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The effects of three regeneration harvest methods on plant diversity and soil characteristics in the southern Appalachians

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Abstract

We evaluated the effects of three regeneration harvest methods on plant diversity and soil resource availability in mixed-hardwood ecosystems. The study area is in the Wine Spring Creek watershed on the Nantahala National Forest of the Southern Appalachian Mountains in western North Carolina. The regeneration treatments were: an irregular, two-aged shelterwood cut (2A), with 5.0 m^2/ha residual basal area; a shelterwood cut (SW), with 9.0 m^2/ha residual basal area; a group selection cut (GS), with 0.10–0.20 ha openings and 25% overstory removal on area basis at first entry; fourth, the control, consisted of two uncut sites (UC). Each harvest treatment was replicated three times across the landscape in similar plant community types. Within each treatment area, permanent plots were marked and inventoried for overstory, midstory, and herbaceous layer plants. In each permanent plot, we collected soil samples in winter (December–March) to reduce temporal variation due to vegetation phenological stage and rainfall events. We analyzed soil samples for extractable calcium (Ca), magnesium (Mg), potassium (K), cation exchange capacity (CEC), pH, bulk density, A-horizon depth, total carbon (C), and nitrogen (N). Species diversity of overstory, understory, and herbaceous layer species was evaluated using species richness (S), Shannon–Wiener's index of diversity (H'), and Pielou's evenness index (E). We used direct gradient analysis (non-metric multidimensional scaling, NMS) to explore the changes in vegetation–site relationships among herbaceous layer abundance, and soil characteristics and overstory basal area between pre-harvest (1994) and post-harvest (2000). Twelve minor overstory species were cut from the 2A treatments and nine species were cut from the SW treatments. Thus, it is not surprising that S and H' were reduced in the overstory on the heavily cut sites. However, most of these species sprouted from cut stumps and were substantially more abundant in the midstory layer after harvest than before. For the midstory, we found higher S and H' on the harvested treatments than the control; however, H' did not differ significantly among the harvest treatments. We measured an increase in herbaceous layer H' on the more heavily cut treatments (2A and SW) after harvest. We found an increase in average distance in the NMS ordination among sites in 2000 compared to 1994, which suggests greater herbaceous species diversity after harvest. However, we did not see a clear separation among harvest treatments in the NMS ordination.

Keywords: Herbaceous flora; *Quercus rubra*; *Rhododendron calendulaceum*; North Carolina; Soil carbon; Soil nitrogen; Non-metric multidimensional scaling; Vegetation dynamics; Disturbance

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1. Introduction

Recent emphasis on the maintenance of biological diversity in forest ecosystems has prompted researchers to evaluate the impacts of forest management techniques on biodiversity (Swindel et al., 1984, 1991; McMinn, 1991, 1992; Roberts and Gilliam, 1995; Roberts and Zhu, 2002). Forest practices that alter site conditions, either as a consequence of a timber harvest or a silvicultural practice intended to promote tree regeneration, may change biological diversity patterns. Harvesting and other disturbances in eastern deciduous forests can change the relative composition of tree species (Parker and Swank, 1982; Elliott and Swank, 1994; Schuler and Gillespie, 2000; Crow et al., 2002; Brashears et al., 2004) and strongly influence species diversity (Elliott and Swank, 1994; Elliott et al., 1997, 1998). A wide variety of other community and ecosystem properties may also be altered (Pastor and Post, 1986; Huston and Smith, 1987). Site diversity is affected by human disturbances, and potentially linked with ecosystem processes (Schulze and Mooney, 1993; Vitousek and Hooper, 1993; Tilman, 1996; Tilman et al., 1997) such as long-term site productivity (see Huston, 1979, 1994; Tilman, 1996). Much of the overall biological diversity at a site depends on plant diversity, because plants provide both energy and habitat for other organisms (Hunter, 1990).

Silvicultural systems designed to enhance or maintain diversity rely on an understanding of factors that allow several plant species to coexist on the same site. Coexistence of plants depends on spatial variation inherent in a site (i.e., micro-site variability), the ability of plants to partition available resources through phenology or stratification (Aarssen, 1989), and site productivity (Grime, 1979; Huston, 1994). In eastern deciduous forests, the greatest species diversity often occurs in the first few years after clearcutting (Clinton et al., 1993; Elliott and Swank, 1994; Brashears et al., 2004), because resource competition is low and/or resource availability is high, which facilitates occupancy by species usually restricted to other habitats. However, because some species are intolerant of disturbance extensive clearcutting may reduce the number of species present on a landscape. Alternative harvest methods may be viable options for removal of commercial timber, establishment of successful tree seedling regeneration, and enhancement of vegetation diversity.

Shelterwood methods establish a new stand by gradually removing the existing stand so that tree seedlings become established under the protection of the older trees (Loftis, 1983, 1990). An important factor of both selection and shelterwood harvesting methods is that they provide vertical stand structure, which will support a more diverse biota (see Hunter, 1990). Single tree or group selection methods may be the best management system for maintaining diversity on forest, ecosystem, or watershed scale, because an uneven-aged forest is maintained by the removal of single trees or small groups of trees. Multiple tree removal provides gaps in forest canopies for recruitment of new species and provides closed canopy areas for the continued viability of forest shrubs and herbs that are not adapted to disturbance. For example, selection harvesting in deciduous forests of eastern Canada has shown no significant negative effects on forest herbs (Reader and Bricker, 1992). At the landscape scale, Hunter (1990) suggests that management include a variety of regeneration methods to create a mosaic of stands of different ages and species compositions.

Forest management can alter soil nutrient availability due to reduced nutrient uptake by vegetation, the addition of material to the forest floor, and changes in vegetation that occur after cutting. The soil nutrient response depends on the harvest method used and the forest type. For example, whole-tree harvest may result in decreased total soil N and C (Knoepp and Swank, 1997a) and exchangeable Ca (Knoepp and Swank, 1997b; Federer et al., 1989) due to the removal of overstory material. On the other hand, commercial sawlog harvest can result in increased soil nutrient content (Knoepp and Swank, 1997a,b) due to the addition of large amounts of readily decomposable material to the forest floor. These changes in nutrient availability may affect forest productivity (Johnson et al., 2002). Few studies have compared the effects of alternative regeneration harvest methods on plant diversity and examined the relationships among soil nutrient responses and herbaceous species composition and diversity following forest regeneration harvesting (Hannerz and Hånell, 1997; Bergstedt and Milberg, 2001; Roberts and Zhu, 2002). Thus, little information is available to assess impacts of

forest harvesting methods on plant diversity in deciduous forests of the southern Appalachians.

We evaluated how two-aged shelterwood, shelterwood, and group selection cutting affected plant diversity and composition, and examined the relationships among species diversity, environmental heterogeneity, and site soil properties. We hypothesized that: (1) the more heavily disturbed sites (shelterwood harvests) would experience increased species diversity and environmental heterogeneity than the less disturbed sites (group selection or uncut controls) and (2) the partial cutting would allow for coexistence of early and late successional herbaceous species by providing suitable micro-environments. We propose that knowledge of vascular plant diversity and changes that occur with disturbance will provide planning information to wildlife biologists, silviculturalists, and other forest managers.

2. Methods

2.1. Site descriptions

The study area is in the Wine Spring Creek watershed on the Nantahala National Forest of the Southern Appalachian Mountains in western North Carolina (35°15′N latitude, 83°35′W longitude). Wine Spring Creek is within the Blue Ridge Mountain District of the Blue Ridge physiographic province. Three tributaries (Wine Spring Creek, Bearpen Creek, and Indian Camp Branch) converge and drain into Nantahala Lake at the western edge of the watershed boundary. Eleven sites ranging from 4.0 to 6.6 ha were chosen based on similarity in overstory and shrub layer composition, topography, and elevation (Fig. 1). Sites were located using the Landscape Ecosystem Classification (LEC) system of McNab and Browning (1992), which classifies sites according to overstory, topography, and elevation. The areas were described as dry, high-elevation (1370–1670 m), intermediate mixed-hardwoods (McNab and Browning, 1992). The dominant overstory species is *Quercus rubra* (northern red oak), with *Rhododendron calendulaceum* (flame azalea), a midstory dominant.

Elevations range from 1380 to 1580 m. Over 10 years, average annual precipitation (Fig. 2) and temperature were 176 cm and 10.8 °C, respectively. Average temperature in January was 1.7 °C, and average temperature in July was 19.7 °C. Sites are located on gneiss and granite bedrock on soils mapped in Plott, Edneyville, and Chestnut series (Thomas, 1996). We examined the soil profile at two locations on all sample plots on all sites to determine the soil series present and estimate the depth of the A-horizon. Plott (coarse-loamy, mixed, mesic Typic Haplumbrepts) was the dominant series occupying 31 of 44 sample plots. Plott soils are characterized by a deep umbric horizon; A-horizon depths for study plots located on Plott soils ranged from 20 to 80 cm. The remaining 13 plots were located on soils in the Edneyville and Chestnut series (coarse-loamy, mixed, mesic Typic Dystrochrepts) alone or in combination (transition sites) with the Plott series. These soils contain less organic matter in the surface horizon; A-horizon depth on these plots ranged from 15 to 25 cm.

2.2. Experimental design

Three types of regeneration treatments and two control areas were used in the experimental design. The regeneration treatments were: (1) an irregular, two-aged shelterwood cut (2A), with 5.0 m^2/ha residual basal area; (2) a shelterwood cut (SW), with 9.0 m^2/ha residual basal area with plans to conduct a removal cutting in 10 years; (3) a group selection cut (GS), with 0.10–0.20 ha openings and 25% overstory removal on an area basis at first entry; (4) two uncut control sites (UC). For the 2A and SW treatments, forest managers used silvicultural prescriptions to promote *Quercus* spp., which were valuable commercial species, and to reduce non-commercial species such as *Acer rubrum*, *Fagus grandifolia*, *Acer pensylvanicum*, *Amelanchier arborea*, *Halesia carolina*, *Nyssa sylvatica*, and *Oxydendrum aboreum*. Each regeneration harvest treatment was replicated three times across the landscape in similar community types (Fig. 1). Wayah Ranger District (Nantahala National Forest, USFS) personnel determined which harvest treatment would be applied among the 11 potential candidate sites (3 regeneration harvest treatments × 3 replications, plus 2 controls). Treatments were distributed across the landscape so that no single harvest treatment was clustered in a small area (Fig. 1).

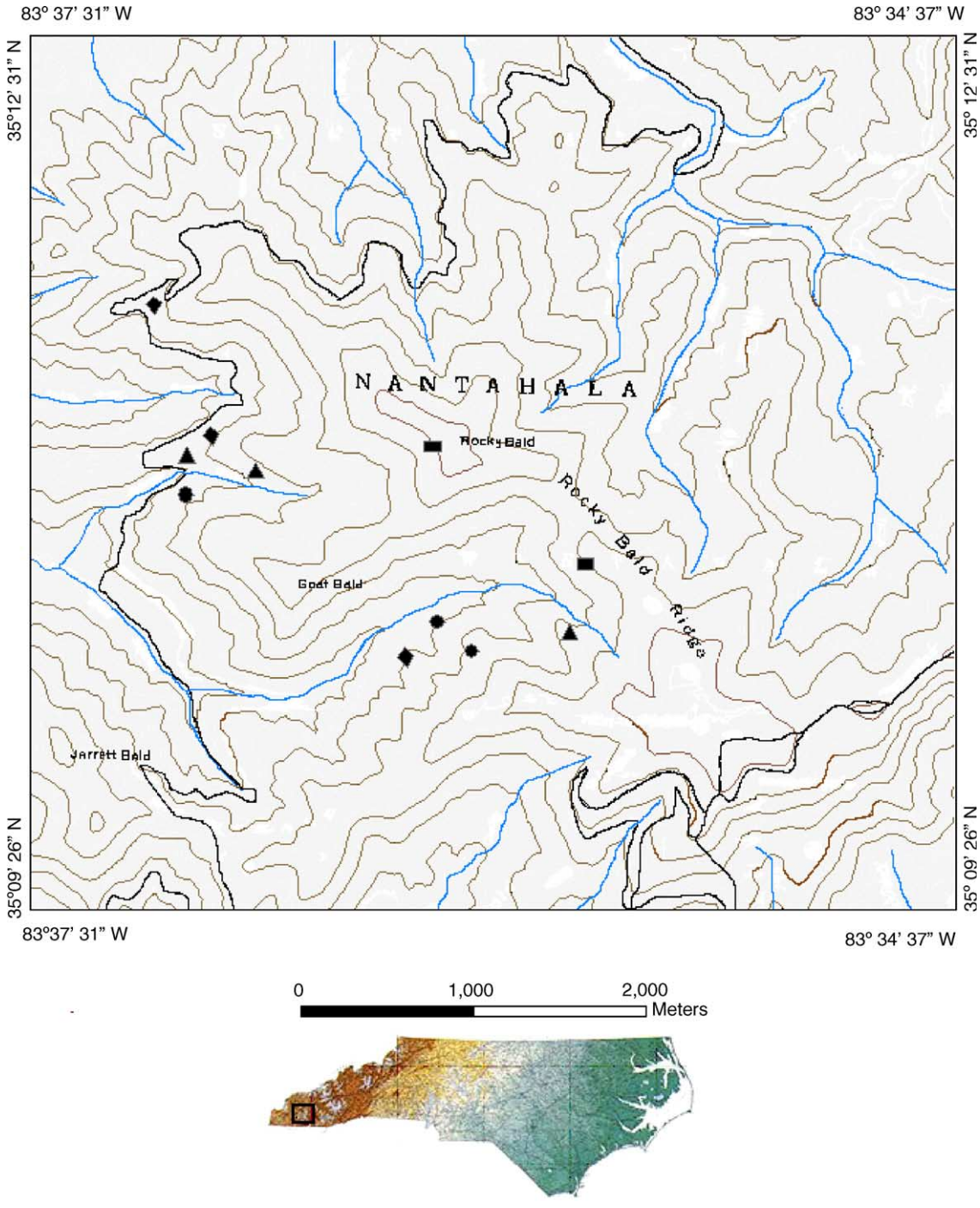

Fig. 1. Topographic map of the Wine Spring Creek watershed, Nantahala National Forest, western North Carolina. The 11 site locations are represented by symbols: uncut control (square); two-aged shelterwood (circle); shelterwood (diamond); group selection (triangle).

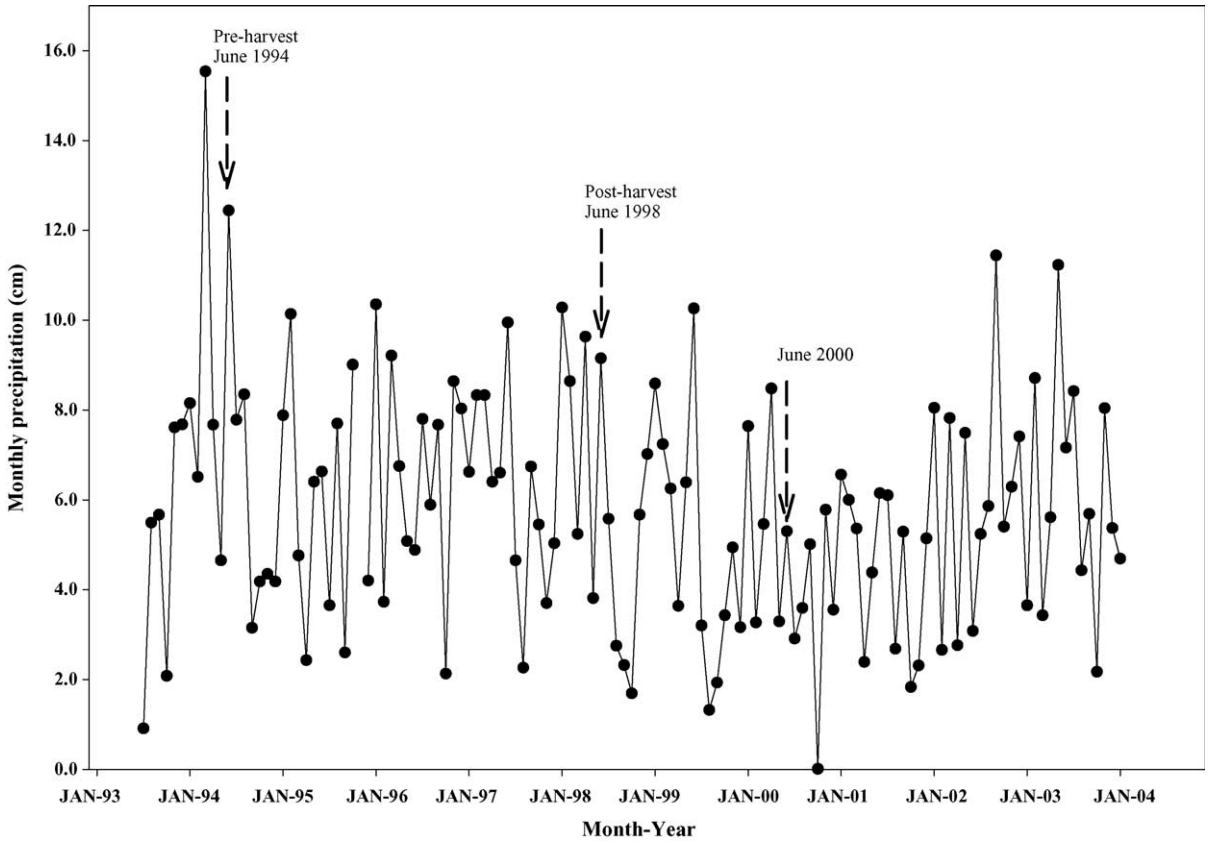

Fig. 2. Monthly precipitation over the sample period before and after harvest treatments for the Wine Spring Creek watershed, western North Carolina.

Within each of the 11 treatment sites, four 0.08 ha (20 m × 40 m) plots were randomly located to inventory vegetation characteristics. Before harvest (spring–summer 1994), permanent plots were marked and inventoried for overstory, midstory, and herbaceous layer plants. The overstory was re-inventoried the first year after harvest (spring–summer 1998), the midstory was re-inventoried the third year after harvest (spring–summer 2000), and the herbaceous layer was re-sampled the first (1998) and third (2000) growing seasons after harvest. For the overstory, diameter of all tree stems ≥5.0 cm dbh was measured to the nearest 0.1 cm and recorded by species in each 0.08 ha plot. For the midstory layer, diameter at the base (5 cm from ground level) was measured on all woody species (stems, <5.0 cm dbh and >1.0 m height) in two 3 m × 5 m subplots in the NW and SE corner of each 0.08 ha plot. Within each 0.08 ha plot, four 2.0 m^2 quadrats were placed diagonally 2.0 m from each corner, and herbaceous layer vegetation (woody species ≤ 1.0 m height and all herbaceous species) was surveyed during June and July. Presence, number, and percent cover of each species within the quadrats were visually estimated in 10% interval classes. Species nomenclature follows Brown and Kirkman (1990) for trees and Gleason and Cronquist (1991) for shrubs and herbs.

2.3. Soil sample collection and chemical analyses

We collected soil samples in the winter months (December–March) to minimize temporal variation due to vegetation phenological stage and diurnal temperature fluctuations. To correspond with the

vegetation measurement years, we sampled soils before the harvest (1994), after 1 year (1998), and after the third year (2000). Samples intended for chemical analysis and bulk density (BD) determination were collected separately. We collected intact soil cores to determine bulk density (at 0–5 and 5–15 cm depths) using a 4.3 cm (i.d.) PVC pipe just outside the permanent plots (1 m from each corner). The four samples were composited and air-dried prior to weighing. Total bulk density (g/cm^3) values represent weight of all inorganic material; we also report weight of materials <2 mm (BD_2). Both values are corrected for coarse materials (>7.6 cm) using the mean value estimated in the Macon County Soil Survey (Thomas, 1996). Soil chemistry samples represent the 0–5 and 5–15 cm depths of each permanent plot. Each sample was a composite of 16–24 individual samples collected using a 2 cm soil probe. Samples were air-dried and sieved (<2 mm) prior to analysis. Extractable soil cations (Ca, Mg, and K) were determined by extracting 10 g soil samples with 50 ml of 1 M NH_4Cl for 12 h using a Century mechanical vacuum extractor. Following an EtOH rinse (1 h), the NH_4 was extracted (12 h) with 1 M KCl to determine cation exchange capacity (CEC). Cation concentrations in NH_4Cl solutions were determined using a Perkin-Elmer Analyst 300 atomic absorption spectrophotometer. Ammonium determinations in KCl solutions were made using a Perstorp Environflow 3599. Soil pH was determined in a 1:1 soil to 0.01 M $CaCl_2$ slurry with a Broadley–James combination electrode and an Orion 611 pH meter.

2.4. Data analyses

We evaluated species diversity using species richness (S), Shannon–Wiener's index of diversity (H'), and Pielou (1966) evenness index (E). Shannon–Wiener's index incorporates both species richness and the evenness of species abundance (Magurran, 1988). The Shannon–Wiener index is most sensitive to the number of species in a sample and considered to be biased toward measuring species richness. Because determining the degree to which each factor contributes to diversity is impossible from the calculated value of H' alone (Peet, 1974; Patil and Taillie, 1982; Christensen and Peet, 1984), a separate measure of evenness (E) was calculated based on the Shannon–Wiener index. For the herbaceous layer, H' and E were calculated based on density and percent cover. For the understory and midstory, H' and E were calculated based on density and basal area. Shannon–Wiener index was calculated as: $H' = p_i \ln p_i$, where p_i = proportion of total density, total basal area, or total percent cover of species i. Species evenness was calculated as: $E = H'/H'_{MAX}$, where H'_{MAX} = max-maximum level of diversity possible within a given population = ln(number of species). H' and E were calculated at the plot level and averaged for each site.

Importance values (IV) for woody species were calculated as: (relative density + relative basal area)/2 and IVs for herbaceous layer species were calculated as: (relative density + relative percent cover)/2. Frequency was calculated as a percentage occurrence of species i from total number of plots sampled. Separate analyses were performed for each vegetative layer (i.e., overstory, midstory, and herbaceous layer). We used a paired t-test to evaluate the changes in S, H', and E between years within a treatment.

We used analysis of covariance (PROC GLM, SAS, 1999) to determine significant differences among regeneration harvest treatments on S, H', and E of each vegetative layer and soil characteristics. Mean site values were used in the analysis with initial pre-harvest data used as the covariate. If the covariate was not significant, then we used analysis of variance to determine significant differences among treatments (PROC GLM, SAS, 1999).

To compare herbaceous layer species composition before and after regeneration harvest treatments, we used multiresponse permutation procedures (MRPP) and non-metric multidimensional scaling (NMS) (McCune and Mefford, 1999; McCune and Grace, 2002). MRPP is a non-parametric multivariate test of differences between a priori groups (Mielke, 1984). NMS is an ordination technique especially suited for ecological applications (Clarke, 1993). For both multivariate analyses, we chose to compare the pre-harvest (1994) and the third growing season, post-harvest (2000) site data. We used herbaceous layer species IVs as the measure of abundance in both the MRPP and NMS analyses. With MRPP we contrasted pre- and post-harvest groups (across treatments between years) and treatment groups (across years

among treatments) using the Sorensen distance measure. With NMS, we explored the vegetation–environment relationships among herbaceous layer abundance (IV), soil characteristics and overstory basal area. Herbaceous layer data was combined for both years into one NMS ordination analysis so that we could determine how far each treatment site moved in ordination space after the harvest (i.e., 1994 versus 2000). NMS was conducted using the Sorensen distance measure with 60 runs of real data along with 50 runs of randomized data (a maximum of 200 iterations for each run) for a Monte Carlo test of significance that similar results could have been achieved by chance alone ($P = 0.020$). Following Monte Carlo testing, a three-dimensional solution was chosen for the final iterative ordination using the best ending point in the preliminary analysis as the starting point in the final run. We report the final stress of the ordination and coefficients of determination (r^2) for each ordination axis calculated as a proportion of the variation explained in the reduced matrix relative to that in the original matrix. Ecological community data sets often have final stress values between 10 and 20. Values in the lower half of this range indicate reliable solutions (McCune and Grace, 2002).

Uncommon species (those occurring in 2 or fewer of the 2.0 m^2 sample quadrats; frequency $\leq 1\%$) were excluded from the ordination analyses. A secondary matrix of soil environmental variables (A-horizon depth, bulk density, pH, total nitrogen, total carbon, calcium, magnesium, potassium, and CEC) and overstory basal area was used to help interpret the ordination results. In the resulting ordination graph, plot points indicate sites and line-vectors indicate environmental variables. The length of each line-vector represents the rate of change in the weighted average as inferred from the biplot, showing how much the species distributions and sites differ along that environmental variable. The most important variables are those with the longest line-vector. Monte Carlo permutations were applied to NMS analyses to determine if the strength of species sorting along the environmental variable was greater than would be expected by chance (ter Braak, 1986; Crowley, 1992). We chose to graph only the environmental variables with an $r^2 \geq 0.35$ and we used PC-ORD version 4 (McCune and Mefford, 1999) for the ordination analysis.

3. Results

3.1. Vegetation dynamics

3.1.1. Overstory

Over all the sites, a total of 32 species were recorded in the overstory (Table 1). The most abundant species were *A. rubrum*, *Q. rubra*, *Quercus prinus*, and *Quercus alba*. These species accounted for 53–75% of the IV before cutting and 61–82% after cutting, depending on treatment. After harvest proportional abundance of species changed on the two heavily cut treatments (2A and SW), but little change in species distributions occurred on the GS or UC treatments (Table 1). In the 2A and SW treatments, fewer species were present in the overstory after harvest decreasing by 11 and 7 species per site, respectively, although before harvest the absent species had low density ($\leq$20 stems/ha) and basal area ($\leq$0.20 m^2/ha) (Table 1). Species richness (S) per plot was significantly lower after harvest on the 2A and SW sites; whereas the GS and UC sites had no change between sample dates (Table 2). The SW treatment had significantly lower H' based on both density and basal area, and E based on basal area after harvest compared to before harvest values (Table 2). None of the diversity measures we used showed significant differences between years on the GS or UC sites.

3.1.2. Midstory

Before harvest, *R. calendulaceum* and *Castanea dentata*, dominated the midstory occupying 64, 65, 61, and 85% of the importance value in the 2A, SW, GS, and UC treatments, respectively (Table 3). These two species declined in importance after harvest to occupy only 23% of the importance value on the 2A, 28% on the SW, and 39% on the GS treatments. After harvest, other species substantially increased in density altering the composition of the midstory layer. As expected, the greatest shift in species composition occurred in the most heavily cut treatments, 2A and SW.

Three years after the harvest (2000), density and basal area significantly increased in the 2A and SW treatments (Table 4). There were no significant changes in density or basal area in the GS and UC sites. Diversity (H') and E were significantly higher on the 2A and SW treatments than the UC sites, but there

Table 1
Dominant overstory species ordered by sequence of maximum importance value in 1994

	Frequency		Density		Basal area		IV	
	1994	1998	1994	1998	1994	1998	1994	1998
2A								
Acer rubrum	100	100	344	25	8.75	2.09	32.18	32.76
Quercus prinus	100	91	92	24	6.16	1.79	15.74	29.50
Quercus rubra	91	73	86	16	5.58	1.11	14.40	18.91
Halesia carolina	54	9	120	2	1.53	0.05	8.40	1.75
Hamamelis virginiana	73	9	104	1	0.52	0.004	5.79	0.69
Fagus grandifolia	27	0	80	0	0.94	0	5.42	0
Amelanchier arborea	100	27	72	4	0.68	0.18	4.57	4.18
Tsuga canadensis	36	36	38	9	0.66	0.37	2.95	8.52
Robinia pseudoacacia	54	0	28	0	0.75	0	2.70	0
SW								
Acer rubrum	100	50	301	11	6.44	1.25	26.31	11.96
Quercus rubra	100	92	86	35	5.80	3.46	14.55	34.67
Quercus prinus	75	67	104	19	4.10	1.19	12.42	14.81
Halesia carolina	33	25	95	3	2.86	0.48	9.76	4.06
Carya spp.	42	25	60	7	2.31	0.60	7.08	6.52
Robinia pseudoacacia	75	17	34	3	1.84	0.12	4.96	2.03
Magnolia acuminate	42	17	41	3	0.78	0.37	3.39	3.42
Nyssa sylvatica	33	8	51	1	0.34	0.04	3.13	0.68
Castanea dentate	92	17	43	2	0.26	0.02	2.57	1.03
Hamamelis virginiana	33	0	38	0	0.12	0	2.08	0
Tsuga canadensis	92	50	23	10	0.46	0.08	1.95	6.10
Quercus alba	25	17	8	3	0.73	0.45	1.71	3.88
Prunus serotinal	25	25	14	3	0.56	0.24	1.67	2.73
Ilex ambigua	50	0	28	0	0.09	0	1.56	0
GS								
Acer rubrum	100	92	406	250	8.76	6.38	35.35	32.99
Quercus rubra	92	83	112	103	5.06	4.34	14.81	17.92
Quercus alba	83	75	49	43	4.88	3.98	11.55	12.96
Quercus prinus	83	83	71	45	3.00	1.71	8.97	7.36
Hamamelis virginiana	67	50	153	106	0.57	0.39	8.12	8.15
Tsuga canadensis	67	58	50	42	0.82	0.92	3.87	5.14
Carya spp.	42	25	25	14	0.74	0.59	2.56	2.40
Robinia pseudoacacia	75	67	20	12	0.78	0.48	2.40	2.07
Rhododendron maximum	42	33	42	19	0.12	0.08	2.15	1.47
Castanea dentate	92	67	35	29	0.21	0.20	2.02	2.47
Amelanchier arborea	75	67	27	24	0.29	0.19	1.80	2.11
UC								
Quercus rubra	100	100	245	243	18.03	19.43	50.26	47.88
Acer rubrum	100	100	173	180	3.42	4.21	18.07	18.38
Quercus alba	86	86	75	75	3.33	3.91	11.29	11.27
Hamamelis virginiana	28	28	111	138	0.50	0.59	8.38	9.60
Amelanchier arborea	86	100	66	75	0.92	1.09	6.16	6.54
Castanea dentate	100	100	43	54	0.25	0.27	3.36	3.81

Notes: Other minor species with an IV < 1.5 in either year: *Acer pensylvanicum*, *Acer saccharum*, *Betula alleghaniensis*, *Betula lenta*, *Fraxinus americana*, *Kalmia latifolia*, *Liriodendron tulipifera*, *Magnolia fraseri*, *Nyssa sylvatica*, *Oxydendrum arboreum*, *Prunus serotina*, *Quercus velutina*, *Rhododendron calendulaceum*, *Sassafras albidum*, *Tilia americana*. Columns are percent frequency, average density (stems/ha), average basal area (m^2/ha), and importance value (IV = (relative density + relative basal area)/2) for the regeneration harvest treatments (two-aged shelterwood (2A), regular shelterwood (SW), group selection (GS), and uncut control (UC)) before harvest (1994) and the first growing season after harvest (1998) at Wine Spring Creek, western North Carolina.

Table 2
Overstory density (stems/ha), basal area (m^2/ha), Shannon–Wiener index of diversity (H' based on density and basal area), Pielou's evenness index (E based on density and basal area), and species richness (S: average number of species per plot and average number of species per site) for the four regeneration harvest treatments (two-aged shelterwood (2A), regular shelterwood (SW), group selection (GS), and uncut control (UC)) before harvest (1994) and the first year (1998) after harvest at Wine Spring Creek, western North Carolina

	2A		SW		GS		UC	
	1994	1998	1994	1998	1994	1998	1994	1998
Density	1094 (34)	84[a] (15) a	1009 (134)	114[a] (29) a	1090 (56)	742[a] (78) b	717 (183)	771[a] (192) b
Basal area	26.7 (0.6)	5.6[a] (0.4) a	28.2 (2.5)	9.1[a] (1.8) a	26.2 (2.2)	19.8[a] (2.0) b	26.6 (0.5)	29.6 (1.1) c
H' density	1.83 (0.13)	1.13[a] (0.16)	1.89 (0.14)	1.32[a] (0.24)	1.78 (0.07)	1.68 (0.02)	1.39 (0.01)	1.43 (0.02)
E density	0.77 (0.02)	0.88[a] (0.01) a	0.79 (0.02)	0.92 (0.03) a	0.74 (0.003)	0.79 (0.01) b	0.74 (0.02)	0.75 (0.02) b
H' basal area	1.56 (0.14)	0.98 (0.16)	1.70 (0.13)	1.19[a] (0.24)	1.56 (0.18)	1.45 (0.10)	0.79 (0.3)	0.81 (0.3)
E basal area	0.66 (0.03)	0.75 (0.04) a	0.70 (0.02)	0.82[a] (0.02) a	0.64 (0.05)	0.69 (0.05) ab	0.43 (0.2)	0.44 (0.2) b
S per plot	11 (1.2)	4[a] (0.5) a	11 (1.2)	5[a] (1.4) a	12 (1.0)	9 (0.4) b	7 (0.4)	7 (0.5) ab
S per site	17 (0.9)	6 (1.2)	16 (1.5)	9 (2.5)	18 (1.5)	15 (1.5)	10 (1.0)	11 (1.5)

Standard errors are in parentheses.
[a] Denotes significant difference (paired t-test, $\alpha \leq 0.05$) between pre-harvest (1994) and post-harvest (1998). For 1998, values across rows followed by different letters (a–c) denote significant difference among treatments ($\alpha \leq 0.05$) based on analysis of covariance with the corresponding initial condition in 1994 as the covariate.

were no significant differences among the three harvest treatments. In addition, S per plot significantly increased on all three treatments after harvesting (Table 4).

After harvest in the 2A treatment, the five top species ranked by IV were *R. calendulaceum*, *H. carolina*, *A. rubrum*, *Gaylussacia baccata*, and *A. arborea*. *H. carolina*, *G. baccata*, *A. arborea*, and *A. rubrum* increased in density by >10-fold. New species, with >1.0 IV, were *A. pensylvanicum*, *Q. alba*, and *Rubus allegheniensis*.

After harvest in the SW treatment, the five top species ranked by IV were *R. calendulaceum*, *A. rubrum*, *C. dentata*, *Robinia pseudoacacia*, *H. carolina*,

Table 3
Dominant midstory woody species ordered by sequence of maximum importance value in 1994

	Frequency		Density		Basal area		IV	
	1994	2000	1994	2000	1994	2000	1994	2000
2A								
Rhododendron calendulaceum	73	73	6660	7337	1.41	1.08	48.52	16.05
Castanea dentata	73	73	2272	1849	0.37	0.60	15.23	6.45
Vaccinium corymbosum	45	64	656	2425	0.19	0.24	6.02	4.42
Hamamelis virginiana	45	73	656	1819	0.12	0.31	4.70	4.34
Magnolia acuminata	54	45	707	637	0.09	0.08	4.20	1.32
Ilex ambigua	45	64	404	2607	0.14	0.28	4.03	4.88
Halesia carolina	36	36	404	4639	0.07	0.90	2.83	11.88
Quercus rubra	45	91	606	3305	0.03	0.21	2.76	5.06
Fagus grandifolia	18	18	303	2274	0.03	0.25	1.68	4.35
Pyrularia pubera	18	36	151	424	0.03	0.03	1.06	0.65
Tsuga canadensis	9	9	50	30	0.04	0.01	1.05	0.13
Gaylussacia ursina	9	45	606	6579	0.02	0.17	0.65	8.15
Robina pseudoacacia	9	45	101	879	0.01	0.19	0.52	2.41
Amelanchier arborea	36	73	252	3486	0.02	0.48	0.34	7.39
Acer rubrum	9	73	50	3365	0.01	0.72	0.29	9.16
Magnolia fraseri	9	9	50	364	0.004	0.20	0.25	1.97
Betula alleghaniensis	9	27	50	758	0.001	0.15	0.20	1.95
Acer pensylvanicum	0	27	0	818	0	0.11	0	1.68
Quercus alba	0	9	0	637	0	0.11	0	1.50
Rubus allegheniensis	0	73	0	3668	0	0.19	0	5.30

Table 3 (*Continued*)

	Frequency		Density		Basal area		IV	
	1994	2000	1994	2000	1994	2000	1994	2000
SW								
Rhododendron calendulaceum	58	58	7175	6837	1.52	1.24	50.14	17.01
Castanea dentata	83	67	2500	2696	0.35	1.18	14.40	11.24
Vaccinium corymbosum	33	42	648	2390	0.20	0.10	5.69	3.79
Ilex ambigua	33	75	648	2362	0.19	0.33	5.43	5.25
Acer rubrum	58	58	833	4058	0.08	1.33	4.23	14.00
Hamamelis virginiana	25	25	278	1390	0.11	0.32	2.80	3.93
Amelanchier arborea	42	50	463	945	0.05	0.09	2.40	1.81
Magnolia acuminata	25	42	370	500	0.06	0.07	2.19	1.12
Quercus rubra	42	83	324	2334	0.06	0.29	2.19	4.96
Carya spp.	17	17	185	834	0.06	0.10	1.63	1.76
Acer pensylvanicum	17	42	92	1278	0.06	0.15	1.42	2.66
Halesia carolina	8	42	231	1751	0.03	0.60	1.34	6.21
Quercus prinus	17	17	231	417	0.003	0.12	0.84	1.35
Prunus serotina	17	58	92	306	0.01	0.12	0.55	1.20
Robina pseudoacacia	8	58	92	1223	0.01	0.74	0.44	6.45
Sassafras albidum	8	17	46	528	0.01	0.09	0.30	1.26
Betula lenta	0	42	0	1167	0	0.10	0	2.18
Nyssa sylvatica	0	33	0	945	0	0.21	0	2.61
Oxydendrum arboretum	0	17	0	611	0	0.08	0	1.36
Rhododendron maximum	0	8	0	917	0	0.08	0	1.71
Rubus allegheniensis	0	75	0	3529	0	0.13	0	5.46
GS								
Rhododendron calendulaceum	100	100	12499	7559	2.15	2.12	55.10	32.16
Castanea dentata	67	75	1435	1890	0.24	0.44	6.20	7.23
Hamamelis virginiana	50	75	1481	3002	0.21	1.04	5.94	14.53
Gaylussacia ursina	25	25	2268	4613	0.08	0.12	5.86	9.24
Fagus grandifolia	25	25	1111	1251	0.16	0.22	4.50	4.12
Pyrularia pubera	17	50	926	1668	0.14	0.17	3.80	4.50
Vaccinium corymbosum	58	67	648	1334	0.17	0.25	3.67	4.56
Kalmia latifolia	33	42	509	556	0.17	0.13	3.30	2.14
Amelanchier arborea	50	42	463	472	0.14	0.14	2.82	2.11
Quercus rubra	50	75	509	639	0.06	0.07	1.86	1.74
Magnolia acuminata	33	42	278	500	0.05	0.12	1.27	1.95
Halesia carolina	42	25	324	445	0.04	0.04	1.26	1.18
Acer rubrum	17	25	278	778	0.01	0.25	0.72	3.59
Nyssa sylvatica	17	8	185	222	0.02	0.11	0.60	1.38
Sassafras albidum	25	42	139	445	0.02	0.07	0.49	1.38
Ilex ambigua	25	33	139	250	0.01	0.06	0.47	1.01
Quercus prinus	17	33	92	667	0.01	0.06	0.34	1.70
Rubus alleghaniensis	8	42	92	806	0.01	0.03	0.27	1.66
UC								
Rhododendron calendulaceum	86	86	14046	12530	3.19	4.80	70.36	65.26
Vaccinium corymbosum	86	57	3016	2002	0.63	0.75	14.41	10.26
Castanea dentate	100	86	1904	2334	0.24	0.52	7.33	9.39
Rubus allegheniensis	28	57	1666	3478	0.07	0.14	4.74	9.19
Quercus rubra	14	14	238	143	0.09	0.02	1.57	0.46
Hamamelis virginiana	28	28	159	619	0.01	0.39	0.53	4.37

Notes: Other minor species with and IV < 1.0 in either year: *Acer saccharum*, *Fagus grandifolia*, *Fraxinus americana*, *Hydrangia arborescens*, *Prunus pensylvanica*, *Rhododendron maximum*, *Tilia americana*, *Vaccinium stamineum*. Columns are percent frequency, average density (stems/ha), average basal area (m^2/ha), and importance value (IV = (relative density + relative basal area)/2) for the regeneration harvest treatments (two-aged shelterwood (2A), shelterwood (SW), group selection (GS), and uncut control (UC)) before harvest (1994) and the third growing season after harvest (2000) at Wine Spring Creek, western North Carolina.

Table 4
Midstory density (stems/ha), basal area (m^2/ha), Shannon–Wiener index of diversity (H' based on density and basal area), Pielou's evenness index (E based on density and basal area), and species richness (S: average number of species per plot and average number of species per site) for the four regeneration harvest treatments (two-aged shelterwood (2A), regular shelterwood (SW), group selection (GS), and uncut control (UC)) before harvest (1994) and the third year (2000) after harvest at Wine Spring Creek, western North Carolina

	2A		SW		GS		UC	
	1994	2000	1994	2000	1994	2000	1994	2000
Density	14258 (2337)	49117[a] (8578) a	14906 (5345)	38269[a] (6364) ab	23701 (4630)	28347 (5187) bc	21225 (856)	21789 (2445) c
Basal area	2.72 (0.40)	6.44[a] (0.66)	2.92 (1.10)	7.64[a] (1.15)	3.74 (0.29)	5.62 (0.70)	4.20 (0.39)	6.50 (1.14)
H' density	1.22 (0.17)	1.85[a] (0.07) a	1.27 (0.14)	1.88[a] (0.10) a	1.31 (0.07)	1.63 (0.14) a	0.80 (0.17)	0.86 (0.08) b
E density	0.49 (0.06)	0.75[a] (0.01) a	0.51 (0.03)	0.76[a] (0.04) a	0.56 (0.07)	0.68 (0.02) ab	0.51 (0.12)	0.54 (0.07) b
H' basal area	1.00 (0.28)	1.69[a] (0.15) a	1.14 (0.10)	1.60[a] (0.11) a	1.21 (0.10)	1.46 (0.22) ab	0.71 (0.23)	0.74 (0.28) b
E basal area	0.40 (0.10)	0.68[a] (0.03)	0.46 (0.04)	0.65[a] (0.04)	0.52 (0.05)	0.61 (0.05)	0.46 (0.16)	0.49 (0.19)
S per plot	6 (0.4)	10[a] (1.7) a	6 (0.5)	10[a] (0.4) a	7 (0.3)	10[a] (1.9) a	4 (0.3)	4 (0.4) b
S per site	14.0 (1.53)	16.3 (1.4)	13.0 (0.6)	17.7 (0.9)	14.7 (1.8)	18.0 (3.2)	6.5 (0.5)	7.5 (1.5)

Standard errors are in parentheses.
[a] Denotes significant difference (paired t-test, $\alpha \leq 0.05$) between pre-harvest (1994) and post-harvest (2000). For 2000, values across rows followed by different letters (a–c) denote significant difference among treatments ($\alpha \leq 0.05$) based on analysis of covariance with the corresponding initial condition in 1994 as the covariate.

and *R. allegheniensis*. New species, with >1.0 IV, were *Betula lenta*, *N. sylvatica*, *Oxydendrum arboreum*, *Rhododendron maximum*, and *R. allegheniensis*.

3.1.3. Herbaceous layer

Overall, 139 herbaceous layer species occurred over the 11 sites with 40 species present on all treatments in all years and 70 species present on all treatments in at least 1 of the sample years (Table 5). Of these, 104 herbaceous species, 26 tree species, and 9 shrubs were recorded. *Carex pensylvanica*, *Prenanthes trifoliolata*, and *Thelypteris noveboracensis* were the most abundant species on all sites, contributing from 36 to 52% to the importance value. *P. trifoliolata* decreased through time on all sites, even the UC sites. *C. pensylvanica* and *T. noveboracensis* increased after harvest on all the harvested sites and remained about the same on the UC sites.

In the 2A treatment, *Acer saccharum*, *Dryopteris intermedia*, *Epigea ripens*, and *Gillenia trifoliatus* were not recorded after the harvest, all were minor species (IV < 0.1). New species that colonized after harvest were *B. lenta*, *Cimicifuga racemosa*, *Collinsonia canadensis*, *Liriodendron tulipifera*, *Lycopo-*

Table 5
Herbaceous layer species importance values (IV = (relative density + relative percent cover)/2) for the regeneration harvest treatments (two-aged shelterwood (2A), regular shelterwood (SW), group selection (GS), and uncut control (UC)) before harvest (1994), the first year (1998) and the third year (2000) after harvest at Wine Spring Creek, western North Carolina

	2A			SW			GS			UC		
	1994	1998	2000	1994	1998	2000	1994	1998	2000	1994	1998	2000
Acer pensylvanicum	0.43	0.34	0.32	0.37	1.14	0.43	0.06	0.13	0.06	0.005	0.14	0
Acer rubrum	0.38	1.46	1.03	0.70	0.57	0.56	0.51	0.85	0.95	0.17	0.27	0.49
Amelanchier arborea	1.03	1.84	0.81	0.47	0.71	0.57	0.80	0.87	0.84	0.26	0.46	0.45
Anemone quinquefolia	2.45	2.20	0.48	3.05	0.82	0.70	4.02	0.83	0.60	4.13	1.60	1.73
Aster divaricata	0.98	1.54	2.02	0.68	0.92	1.00	0.58	0.56	0.38	0.39	0.36	0.36
Athyrium filix-femina	0.76	0.07	0.18	0.92	0	0.49	0.22	0	0	0.46	0	1.25
Aureolaria flava	0.28	0.09	0.41	0.16	0.24	0.11	1.06	0.58	0.54	0.86	0.85	0.76
Carex pensylvanica	12.32	11.88	22.48	5.76	5.33	6.89	7.36	8.98	16.21	11.48	12.98	11.85
Castanea dentate	0.40	0.59	0.06	1.04	0.78	0.09	0.75	0.50	0.58	0.15	0.18	0.09
Clintonia umbellulata	0.53	0.70	0.63	0.51	0.44	0.39	0.37	0.90	0.89	0.74	0.96	1.28
Collinsonia canadensis	0	0.07	0.48	0.82	0.33	1.20	0.07	0.06	0.06	0.35	0.19	0.44

Table 5 (*Continued*)

	2A			SW			GS			UC		
	1994	1998	2000	1994	1998	2000	1994	1998	2000	1994	1998	2000
Dennstaedtia punctilobula	0.65	1.96	2.52	0.72	2.88	3.74	1.52	1.75	1.99	2.58	2.27	1.97
Dioscorea quaternata	0.59	1.08	0.74	1.11	1.19	1.27	1.41	1.51	1.42	1.69	2.20	2.99
Eupatorium rugosum	0.24	0.48	0.40	0.42	5.64	1.49	0.01	0.19	0.35	0.36	0.81	0.43
Galax aphylla	3.59	3.68	5.42	10.06	9.33	14.44	1.30	1.29	0.80	0	0	0
Galium lanceolatum	0.01	0	0.08	0.11	0.46	0.42	0.10	0.09	1.02	0.10	0.20	0.11
Gaylussacia baccata	11.15	4.06	5.55	6.90	1.58	4.52	3.58	1.16	1.52	1.23	0.76	0.88
Gentiana saponaria	0.50	0.40	0.20	0.27	0.30	0.48	0.54	1.00	0.71	0.18	0.65	0.31
Halesia carolina	0.27	1.96	2.58	0.07	2.19	1.03	0.13	0.52	0.34	0	0	0.01
Hamamelis virginiana	0.90	1.00	0.66	0.19	0.35	0.32	0.95	1.27	1.04	0.07	0.42	0.29
Hedyotis caerulea	0	0	0	1.18	0.23	2.69	0.53	0.12	0.14	0.31	0.11	0.01
Hedyotis purpurea	0.02	0.33	3.78	0.28	0.48	2.32	1.26	1.30	3.47	0.80	0.96	1.18
Hieracium paniculatum	0.44	0.39	0.31	0.43	0.61	0.66	1.54	1.28	0.82	0.86	0.89	0.51
Ilex ambigua	0.50	1.00	0.15	0.65	0.53	0.24	0.65	0	0.05	0	0.01	0
Ligusticum canadense	2.05	1.20	1.99	0.61	0.66	0.70	1.16	0.62	0.78	2.82	2.65	5.07
Lysimachia quadrifolia	0.76	0.72	1.33	0.56	0.83	1.93	1.26	1.55	1.62	0.79	0.97	0.91
Medeola virginiana	5.44	6.01	3.89	2.02	1.37	1.47	1.64	2.14	1.93	1.65	2.26	2.34
Melampyrum linear	1.86	2.01	0.35	1.91	1.49	0.54	3.40	1.50	0.83	0.005	0.10	0.22
Panicum spp.	0.02	0.52	1.47	0.31	0.82	1.35	1.72	1.76	3.00	0.49	0.46	0.79
Pedicularis canadensis	0.18	0.17	0	0.33	0.09	0.06	1.30	1.38	0.35	0.66	0.87	0.77
Poa spp.	0.45	0.64	0.87	0.36	1.38	0.74	1.11	1.87	1.97	0.87	0.90	0.50
Polygonatum biflorum	0.55	0.73	0.29	1.55	1.50	1.28	0.36	0.29	0.25	0.16	0.42	0.14
Potentilla canadensis	0.004	0.08	0.18	0.34	0.70	1.67	1.64	1.28	0.78	1.14	1.28	1.09
Prenanthes trifoliolata	25.58	14.99	0.98	17.85	4.40	1.05	12.26	4.36	2.03	4.83	1.70	2.13
Pyrularia pubera	0.28	0.07	0.12	0.004	0.05	0	1.36	1.06	1.32	0	0	0
Quercus rubra	1.66	2.59	3.39	0.92	1.91	2.05	0.43	1.40	2.19	0.76	2.33	2.87
Rhododendron calendulaceum	1.27	1.59	1.63	1.25	1.34	1.23	1.73	1.20	1.40	0.65	1.92	1.46
Rubus allegheniensis	0	0.37	0.67	0.53	0.99	0.94	0.08	0.18	0.42	2.19	1.92	1.46
Smilacina racemosa	0.34	0.26	0.16	1.37	0.98	0.91	0.62	0.42	0.40	0.42	0.29	0.10
Smilax herbacea	0.46	0.76	0.30	0.24	0.54	0.48	0.18	0.29	0.29	0.90	1.22	0.86
Smilax rotundifolia	1.25	1.54	2.42	1.65	1.47	2.62	2.59	1.71	1.81	0.11	0.12	0
Solidago arguta	0.97	0.55	1.22	1.14	0.69	1.44	2.81	2.10	2.60	1.64	1.63	1.93
Solidago curtisii	1.56	2.56	2.06	2.53	2.37	2.10	1.10	2.16	1.61	2.57	2.69	3.42
Thelypteris noveboracensis	5.10	11.84	12.73	9.41	20.72	13.98	16.36	31.97	26.92	35.63	42.80	40.25
Vaccinium spp. (corymbosum)	1.27	0.84	3.36	1.26	0.84	0.91	2.15	2.06	3.02	0.03	0.48	0.33
Viola cucullate	0.18	1.04	1.30	1.03	1.90	1.53	1.76	2.46	1.85	0.84	0.74	1.00
Viola hastate	5.22	3.78	0.16	6.09	2.91	0.88	6.59	2.42	0.70	5.93	0.23	0.35
Viola rotundifolia	0.73	1.44	0.94	0.77	1.17	0.55	0.23	0.48	0.31	0	0	0
S per plot	30 (3)	31 (4)	32 (2)	38 (2)	39 (2)	39 (2)	39 (2)	38 (2)	38 (2)	37 (1)	34 (3)	31 (2)

Notes: Other minor species with an IV < 1.0 in any year: *Acer saccharum*, *Actaea pachypoda*, *Aesculus flava*, *Amphicarpaea bracteata*, *Aralia nudicaulis*, *Arisaema triphyllum*, *Aruncus dioicus*, *Asclepias exaltata*, *Aster lateriflorus*, *Aster macrophyllus*, *Aster undulatus*, *Athyrium filix-femina*, *Betula lenta*, *Botrychium virginianum*, *Cacalia atriplicifolia*, *Campanula divaricata*, *Cardamine flagellifera*, *Carya* spp., *Caulophyllum thalictroides*, *Chelone glabra*, *Chimaphila maculata*, *Cimicifuga racemosa*, *Clethra acuminata*, *Coreopsis major*, *Crataegus flava*, *Cypripedium acaule*, *Cuscuta gronovii*, *Dactylis glomerata*, *Desmodium nudiflorum*, *Disporum lanuginosum*, *Dryopteris intermedia*, *Erechtites hieracifolia*, *Erigeron pulchellus*, *Epigea repens*, *Eupatorium purpureum*, *Eupatorium steelei*, *Fragus grandifolia*, *Festuca octoflora*, *Fraxinus americana*, *Galium lanceolatum*, *Gillenia trifoliatus*, *Gnaphalium obtusifolium*, *Goodyera pubera*, *Helianthus* spp., *Hypoxis hirsuta*, *Impatiens capensis*, *Isotria verticillata*, *Lactuca canadensis*, *Lilium michauxii*, *Liriodendron tulipifera*, *Luzula acuminata*, *Lycopodium obscurum*, *Magnolia acuminata*, *Magnolia fraseri*, *Maianthemum canadense*, *Monarda clinopodia*, *Nyssa sylvatica*, *Oenothera fruticosa*, *Osmunda cinnamomea*, *Oxypolis rigidior*, *Phlox carolina*, *Plantago major*, *Polystichum acrostichoides*, *Polygonum virginianum*, *Prunus pensylvanica*, *Prunus serotina*, *Prunella vulgaris*, *Pycnantheumum incanum*, *Quercus alba*, *Quercus prinus*, *Ranunculus* spp., *Rhododendron maximum*, *Robinia pseudoacacia*, *Rudbeckia hirta*, *Sanguisorba canadensis*, *Sassafras albidum*, *Saxifrage michauxii*, *Silene virginica*, *Smilax glauca*, *Stachys* spp., *Stellaria pubera*, *Taraxacum officinale*, *Thalictrum dioicum*, *Tiarella cordifolia*, *Tilia americana*, *Toxicodendron radicans*, *Tradescantia virginiana*, *Trifolium repens*, *Trillium* spp., *Tsuga canadensis*, *Uvularia perfoliata*, *Uvularia pudica*, *Veratrum parviflorum*, *Viburnum acerifolium*.

dium obscurum, *Phlox carolina*, and *R. allegheniensis*. Transient species (present in low numbers and only one of the two post-harvest sample years) were *Asclepias exaltata*, *Cardamine flagellifera*, *Cuscuta gonovii*, *Erigeron pulchellus*, *Festuca octoflora*, *Hypoxis hirsuta*, *Maianthemum canadense*, *N. sylvatica*, *Prunus pensylvanica*, *Pycnanthemum incanum*, *Rudbeckia hirta*, *Sanguisorba canadensis*, *Sassafras albidum*, *Silene virginica*, *Tiarella cordifolia*, and *Viburnum acerifolium*.

In the SW treatment, species not present after harvest were *Luzula acuminata*, *F. grandifolia*, *Stachys* spp., *A. saccharum*, *Isotria verticillata*, *Tradescantia virginiana*, and *P. pensylvanica*. New species that colonized after harvest were *Lilium michauxii*, *A. exaltata*, *Pycananthemum incanum*, *Carya* spp., *Dactylis glomerata*, *Monarda clinopodia*, *Prunella vulgaris*, *Smilax glauca*, and *Trifolium repens*. Transient species were *Dryopteris interupta*, *Magnolia fraseri*, *C. racemosa*, *Cuscuta gronovii*, *F. octoflora*, *P. carolina*, *S. virginica*, *Clethra acuminata*, *Erechtites hieraciifolia*, *Gnaphalium obtusifolium*, *Lactuca canadensis*, *Ranuculus* spp., *Saxifrage michauxii*, and *Taraxacum officinale*.

In the GS treatment, species not present after harvest were *Athyrium filix-femina*, *E. ripens*, *Chimaphila maculata*, *Stachys* spp., *A. saccharum*, *I. verticillata*, *Fraxinus americana*, *Desmodium nudiflorum*, *Tsuga candensis*, *Oenothera fruticosa*, and *Aesculus flava*. New species that colonized after harvest were *Magnolia acuminata*, *Disporum lanuginosum*, *R. pseudoacacia*, and *S. glauca*. Transient species were *Thalictrum dioicum*, *C. flagellifera*, *F. octoflora*, *P. incanum*, *T. cordifolia*, *V. acerifolium*, *Polygonum virginianum*, *T. virginiana*, *Platago major*, and *Toxidodendron radicans*.

Species composition also differed on the UC sites among sample years. In the UC sites, species lost were *M. acuminata*, *Coreopsis major*, *Stellaria pubera*, *Arisaema triphyllum*, *G. trifoliatus*, *H. hirsuta*, *Campanula divaricata*, *Ranuculus* spp., *Amphicarpaea bracteata*, *Chelone glabra*, *Cacalia atriplicifolia*, and *Oxypolis rigidior*. New species were *D. lanuginosum*, *Goodyera pubescens*, *C. maculata*, *P. incanum*, and *Crataegus flava*. Transient species were *Ilex ambigua*, *Q. prinus*, *B. lenta*, *C. racemosa*, *S. canadensis*, *S. albidum*, *Caulophyllum thalictroides*, and *S. glauca*.

For the UC sites, diversity (H' and E) based on density were significantly lower in 1998 (1 year after harvest) than in 1994 (before harvest) (Fig. 3), but returned to the 1994 level by 2000. However, herbaceous layer density (Fig. 3) and species richness per plot (Table 5) were significantly lower in 2000 (3 years after harvest) than before harvest treatments were implemented.

Herbaceous layer density and percent cover differed significantly among treatments in the first year after harvest (1998) (Figs. 3 and 4). Density was

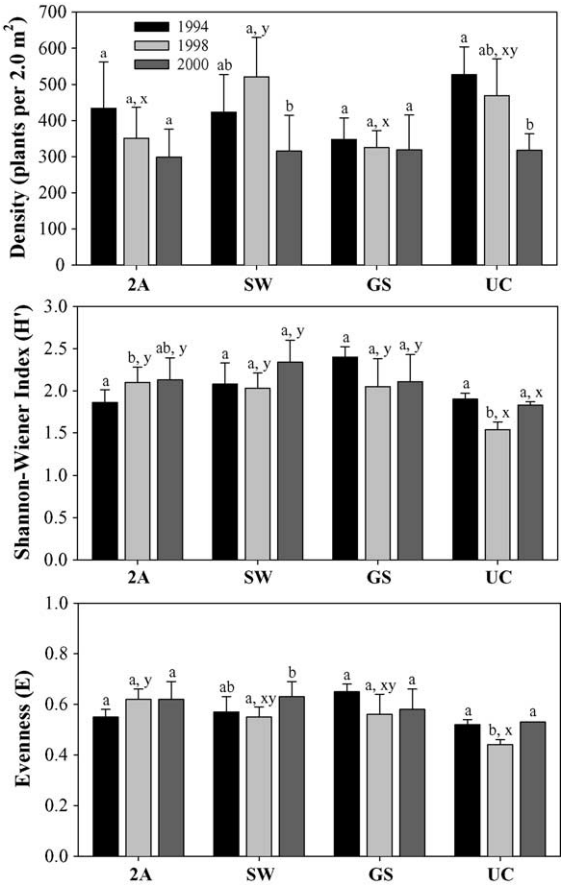

Fig. 3. Herbaceous layer density and diversity (Shannon–Wienner index: H' and evenness: E) based on density for the regeneration harvest treatments (UC: uncut control; 2A: two-aged shelterwood; SW: shelterwood; GS: group selection) in the Wine Spring Creek watershed, western North Carolina. Values with standard error bars are for pre-harvest (1994), post-harvest 1998 (first growing seasons after harvest) and 2000 (third growing season after harvest). Bars within a treatment with different letters (a–c) denote significant difference among years. Bars within a year with different letters (x–z) denote significant difference among harvest treatments.

significantly higher in the SW treatment than the 2A or GS treatments, but not significantly different than the UC sites. Percent cover was significantly higher in the SW treatment than the 2A treatment. The UC sites had significantly lower H' and E than the other harvested treatments in 1998, but no significant differences were detected in 2000. No significant differences were detected for the diversity indices (H' or E) among the three harvested treatments (Figs. 3 and 4).

H' and E based on percent cover were significantly higher the first year after harvest (1998), than before harvest (1994) on all regeneration harvest treatments (Fig. 4). By the third year after harvest (2000), H' and E did not differ significantly from before harvest values for any of the harvested treatments. However, species richness per plot was significantly lower on the UC and 2A treatments compared to the SW and GS treatments (Table 5).

3.2. Soil characteristics

3.2.1. Soil responses

Soil total C and total N content averaged 14 and 7% C in the 0–5 cm layer and 0.62 and 0.33% N in the 5–15 cm layer (Table 6). Soils were acidic with pH values averaging 3.8 and 4.2 in the two surface horizons. Soils were variable among both sites and treatments, as demonstrated by the range in A-horizon depth, which averaged 23 cm in the GS sites and 46 cm in the SW sites. This variation was evident also in some of the soil chemical characteristics measured. For example, extractable Ca concentrations ranged from a mean of 131 mg/kg in the 2A sites to 297 mg/kg in SW sites.

The analysis of covariance showed few significant changes in soil characteristics due to harvest treatment when compared to UC sites (Table 6). There was a significant decrease in total% C after harvest in the 5–15 cm layer in both post-harvest sample years in all three harvest treatments (Table 6). Extractable Ca increased after harvest, but only in the 2A site in the 0–5 cm soil layer. Paired t-test comparisons of pre- and post-harvest values showed a decrease in soil bulk density at the 5–15 cm depth after harvest for all treatments; decreases occurred in both post-harvest sample dates. Bulk density did not differ among sample dates on UC. Analyses also showed increased

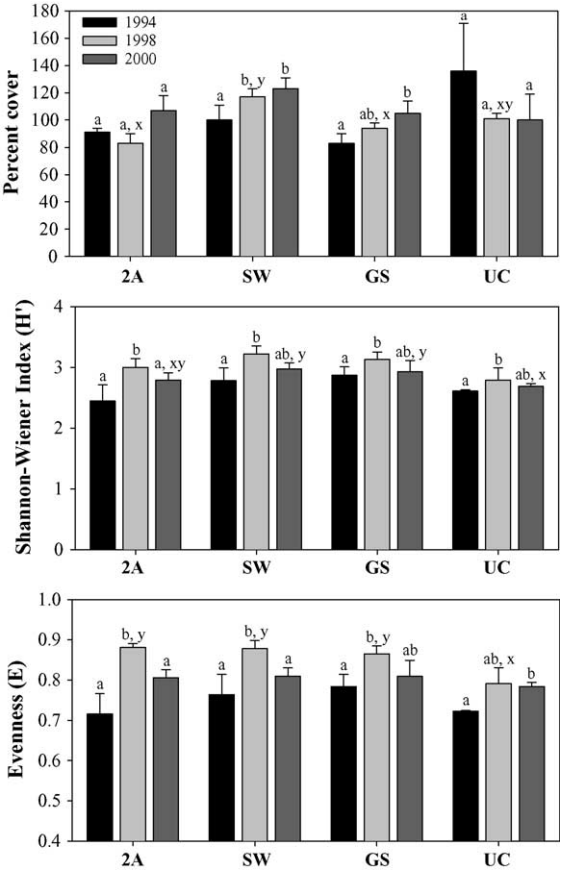

Fig. 4. Herbaceous layer percent cover and diversity (Shannon–Wienner index: H' and evenness: E) based on percent cover for the regeneration harvest treatments (UC: uncut control; 2A: two-aged shelterwood; SW: shelterwood; GS: group selection) in the Wine Spring Creek watershed, western North Carolina. Values with standard error bars are for pre-harvest (1994), post-harvest 1998 (first growing seasons after harvest) and 2000 (third growing season after harvest). Bars within a treatment with different letters (a–c) denote significant difference among years. Bars within a year with different letters (x–z) denote significant difference among harvest treatments.

CEC on all treatments after harvest in 1998 and 2000, but CEC also increased on UC sites.

3.2.2. Vegetation–soil relationships

Herbaceous layer species composition differed significantly after harvest (MRPP: $P = 0.011$) compared to what was present before. The UC group was the only one that decreased in average distance between pre- and post-harvest time periods (UC

Table 6
Soil characteristics for the regeneration harvest treatments (two-aged shelterwood (2A), regular shelterwood (SW), group selection (GS), and uncut control (UC)) before harvest (winter 1994–1995), the first year (winter 1998–1999), and the third year (winter 2000–2001) after harvest at Wine Spring Creek, western North Carolina

	0–5 cm soil depth				5–15 cm soil depth			
	2A	SW	GS	UC	2A	SW	GS	UC
A-horizon depth								
1994	30.7 (3.0)	45.8 (10.1)	23.5 (1.0)	38.0 (2.0)				
Bulk density (g/cm^3)								
1994	0.44 (0.04)	0.45 (0.03)	0.44 (0.04)	0.46 (0.004)	0.60 (0.04) x	0.58 (0.04) x	0.62 (0.01) x	0.58 (0.002)
1998	0.40 (0.06)	0.33 (0.02)	0.43 (0.03)	0.40 (0.01)	0.50 (0.02) y	0.49 (0.07) y	0.57 (0.01) y	0.56 (0.09)
2000	0.44 (0.05)	0.40 (0.04)	0.51 (0.04)	0.40 (0.06)	0.50 (0.04) y	0.50 (0.03) y	0.55 (0.02) y	0.49 (0.03)
pH								
1994	3.7 (0.04)	3.9 (0.05)	3.8 (0.09)	3.8 (0.04)	4.2 (0.01)	4.2 (0.02)	4.2 (0.02)	4.2 (0.01)
1998	3.6 (0.14)	3.9 (0.15)	3.8 (0.07)	3.8 (0.02)	4.1 (0.02)	4.2 (0.05)	4.1 (0.05)	4.2 (0.02)
2000	3.9 (0.05)	4.0 (0.04)	3.9 (0.04)	3.8 (0.03)	4.2 (0.02)	4.2 (0.03)	4.2 (0.04)	4.2 (0.04)
Total nitrogen (%)								
1994	0.62 (0.08)	0.64 (0.14)	0.54 (0.48)	0.68 (0.12)	0.29 (0.06)	0.34 (0.10)	0.27 (0.04) x	0.41 (0.03)
1998	0.62 (0.07)	0.54 (0.12)	0.48 (0.04)	0.66 (0.04)	0.30 (0.05)	0.32 (0.06)	0.26 (0.03) x	0.40 (0.01)
2000	0.44 (0.05)	0.49 (0.12)	0.42 (0.01)	0.48 (0.01)	0.20 (0.03) a	0.30 (0.09) a	0.22 (0.03) a, y	0.45 (0.07) b
Total carbon (%)								
1994	13.3 (1.0)	13.2 (1.7)	13.6 (1.1) y	15.6 (1.0)	6.6 (0.9)	7.4 (1.2)	6.0 (0.6)	8.0 (0.2)
1998	13.2 (1.3)	10.4 (1.3)	10.0 (1.0) x	12.3 (0.3)	6.6 (0.8) a	6.4 (1.0) b	5.4 (0.4) b	7.9 (0.3) a
2000	9.9 (0.4)	9.7 (1.5)	9.1 (0.1) x	9.6 (0.7)	4.5 (0.8) a	6.5 (1.5) a	5.0 (0.5) a	9.2 (0.9) b
Calcium (mg/kg)								
1994	131 (42)	297 (110)	200 (51)	143 (31)	26 (4.6)	60 (19) x	34 (7.3)	41 (15)
1998	183 (22) a	248 (68) ab	193 (43) ab	127 (26) b	33 (7.4)	41 (14) y	30 (1.8)	23 (2.2)
2000	160 (45)	254 (87)	182 (48)	168 (13)	91 (46)	90 (32) x	56 (29)	25 (7.4)
Magnesium (mg/kg)								
1994	59.1 (4.9) x	83.9 (15.5)	68.5 (11.5)	62.9 (3.1) x	19.8 (2.0) b, x	29.0 (4.4) a, x	18.5 (0.5) b	21.5 (1.2) ab
1998	61.1 (5.5) x	61.3 (3.6)	57.2 (3.7)	55.2 (4.0) y	21.3 (1.6) x	20.8 (3.6) y	18.9 (2.0)	19.3 (1.2)
2000	44.9 (7.8) y	60.2 (15.1)	53.3 (5.0)	64.1 (2.0) x	12.8 (1.1) y	18.5 (2.6) y	16.0 (2.0)	18.6 (1.3)
Potassium (mg/kg)								
1994	230 (3.9)	297 (35.0) x	257 (34.6)	259 (13.0) x	130 (10.0) y	13 (14.6) x	118 (6.8)	136 (4.6)
1998	184 (8.4)	204 (17.1) y	198 (34.5)	180 (9.2) y	119 (5.8) xy	115 (10.9) y	108 (8.9)	102 (9.2)
2000	206 (25.6)	227 (31.2) y	213 (8.6)	227 (23.4) xy	91 (13.9) x	115 (11.7) y	106 (2.2)	111 (11.0)
CEC (meq/100 g)								
1994	12.2 (1.2) x	15.2 (1.9)	11.5 (0.6) x	12.3 (0.1) x	7.4 (0.7) x	9.4 (1.4) x	7.0 (0.7)	7.7 (0.5) x
1998	19.9 (1.9) y	19.1 (1.5)	15.8 (1.6) y	19.9 (1.1) z	12.6 (1.5) y	13.5 (1.2) y	10.1 (1.6)	14.2 (0.1) y
2000	16.7 (1.4) y	16.7 (2.8)	14.5 (0.7) y	16.1 (0.2) y	10.7 (0.9) y	13.1 (1.4) y	8.7 (1.0)	12.2 (0.8) xy

Notes: Values in rows followed by different letters (a–c) denote significant differences (analysis of covariance or analysis of variance, $\alpha \leq 0.1$) among treatments within a year. Values in columns followed by different letters (x–z) denote significant differences (pairwise, paired *t*-tests, $\alpha \leq 0.05$) among years within a treatment. Mean soil properties for the 0–5 and 5–15 cm soil depths are bulk density, pH, total nitrogen, total carbon, extractable calcium, extractable magnesium, extractable potassium, and cation exchange capacity (CEC). Standard errors of the mean are in parentheses.

group: average distance was 0.364 in 1994 versus 0.264 in 2000); all harvested groups (i.e., 2A, SW, and GS) increased in average distance. With the exclusion of the UC sites, average distance of the pre-harvest group was 0.530 and increased to 0.551 after harvesting, indicating greater heterogeneity among harvested sites after disturbance. However, no significant differences were detected among the treatment groups before harvest (MRPP: $P = 0.169$) or after harvest (MRPP: $P = 0.406$).

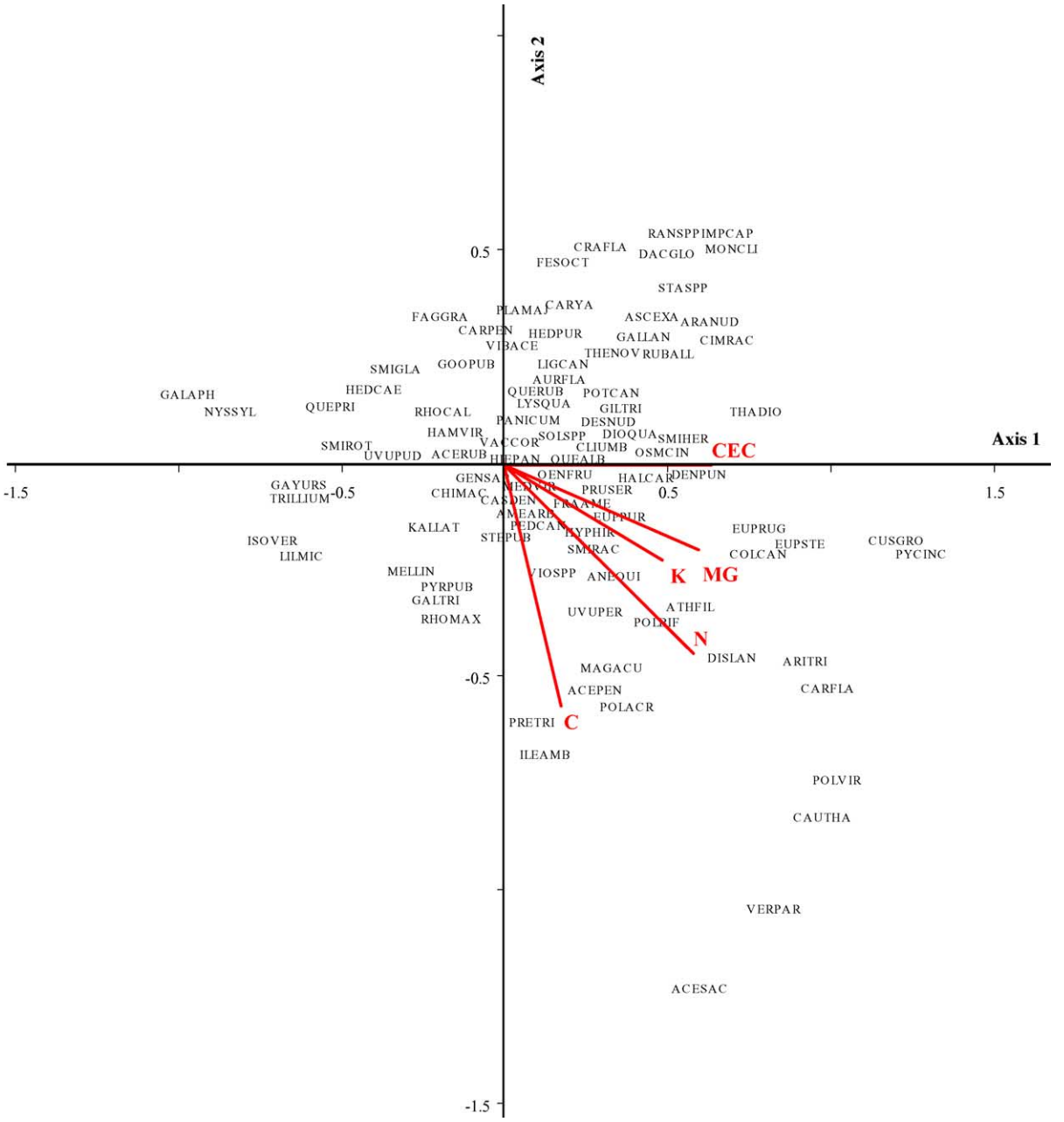

Fig. 5. Wine Spring Creek regeneration harvest sites pre-harvest (1994) and post-harvest (2000); non-metric multidimensional scaling ordination diagram of species scores and environmental variables. Species codes—ACEPEN: *Acer pensylvanicum*, ACERUB: *Acer rubrum*, ACESAC: *Acer saccharum*, ACTPAC: *Actaea pachypoda*, AMEARB: *Amelanchier arborea*, AMPBRA: *Amphicarpaea bracteata*, ANEQUI: *Anemone quinquefolia*, ARANUD: *Aralia nudicaulis*, ARITRI: *Arisaema triphyllum*, ATHFIL: *Athyrium filix-femina*, ASCEXA: *Asclepias exaltata*, AURFLA: *Aureolaria flava*, BETLEN: *Betula lenta*, CAMDIV: *Campanula divaricata*, CARFLA: *Cardamine flagellifera*, CARPEN: *Carex pensylvanica*, CARYA: *Carya* spp., CASDEN: *Castanea dentata*, CAUTHA: *Caulophyllum thalictroides*, CHIMAC: *Chimaphila maculata*, CIMRAC: *Cimicifuga racemosa*, CLIUMB: *Clintonia umbellulata*, COLCAN: *Collinsonia canadensis*, CORMAJ: *Coreopsis major*, CRAFLA: *Crataegus flava*, CUSGRO: *Cuscuta gronovii*, DACGLO: *Dactylis glomerata*, DENPUN: *Dennstaedtia punctilobula*, DESNUD: *Desmodium nudiflorum*, DIOQUA: *Dioscoria quaternata*, DISLAN: *Disporum lanuginosum*, EUPPUR: *Eupatorium purpureum*, EUPRUG:

Table 7
Non-metric multidimensional scaling (NMS) correlations for the 10 environmental variables with the first 3 ordination axes for the herbaceous layer species in Wine Spring Creek regeneration harvest treatment plots

	Axis 1		Axis 2		Axis 3	
	r	tau	*r*	tau	*r*	tau
A-horizon depth	0.457	0.389	−0.586	−0.352	−0.025	0.054
Bulk density	−0.129	−0.074	0.352	0.342	0.217	0.195
Soil potassium	0.574	0.481	−0.623	−0.489	0.039	0.039
Soil calcium	0.581	0.403	−0.569	−0.307	0.138	0.152
Soil magnesium	0.638	0.406	−0.672	−0.455	0.094	0.074
Cation exchange capacity	0.647	0.419	−0.539	−0.342	0.436	0.342
Soil pH	0.306	0.195	−0.105	−0.030	0.450	0.238
Soil carbon	0.348	0.160	−0.548	−0.377	−0.322	−0.299
Soil nitrogen	0.626	0.430	−0.792	−0.639	−0.119	−0.083
Overstory basal area	0.181	0.160	0.346	−0.255	−0.280	−0.143
Coefficients of determination	0.376		0.282		0.259	
Monte Carlo test for stress in real data	0.0196		0.0196		0.0196	
Cumulative % variance explained	37.6		65.7		91.6	

Notes: Pearson's parametric (*r*) and Kendall's non-parametric (tau) correlations with ordination axes, $N = 22$. Before harvest (1994) and the third year (2000) after harvest data sets were combined into a single analysis.

The NMS ordination included 101 species after uncommon species were deleted and converged on three axes for the final solution (McCune and Mefford, 1999). The final stress for the three-dimensional solution was 7.998. The proportion of variance explained for each ordination axis was 38% for Axis 1, 28% for Axis 2, and 26% for Axis 3 (cumulative $r^2 = 91.6\%$ for the first three ordination axes) (Table 7). Unlike other ordination techniques, axis order in NMS does not correspond to the relative importance of each axis. Because Axis 1 and Axis 2 explained more of the variation than Axis 3 in the NMS results, we chose to graph these two axes in the ordination diagram (Figs. 5 and 6). When assessed from a secondary matrix, Axis 1 was positively correlated with A-horizon depth, extractable K, Ca, Mg, CEC, and total N (Table 6, $r^2 \geq 0.20$). Axis 2 was negatively correlated with total N and C. Axis 3 was positively correlated with soil bulk density (Fig. 5; Table 7). In the NMS ordination diagram, herbaceous layer species that were most positively related to Axis 1 were *R. allegheniensis* (tau = 0.563), *Smilax herbacea* (tau = 0.557), and *C. canadensis* (tau = 0.531); species most negatively related were *Galax aphylla* (tau = −0.692), *Smilax*

Eupatorium rugosum, EUPSTE: *Eupatorium steelei*, FAGGRA: *Fagus grandifolia*, FESOCT: *Festuca octandra*, FRAAME: *Fraxinus americana*, GALAPH: *Galax aphylla*, GALLAN: *Galium lanceolatum*, GALTRI: *Galium triflorum*, GAYURS: *Gaylussacia ursina*, GENSAP: *Gentiana saponaria*, GILTRI: *Gillenia trifoliatus*, GOOPUB: *Goodyera pubera*, HALCAR: *Halesia carolina*, HAMVIR: *Hamamelis virginiana*, HEDCAE: *Hedyotis caerulea*, HEDPUR: *Hedyotis purpurea*, HELSPP: *Helianthus* spp., HIEPAN: *Hieracium paniculatum*, HYPHIR: *Hypoxis hirsuta*, ILEAMB: *Ilex ambigua*, IMPCAP: *Impatiens capensis*, ISOVER: *Isotria verticillara*, KALLAT: *Kalmia latifolia*, LIGCAN: *Ligusticum canadense*, LILMIC: *Lilium michauxii*, LYSQUA: *Lysimachia quadrifolia*, MAGACU: *Magnolia acuminata*, MEDVIR: *Medeola virginiana*, MELLIN: *Melampyrum linear*, MONCLI: *Monarda clinopodia*, NYSSYL: *Nyssa sylvatica*, OENFRU: *Oenothera fruticosa*, OSMCIN: *Osmunda cinnamomea*, PANICUM: *Panicum* spp., PEDCAN: *Pedicularis canadensis*, PHLCAR: *Phlox carolina*, PLAMAJ: *Plantago major*, POLARC: *Polystichum acrostichoides*, POLBIF: *Polygonatum biflorum*, POLVIR: *Polygonum virginianum*, POTCAN: *Potentilla canadensis*, PRETRI: *Prenanthes trifoliolata*, PRUSER: *Prunus serotina*, PYCINC: *Pycnantheumum incanum*, PYRPUB: *Pyularia pubera*, QUEALB: *Quercus alba*, QUEPRI: *Quercus prinus*, QUERUB: *Quercus rubra*, RHOCAL: *Rhododendron calendulaceum*, RHOMAX: *Rhododendron maximum*, RUBALL: *Rubus allegheniensis*, RUDHIR: *Rudbeckia hirta*, SASALB: *Sassafrass albidum*, SMIRAC: *Smilacina racemosa*, SMIGLA: *Smilax glauca*, SMIHER: *Smilax herbacea*, SMIROT: *Smilax rotundifolia*, STASPP: *Stachys* spp., STEPUB: *Stellaria pubera*, THADIO: *Thalictrum dioicum*, THENOV: *Thelypteris noveboracensis*, TRILLIUM: *Trillium* spp., TSUCAN: *Tsuga canadensis*, UVUPER: *Uvularia perfoliata*, UVUPUD: *Uvularia pudica*, VACCOR: *Vaccinium corymbosum*, VERPAR: *Veratrum parviflorum*, VIBACE: *Viburnum acerifolium*, VIOSPP: *Viola* spp. Soil environmental variable codes—CEC: soil cation exchange capacity, K: extractable soil potassium, Ca: extractable soil calcium, Mg: extractable soil magnesium, N: total soil nitrogen, and C: total soil carbon. Only environmental variables with an $r^2 \geq 0.35$ were included in the ordination diagram. Not all species are displayed in ordination diagram; 133 species were recorded across all sites in years 1994 and 2000, only 101 species were used in the NMS ordination.

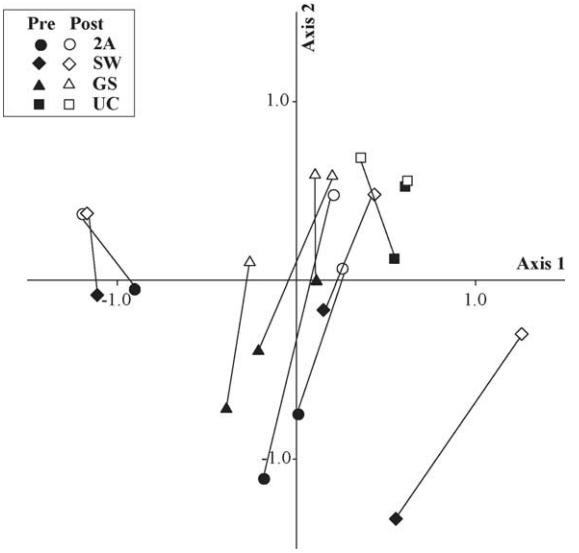

Fig. 6. Wine Spring Creek regeneration harvest sites pre-harvest (1994) and post-harvest (2000); non-metric multidimensional scaling (NMS) ordination diagram of site. The regeneration harvest treatments are two-aged shelterwood (2A), shelterwood (SW), group selection (GS), and uncut control (UC). For each site, lines are drawn between pre- and post-harvest. The length of the line is an indication of the amount of species' change between pre- and post-harvest sites.

rotundifolia (tau = −0.522), and *L. michauxii* (tau = −0.520) (Fig. 5). Species that were most positively related to Axis 2 were *Thelypteris noveaborensis* (tau = 0.498) and *Hedyotis purpurea* (tau = 0.408); species most negatively related were *I. ambigua* (tau = −0.560), *Viola* spp. (tau = −0.481), and *P. trifoliolata* (tau = 0.730). Species that were most positively related to Axis 3 were *R. hirta* (tau = 0.575) and *Potentilla canadensis* (tau = 0.559); species most negatively related were *C. pensylvanica* (tau = −0.584) and *Gaylussacia ursina* (tau = −0.485) 0.485) (Fig. 6).

4. Discussion

4.1. Vegetation dynamics

4.1.1. Overstory

Harvesting significantly reduced species richness and altered overstory composition in the two heavily cut treatments (2A and SW). Importance value of *A. rubrum* remained about the same on the 2A treatment before and after harvest, but was considerably less on the SW treatment, whereas importance values for *Q. rubra* and *Q. prinus* were considerably higher after harvest than before harvest on both the 2A and SW treatments. For the GS treatment, relative composition of the dominant species was similar before and after harvest; even though density and basal area were reduced. Because the intention of silvicultural prescription was to promote *Quercus* spp. and reduce the abundance of non-commercial species, 12 minor overstory species were cut from the 2A treatments and 9 species were cut from the SW treatments. Thus, it is not surprising that S and H' were reduced in the overstory on the heavily cut sites. However, most of these species sprouted from cut stumps and were substantially more abundant in the midstory layer after harvest than before.

4.1.2. Midstory

We found higher S and H' on the harvested treatments than on the UC sites; however, H' did not differ significantly among the harvested treatments. Jenkins and Parker (1998) investigated harvested stands in central Appalachian deciduous forests that ranged in age from 8 to 27 years, much older than our 1–3 years since harvest. In their study, group selection and clearcut stands had higher diversity than either single tree selection or reference stands, but there was no difference between the group selection and clearcut stands. By contrast, in northern hardwood stands in Wisconsin, Lu and Buongiorno (1993) compared six alternative cutting methods and reported lower diversity on the most heavily cut stands, which ranged from 6- to 16-year olds.

In our study, S and H' significantly increased on the 2A and SW sites after harvest. Harvesting in the 2A and SW treatment sites favored regeneration from *A. rubrum* because that species recruits prolifically by both sprout and seed origin after cutting (Elliott et al., 1997). This response was similar to what others have found in eastern deciduous forests after disturbance (Arthur et al., 1997; Wang and Nyland, 1993; Hix and Lorimer, 1991). The most abundant woody species on all our sites before harvest was *R. calendulaceum*. After harvest, it had lower basal area and IV on all sites; its reduced IV corresponded to a substantial increase in density and IV of other species.

4.1.3. Herbaceous layer

Seasonal and annual climate differences among sample years could have affected species composition and diversity, particularly in the herbaceous layer. Based on the 10 years (1994–2003) average annual precipitation recorded at Wine Spring Creek (Fig. 2), annual precipitation was 176 cm; whereas average annual precipitation for the 3 years from 1999 to 2001 was only 143 cm, a deficit of about 33 cm. In addition, growing season (May–September) precipitation averaged 79 cm/year from 1994 to 1997 and averaged 56 cm/year from 1998 to 2000, a substantial difference of more than 20 cm/year. Based on the long-term average annual precipitation recorded at Coweeta Hydrologic Laboratory (>65 years record since 1935), precipitation was 22, 56, and 40 cm below average for 1999, 2000, and 2001, respectively. This deficit in annual precipitation for 1999 and 2000, and growing season precipitation from 1998 to 2000, could have contributed to the reduced number of species observed on the uncut sites. For example, the UC sites had lower H' and E in 1998 than in 1994 (pre-harvest sample year), then values returned to the pre-harvest level by 2000. In addition, S per plot was lower in 1998 and 2000 than in the pre-harvest sample year on the UC sites. We found no changes in S after harvest in any of the regeneration harvest treatments and H' increased after harvest in the most heavily cut treatments (i.e., 2A and SW). By contrast, Reader and Bricker (1992) found that the percentage of herbaceous species disappearing from plots in an uncut forest (9–13%) was similar to that within a harvested forest (3–12%). In a study of herbaceous layer diversity in the central Appalachian region, Gilliam (2002) did not find any significant effects of cutting after 20 years of recovery. We suspect H' increases would have been greater on the heavily cut treatment sites if rainfall had not been below normal for the sample years after harvest.

We measured an increase in herbaceous layer diversity on the more heavily cut treatments (2A and SW) after harvest. This differed from the findings on clearcut forests in the southern Appalachians (Elliott et al., 1997, 1998). In a high-elevation mixed-oak forest type in the southern Appalachians, Elliott et al. (2002) studied how salvage logging after hurricane blow-down affected species diversity. They found that residual density was 67 stems/ha (16% of precut forest) and residual basal area was 6.5 m^2/ha (17% of the precut forest), comparable to the 2A treatment in our study. Elliott et al. (2002) concluded that herbaceous layer H' was higher on the salvage-logged site than in an adjacent undisturbed forest, whereas no difference was found for the midstory layer H'. However, the SW methods we studied were less severe than clearcutting methods.

In other forest types using alternative harvesting methods, diversity was greater following less-intensive cutting methods, such as shelterwood, strip-cutting, or thinning, when compared to clearcutting (Gove et al., 1992; Hannerz and Hånell, 1997; Bråkenhielm and Liu, 1998; Crow et al., 2002). For example, in a northern hardwoods forest, Gove et al. (1992) compared diversity trends after strip-cutting and clearcutting; strip-cutting had the highest diversity both 1 and 10 years after harvesting. In a study of Norway spruce forests in Sweden, Hannerz and Hånell (1997) found that vascular plant diversity was favored by shelterwood cutting over clearcutting. Hammond et al. (1998) found that clearcutting in mixed-oak forests of Virginia resulted in greater changes in herbaceous layer species than other harvest techniques such as group selection and shelterwood cutting. Fredericksen et al. (1999) concluded that only the most intensive levels of harvesting negatively affected herbaceous layer richness, diversity, and composition in northern hardwood and oak-hickory forests of Pennsylvania. Kochenderfer and Wendel (1983) reported changes in composition and dominance of herbaceous layer species during the first 10 years of recovery from clearcutting in a central Appalachian hardwood forest. In a recent paper, Roberts and Gilliam (2003) reviewed the response of herbaceous layer diversity to anthropogenic disturbances in eastern deciduous forests. They concluded that the lack of consistency in findings, from the wide range of studies they examined, demonstrates the site-specific nature of herb layer response to disturbances, precluding broad generalizations and emphasizing the need for in-depth study of different forest types and disturbance regimes.

4.2. Soil characteristics

4.2.1. Soil responses

We found few significant forest harvest effects on soil physical or chemical properties either, among

regeneration harvest treatments (SW, 2A, GS, or UC) or between years (pre- and post-harvest sampling periods). Many studies of how forest harvest impacts soil chemistry have noted significant harvest effects. In sawlog harvest treatments there is often an increase in available nutrients such as Ca, K, and Mg due to the large input of organic material (Knoepp and Swank, 1997b). An increase in soil cations also was measured in sites where less intensive forest practices such as thinning have been carried out (Boerner and Sutherland, 1997). Johnson et al. (2002) examined the long-term impacts of forest harvest techniques; sawlog, whole-tree, and complete-tree (includes removal of stumps >15 cm) on soil C content. They found that while some studies measured significant effects 1–3 years following treatment, few impacts were discernable 15–16 years later. However, soil C increased 15–16 years after sawlog and whole-tree harvest in the southern Appalachians (Knoepp and Swank, 1997a). In our study, the high-elevation soils (1000 m) had relatively high concentrations of soil cations, total C, and total N (Table 5). Small responses (+/−) to a relatively large initial pool may make the effects of these forest treatments difficult to detect.

4.2.2. *Vegetation–soil relationships*

Composition and structure of forest ecosystems are influenced by climatic, edaphic, and physiographic variation within local landscapes (Roberts and Christensen, 1988; Nowacki et al., 1990). We chose sites as similar in composition and structure as possible using landscape classification (McNab and Browning, 1992) and site reconnaissance. To account for additional variation within and among sites, we measured soil physical and chemical properties on each plot before and after harvest treatments. Although harvesting seldom had statistically significant effects on the soil properties we measured, soil variables influenced species composition.

Other researchers have reported similar species–soil variable relationships in eastern deciduous forests (Gilliam, 2002; Searcy et al., 2003; Gilliam and Roberts, 2003). For example, in eastern deciduous forests of Massachusetts, Searcy et al. (2003) measured the effect of soil nutrient availability on species richness in the tree and herbaceous layers. They found that soil factors regulated by bedrock type (such as nutrient availability), explained 51% of the variation in plant species richness.

We found an increase in average distance in the NMS ordination for sites in 2000 compared to 1994, which suggests greater herbaceous species diversity after harvest across the landscape (Palmer, 1993). However, we did not see a clear separation among harvest treatments in either the pre- or post-harvest sites in the NMS ordination. In general, the UC sites were less variable (i.e., clustered closer together in the ordination) than the SW sites, which were spread across the ordination axes. The harvesting treatments only enhanced this general landscape pattern of diversity (i.e., NMS ordination, 1994 versus 2000).

Without question, timber harvest has caused significant changes in the composition and structure of mixed-hardwood forests that were long dominated by *Q. rubra* in the overstory and *R. calendulaceum* in the understory. As part of the harvest treatments, commercially favored tree species were marked for retention. Harvesting methods reduced tree density and stand basal area. As a result, large gaps were created in the canopy allowing understory development and regeneration from cut stumps. Soil properties strongly influenced herbaceous layer species composition, a relationship that was strengthened following harvest. Increased diversity was very short-term; by 3 years after harvest, diversity had returned to pre-treatment levels. Our results also emphasize the site-specific nature of herbaceous layer response to forest management practices, similar to studies reviewed by Roberts and Gilliam (2003). Response of vegetation composition and diversity must be determined for different forest types and harvest techniques. Forest management systems used throughout eastern deciduous forests represent a gradient of disturbance intensity, from the least intense with single tree selection to the most intense with clearcutting.

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