banksiana* forests in Alberta to be between 500 and 2600 seeds/m^2. The comparatively low seed bank densities found in this study suggested assessment of the methodology.

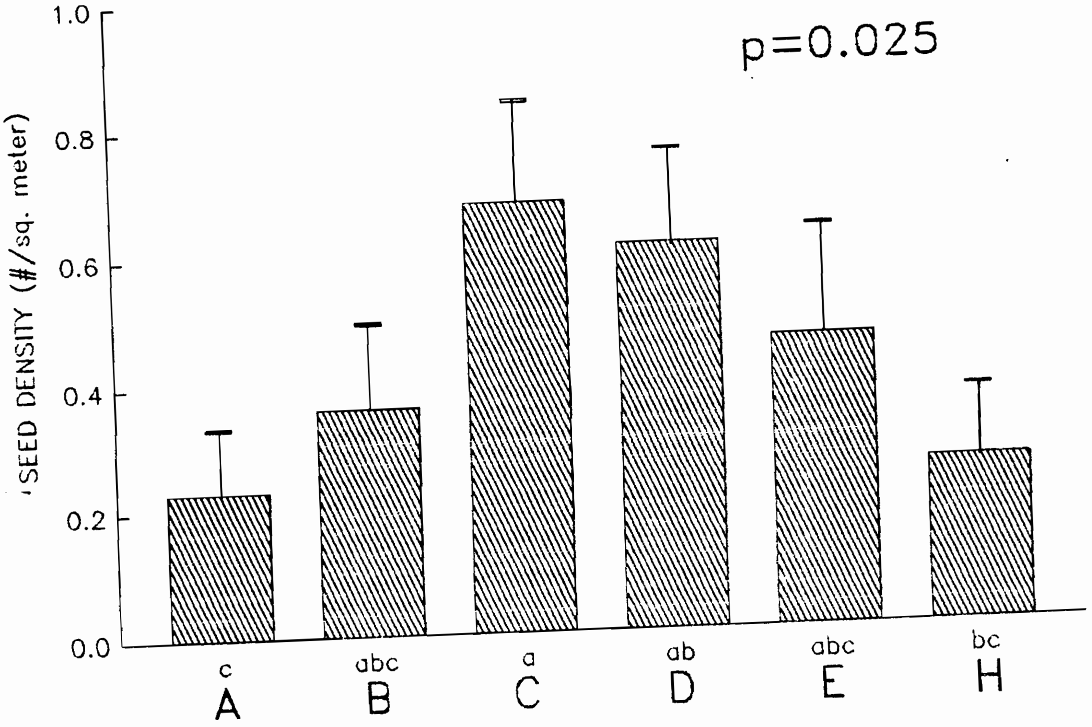


Figure 16. Density of seeds (mean ± S.E.) found in forest floor and surface soil detritus at each of the 6 spur-ridge sites. The greenhouse germination and visual search data were pooled to produce these values. Lower-case letters along x-axis indicate groupings produced by Duncan's multiple range test (alpha=0.05).

If the greenhouse environment had been unfavorable for germination of important species, seed bank densities might have been greatly underestimated. The low seed density observed for the greenhouse samples, however, was corrobrated by the visual search. Of course, some seeds may have still gone undetected. Rhododendron, for example, produces minute seeds (< 1 mm) that may have passed through the sieves used to remove seeds from the soil and forest floor detritus. In addition, the seeds of Gaylussacia baccata strongly resemble root fragments and might have been missed by the visual search.

2. Additional Evidence of Sparse Seed Banks

Vegetation in canopy gaps often reflects the composition of the buried seed bank (Schaetzl et al. 1989). Therefore, vegetation on 10 tip-up mounds (mounds of disturbed soil produced when trees fall) were surveyed using 1.0 m^2 circular sampling plots. These mounds were located in forest adjacent to the 0.09 ha research quadrats. While the lengths of time since tree fall were not known, the degree of tree decay indicated that these mounds had been created several years prior to sampling.

Tip-up mound plant densities were low, averaging only 3.6 stems/m^2 (Table 8). Two mounds supported only patches of moss. The species richness of the mounds was also low (mean

Table 8. Density (stems/m^2) of species occurring on 10 tip-up mounds. Vegetation on 2 mounds per spur-ridge was surveyed, except at spur-ridges C and H where only 1 mound was found.

	TIP-UP MOUND									
SPECIES	A1	A2	B1	B2	C1	D1	D2	E1	E2	H1
Tree species:										
Acer rubrum	-	3	-	2	-	-	-	5	3	-
Amelanchier arborea	-	-	-	-	1	-	-	-	-	-
Ostrya virginiana	-	-	2	-	-	1	-	-	-	-
Shrub species:										
Rhododendron sp.	-	-	4	-	-	-	-	2	-	-
Vaccinium vacillans	-	1	-	-	-	-	-	-	-	-
Viburnum acerifolium	-	-	-	2	-	-	-	-	1	-
Forest Herb species:										
Danthonia spicata	-	-	-	-	3	-	-	-	-	3
Heuchera americana	-	-	-	-	-	-	-	-	2	-
Houstonia longifolia	-	1	-	-	-	-	-	-	-	-
TOTALS:	0	5	6	4	4	1	0	7	6	3

number of species present = 1.6/m^2). About half of the 9 species found on the mounds also occurred in the seed banks. While the densities of plants on the mounds exceeded estimated seed bank densities, some of the tip-up mound plants may not have been derived from the seed bank, but instead from propagules dispersed following tree fall. Still, the relatively low densities of tip-up mound plants and their general similarity in species composition to the seed banks supports the finding that the buried seed bank on Brush Mountain was very depauperate.

E. Postdisturbance Vegetation (1987 and 1988)

1a. Understory Structure

Predisturbance differences in understory patchiness among sites B, C, D, and E remained in the postdisturbance environment. The shape of the cover distributions changed very little (Figure 17). The large differences between C (mean cover in 1988 = 70.7%) and E (mean cover in 1988 = 35.2%) persisted. Two sampling plots at E still contained no understory plants in 1988. Fluctuations in cover between years was also apparent, reflecting mortality that was probably associated with severe summer drought in 1987 (National Oceanic and Atmospheric Administration 1988).

Total densities of understory vegetation increased minimally from 1986 to 1988. Expansion in size of existing

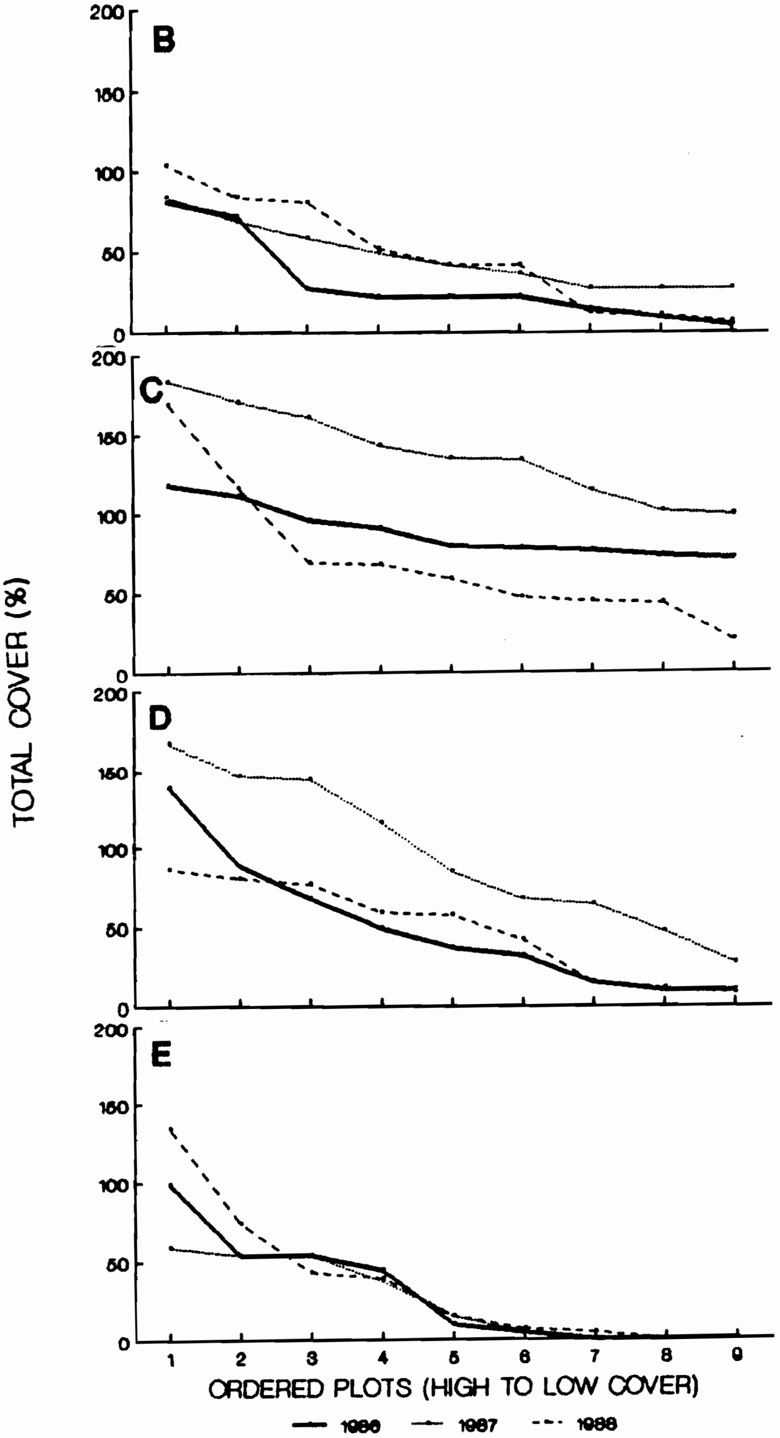


Figure 17. Cover distributions of understory stratum vegetation at sites B, C, D, and E in 1986 (prior to the disturbance) and 1987 and 1988 (following the disturbance). Distributions were produced by ordering the 9 understory sampling plots at each site from highest to lowest percent cover.

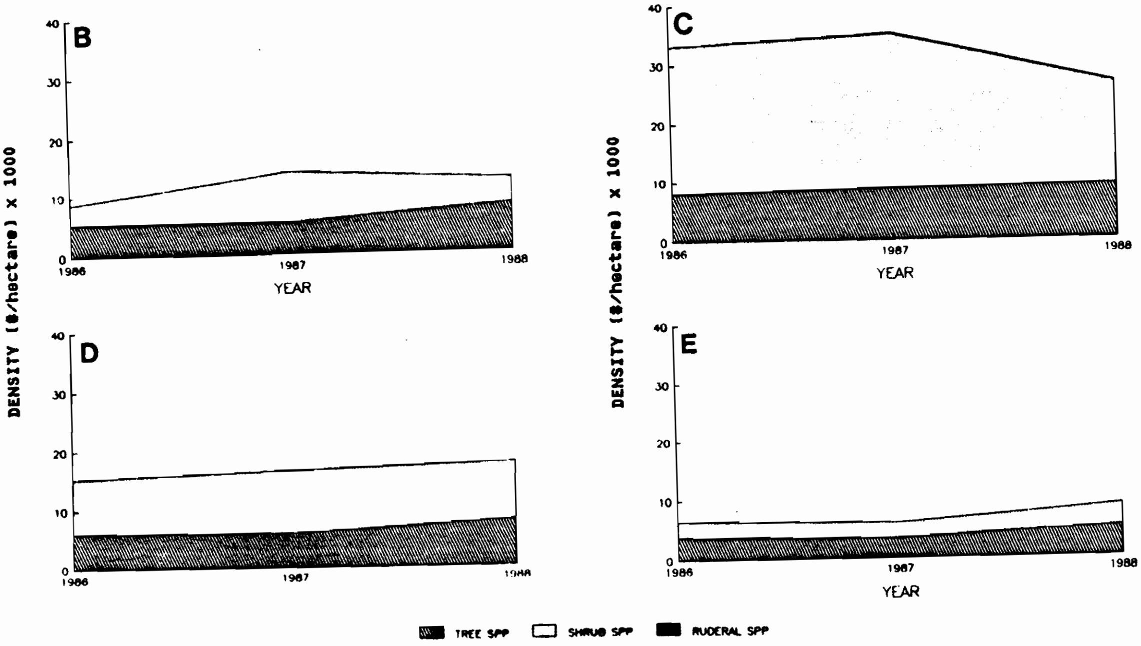


Figure 18. Postdisturbance changes in the density of tree, shrub, ruderal species in the understory stratum of sites B, C, D, and E.

1b. Understory Composition

The postdisturbance understory vegetation strongly resembled that of the predisturbance condition. Acer pensylvanicum, Quercus prinus, and Vaccinium vacillans were again observed at all 4 sites in 1987 and 1988. In addition, Quercus coccinea colonized the understory at E in 1987, thereby occurring in the postdisturbance flora of all 4 disturbed sites. Acer rubrum, however, had occurred in low density (160 stems/ha) at D in 1986 and 1987, but was not found there in 1988.

The densities of Acer pensylvanicum, Quercus coccinea, and Quercus prinus did not change appreciably following disturbance. These 3 ubiquitously distributed species continued to occur in densities that did not differ statistically among sites ($p>0.05$). Vaccinium vacillans, which had differed statistically among sites in 1986 ($p=0.033$), continued to vary considerably in 1988 ($p=0.006$). The densities of this shrub species remained much greater at C and D than at B and E (Figure 19).

Total understory plant density also differed greatly among sites during the 2 years following disturbance (Figure 20). Ubiquitious species (species observed in similar densities at all sites, $p>0.05$) accounted for smaller proportions of the total understory than did the more locally abundant species. At site C in 1988, for example, ubiquitous

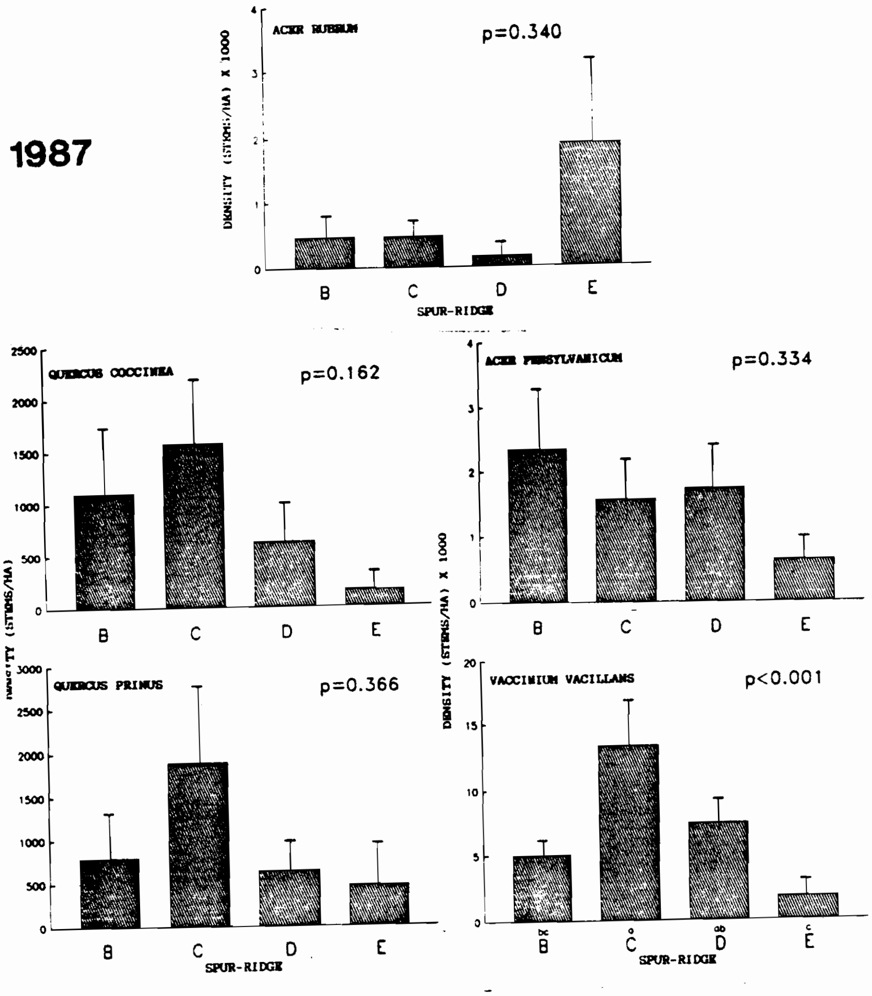


Figure 19. Density (mean ± S.E.) of 5 species found in the understory stratum of all 4 disturbed spur-ridge sites in 1987, and of 6 species found at all sites in 1988. Note: y-axis scales differ. Lower-case letters along x-axis indicate groupings produced by Duncan's multiple range test (alpha=0.05).

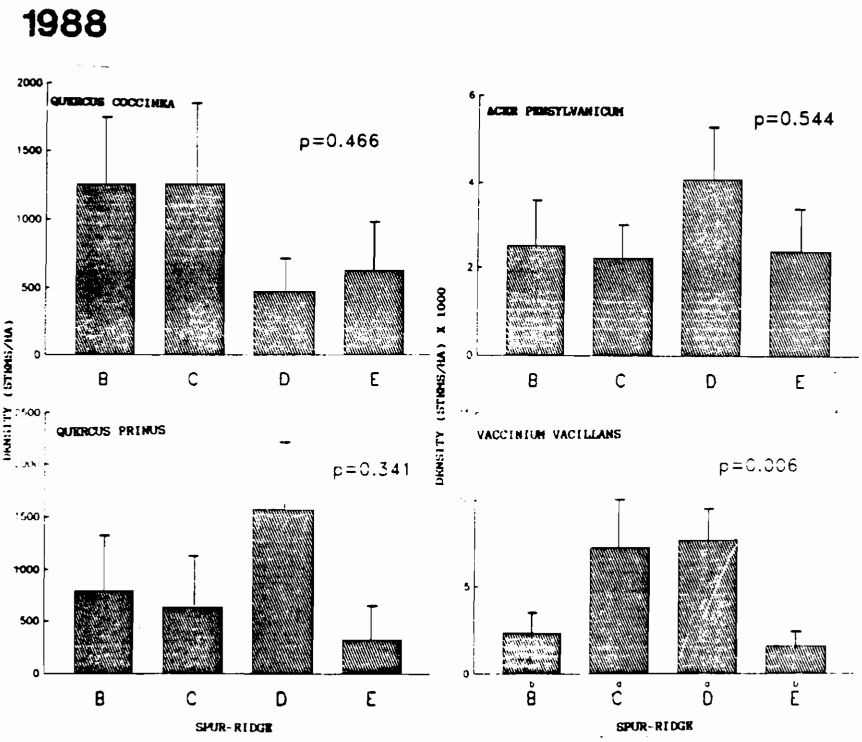


Figure 19. (CONTINUED)

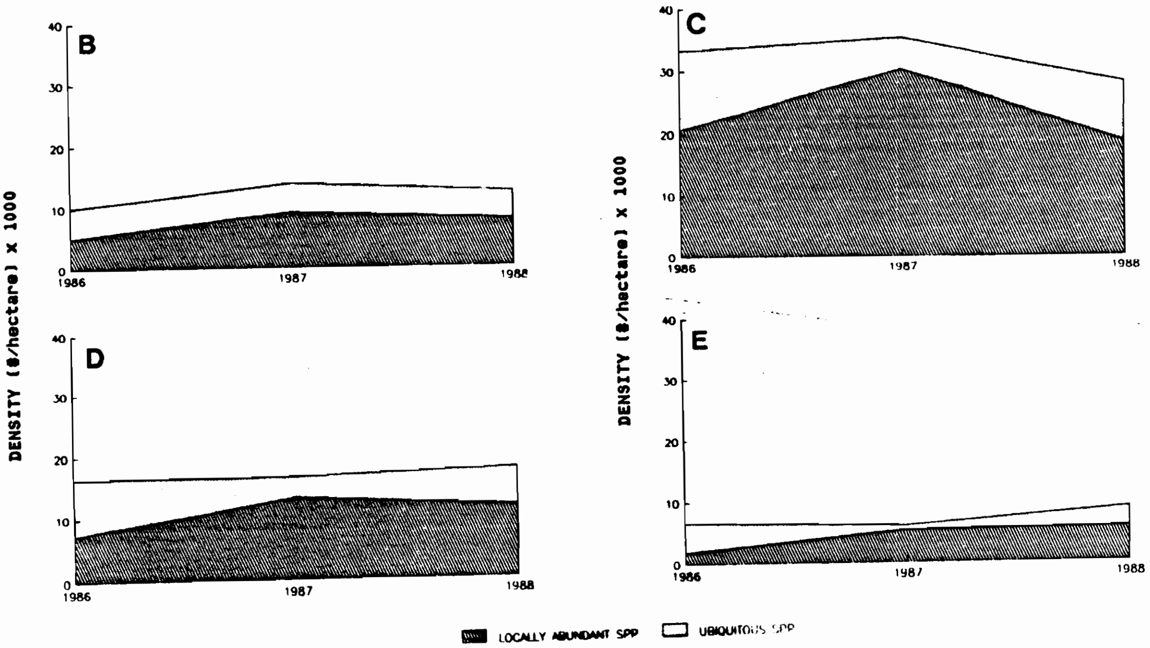


Figure 20. Postdisturbance changes in the total density of species found in the understory stratum that occurred ubiquitously on the Brush Mountain spur-ridges ($p>0.05$) or were only locally abundant ($p<0.05$).

species had a total density of 9380 stems/ha, while the total density of these species at E was only 3300 stems/ha.

Varied combinations of 5 tree species, 9 shrub species, and 1 ruderal species comprised the rest of the understory at the 4 disturbed sites (Table 9). These locally abundant species typically occurred in low average densities (<2000 plants/ha). One exception was Gaylussacia baccata where, in 1987, 5973 stems/ha were found at C while none occurred at the other 3 sites (Table 9).

From 1986 to 1988, sites B, C, and E experienced small net increases in understory species richness (Figure 21). Richness at D declined somewhat over this period. At the 3 sites where increases occurred, the newly colonized species, were found in relatively low densities (<1000 stems/ha; Table 9). Vegetative expansion by existing understory plants, a process that did not alter species richness, had a more important effect on the overall structure of these forests.

While all of the species in the understory were capable of sexual reproduction, plants that reproduced by vegetative means predominated (Figure 22). Individuals derived from propagules were observed in much lower densities. Following the disturbance, the density of plants that combined vegetative reproduction with germination from seeds increased somewhat (Figure 22). The high relative importance of vegetative reproduction at these sites was one reason why

Table 9. Species that occurred in the understory stratum at fewer than all 4 disturbed spur-ridge sites in 1987 and 1988.

	SPUR-RIDGE							
SPECIES	B		C		D		E	
	87	88	87	88	87	88	87	88
Trees:								
Acer rubrum	470	2672	470	1257	160	-	1890	1729
Amelanchier arborea	-	314	1886	2357	157	-	-	-
Carya glabra	-	-	-	157	-	-	-	-
Cornus florida	-	-	1257	1100	-	-	-	-
Ostrya virginiana	629	314	-	-	2672	1886	157	-
Sassafras albidum	157	-	1257	943	157	-	-	-
Shrubs								
Castanea dentata	-	-	-	-	157	157	157	-
Dryopteris marginalis	-	-	-	471	-	157	-	157
Gaylussacia baccata	-	-	5973	3615	-	786	-	-
Hamamelis virginiana	-	314	3615	409	-	-	314	1729
Kalmia latifolia	-	-	314	157	-	-	314	314
Rhododendron sp.	-	157	-	-	314	-	-	-
Vaccinium stamineum	2358	1415	629	-	943	471	157	-
Viburnum acerifolium	943	157	1257	786	1572	314	-	-
Ruderals:								
Robinia pseudo-acacia	-	-	157	157	-	-	-	-

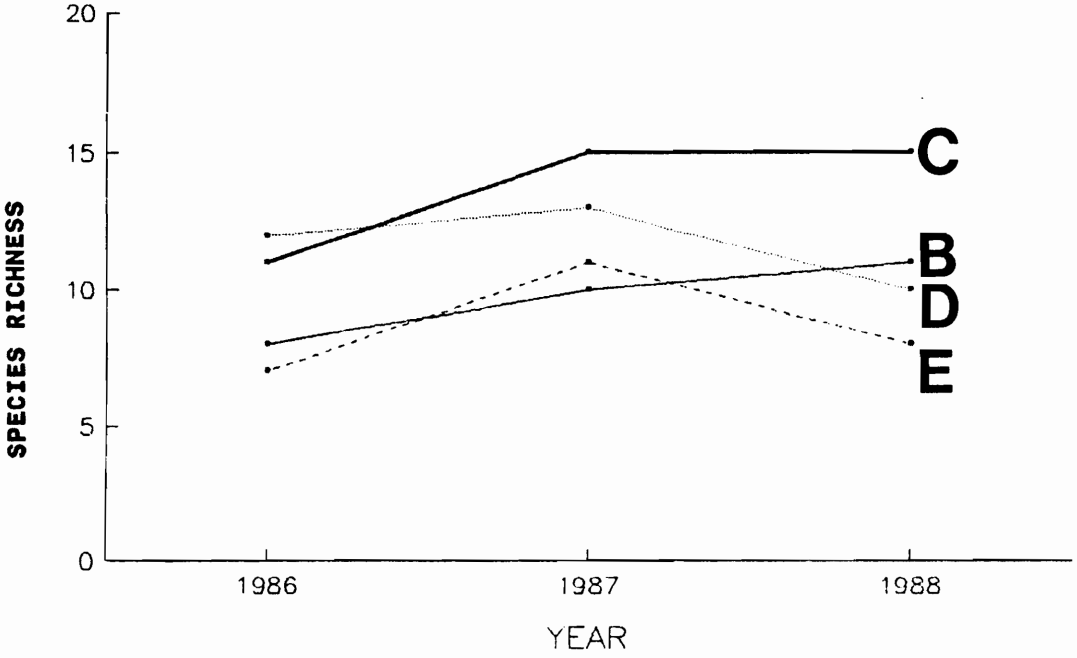


Figure 21. Postdisturbance changes in understory stratum species richness at sites B, C, D, and E.

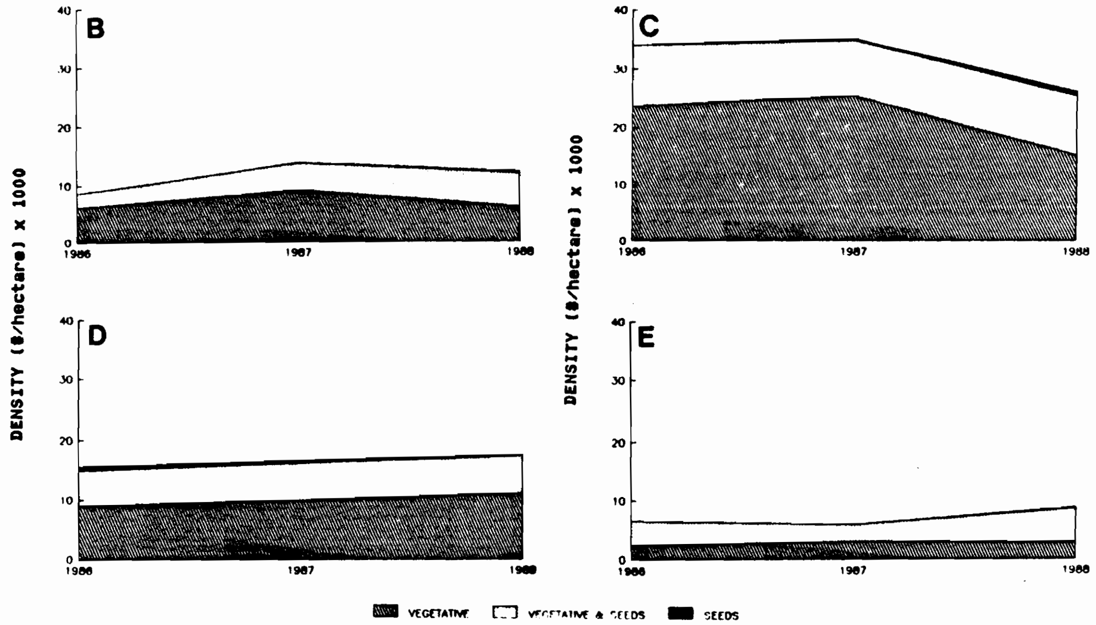


Figure 22. Postdisturbance changes in the total density of understory stratum species that reproduced primarily vegetatively, primarily from seeds, or by a combination of both means.

drastic compositional changes did not occur in the understory following disturbance. Most of the species established at these sites survived after the removal of canopy cover and some ~~then went~~ on to propogate themselves vegetatively.

The degree of similarity among sites, as indicated by trajectories of Sorensen's coefficients of similarity and Pearson product-moment correlation coefficients, remained uniformly low and at approximately the same levels from 1986 to 1988 (Figure 23). Sites, such as C and E which had exhibited only minimal similarity in 1986 remained very dissimilar following the disturbance.

2a. Groundlayer Structure

Leaf litter had been removed from half of the groundlayer sampling plots at the time of disturbance. Although some studies have shown that leaf litter on the forest floor inhibits groundlayer colonization (Beatty 1984, Beatty and Sholes 1988), t-tests performed on data collected in 1987 and 1988 showed that there had been no statistically significant differences in plant density or species richness between the 2 types of plots at any of the spur-ridge sites ($p>0.05$, d.f.=18 for each site in 1987 and 1988). Therefore, the data were pooled for all analyses.

The overall form of pre- and postdisturbance cover distributions for groundlayer vegetation were very similar

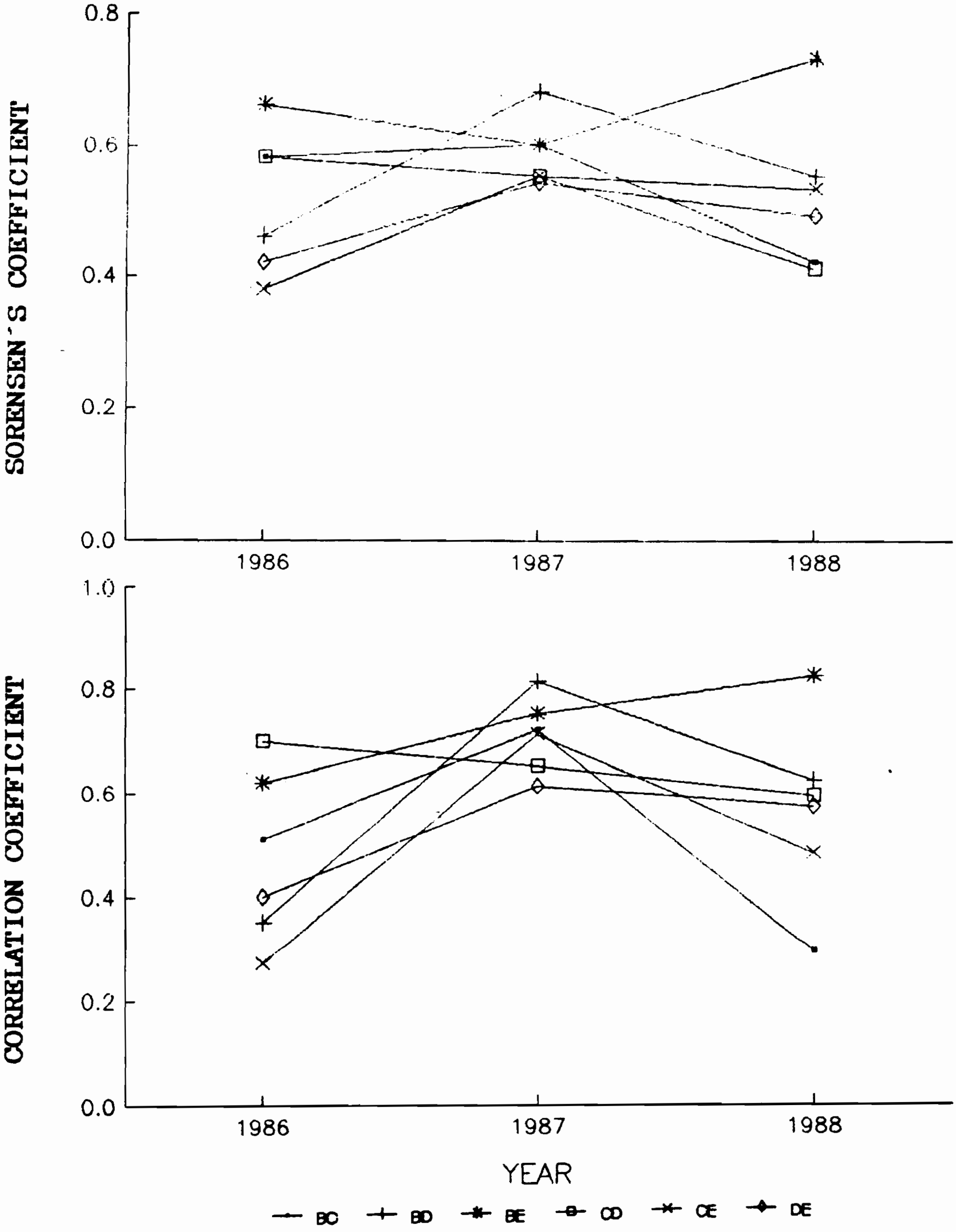


Figure 23. Postdisturbance changes in understory stratum similarity as indicated by Sorensen's coefficients of similarity (upper graph) and Pearson product-moment correlation coefficients (lower graph).

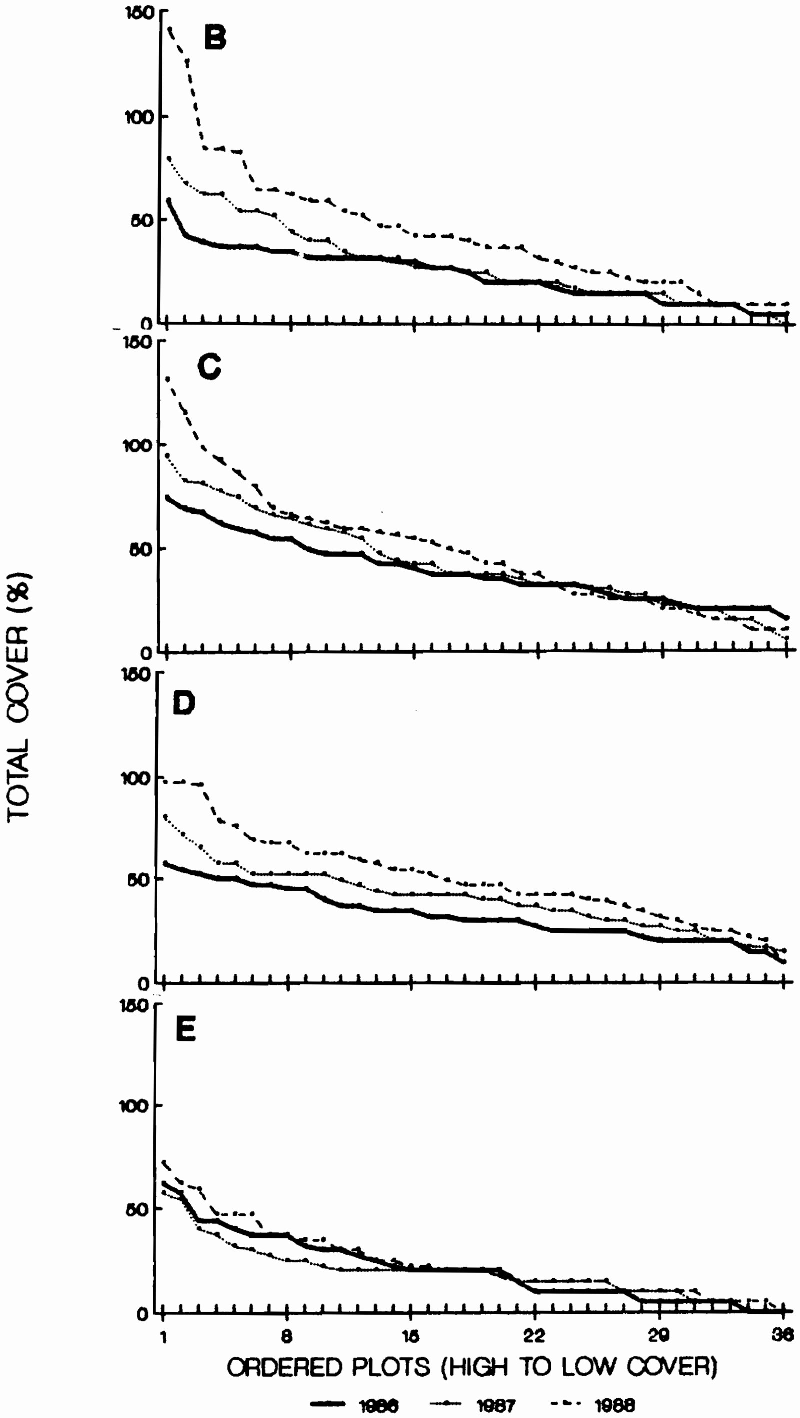


Figure 24. Cover distributions of groundlayer stratum vegetation at sites B, C, D, and E in 1986 (prior to the disturbance) and 1987 and 1988 (following the disturbance). Distributions were produced by ordering the 36 groundlayer sampling plots at each site from highest to lowest percent cover.

(Figure 24). This general similarity from year to year indicated that the spatial heterogeneity had not been severely affected by the removal of canopy cover. In 1987, groundlayer sampling plots at sites C and D still contained vegetation with more overall cover than B and E.

Groundlayer cover did increase at all 4 sites, however. The greatest increase in cover was observed at B. By 1988, cover at that site (mean cover = 44.1%) was nearly as extensive as at C (mean cover = 48.1%) and D (mean cover = 50.3%). More than one-third of the plots at these 3 sites had vegetation covering 50% or more of the ground. Groundlayer cover at E in 1988 was much less extensive (mean cover = 24.1%). Only 3 out of 36 sampling plots at E contained vegetation with cover of 50% or more. One sampling plot contained no plants at all in 1988 (Figure 24).

Groundlayer densities did not increase during the first growing season following the disturbance (1987). The drought that summer (total precipitation for June, July and August, 1987 was 12.7 cm; average precipitation for these 3 months, 1959 - 1987 was 27.6 cm; National Oceanic and Atsmospheric Administration 1988) probably inhibited plant recruitment and growth (sprouting). Actually, mortality that year resulted in decreased total groundlayer plant densities at each site (Figure 25). Climatic conditions in 1988 (total rainfall for June, July and August = 29.7 cm; National Oceanic and

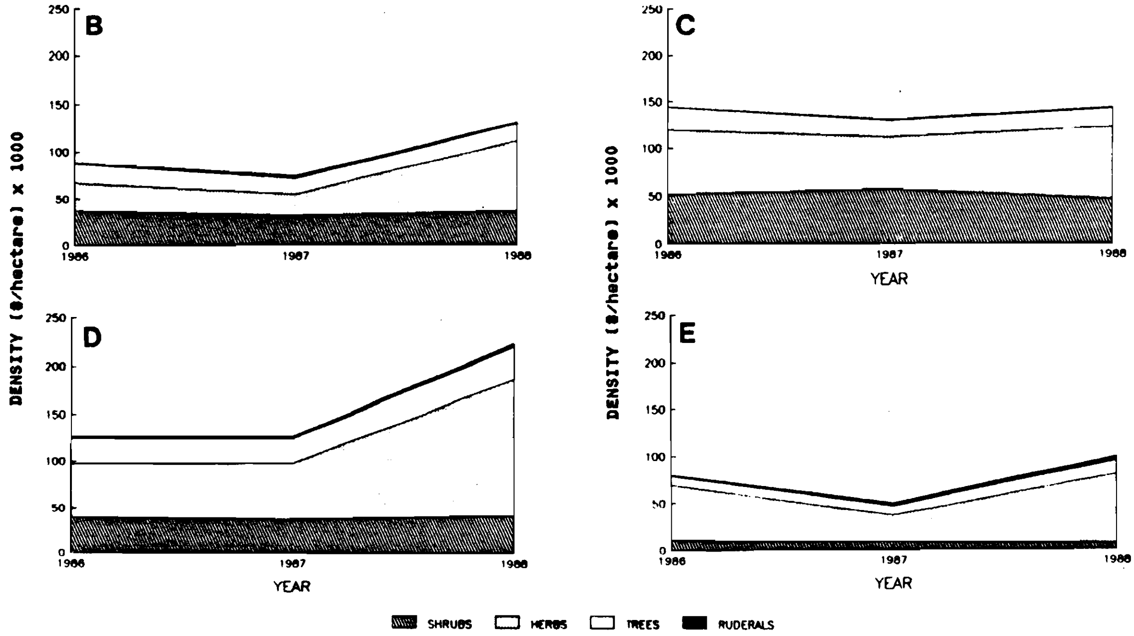


Figure 25. Postdisturbance changes in the density of tree, shrub, forest herb, and ruderal species in the groundlayer stratum of sites B, C, D, and E.

Atmospheric Administration 1988), however, were more conducive to growth.

While increases in understory cover had been primarily due to growth in size of existing plants, the observed increases in groundlayer cover that occurred in 1988 were directly attributable to recruitment of new plants. Although the density of groundlayer vegetation increased at each site, the extent of these increases varied greatly among sites (Figure 25). Site D experienced the largest net increase in density (105390 stems/ha [83.4%]). Recruitment of groundlayer plants at B and E resulted in more moderate net increases in density (42590 stems/ha [48.5%] at B; 21700 stems/ha [27.4%] at E). In contrast, at C, where the density of plants in the groundlayer stratum was quite high prior to the disturbance (143640 plants/ha), the net increase in density was extremely small (120 stems/ha [0.08%]).

Recruitment of forest herbs and ruderals caused the observed increases in groundlayer density (Figure 25). Sites that had relatively high numbers of forest herbs and ruderals in 1986 continued to do so in 1987 and 1988. Clearly, predisturbance vegetation density influenced the structure of the postdisturbance groundlayer stratum at each site.

2c. Groundlayer Composition

In 1987, 16 species were found in the groundlayer stratum of all 4 disturbed sites. The following year, this number increased to 17 (Figure 26). Several of these species (13 in 1987 and 9 in 1988) occurred in densities that did not differ statistically among sites ($p>0.05$). The total densities of these ubiquitous species at each spur-ridge site remained small and relatively stable from 1986 to 1988 (Figure 27). Therefore, increases in the total density of the groundlayer stratum were primarily due to colonization and increases in density by existing locally abundant species.

Locally abundant species were particularly important constituents of the groundlayer. Six tree species, 5 shrub species, 18 forest herb species, and 9 ruderal species were found in the groundlayer of 3 or fewer sites in 1987 and 1988 (Table 10). In addition, several species occurred at all 4 disturbed sites in densities that differed significantly among sites ($p<0.05$). These locally abundant species occurred in vastly different combinations and densities at each spur-ridge site.

The density of certain locally abundant species was very high, resulting in their dominance of some sites. In 1988, for example, the density of Danthonia spicata at D exceeded 45000 stems/ha. This species was also a dominant at C, where

1987

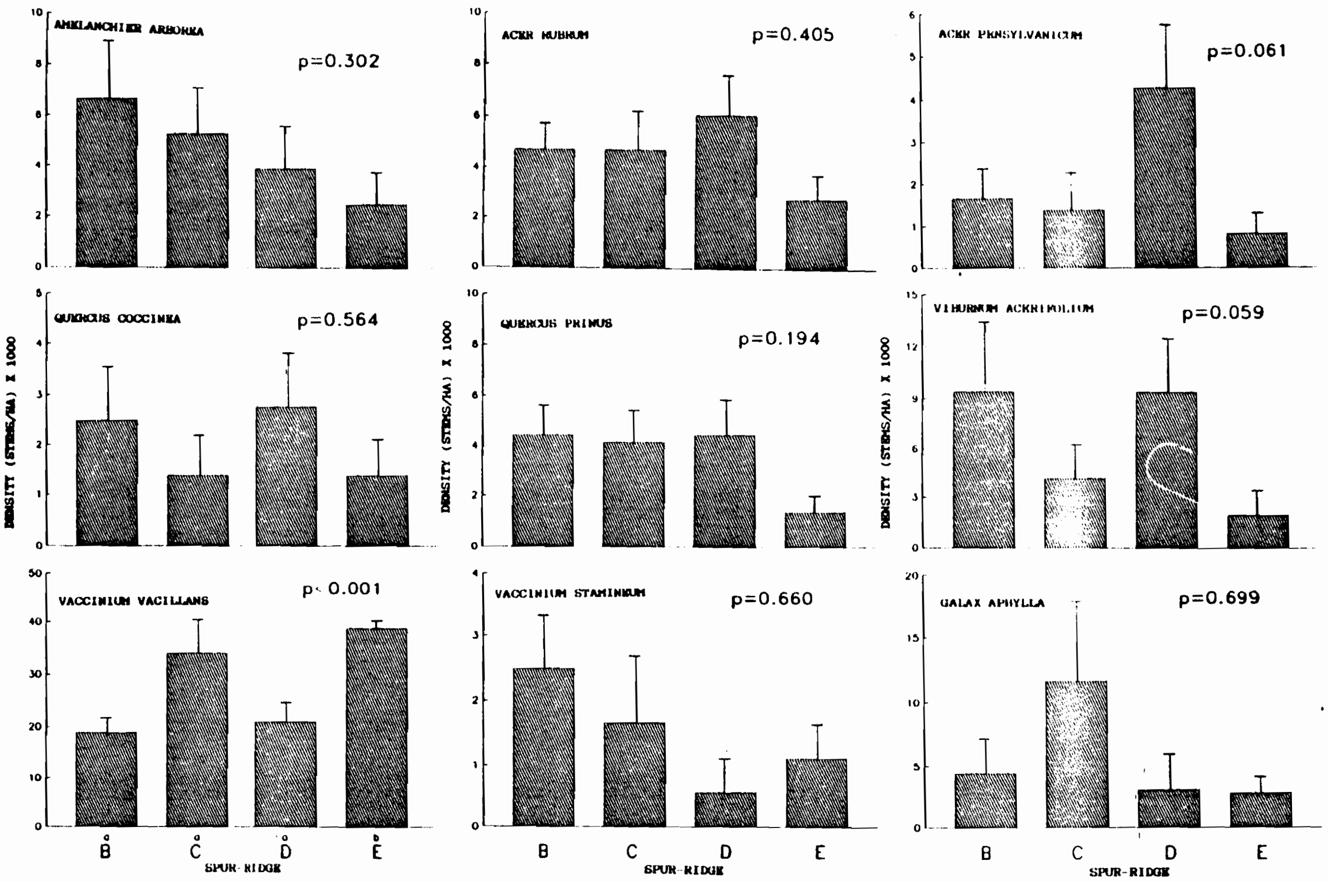
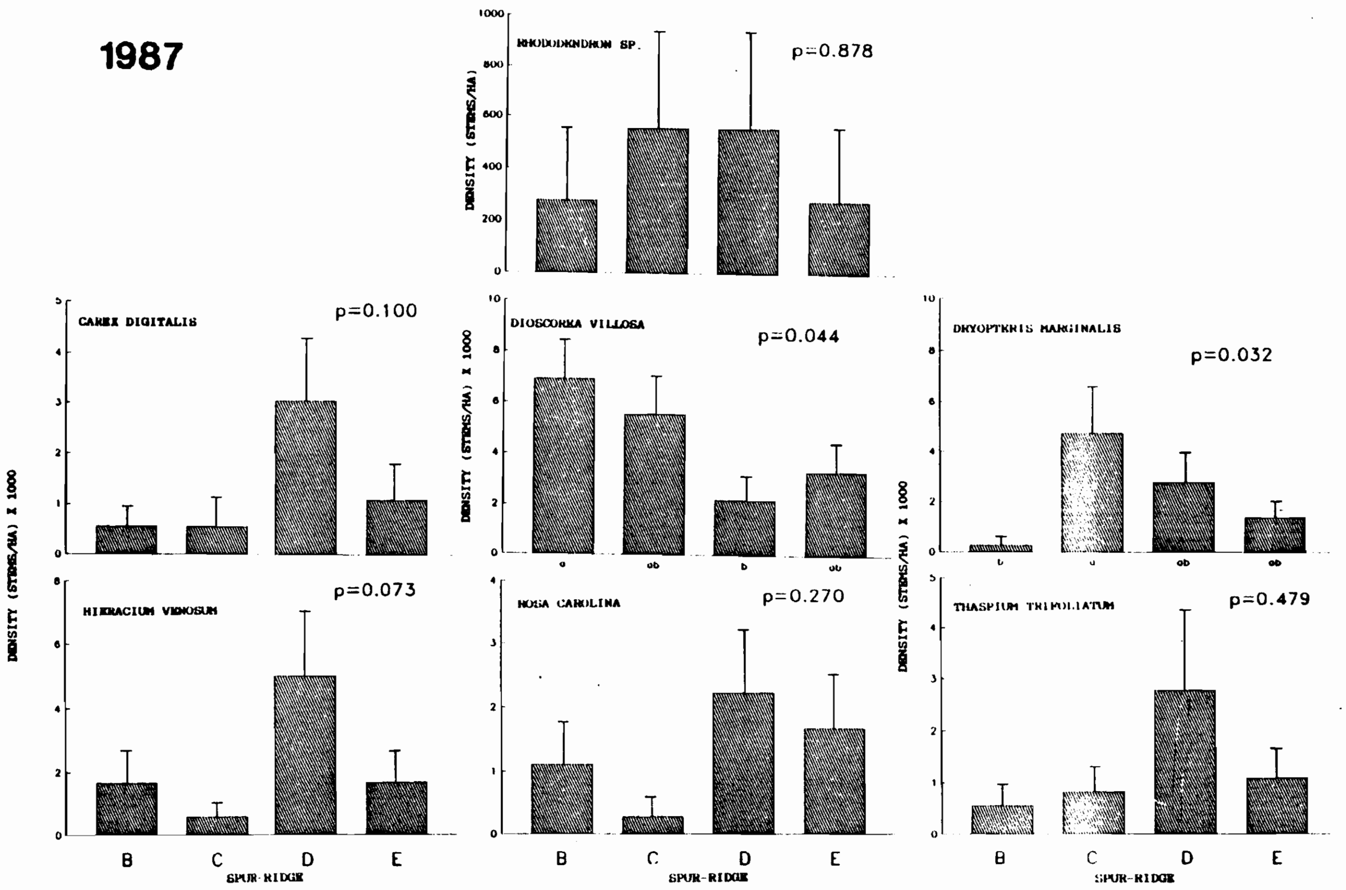


Figure 26. Density (mean ± S.E.) of 16 species found in the groundlayer stratum of all 4 disturbed spur-ridge sites in 1987, and of 17 species found at all sites in 1988. Note y-axis scales differ. Lower-case letters along the x-axis indicate groupings produced by Duncan's multiple range test (alpha=0.05).



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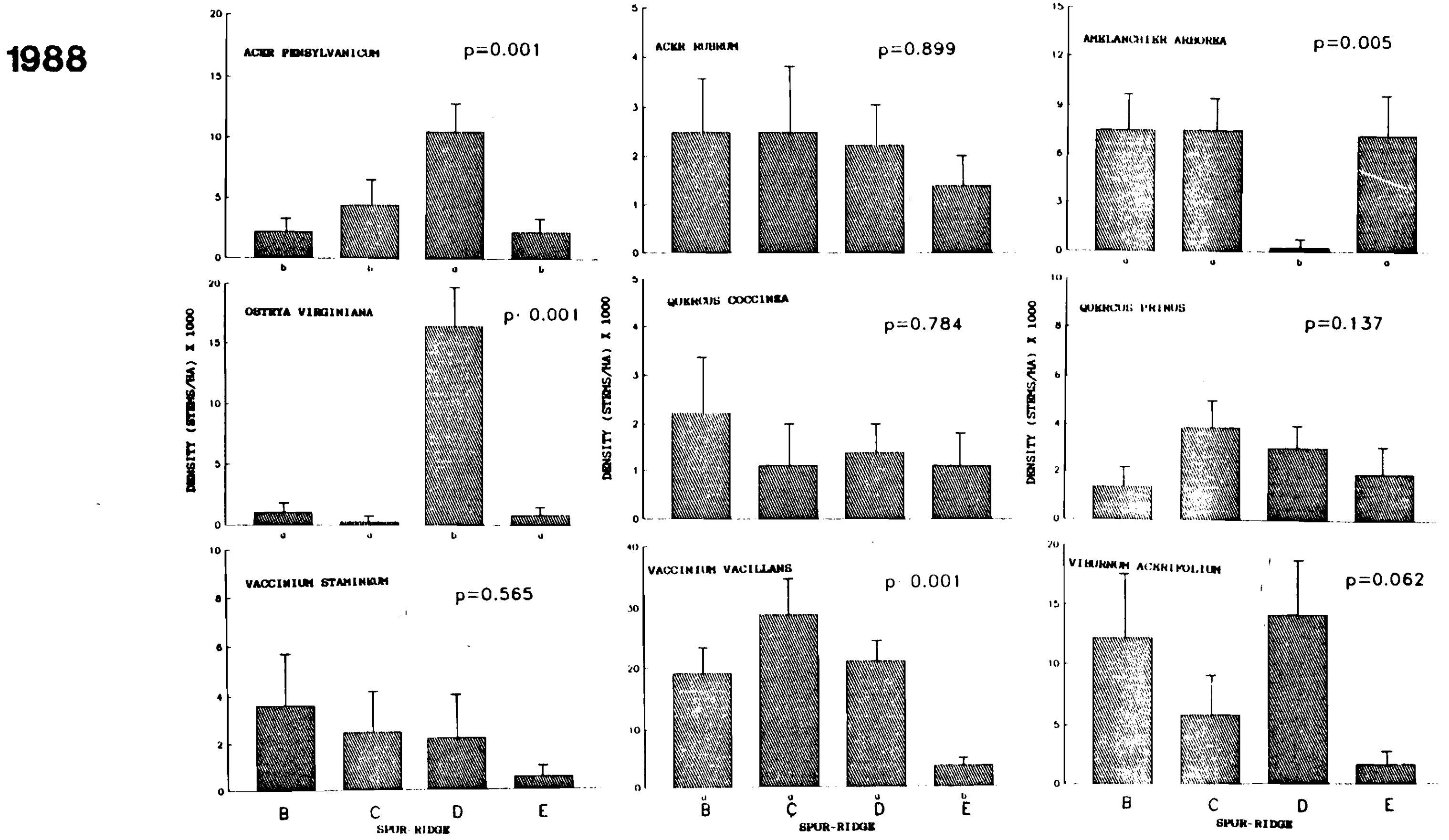

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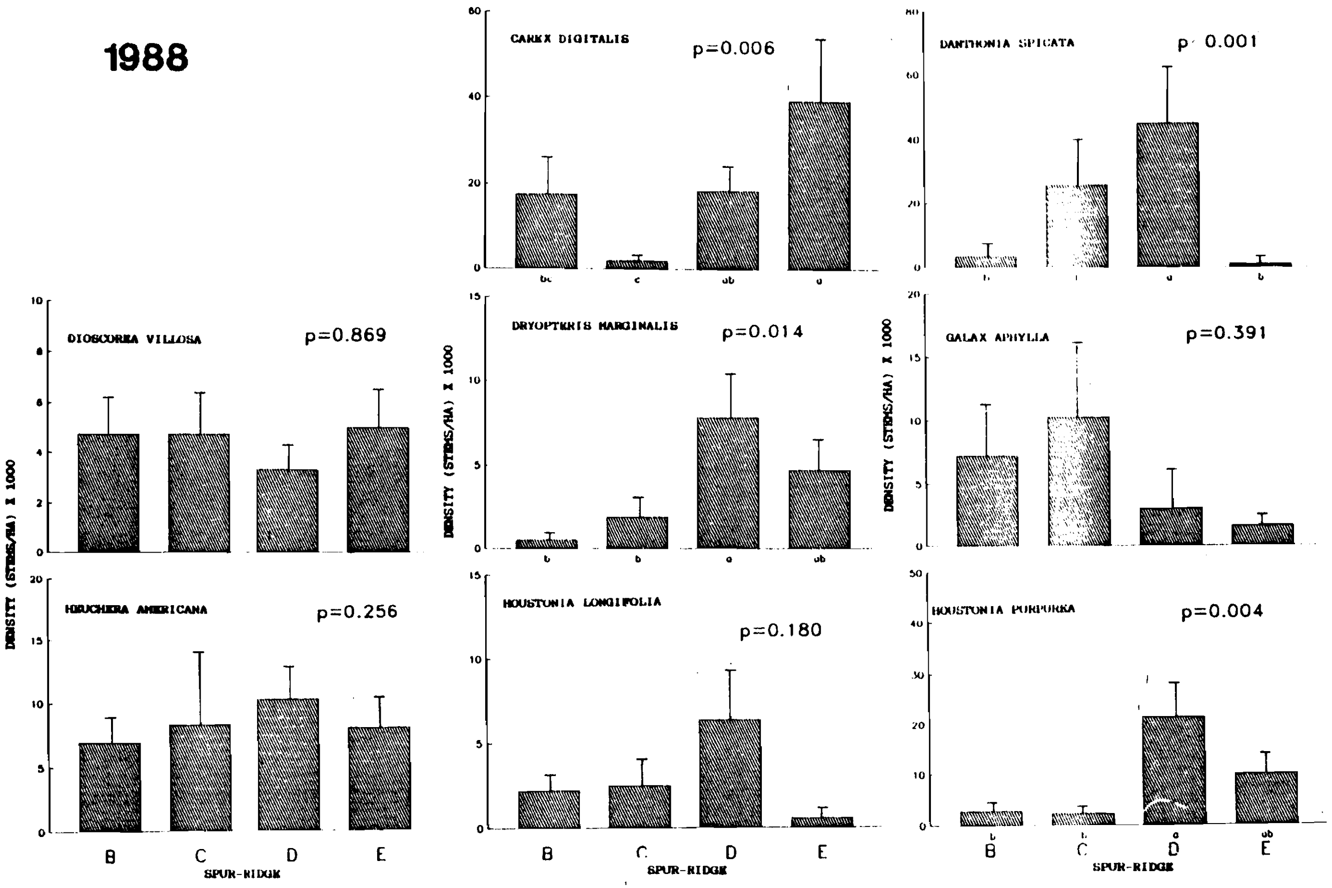

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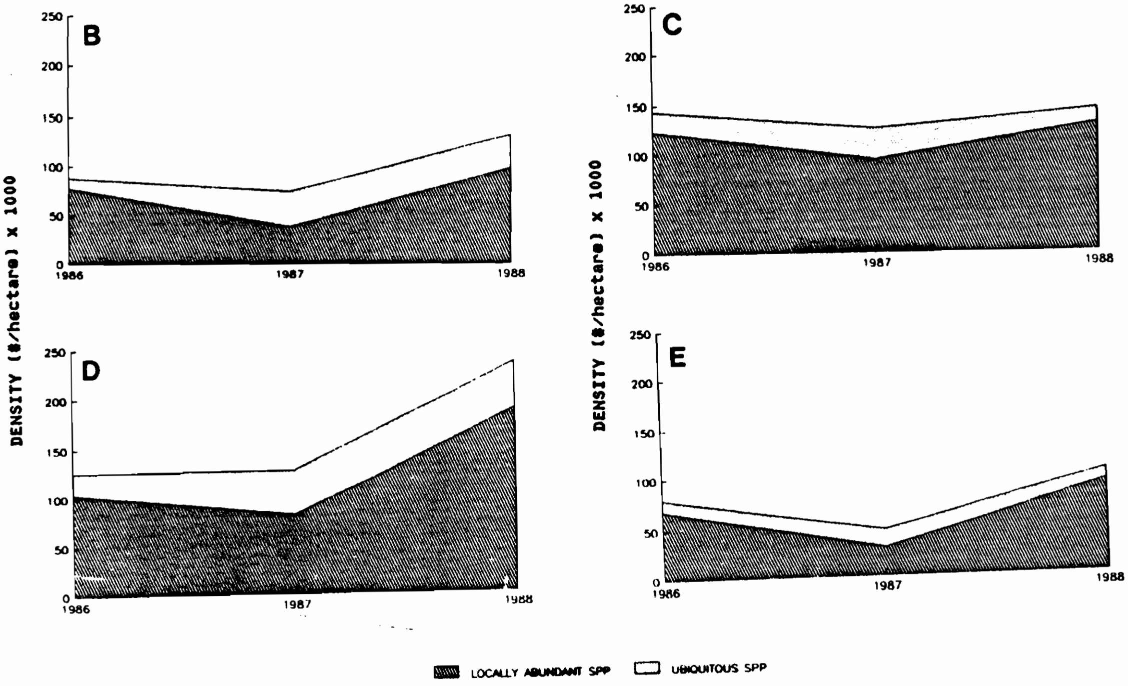

Figure 27. Postdisturbance changes in the total density of species found in the groundlayer stratum that occurred ubiquitously on the Brush Mountain spur-ridges ($p>0.05$) or were only locally abundant ($p<0.05$).

Table 10. Species that occurred in the groundlayer stratum at fewer than all 4 disturbed spur-ridge sites in 1987 and 1988.

SPECIES	SPUR-RIDGE							
	B		C		D		E	
	1987	1988	1987	1988	1987	1988	1987	1988
Forest Trees:								
Acer rubrum	-	2500	4722	2500	6111	2222	2778	1389
Cornus florida	278	-	1111	1111	-	278	833	-
Carya glabra	-	-	-	-	278	-	-	-
Ostrya virginiana	-	1111	-	278	4722	16389	-	830
Pinus pungens	-	1111	-	-	-	278	-	-
Pinus strobus	278	-	-	-	-	-	-	-
Forest Shrubs:								
Gaylussacia baccata	-	833	7778	4444	4444	1944	-	-
Hamamelis virginiana	-	556	3611	1667	278	-	556	-
Rhododendron sp.	278	-	556	833	556	8333	278	278
Sassafras albidum	-	-	5000	2222	-	278	-	-
Smilax rotundifolia	-	-	-	-	278	-	833	-
Forest Herbs:								
Antennaria plantaginifolia	-	-	-	-	1111	-	-	-
Asplenium platyneuron	-	1111	278	-	556	-	-	-
Convallaria majalis	-	1389	-	556	-	-	6389	1111
Cunila oreganoides	-	1111	-	-	-	5833	-	-
Carex platyphylla	278	11944	-	1667	3611	19444	-	-
Danthonia spicata	2778	3333	11667	25867	19444	45278	-	1111
Geranium maculatum	-	-	278	833	278	-	278	556
Gaultheria procumbens	1111	-	1389	-	-	-	2778	-
Gillenia trifoliata	-	-	-	1667	-	-	-	278
Houstonia longifolia	-	556	1389	2500	1667	6390	2222	556
Houstonia purpurea	3333	2778	4167	2222	8056	21389	-	10000
Polygonatum biflorum	-	556	-	-	-	-	-	278
Potentilla canadensis	-	278	833	5000	833	1111	-	-
Polygala pauciflora	-	-	1111	1944	-	-	-	-
Polypodium virginianum	833	6944	5278	-	556	-	-	-
Solidago sp.	-	2222	-	-	-	1667	-	556
Thaspium trifoliatum	-	-	-	278	-	-	-	833
Viola palmata	556	-	833	278	2778	1944	1111	-
Ruderals:								
Barbarea vulgaris	-	-	-	-	-	-	-	278
Carduus lanceolatus	-	556	-	-	-	-	-	556
Erechtites hieracifolia	556	-	-	556	-	833	-	556
Phytolacca americana	-	-	-	-	-	-	278	-
Rosa carolina	1111	278	278	-	2222	2222	1667	2778
Robinia pseudo-acacia	278	556	-	-	-	278	556	-
Rubus sp.	-	-	278	-	-	-	556	-
Taraxacum officinale	556	-	-	-	-	-	-	-
Verbascum thapsus	278	-	-	-	-	-	-	-

nearly 30000 stems were found. Site E, however, had only 1111 stems/ha. Similarly, the density of *Ostrya virginiana* at D in 1988 was 16390 stems/ha, while fewer than 1500 stems/ha were found at the 3 other disturbed sites. The high density of *O. virginiana* at D was particularly interesting because several individuals were also found in the understory and predisturbance canopy at that site. The larger individuals apparently were an important local source of seeds and vegetative sprouts. The canopy and understory strata at sites B, C, or E did not include many *O. virginiana* individuals, and this was reflected by the much lower groundlayer densities of this species at those sites.

Postdisturbance regeneration occurred primarily by vegetative reproduction. This was particularly true at E, where the density of species that reproduced primarily by vegetative means increased by 56.1%, an increase of 44430 stems/ha (Figure 28, Table 11). Species that increased in density through a combination of vegetative reproduction and seed germination also made up increasing proportions of the groundlayer at each site.

In 1988, 89% of the ubiquitously distributed species reproduced vegetatively, or by both seed germination and vegetative reproduction. Only 26% of the locally abundant species at the spur-ridge sites were vegetative reproducers. Many of these species (e.g. *Vaccinium vacillans*, *Danthonia*

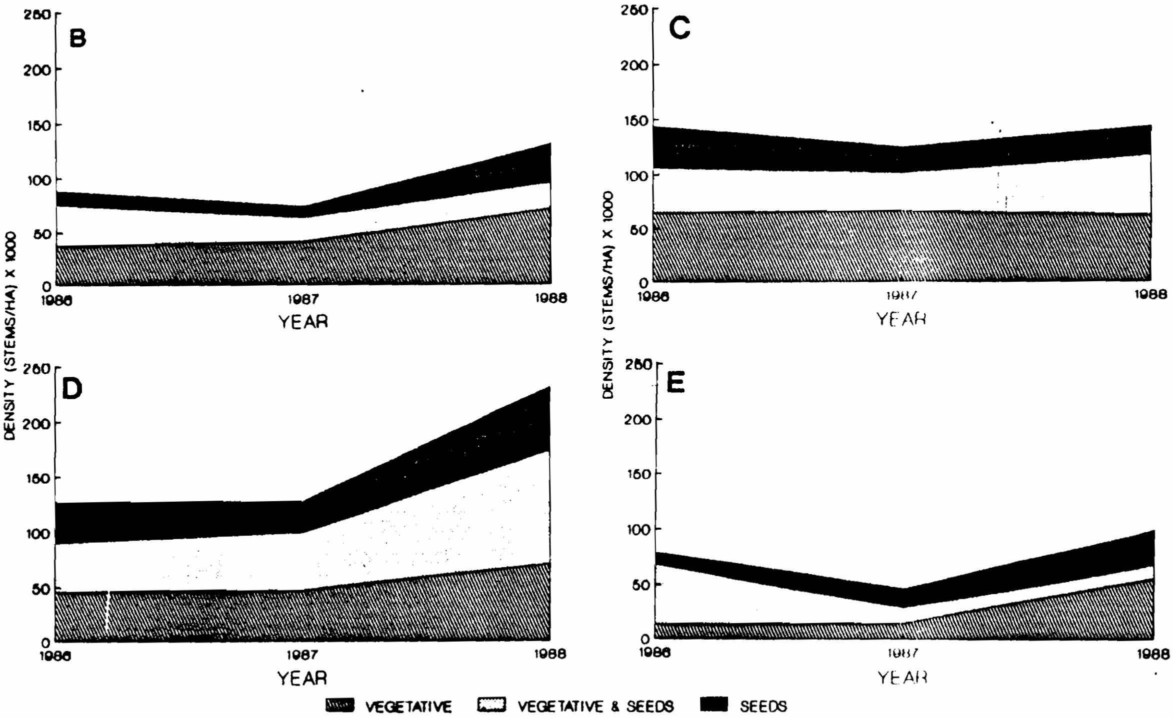

Figure 28. Postdisturbance changes in the total density of groundlayer stratum species that reproduced primarily vegetatively, primarily from seed, or by a combination of both means.

Table 11. Observed primary mode of reproduction by species found at the spur-ridge sites. "V"=vegetative, "S"=seeds (or spores), "VS"=combination of both.

SPECIES	OBSERVED PRIMARY MODE OF REPRODUCTION
Tree species:	
Acer pensylvanicum	VS
Acer ruburm	VS
Amelanchier arborea	V
Carya glabra	S
Ostrya virginiana	VS
Cornus florida	VS
Pinus pungens	S
Pinus strobus	S
Quercus coccinea	V
Quercus prinus	V
Shrub species:	
Gaylussacia baccata	V
Castanea dentata	V
Hamamelis virginiana	VS
Kalmia latifolia	V
Rhododendron sp.	S
Sassafras albidum	VS
Smilax rotundifolia	S
Vaccinium stamineum	V
Vaccinium vacillans	V
Viburnum acerifolium	VS
Forest Herb species:	
Antennaria plantaginifolia	S
Asplenium platyneuron	S
Carex digitalis	V
Carex platyphylla	V
Convallaria majalis	VS
Danthonia spicata	VS
Dioscorea villosa	VS
Dryopteris marginalis	S
Galax aphylla	V
Gaultheria procumbens	S
Geranium maculatum	S
Gillenia trifoliata	S
Epigaea repens	S
Heuchera americana	VS
Houstonia longifolia	S
Houstonia purpurea	S
Polygala pauciflora	S
Polygonatum biflorum	S
Potentilla canadensis	S
Polypodium virginianum	S
Thaspium trifoliatum	S
Viola palmata	S
Ruderal species:	
Barbarea vulgaris	S
Carduus lanceolatus	S
Erechtites hieracifolia	S
Phytolacca americana	S
Rosa carolina	S
Robinia pseudo-acacia	S
Rubus sp.	S
Solidago sp.	S
Taraxacum officinale	S
Verbascum thapsus	S

spicata, *Carex digitalis*, *Ostrya virginiana*, *Amelanchier arborea*), however, occurred in very high densities at one or more sites. Once established at a particular site, the ability to reproduce by sprouting enabled these species to rapidly become local dominants. Seventy-four percent of the locally distributed abundant species appeared to rely completely upon seed germination for reproduction in 1988. Perhaps because seed germination is a slower and less certain means of recruitment than vegetative sprouting, most of these species occurred in low densities, making them somewhat less important groundlayer constituents.

The 2 relatively sparse and less diverse sites, B and E, experienced the most new colonizations in 1987 and 1988 (Table 12). These colonists, which were largely forest herb and ruderal species, were derived from seed. Colonizations increased the species richness at each site considerably (44.0% at B and 52.3% at E; Figure 29). Fewer new species were found at C and D after the disturbance. The groundlayer stratum at these 2 sites, however, had been much more diverse than at B and E in 1986. Due to the colonizations at B and E, all 4 sites had similar levels of species richness in 1988 (B=36, C=36, D=35, E=33 species). The combinations of species and their densities differed greatly among sites, however.

Table 12. Labile species in the 4 disturbed spur-ridge sites. "C"=colonization, "E"=local extinction, "-"=never present, "+"=present since 1986.

	SPUR-RIDGE			
LABILE SPECIES	B	C	D	E
Carya glabra	-	-	C	-
Cornus florida	C	+	-	C
Pinus pungens	C	-	C	-
Pinus strobus	C	-	-	-
Castanea dentata	-	-	-	C
Gaylussacia baccata	C	+	+	-
Hamamelis virginiana	C	+	C	E
Kalmia latifolia	-	E	-	E
Rhododendron sp.	C	+	+	+
Sassafras albidum	-	-	-	C
Smilax rotundifolia	E	-	E	E
Antennaria plantaginifolia	-	C	E	-
Asplenium platyneuron	+	E	E	-
Convallaria majalis	+	C	E	+
Cunila oreganoides	C	-	+	C
Danthonia spicata	+	+	+	C
Geranium maculatum	-	C	E	C
Hieracium venosum	E	E	E	E
Gaultheria procumbens	C	C	-	C
Gillenia trifoliata	C	+	-	C
Houstonia longifolia	C	+	+	C
Polygonatum biflorum	C	-	-	C
Potentilla canadensis	C	+	+	-
Polygala pauciflora	E	+	-	-
Polypodium virginiana	E	+	+	-
Solidago sp.	C	E	+	C
Thaspium trifoliatum	E	+	E	+
Viola palmata	C	C	C	-
Barbarea vulgaris	-	-	-	C
Carduus lanceolatus	C	-	-	C
Erechtites hieracifolia	C	C	C	C
Phytolacca americana	-	-	-	C
Robinia pseudo-acacia	C	-	C	C
Rosa carolina	C	C	+	+
Rubus sp.	E	C	-	-
Taraxacum officinale	C	-	-	-
Verbasucum thapsus	C	-	-	-

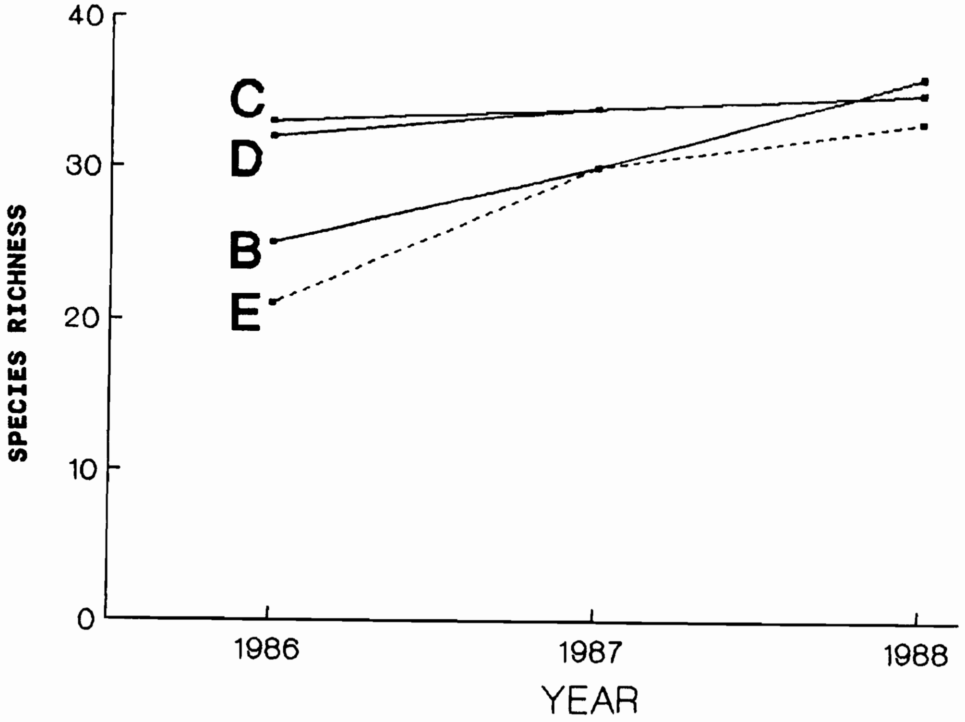

Figure 29. Postdisturbance changes in groundlayer stratum species richness at sites B, C, D, and E.

Some of the colonizing species were probably derived form the buried seed bank. Although the seed banks at these sites were found to be quite sparse, there was some correspondence between seed bank composition of a particular site and the composition of the postdisturbance vegetation at that site. Sixty-eight percent of the species found in seed bank samples were found in the groundlayer of the corresponding sites.

Seeds produced in the surrounding forest and dispersed to these sites were probably another source of new plants. The low numbers of seeds trapped by the 9 traps at each site (Table 13) suggest that the traps may not have adequately sampled seed inputs. The majority of seeds trapped were produced by trees and were wind dispersed (*Acer pensylvanicum*, *Acer rubrum*, *Betula lenta*, *Liriodendron tulipifera*, *Ostrya virginiana*, *Pinus pungens*). The traps were apparently not appropriate for trapping seeds of colonizing forest herbs and ruderal species. The small seeds of these species might have been more effectively captured by sticky traps (Werner 1975).

Of course, dispersal of seeds to a site does not guarantee their establishment. *Liriodendron tulipifera* seeds were trapped at each site. Yet this species, which typically occurs in mesic habitats, was not present on these xericspur-ridges. Likewise, *Betula lenta* seeds were trapped at C, but

Figure 13. Density of seeds (seeds/m^2) collected in seed traps at the 4 disturbed sites in 1987 and 1988.

	SPUR-RIDGE							
	B		C		D		E	
SPECIES	´87	´88	´87	´88	´87	´88	´87	´88
Acer pensylvanicum	-	-	0.44	-	0.44	-	1.33	-
Acer rubrum	1.78	-	1.33	-	-	-	1.44	-
Betula lenta	-	-	3.56	-	-	-	0.89	-
Cornus florida	-	0.89	-	-	-	2.67	-	-
Liriodendron tulip.[1]	1.78	0.44	0.89	2.22	1.78	-	-	0.89
Ostrya virginiana	0.89	0.44	-	0.89	12.00	4.00	-	0.44
Pinus pungens	0.44	-	-	-	-	-	-	-
Unknown #1	-	-	4.44	-	-	-	-	-
Unknown #2	-	-	-	-	-	-	-	0.89
Unknown #3	-	-	-	-	-	-	-	0.44
TOTALS:	4.89	1.77	10.66	3.11	14.22	6.67	3.66	2.66

[1] Liriodendron tulipifera

it was not present in the vegetation at any site. *Betula lenta* was also found in the seed bank at site C.

The trajectories of Sorensen´s coefficients of similarity over time clearly reflect the consistent differences in density and composition among sites (Figure 30). Coefficients that represented pairwise comparisons of groundlayer density at E with the other sites were consistently lower than the other coefficients in 1986 and remained lower in 1987 and 1988. Not surprisingly, E exhibited the greatest amount of similarity with B and the least with C. The same pattern was also indicated by the trajectories of Pearson product-moment correlation coefficients (Figure 29). Moreover, the low coefficients for all pairs of sites reflect the importance of locally abundant species at each site. The general constancy of the coefficients from 1986 to 1988 indicates that the differences in groundlayer stratum structure and composition prior to the disturbance remained evident during the 2 years following canopy removal.

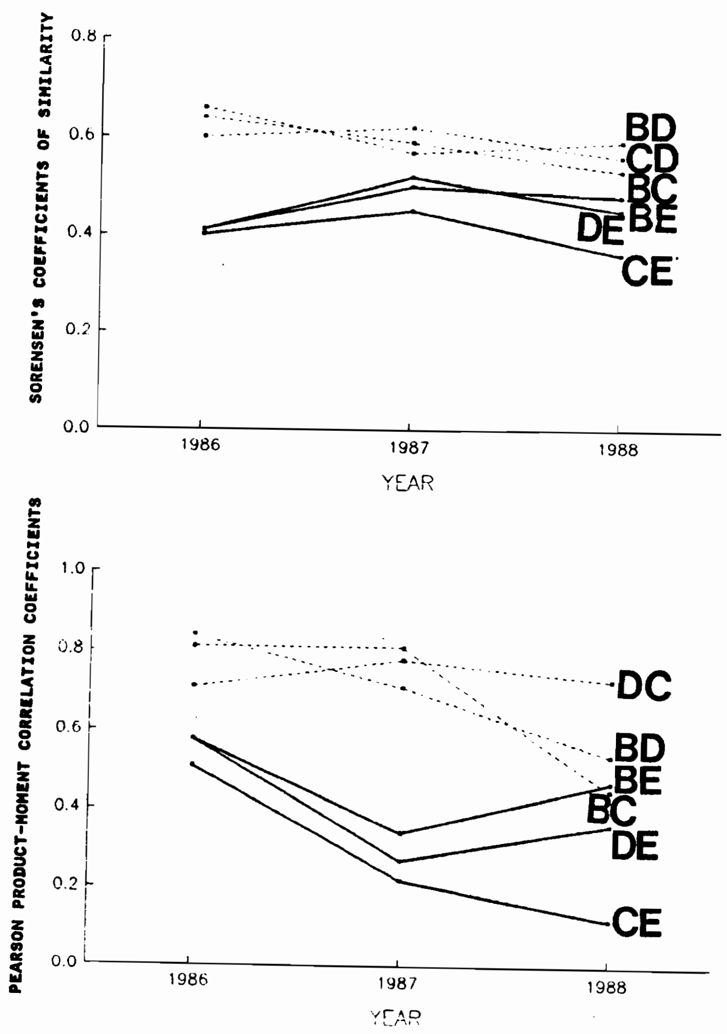

Figure 30. Postdisturbance changes in groundlayer stratum similarity as indicated by Sorensen's coefficients of similarity (upper graph) and Pearson product-moment correlation coefficients (lower graph).

IV. DISCUSSION

A. Predisturbance Vegetation

1. Canopy

The structural and compositional similarity of canopy stratum vegetation at the 6 Brush Mountain spur-ridges in 1986 supported the theory that similar vegetation occurs on environmentally similar sites. Domination of each site by _Quercus prinus_ and _Quercus coccinea_ was clearly responsible for much of the overall similarity among canopies. Together these 2 species accounted for more than 60% of the density and 80% of the basal area of each canopy.

Life history characteristics of these species, suggest that the canopy vegetation at these sites had been similar in structure and composition for a very long period of time. Oaks sprout vigorously from the base and roots following distubances such as fire or cutting (Hibbs and Fischer 1979, Ross et al. 1982, 1986, Whitney and Johnson 1984, Crow 1988, Harrison et al. 1989). _Amelanchier arborea_ and _Acer rubrum_, 2 other important canopy species, also reproduce by sprouting (Hibbs and Fischer 1979, Boring et al. 1981, Scheiner 1988). Following canopy disturbances in the past, sprouting by trees with established root systems would have enabled them to rapidly regain positions in the forest canopy (Hibbs and Fischer 1979, Ross et al. 1982, 1986) and, therefore, maintain the predisturbance composition..

Moreover, rapid postdisturbance regeneration by large numbers of sprouting oaks probably inhibited the establishment and growth of other potential canopy species, especially colonists derived from seeds. Since postdisturbance colonization can be a very stochastic process (Gleason 1927, Matthews 1979, Boerner 1985, McCune and Allen 1985a, 1985b, Schafale and Christensen 1986, Walker et al. 1986, Walker and Chapin 1987, Wood and del Moral 1987), sprouting would have limited the role of stochasticity that might have otherwise altered forest structure and composition. Locally abundant species whose presence at a particular site could be attributable to stochastic events, comprised only 1.5 - 7.8% of the total density and 0.8 - 3.2% of the total basal area.

The high degree of compositional similarity among Brush Mountain sites contrasts markedly with the findings of McCune and Allen (1985a, 1985b). They found large compostional differences among old-growth forests in a series of environmentally replicated canyons in western Montana. Unlike the trees in the forest on Brush Mountain, western United States coniferous forests do not regenerate by sprouting. Therefore, postdisturbance colonization events may have been very important determinants of vegetation composition in the canyons (McCune and Allen 1985a). In addition, 3 of the canopy species (*Abies grandis*, *Taxus brevifolia*, *Thuja plicata*) were near the edge of their natural range in the canyons (McCune and Allen 1985a), and so would be expected to be patchy in distribution.

In another study, Matthews (1979) found significantly different late successional species assemblages on deglaciated land in Norway. These differences, however, were observed on sites that differed by as much as 350 m in elevation. Since a steep environmental gradient must have existed among these sites, large differences in community composition should have been expected (Whittaker 1967). Likewise, variation in environmental parameters along a 60 km latitudinal gradient in Montana might have been the cause of some of the canopy variability observed by McCune and Allen (1985a, 1985b).

The structure of the canopy on Brush Mountain was remarkably uniform from site to site, and did not indicate any site differences in resource availablility. The structural similarity also indicated that these sites had similar disturbance histories. Although little is known about distubances prior to the 1930´s, the strong similarity of canopy density-diameter distributions among sites indicated that the stand-initiating disturbance at these sites was of similar type, timing, and intensity. The density-diameter distributions should have reflected any significant differences in past disturbance among the sites.

2. Understory and Groundlayer

The structure of understory and groundlayer vegetation was similar, in a general sense, among sites. The subcanopy strata of each site consisted of vegetation with broadly similar cover distributions, indicating similar levels of vegetation patchiness. Moreover, the subcanopy strata were made up of species with similar growth forms (understory: trees and shrubs; groundlayer: trees, shrubs, forest herbs, ruderals).

Despite this basic structural similarity, subcanopy species composition varied greatly among sites. Although the sites had several species in common, only fractions of the groundlayer (23.5%) and understory (28.5%) species occurred at all 6 sites. More than 80% of the species found in each subcanopy stratum had limited, locally abundant distributions. Furthermore, only 17.6% of the groundlayer and 11.9% of the understory species were observed in densities that did not differ significantly among sites ($p>0.05$). Approximately half of the density of each subcanopy stratum was made up of locally abundant species with densities that differed significantly from site to site.

It is unlikely that the variability of subcanopy vegetation was actually caused by environmental differences among sites, at least based on evaluation of modern samples. While the site selection analyses indicated that some environmental parameters varied slightly among sites, the degree of variability was extremely low. In particular, the small site differences in soil nutrient status (e.g. phosphorus and potassium) were probably not sufficient to have affected forest composition (Collins and Good 1987, Christensen and Peet 1984, Schafale and Christensen 1986). The 6 spur-ridge sites were located at midslope, and were northeast-facing, and, therefore, had similar site quality and soil moisture availability (Meiners et al. 1983, Callaway et al. 1987). Furthermore, ordination analysis indicated that the group means for environmental variables measured at C and E were very close, indicating that the environmental parameters measured at the sites were similar. Yet, the subcanopy vegetation at these sites was quite different. Site C supported vegetation that averaged twice the density and cover of E, and was much more diverse compositionally.

Subcanopy species composition at these environmentally similar sites was probably strongly influenced by stochastic processes. For example, random colonization of site E by _Convallaria majalis_ and its subsequent local spread is the only apparent reason why this forest herb dominated that site but was rare or absent at the other sites. Such chance colonizations by many species would have resulted in the varied subcanopy vegetation observed in 1986. Several authors (e.g. Gleason 1939, Grieg-Smith 1979, McCune and Allen 1985) have noted that stochastic colonization events can be important determinants of vegetation composition.

Perhaps variation in subcanopy vegetation was associated with undetected past disturbances. Although the similarity of canopy vegetation at these sites did not reflect gross differences in past disturbances, low intensity disturbances (e.g. ground fires, heavy deer browsing, cattle grazing) might have affected the lower strata at some sites while leaving the taller, more resistant canopy trees virtually unaffected. The presence of fire scarred trees at the Brush Mountain sites indicated that they had burned sometime after canopy establishment. Since fires are typically hottest at the level of the forest floor, and can vary greatly in intensity from place to place (Williamson and Black 1981), it is possible that plants in the lower vegetation strata at some sites could have been more severely burned than at other sites. Given the eroding nature of the soil (Inceptisols), and the apparently very sparse buried seed bank at these sites, regrowth of understory and groundlayer plants following a relatively intense ground fire might have been a slow, variable process, resulting in measurable differences in vegetation structure and composition many years later. Perhaps such a past occurrence explains the very low subcanopy plant density and species diversity at E. Difficult to detect disturbances that differentially alter the structure and composition of vegetation at otherwise environmentally similar sites could be described as stochastic processes (Keever 1983, Grimm 1984, Abrams et al. 1985, Schafale and Christensen 1986, Halpern 1989). Abrams et al. (1985) found large postfire differences in groundlayer species composition among generally similar sites in Michigan.

Lastly, it is possible that some species that were found to be only locally abundant were actually more widely distributed on Brush Mountain than was detected within the area of the sampling plots. The 0.09 ha quadrat covered about half of the midslope area (at elevation 730 m) on each northeast-facing spur-ridge slope. Therefore, the presence of some very rare species may have been missed (Brown 1984). If this were true, then the number of ubiquitously occurring species at these sites may have been underestimated, and the role of stochasticity in determining the composition of the subcanopy vegetation, overestimated. Connell and Sousa (1983) and Rahel et al. (1984) note that the spatial scale of a study can be an important factor when judging whether differences in species abundances are due to stochastic or deterministic processes. While it is unlikely that high density species would have been undetected or their densities grossly underestimated, the presence of low density, infrequently occurring species may have escaped detection at one or more of the sites. Because of their relative rarity, however, these additional ubiquitous species would not have counterbalanced the tremendous variability among sites exhibited by many of the more common species (e.g. *Vaccinium vacillans*, *Heuchera americana*, *Dioscorea villosa*, *Gaylussacia baccata*, *Danthonia spicata*). Therefore, it is unlikely that the estimated importance of locally abundant species at these sites was merely an artifact of the sampling scheme.

To summarize, the subcanopy species composition at 6 environmentally similar forest sites on Brush Mountain differed, possibly reflecting both the stochastic nature of past low intensity disturbances and the stochastic nature of the response of vegetation to those disturbances. In addition, what appeared to be stochastic responses of vegetation to disturbance were long lasting, reflected by differences in vegetation among sites many years later.

B. Postdisturbance Vegetation

Because the Brush Mountain spur-ridges had supported canopy trees with virtually identical densities and basal areas, it is likely that the removal of canopy cover affected the subcanopy environment similarly at each site. Moreover, since the intensity of disturbance was similar, differences in postdisturbance species composition among sites should have been due to biotic differences rather than directly linked to the disturbance itself.

The importance of stochastic events as determinants of vegetation composition and structure, are thought to be greatest during the first few years following disturbance (Smith 1975, White 1979, Christensen and Peet 1984, Walker and Chapin 1987). The response of the Brush Mountain understory and groundlayer vegetation to the removal of canopy cover, however, was not dramatic. Densities of some species increased and a few new species colonized each site, but predisturbance vegetation patterns remained evident during the initial postdisturbance years. The lower strata vegetation at each spur-ridge site continued to be characterized by a similar degree of spatial heterogeneity but very different species composition.

Differences in vegetation among sites that had been apparent prior to the disturbance in 1986 continued to exist in 1987 and 1988. For example, the density, cover and species richness of lower strata vegetation at site C remained greater than at E. This constancy may have been in part due to the indirect way in which the removal of canopy cover affected understory vegetation. While disturbances such as fire, grazing, and cultivation can severely damage subcanopy plants by destroying vegetative structures, the direct results of canopy removal were changes in microclimatic regime. The response of subcanopy vegetation was, therefore, primarily a response to postdisturbance microclimatic change, rather than to physical disturbance. Removal of forest canopy cover by clearcutting would have altered microclimate in a generally similar manner.

After removal of canopy cover, the intensity of solar irradiance at the level of the forest floor increases, raising air and soil temperatures (Boring et al. 1981). Without a dense transpiring canopy, soil moisture is greater and the relative humidity of the air, lower. As tree roots decay, the availability of soil nutrients is also increased (Pritchett 1979). Many of the species established on these steep, rocky, nutrient poor sites typically occur in marginal and xeric forest habitats, and were probably not especially sensitive to changes in microclimate caused by removal of canopy cover (Whitney and Johnson 1984).

Species life history characteristics are important determinants of vegetation response to disturbance (Cattelino et al. 1979, White 1979, Noble and Slatyer 1980, Armesto and Pickett 1985, Walker et al. 1986, Pickett et al. 1987, Halpern 1988, 1989). At the Brush Mountain spur-ridge sites, the structural and compositional resemblence of postdisturbance vegetation to that which existed prior to the disturbance was clearly related to the life histories of the subcanopy species. The lower strata of each site were dominated by species that reproduced by vegetative means. Following canopy removal at these sites, increases in species densities were largely due to vegetative reproduction. This mode of reproduction enabled existing disturbance-resistant species, such as Vaccinium vacillans, Acer pensylvanicum, and Danthonia spicata, to rapidly exploit new resources made available by the disturbance. Because vegetatively reproducing species were already present at the time of disturbance, increases in density were not necessarily accompanied by changes in species composition or increases in species richness.

Several investigators have found that disturbances which remove only canopy cover sometimes have little effect on the composition of the subcanopy plants (Ehrenfeld 1980, Metzger and Schultz 1981, Whitney and Johnson 1984, Pickett et al. 1988). Furthermore, Ehrenfeld (1980) noted that the response of forest vegetation to canopy disturbance could be predicted by examining the pattern and species composition of vegetation in the subcanopy strata. Because of the importance of vegetative reproduction at the Brush Mountain sites and the resistence of many subcanopy strata plants to the disturbance, quantifying the effects of stochastic processes that were directly associated with canopy removal was difficult. Vegetation differences among sites in 1987 and 1988 had largely been apparent prior to the disturbance and reflected the effects of long past stochastic processes.

Postdisturbance colonization is generally a very stochastic process (Smith 1975, Grieg-Smith 1979, Marks and Mohler 1985, McCune and Allen 1985a, McCune and Cottam 1985, Schafale and Christensen 1986, Walker and Chapin 1987). Following removal of canopy cover, each site was colonized by a few new species. These colonists, primarily forest herb and ruderal species, occurred in very low densities. The combinations of colonist species varied among sites. Only _Erechtites hieracifolia_, a ruderal that had also been observed in seed banks, colonized all of the disturbed sites. The local abundance of colonizing species indicates that their presence at one particular site and not another was largely due to chance occurrences associated with seed availability, germination, and seedling survivorship.

Specific sources of seeds from which stochastic colonizations originated were frequently uncertain. Usually, plants derived from the buried seed bank dominate the colonization phase following disturbance (Livingston and Allessio 1968, Moore and Wein 1977, Cook 1980, Marks and Mohler 1985). Because seeds, particularly ruderal species, can accumulate and remain viable in the soil for many years

(Kivilaan and Bandurski 1981), vegetation derived from seed banks can be very diverse (Livingston and Allesio 1968, Thompson 1978, Donelan and Thompson 1980). Only very sparse seed banks were found at each of the Brush Mountain sites, however.

The very low buried seed densities found at the Brush Mountain sites (< 1 seed/m) were quite unusual. It is unlikely that these steep, rocky spur-ridges had ever been cultivated. Therefore, the abundance of weed seeds characteristic of old field forest seed banks (Livingston and Allessio 1968, Marks and Mohler 1985, Thompson 1978, Thompson and Grime 1979, Donelan and Thompson 1980) would not be expected. Thompson (1978) noted that seed banks of mature forests on nutrient poor soils tend to be the most depauperate. While this clearly suggests that sparse seed banks would be found on Brush Mountain, only a few studies have yielded comparably low seed densities (Whipple 1978, Donelan and Thompson 1980).

Dispersal of seeds to the 4 disturbed sites from the surrounding area was another possible source of colonists. In heterogeneous landscapes, the potential for stochastic dispersal events to significantly alter the structure and composition of disturbed habitats can be very high (Johnson et al. 1980, McDonnell and Stiles 1983, Walker et al. 1986). The forest on Brush Mountain, however, was extensive and relatively unfragmented. Therefore, there was a paucity of open, disturbed habitats that might have served as sources of colonists to the sites. Short distance dispersal of locally produced seeds was the most likely source of colonizing species. In particular, seeds of colonizing forest herb, shrub, and tree species, which occurred throughout the surrounding forest, were probably not dispersed long distances.

Although each site was colonized by a different combination of new species, these chance colonizations had relatively little effect on the overall vegetation composition of these sites during the first 2 years following canopy removal. The impact of these colonizations on postdisturbance vegetation composition may, however, become more significant in the future. Over a period of several years, successful colonists at a particular spur-ridge site may reproduce and increase in density, possibly greatly altering the composition and structure of the vegetation at the sites at which they occur (Gleason 1939, Egler 1954, McCune and Allen 1985a). This local expansion phenomenon was already exhibited by a few species on these spur-ridges. Approximately 3000 stems/ha of _Danthonia spicata_, a locally abundant grass species, were found at D in 1986. By 1988, the density of this species had increased more than 15 fold. This species occurred in high density only at D, and clearly contributed to the compositional uniqueness of the vegetation at that site.

Locally abundant species, such as _D. spicata_, which reproduce both vegetatively and from seed became increasingly abundant constituents of the understory and groundlayer strata at the Brush Mountain sites. Species that reproduce vegetatively avoid the initially high mortality rates that characterize species that grow only from seeds. They are also frequently more resistant to the effects of low intensity disturbances. By being able to disperse more rapidly over larger areas, species that also grow from seeds can exploit the environment even more efficiently. Therefore, it is likely that these species will become increasingly dominant at the Brush Mountain sites. Because the species composition varied widely among sites, the local expansion of a few species at each site could result in even more extensive divergence of species composition. At site E, in particular, where existing vegetation was sparsest and successful colonizations most frequent, the potential for compositional divergence is especially large.

V. CONCLUSIONS

Mature canopy vegetation of similar structure and species composition was found at environmentally similar sites on Brush Mountain. Locally abundant species comprised less than 8% of the total canopy tree density at these sites. Because the dominant species in this stratum (_Quercus prinus_, _Q. coccinea_, _Acer ruburm_, _Amelanchier arborea_) were vigorous sprouters, it is likely that these sites have had similar canopy vegetation for a very long time. Rapid postdisturbance regeneration by sprouting trees would have limited the impact of stochastic colonization events on canopy development. These findings support the long-held ecological theory that vegetation development is largely enviromentally determined.

In contrast, the species composition of the subcanopy strata vegetation differed significantly at these sites. Only 11.9% of the understory and 17.6% of the groundlayer species were found in densities that did not differ statistically between the spur-ridges. The data suggest that the development of subcanopy vegetation on Brush Mountain was a much less deterministic process. Stochastic biotic processes (e.g. seed dispersal) as well as undetected differences in past disturbance probably resulted in the development of site-to-site differences in the understory and groundlayer composition. Interestingly, these strong compositional differences existed among sites despite their general similarity in subcanopy vegetation structure.

Site differences in subcanopy vegetation remained apparent during the 2 years following the disturbance (1987 and 1988). In particular, species density, cover, and richness at site C continued to be greater than at site E. These differences among sites remained mainly because vegetative reproduction by existing disturbance-resistent species (e.g. Vaccinium vacillans, Acer pensylvanicum, and Danthonia spicata) was the primary means of regeneration. Therefore, most of the postdisturbance subcanopy differences reflected the effects of stochastic processes that occurred when these species first became established at each site.

The disturbed sites were also colonized by plants derived from seeds (mostly forest herb and ruderal species). Since the Brush Mountain buried seed bank was extremely sparse (< 1 seed/m^2), most colonists probably dispersed into the sites from the surrounding forest. Postdisturbance stochastic colonization events had relatively little immediate effect on the overall vegetation composition at the spur-ridge sites. In the future, however, as some colonist species reproduce and increase in density, species derived from seeds may become more important. Stochastic processes associated with seed dispersal and seedling establishment may, therefore, significantly alter the vegetation structure and composition of these environmentally similar Brush Mountain spur-ridges.

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VII. APPENDIX

Plant species found on Brush Mountain subdivided into tree, shrub, forest herb, and ruderal growth form groups.

Tree species:
Acer pensylvanicum
Acer ruburm
Amelanchier arborea
Carya glabra
Ostrya virginiana
Cornus florida
Pinus pungens
Pinus strobus
Quercus coccinea
Quercus prinus

Shrub species:
Gaylussacia baccata
Castanea dentata
Hamamelis virginiana
Kalmia latifolia
Rhododendron sp.
Sassafras albidum
Smilax rotundifolia
Vaccinium stamineum
Vaccinium vacillans
Viburnum acerifolium

Ruderal species:
Barbarea vulgaris
Carduus lanceolatus
Erechtites hieracifolia
Phytolacca americana
Rosa carolina
Robinia pseudo-acacia
Rubus sp.
Solidago sp.
Taraxacum officinale
Verbascum thapsus

Forest Herb species:
Antennaria plantaginifolia
Asplenium platyneuron
Carex digitalis
Carex platyphylla
Convallaria majalis
Danthonia spicata
Dioscorea villosa
Dryopteris marginalis
Galax aphylla
Gaultheria procumbens
Geranium maculatum
Gillenia trifoliata
Epigaea repens
Heuchera americana
Houstonia longifolia
Houstonia purpurea
Polygala pauciflora
Polygonatum biflorum
Potentilla canadensis
Polypodium virginianum
Thaspium trifoliatum
Viola palmata

VII. Vita

Paula M. (Polly) Schiffman was born in Los Angeles, California on December 7, 1959. She grew up in the Pasadena area and graduated from San Marino High School in June 1977. Polly then attended the University of California, Riverside. While a student at UCR, she worked part-time as a greenhouse waterer, and later as a laboratory technician. In 1980, she enrolled in the UC Santa Cruz Sierra Institute program and spent spring quarter in the high country of Yosemite National Park studying forest ecology and natural history. Polly received a B.S. in biology from UCR in June 1981.

Following graduation, she remained at UCR and continued working as a laboratory technician studying postharvest physiology of avocado fruit. Soon Polly made 2 very important realizations: (1) she was not terribly interested in physiology, and (2) she did not want to be a lab technician for the rest of her life. In August 1982, Polly moved to Blacksburg, Virginia and began graduate school at Virginia Polytechnic Institute and State University. Her masters research involved an examination of phytomass and detrital carbon storage during forest regrowth. After receipt of her M.S. in botany in June 1985, she remained at Virginia Tech and began working on her doctorate.

Polly has accepted a position as Assistant Professor of Biology at California State University-Northridge. Although she is beginning a study of vegetation patchiness in the desert of southern California, Polly plans to return periodically to the wilds of Brush Mountain. Her doctoral research is meant to be the first phase of a long-term study of forest regeneration.

Paula M. Schiffman