ELSEVIER

Forest Ecology and Management 116 (1999) 129–139

Forest Ecology and Management

Short-term understory plant community responses to timber-harvesting intensity on non-industrial private forestlands in Pennsylvania

Todd S. Fredericksen[1,a,*], Brad D. Ross[b], Wayne Hoffman[c], Michael L. Morrison[d], Jan Beyea[e], Bradley N. Johnson[f], Michael B. Lester[g], Eric Ross[h]

[a] Top Bol #5053, PO Box 52-0777, Miami, FL 33152-0777, USA
[b] National Audubon Society, 204 Ferguson Building, The Pennsylvania State University, University Park, PA, 16802, USA
[c] National Audubon Society, 115 Indian Mound Trail, Tavernier, FL 44070, USA
[d] Department of Biological Sciences, California State University, Sacramento, CA 95819, USA
[e] Consulting in the Public Interest, 53 Clinton Street, Lambertville, NJ 08530, USA
[f] The Proctor & Gamble Company, 6100 Center Hill Avenue, Cincinnati, OH 45224, USA
[g] The Procter & Gamble Company, P.O. Box 32, Mehoopany, PA 18629-0032, USA
[h] Department of Forestry, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA

Received 10 March 1998; accepted 21 July 1998

Abstract

Understanding harvesting impacts on non-industrial private forestlands is important, since they represent 75% of all commercial forestlands in the State of Pennsylvania, as well as a large percentage of most of the eastern United States. This study measured species composition, richness, and diversity of herb- and shrub-layer plant communities on a total of 40 non-industrial private forest stands in northeastern Pennsylvania. These northern hardwood and oak–hickory stands had been recently harvested at different intensities. Remaining basal area was used as an indicator of harvest intensity. Species richness and diversity were not significantly related to basal area for summer or vernal herb understory plant communities for either forest type, although there was some evidence of a weak negative relationship between plant species richness and remaining basal area on more intensively harvested northern hardwood stands. Summer plant-species richness and diversity were related to percent litter cover and percent slope on northern hardwood stands, and percent *Vaccinium* cover and percent slope on oak–hickory stands. Ground- and shrub-layer cover significantly increased with increasing harvest intensity. Species composition of vernal herb communities did not vary in stands with differing amounts of basal area. Species composition of summer forest-floor communities differed with amount of basal area remaining, but only for northern hardwood stands. Shade-intolerant ruderal species dominated northern hardwood stands with low basal area, while more shade-tolerant plants dominated northern hardwood stands with high basal area. Summer plant understories of northern hardwood stands were generally dominated by fern and/or *Rubus* spp. (blackberry and raspberry), while oak–hickory stands were dominated by *Vaccinium* (blueberry) species. Litter cover, *Vaccinium* cover, fern cover, total ground cover, and forest type were significant variables related to species composition of vernal herb communities. Based on these results, forest landowners in this region should not expect significant short-term changes in vernal herbaceous or summer understory plant richness or diversity on their lands, regardless of the intensity of logging. However, short-term changes in vegetation structure (increased growth of forest-floor and shrub

*Corresponding author. E-mail: nelltodd@bibosi.scz.entelnet.bo
[1]Current address: Tropical Research and Development Inc., Proyecto BOLFOR, Santa Cruz, Bolivia.

PII: S0378-1127(98)00452-6

layers) should be expected for both oak–hickory and northern hardwood stands and a slight shift in species composition should be anticipated with intensive harvesting of northern hardwood stands.

Keywords: Forest harvesting; Logging; Non-industrial private forests; Northern hardwood forests; Oak–hickory forests; Pennsylvania; Herb-layer vegetation; Plant-species diversity; Plant-species richness

1. Introduction

Non-industrial private forestlands (NIPF) comprise the majority of commercial forestlands in most of the eastern United State. In Pennsylvania, 75% of commercial forestlands are categorized as NIPF, representing over one-half million tracts of land with an average size of only 15 hectares (Widmann, 1995). While industry and government forestlands are often managed by professional foresters, only 20% of harvests on Pennsylvania NIPF lands are guided by foresters or other natural-resource professionals, and only 6% of NIPF lands have a written management plan (Birch and Stelter, 1993). Determining whether current forest practices are sustainable is an important question for this forestland ownership class (Jones et al., 1995).

There is also a growing concern about the maintenance of biodiversity among the public and land managers for all classes of forest lands (O'Connell and Noss, 1992; Thorne et al., 1995; Roberts and Gilliam, 1995). Some recent reports (Duffy and Meier, 1992; Bratton et al., 1994; Meier et al., 1995) have suggested that current rates of logging in eastern forests may be incompatible with the long-term maintenance of plant diversity. In addition to long-term changes, may NIPF landowners are also interested, mostly for aesthetic reasons, in short-term responses of vegetation to forest harvesting.

There is little documentation of plant-community responses to harvesting on NIPF lands in the United States. Studies from public and research forests suggest that logging may, at least temporarily, increase species richness and diversity in forest stands. Bormann and Likens (1979) hypothesized that species diversity in northern hardwood stands should be highest during early succession and again during the late succession, steady-state phase of plant-community development. Moreover, while harvesting may lead to the reduction of disturbance-sensitive species, increased amounts of light to the forest floor may help increase the growth of sapling and shrub species that are currently restricted by fern and deer in the region (Behrend and Patric, 1969; Kelty and Nyland, 1981; Niese and Strong, 1992; Fredericksen et al., 1998). Logging slash, in the form of felled cull trees and unutilized tree tops may also protect plants from deer (Tilghman, 1989).

We studied patterns of species richness, diversity, composition, and vegetation structure within plant communities and their relation to basal area remaining, and other site variables on 40 non-industrial private forest stands, in northeastern Pennsylvania (Table 1). Specifically, we hypothesized that a reduction in basal area caused by forest harvesting would correlate with a short-term increase the species richness and diversity of forest understory plants. However, we also hypothesized that the richness and diversity of spring wildflowers would decrease with decreasing basal area remaining in stands due to reduction in litterfall and soil disturbances caused by harvesting. Further, we also hypothesized that plant-community composition would differ in stands with differing harvest intensity due to differing tolerances of light intensity and sensitivity to soil disturbance with a shift towards ruderal and shade-intolerant species in more intensively-harvested stands.

2. Methods

2.1. Study sites

Study stands were located in five countries (Monroe, Pike, Susquehanna, Wayne, and Wyoming) in northeastern Pennsylvania (41°25′ N, 75°25′ W). This area lies within the glaciated low plateau and glaciated Pocono Plateau sections of the Allegheny Plateau Physiographic province with elevations ranging from 110 to 895 m. Rainfall averages 110 cm per year and soils are derived from sandstone and siltstone (Widmann, 1995).

Table 1
Stand characteristics for 40 non-industrial private forest ownerships (NIPF) sampled in northeastern Pennsylvania

Stand	Type [a]	Basal area (m^2/ha)	Year cut	Harvest method
1	NH	24.3	1992	selection
2	NH	0.5	1992	clearcut
3	NH	19.5	1991	selection
4	NH	20.2	1991	selection
5	NH	37.8	uncut	none
6	NH	4.8	1994	selection
7	NH	0.6	1994	clearcut
8	NH	30.1	none	uncut
9	NH	8.0	1995	selection
10	NH	37.5	none	uncut
11	NH	18.5	1988	selection
12	NH	24.0	1993	selection
13	NH	27.8	1990	selection
14	NH	25.0	1989	selection
15	NH	25.1	1994	selection
16	NH	22.3	1992	selection
17	NH	19.5	1993	selection
18	NH	20.3	1994	selection
19	NH	17.5	1991	selection
20	NH	5.5	1993	diameter-limit
21	NH	14.9	1995	selection
22	NH	28.7	1991	selection
23	NH	42.3	uncut	none
24	NH	25.1	uncut	none
25	NH	24.5	1988	diameter-limit
26	NH	40.5	uncut	none
27	OH	21.5	uncut	none
28	OH	6.9	1993	selection
29	OH	11.6	1993	selection
30	OH	21.3	uncut	none
31	OH	11.6	1993	selection
32	OH	7.3	1993	selection
33	OH	17.8	1994	selection
34	OH	19.3	1989	selection
35	OH	4.0	1994	clearcut
36	OH	15.0	1993	selection
37	OH	24.6	uncut	none
38	OH	20.0	1993	selection
39	OH	24.6	1989	selection
40	OH	12.8	1994	selection

[a] NH, Northern hardwood; OH, oak–hickory.

Stands represented a wide spectrum of the NIPF in northeastern Pennsylvania, incorporating a large amount of topographic variation, harvesting methods, and land uses. Timber harvesting, hunting, dog training, wildlife observation, nature protection, and cattle grazing were among the management objectives for the forest stands in this study. Sampling from such a range of variation makes it easier to generalize these results across many stands, although precision for determining responses on any one type of stand may be low. Out study is thus a retrospective analysis of understory plant communities associated with different amounts of basal area remaining after differing harvesting intensities.

Stands were selected to represent the two major forest types in northeastern Pennsylvania, oak–hickory (14 stands) and northern hardwoods (26 stands), and a range of tree basal area from nearly zero to mature forest with high basal area (35–40 m^2/ha). However, northern hardwood stands had a much larger range of remaining basal area (0–40 m^2/ha) compared to oak–hickory stands (4–25 m^2/ha). Most stands were harvested within 2–8 years, using some type of selective cutting, the most common type of harvesting on NIPF lands in the northeastern United States. However, four stands had been recently clearcut and nine stands had no harvesting, at least within the past seventy years.

Like much of the eastern United States, forest type associations in the Appalachian Plateau province of Pennsylvania are driven by soil moisture and soil type, often related to topography (Whitney, 1990). Oak–hickory stands in our study area occurred either on dry, and often steep, southern aspect slopes of the Endless Mountain region and east of the Pocono Plateau. Oak–hickory stands were dominated by understory plant species typical of acidic soils and drier moisture conditions, such as blueberry. In contrast, northern hardwood stands occurred on more northerly aspects or flat terrain and their understories were often dominated by fern species, which require abundant moisture for spore germination. Historically, nearly all stands in the area have been subjected to episodes of disturbance (Widmann, 1995). For example, nearly all stands were clearcut, or at least heavily logged, around the turn of the century. More recently, stands have been subjected to periodic outbreaks of gypsy moth (*Lymantria dispar*), tent caterpillars (*Malacosoma disstria*) and other defoliators at irregular intervals. Deer densities have also had a large impact on the study area (Fredericksen et al., 1998).

The most abundant tree species in oak–hickory stands included (*Quercus prinus*, *Q. alba*, *Q. ilicifolia*, *Q. rubra*, *Q. coccinea*, *Q. velutina*), hickories (*Carya tomentosa*, *C. glabra*), sassafras (*Sassafras albidum*), dogwood (*Cornus florida*), and pitch pine (*Pinus rigida*). Northern hardwood associates included basswood (*Tilia americana*), sugar maple (*Acer saccharum*), black cherry (*Prunus serotina*), American beech (*Fagus grandifolia*), eastern hemlock (*Tsuga canadensis*), and yellow birch (*Betula allegheniensis*). Generalists species, not aligned with either forest type, included red maple (*Acer rubrum*), white pine (*Pinus strobus*), black birch (*Betula lenta*), and downy serviceberry (*Amelanchier arborea*). Conifers made up less than 10% of the basal area of oak–hickory stands (except for one stand with 27%), while some northern hardwood stands had more than half of the basal area composed of conifers, the majority of which was eastern hemlock.

The shrub stratum of oak–hickory stands was dominated by blueberry (*Vaccinium* spp.) and/or mountain laurel (*Kalmia latifolia*). Although sparse in total cover, dominance within the shrub stratum of northern hardwood stands was shared by a large number of species including arrowwood (*Viburnum dentatum*), maple-leaf viburnum (*V. acerifolum*), and witch-hazel (*Hamamelis virginiana*).

2.2. Field sampling

Sampling of understory plant communities (vascular plants $\leq$1 m tall) was carried out in 1996 (27 stands) and 1997 (13 stands). Sampling of summer plant understories was conducted in July and August, the period when understory vegetation biomass was at, or near, its maximum. In each stand, fifteen 1 m^2 plots were randomly located using a stratified sampling design. For each plot, the percent cover of each plant species was estimated. Plant-species nomenclature followed that of Gleason and Cronquist (1991). Sample size was based on a pilot study conducted during 1995 on 14 stands of percent vegetation cover and understory plant-species richness.

During May, transects were established in each stand to determine the species richness and composition of vernal herb communities. At 12 sampling points along a random transect through each stand, a 3-m radius circular plot was established, within which the occurrence of all species of Spring-flowering (March–May) herbaceous species were recorded. The frequency of occurrence for each vernal herb species over all the plots was then determined.

Sampling of various site variables was also included for the purposes of determining their relationships to understory plant-species richness, diversity, and composition. During the year of sampling for each stand, 20 prism plots (10-basal area factor) were established to determine tree-species composition and live basal area. Plots were located using a stratified random design, set along transects determined by stand size in order to cover all parts of the stand. In addition, for each of the 15 summer understory plant plots, separate visual estimates of cover were made for overall ground (<1 m) cover, shrub-layer cover (1–3 m), leaf litter, and logging slash during July and August.

Soil moisture and soil type often exert strong influences on vegetation in this region (Whitney, 1990). Because of difficulties in sampling and integrating soil moisture and soil type at the stand level for a large number of stands, we used percent slope and aspect as surrogate measures. Average slope and aspect were recorded in all stands with a clinometer and compass, respectively.

2.3. Data analysis

The experimental unit for statistical analyses was the stand, with sampling units consisting of within-stand plots. Response variables sampled were the relative cover of individual species or species groups, species richness, and species diversity; calculated as the Shannon–Weiner index (H') in natural log base (Shannon and Weaver, 1949). Hypotheses were tested using regression analysis with basal area against the response variables. Stand age since harvest was used as a covariate, because of its possible influence on response variables. In addition, stepwise regression was used to determine the relative influence of other site factors in explaining understory plant richness and diversity. A probability value of 0.10 was the criteria used for entry in the model. Aspect was converted to an ordinal variable for purposes of regression. Northeast slopes were coded as 4 (wettest) and southwest slopes as 1 (driest). Northwest and southeast slopes were given values of 3 and 2, respectively. Student's *t*-test was used to detect differences in plant cover between forest types. In addition, we investigated plant species composition relationships with basal area with the use of detrended correspondence analysis (DCA) (Gauch, 1982). Correlation analysis was used to determine the strength of relationships between DCA axes and other stand variables. All statistical relationships were considered significant at $p<0.10$.

3. Results

3.1. Summer understory vegetation

Basal area remaining was not significantly related to understory plant-species richness (OH: $p=0.11$; NH: $p=0.281$) nor species diversity (OH: $p=0.79$; NH: $p=0.46$) for either forest type. Age since harvesting was not a significant covariate in any of the regressions. Mean plant species richness did not differ significantly between oak–hickory (OH) and northern hardwood (NH) forest types (OH=48.4; NH=39.6; $t=1.68$, $p=0.11$), nor did the mean plant-species diversity (OH=2.53 and NH=2.39; $t=0.68$; and $p=0.50$).

A significant negative relationship was observed between summer ground cover and basal area for both forest types (NH: $r^2=0.38$, $p=0.06$; OH: $r^2=0.45$, $p=0.03$). A similar pattern was observed for summer shrub cover and basal area (NH: $r^2=0.24$, $p=0.02$; OH: $r^2=0.37$, $p=0.01$). Again, age since harvest was not a significant covariate.

Stepwise regression for northern hardwood stands indicated that plant richness on northern hardwood stands was significantly and inversely related to litter cover, and positively related to percent slope (Table 2). Only percent litter cover was a significant variable (negatively related) in the stepwise regression model for plant diversity. Stepwise regression for oak–hickory stands explained much more variation in plant species richness and diversity than the stepwise regression for northern hardwood stands (Table 2). Both plant richness and plant diversity in oak–hickory stands were significantly and negatively related to blueberry cover and percent slope. Other variables, including basal area, stand age, ground cover, shrub cover, fern cover, blackberry cover, and percent of slash cover, did not enter as significant variables in stepwise regressions.

In general, summer understory plant communities were typically dominated by one of the three types of vegetation: fern, blackberry, or blueberry. Overall ground cover did not differ significantly by forest type (Table 3). Blueberry dominated the understory of oak–hickory stands. Oak–hickory stands averaged 35% blueberry cover, while northern hardwood stands averaged 0.5% blueberry cover. Fern and *Rubus* cover were both significantly greater in northern hardwood compared to oak–hickory stands. Grass and sedge cover did not differ between forest types.

Understory plant-species composition was most closely aligned with forest type. A detrended correspondence analysis (DCA) ordination of summer understory vegetation placed oak–hickory and northern hardwood stands on opposite ends of the first axis, which explained 62% of the variation in plant-species composition (Fig. 1). The second axis, explaining 29% of the variation, separated more heavily har-

Table 2
Independent environment variables entered at $p<0.10$ in stepwise regression to determine relationships with plant-species richness and species diversity of summer understory communities. Data are from northern hardwood and oak–hickory forests in northeastern Pennsylvania. Coefficients of determination and the probability of a type I error are presented. The direction of the relationship between species richness of diversity for each variable is given in parentheses

Northern hardwood			Oak–hickory		
variable	r^2	p	variable	r^2	p
Plant-species richness					
Litter cover (−)	0.32	0.003	blueberry cover (−)	0.54	0.003
Percent slope (+)	0.10	0.06	percent slope (−)	0.27	0.002
Plant-species diversity					
Litter cover (−)	0.19	0.02	blueberry cover (−)	0.27	0.06
			percent slope (−)	0.24	0.04

Table 3
Summary of mean percent cover for dominant understory plant species by forest type. One standard error of the mean is given in parenthesis. Results of t-tests for differences between forest types are also presented

Growth form	Northern hardwood	Oak–hickory	t	$p>t$
All	68.0 (4.4)	64.4 (4.3)	0.53	0.60
Fern	30.2 (4.2)	10.8 (2.7)	3.88	0.0004
Grass/sedge	9.5 (2.3)	8.9 (2.6)	0.15	0.88
Rubus	23.4 (4.6)	4.4 (2.1)	3.77	0.0006
Vaccinium	0.4 (0.2)	35.0 (7.4)	4.71	0.0004

vested northern hardwood stands from less intensively harvested northern hardwoods (Fig. 1). The second DCA axis was significantly ($r=-0.66$, $p=0.0001$) correlated with basal area (Fig. 2). Species associated with oak–hickory stands on the first DCA axis were wild columbine (*Aquilegia canadensis*), fairly bells (*Disporum lanuginosum*), blueberry species (*Vaccinium stamineum*, *V. vacillans*, and *V. angustifolium*), oak seedlings (*Quercus* spp.), mountain laurel (*Kalmia latifolia*), sheep laurel (*K. angustifolium*), teaberry (*Gaultheria procumbens*), bracken fern (*Pteridium aquilinum*), cow-wheat (*Melampyrum lineare*), wild sarsparilla (*Aralia nudicaulis*), whorled loosestrife (*Lysimachia quadrifolia*), indian cucumber (*Medeola virginiana*), and dwarf ginseng (*Panax trifolius*). Species associated with northern hardwood stands on the first DCA axis with low basal area were mostly shade-intolerant ruderal plants, such as pokeweed (*Phytolacca americana*), multiflora rose (*Rosa multiflora*), jewelweeds (*Impatiens pallida* and *I. capensis*), upright wood sorrel (*Oxalis stricta*), goldenrod species (*Solidago gigantea*, *S. rugosa*, and *S. tenuifolia*) and wild strawberry (*Fragaria virginiana*). Northern hardwood stands with high basal area had spinulose wood fern (*Dryopteris spinulosa*), hay-scented fern (*Dennstaedtia punctilobula*), mountain wood sorrel (*Oxalis montana*), and partridgeberry (*Mitchella repens*) as major associates.

3.2. Vernal herbs

Basal area remaining after harvest was not significantly related to either species richness (OH: $p=0.99$;

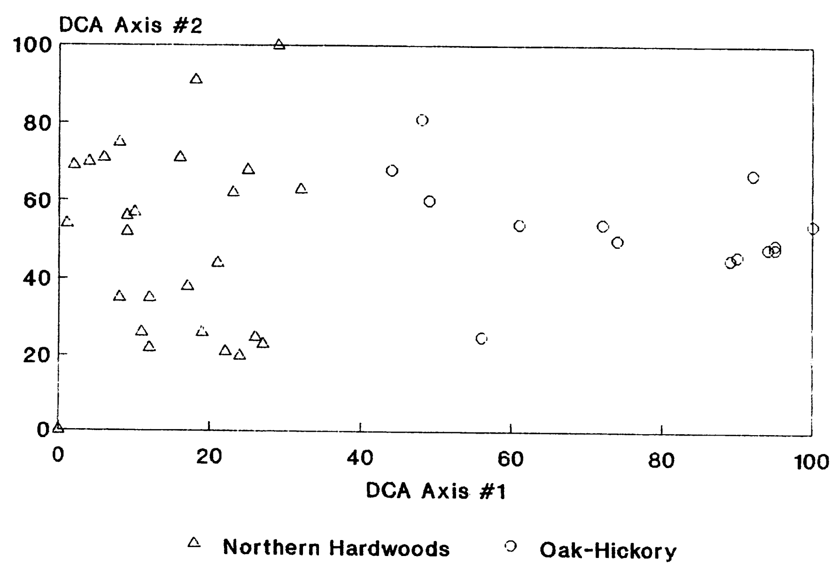

Fig. 1. Ordination of stands along the first two axes produced by detrended correspondence analysis ordination (DCA) of study stands based on summer understory plant-species composition.

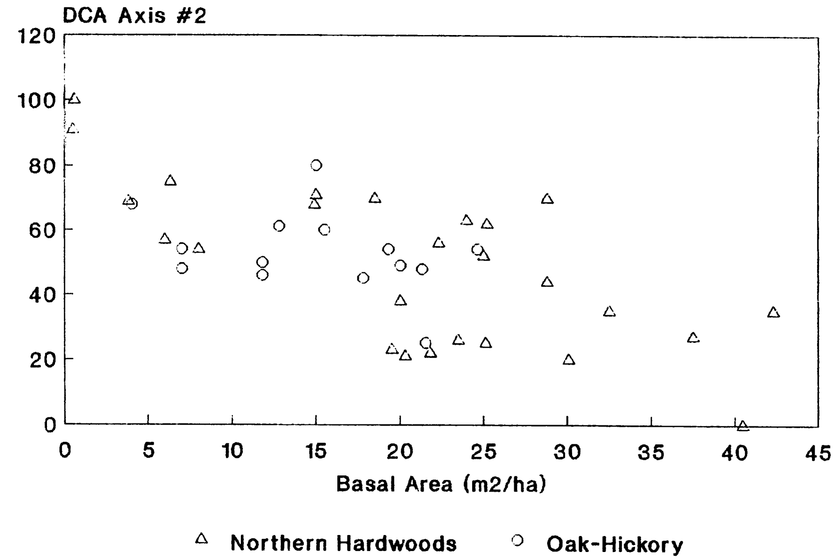

Fig. 2. Correlation of DCA axis 2 with basal area for summer understory plant communities for oak–hickory and northern hardwood forest stands in northeastern Pennsylvania ($r=-0.66$, $p=0.0001$).

NH: $p=0.93$) or species diversity (OH: $p=0.83$; NH: $p=0.66$) for either forest type. For stepwise regressions, neither basal area or any other environmental variable entered significantly into any of the models of plant diversity or plant richness for either forest type. For vernal herb composition analysis, the first DCA axis was significantly and negatively correlated with litter cover ($r=-0.57$, $p=0.0001$), blueberry cover ($r=-0.39$, $p=0.01$), and fern cover ($r=-0.28$, $p=0.08$) (Fig. 3) This axis explained 47% of the variation in the data.

Species associated with low litter, blueberry and fern cover included early saxifrage (*Saxifraga virginiensis*), Selkirk's violet (*Viola selkirkii*), thyme-leaved speedwell (*Veronica serpyllifolia*), fairy bells (*Disporum lanuginosum*), winter cress (*Barbarea vulgaris*), round-leaved hepatica (*Hepatica americana*), wild leek (*Allium tricoccum*), rue anemone (*Anemonella thalictroides*), and kidney-leaved buttercup (*Ranunculus cucullaria*). Species associated with high litter, blueberry, and fern cover included several bellwort species (*Uvularia grandiflorum*, *U. sessilifolium*, and *U. perfoliata*), pale corydalis (*Corydalis flavula*), goldthread (*Coptis groenlandica*), starflower (*Trientalis borealis*), painted trillium (*Trillium undulatum*), and lousewort (*Pedicularis canadensis*).

The second DCA axis appeared to be weakly related to forest type (Fig. 3). Species located near the axis terminus associated with northern hardwood stands included wild leek (*Allium tricoccum*), kidney-leaved buttercup (*Ranunculus cucullaria*), Canada violet (*Viola canadensis*), squirrel corn (*Dicentra canadensis*), blue cohosh (*Caulophyllum thalictroides*), and long-spurred violet (*Viola rostrata*). Species located near the oak–hickory terminus of the axis included Selkirk's violet (*Viola selkirkii*), LeConte's violet (*V. affinis*), downy yellow violet (*V. pubescens*), perfoliate bellwort (*Uvularia perfoliata*), pink ladyslipper (*Cypripedium calceolus*), solomon's seal (*Polygonatum biflorum*), and rue anemone (*Anemonella thalictroides*).

4. Discussion

For the broad array of basal area remaining on the non-industrial private forestlands sampled in this study, harvesting did not significantly affect understory plant richness or diversity in the years immediately following logging. The hypothesized increase in summer plant richness and diversity and decrease in vernal herb richness and diversity with increasing

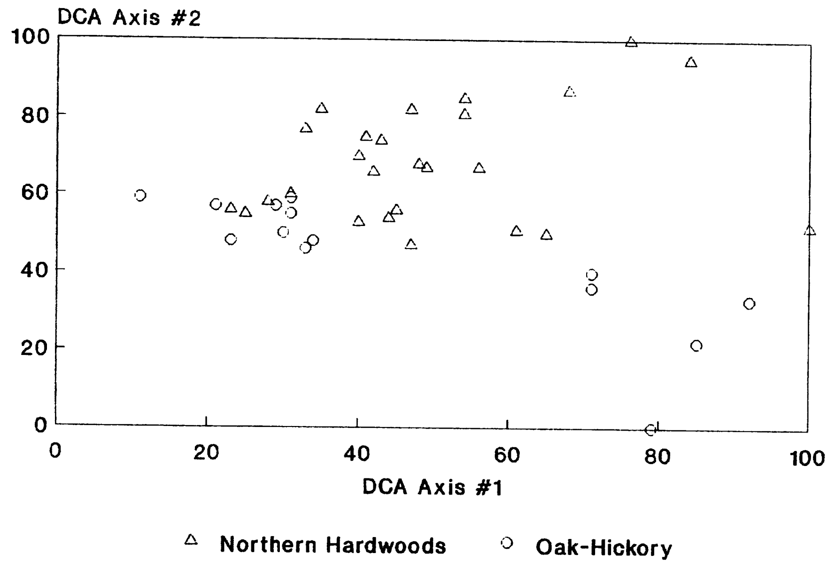

Fig. 3. Ordination of stands along the first two axes produced by DCA ordination of vernal herb communities for oak–hickory and northern hardwood forest stands in northeastern Pennsylvania.

harvest intensity was not observed in these study stands. However, species composition did shift, as hypothesized, to more shade-intolerant species with increasing harvest intensity, but only for summer understory plants in northern hardwood stands.

There is some evidence from these data, however, that plant richness may increase with increasing harvesting intensity for northern hardwood stands. Despite any significant relationships across the basal area gradient with all stands included in the model, removal of an outlier stand (#34, with 15 m^2/ha basal area and high species richness) produced a significant, but weak (r^2=0.15, p=0.06) negative relationship between plant-species richness and remaining basal area for northern hardwood stands. It is also interesting to note that the three northern hardwood stands with <4 m^2/ha of basal area had over twice the plant-species richness (49.3 vs. 24.0 species), compared to the three stands with basal area >35 m^2/ha. Thus, there is some indication that very intensively harvested stands may have higher plant richness than unharvested stands or stands with very high basal areas.

Studies of changes in species richness and diversity after different intensities of logging have yielded mixed results. Most studies have been long-term retrospective studies of clearcut and unlogged stands many years after logging took place. Gilliam et al. (1995) found that herbaceous layer species diversity did not vary significantly between mature selectively logged stands and young (<20-year old) clearcut stands in the central Appalachians, although changes in species composition occurred in the understory due to complete removal of the overstory layer in clearcut stands. Smith and Miller (1987) found that species richness of woody vegetation in Appalachian hardwood stands 34 years after cutting was greatest in stands with the most intensive overstory removal.

Other studies, however, have indicated that logging and other human-associated disturbances may lead to longer term decreases in herbaceous plant richness or diversity. In a study of overbrowsed primary and secondary hemlock–northern hardwood stands in western Pennsylvania, Rooney and Dress (1997) found higher stand-level diversity in primary forests, compared to secondary forests. In the southern Appalachians, Duffy and Meier (1992) found significantly lower herbaceous plant species richness in second growth stands compared to old growth stands. In addition, Bratton et al. (1994) studied cover and plant diversity of vernal herbs on floodplain forests of the lower Susquehanna River gorge in Pennsylvania and Maryland and found that mature forest stands had greater vernal herb cover and species diversity than early successional stands. The lack of strong relationships between plant richness or diversity observed in the stands of our study do not necessarily contradict those of other studies because nearly all of our study areas were second growth stands, between 1–7 years in age. Only one stand in this study could be described as old growth (Stand #26). This stand actually had the lowest summer forest-floor plant diversity of all stands, yet it was also heavily impacted by deer browsing.

While basal area was not a significant factor in explaining understory summer plant richness or diversity, other variables were significantly (although not always strongly) related to species richness and diversity. Litter cover was important in explaining species richness and diversity in norther hardwood stands. Stands with greater amounts of litter cover tended to have lower understory plant richness and diversity. The mechanism behind this relationship is unclear, except that heavy litter cover, like heavy slash cover (Smith, 1986), may impede germination and early growth of many plant species. In oak–hickory stands, blueberry cover was inversely correlated with both understory species richness and diversity. Drier oak–hickory sites dominated by blueberry species may be less favorable to growth. Plant species richness and diversity may be restricted on these sites, because a smaller subset of plants are adapted to these conditions. For northern hardwoods, percent slope was positively related to plant richness. Interestingly, however, percent slope was negatively related to both, plant species richness and diversity for oak–hickory stands. The mechanisms for these dichotomous relationships are also unclear, although soil drainage might be an underlying factor. Better soil drainage due to steeper slopes on moist northern hardwood sites might encourage colonization and growth by more plant species, whereas steeper slopes on drier oak–hickory sites might restrict the growth of many species. These environmental associations with plant richness and diversity should be viewed as hypotheses to be tested in future studies.

As expected, forest-floor vegetation and shrub cover increased with decreasing basal area remaining on stands. This response is typical of recently harvested stands due to an increase in the relative availability of resources after harvesting, especially light (Marks, 1974; Bormann and Likens, 1979; Gilliam et al., 1995). Niese and Strong (1992) found similar results in a study of northern hardwood stands. Thus, despite few changes in species richness or diversity with intensity of logging, the vegetation structure of stands was significantly altered in stands in the years immediately following logging; manifested by increased growth of the forest floor and shrub layers.

Fern species dominated many stands with moderate-to-high basal area and overstory tree cover, especially for the more moist northern hardwood stands. Fern species that reproduce by rhizomes, including hay-scented and New York fern, often quickly colonize stands, especially after soil disturbances such as logging (Groninger and McCormick, 1992). Dense fern stands, present throughout the growing season, may inhibit the germination and growth of other plants (Horsley and Marquis, 1983; Tilghman, 1989; DeCalesta, 1994). In general, fern cover was not a significant factor related to plant diversity or richness in this study. However, of the six northern hardwood stands, where the summer understory plant diversity index was <2.0, four had an average cover of fern >55%. Another low diversity stand (34% fern cover) was an old-growth stand with heavy understory shade from a dense canopy of eastern hemlock. Thus, there is some evidence from this study that fern may restrict plant diversity of some northern hardwood sites.

The composition of understory plant communities in northern hardwood stands shifted from more shade-tolerant herbaceous species to more shade-intolerant species with decreasing basal area remaining in stands. These results were expected because of increased light availability in more heavily harvested stands (Marks, 1974; Bormann and Likens, 1979; Niese and Strong, 1992; Gilliam et al., 1995). Interestingly, however, no such changes in plant species composition were observed in oak–hickory stands. It is possible that competition for light might be secondary to soil moisture and nutrient factors on these sites. In any case, landowners of oak–hickory stands should expect fewer short-term changes in the species composition of understory plant communities when harvesting timber than the owners of northern hardwood stands.

Neither basal area remaining or other variables in this study appeared to be strongly related to vernal herb-species richness or diversity. The species composition of these communities appears to be most strongly related to the amount of litter cover, forest type, and presence of some plant-species groups, such as fern and blueberry. A group of early spring plants adapted to moist, disturbed soils appeared to colonize sites without abundant litter, blueberry, or fern cover. Typical of this group were early saxifrage, thyme-leaved speedwell, and winter cress. Bellworts (*Uvularia* sp.) appear to be closely associated with sites with high litter. Although usually lower in priority than timber income, we have observed that many landowners often weigh aesthetic considerations, such as the abundance and diversity of spring wildflower communities, into their harvest decisions. More detailed studies of the site requirements and responses to harvesting of these species would be beneficial.

It is important to recognize that the results of our study are limited by a large number of factors which could not be controlled in a retrospective study. Stand conditions prior to harvesting and other disturbances, such as insect outbreaks and past amounts of deer browsing could not be assessed. Deer browsing and grazing on both woody and herbaceous understory plants have a large impact on plant communities in Pennsylvania (Horsley and Marquis, 1983; Tilghman, 1989; Miller et al., 1992; DeCalesta, 1994; Rooney and Dress, 1997; Fredericksen et al., 1998). It is possible that the impact of deer is overshadowing the effect of harvesting on these stands. These uncontrolled factors most likely accounted for the high variability observed in many regression relationships.

In summary, no strong relationships were detected between vernal herb or summer understory plant richness or diversity and harvesting intensity for either forest type across the broad range of NIPF stands sampled. Percent litter cover, blueberry cover, and percent slope were variables significantly related to summer understory plant richness and diversity on these stands. However, species composition varied with the amount of basal area remaining after harvest on northern hardwood forestlands, where plant species characterized by open, disturbed environments replaced shade-tolerant plant species on more intensively harvested stands. No such changes were observed in oak–hickory stands. For both forest types, however, the understory vegetation structure of stands was changed due to harvesting as ground and shrub-layer cover increased with increasing basal area removal.

Acknowledgements

Funding for this study was provided by The Procter & Gamble Company and the Heinz Endowment. The authors also wish to thank the following institutions and organizations for their support of this study: The School of Forest Resources at the Pennsylvania State University, The Bureau of Forestry of the Pennsylvania Department of Conservation and Natural Resources, The Pennsylvania Game Commission, and The Nature Conservancy of Pennsylvania. In addition, we are grateful for the staff and field support from Alys Campaigne, Nell Fredericksen, Cynthia Jones, Chris Snyder, and Floyd Schnackenberg.

References

Behrend, D.F., Patric, E.F., 1969. Influence of site disturbance and removal of shade on regeneration of deer browse. J. Wildl. Manage. 33, 394–398.

Birch, T.W., Stelter, C.M., 1993. Trends in owner attitudes. In: Finley, J.C., Jones, S.B. (Eds.), Penns Woods – Change and Challenge. The Pennsylvania State University, University Park, PA.

Bormann, F.H., Likens, G.E., 1979. Pattern and Process in a Forested Ecosystem. Springer-Verlag, New York, NY.

Bratton, S.P., Hapeman, J.R., Mast, A.R., 1994. The lower Susquehanna River gorge and floodplain (USA) as a riparian refugium for vernal, forest floor herbs. Conserv. Biol. 8, 1069–1077.

DeCalesta, D.S., 1994. Effect of white-tailed deer on songbirds within managed forests in Pennsylvania. J. Wildl. Manage. 58, 711–718.

Duffy, D.C., Meier, A.J., 1992. Do Appalachian herbaceous understories ever recover from clearcutting?. Conserv. Biol. 6, 196–201.

Fredericksen, T.S., Ross, B., Hoffman, W., Lester, M., Beyea, J., Morrison, M., Johnson, B.N., 1998. Adequacy of natural hardwood regeneration on recently-harvested northeastern Pennsylvania forestlands, N.J. Appl. For., in press.

Gauch, H.G., 1982. Multivariate Analysis in Community Ecology. Cambridge Studies in Ecology. Cambridge University Press, Cambridge, UK.

Gilliam, F.S., Turrill, N.L., Adams, M.B., 1995. Herbaceous layer and overstory species in clearcut and mature central Appalachian hardwood forest. Ecol. Appl. 5(4), 947–955.

Gleason, H.A., Cronquist, A., 1991. Manual of vascular plants of northeastern United States and adjacent Canada. Van Norstrand. pp. 810.

Groninger, J.W., McCormick, L.H., 1992. Effects of soil disturbance on hay-scented fern establishment. North. J. Appl. For. 9, 29–31.

Horsley, S.B., Marquis, D.A., 1983. Interference by weeds and deer with Allegheny hardwood reproduction. Can. J. For. Res. 13, 61–69.

Jones, S.B., Luloff, A.E., Finely, J.C., 1995. Another look at NIPFs: Facing our "myths". J. For. 93, 41–44.

Kelty, M.J., Nyland, R.D., 1981. Regenerating Adirondack and northern hardwoods by shelterwood cutting and control of deer density. J. For. 79, 22–26.

Marks, P.L., 1974. The role of pin cherry (*Prunus pensylvanica* L.) in the maintenance of stability in Northern hardwood forests. Ecol. Monogr. 44, 73–88.

Miller, S.G., Bratton, S.P., Hadidan, J., 1992. Impacts of white-tailed deer on endangered and threatened vascular plants. Nat. Areas J. 12, 67–74.

Meier, A.J., Bratton, S.P., Duffy, D.C., 1995. Possible ecological mechanisms for loss of vernal herb diversity in logged eastern deciduous forests. Ecol. Appl. 5(4), 935–946.

Niese, J.N., Strong, T.F., 1992. Economic and tree diversity tradeoffs in managed northern hardwoods. Can. J. For. Res. 22, 1807–1813.

O'Connell, M.A., Noss, R.F., 1992. Private land management for biodiversity conservation. Environ. Manage. 16, 435–450.

Roberts, M.R., Gilliam, F.S., 1995. Patterns and mechanisms of plant diversity in forested ecosystems: implications for forest management. Ecol. Appl. 5(4), 969–977.

Rooney, T.P., Dress, W.J., 1997. Patterns of plant diversity in overbrowsed and mature secondary hemlock–northern hardwood forest stands. J. Torrey Bot. Soc. 124, 43–51.

Shannon, C.E., Weaver, W., 1949. The Mathematical Theory of Communication. University of Illinois Press, Urbana, IL.

Smith, D.M., 1986. The Practice of Silviculture. Wiley & Sons, NY. pp. 527.

Smith, H.C., Miller, G.W., 1987. Managing Appalachian hardwood stands using four regeneration practices – 34-year results. North. J. Appl. For. 4, 180–185.

Thorne, S., Kim, K.C., Steiner, K.C., 1995. Conserving Pennsylvania's Native Biological Diversity. PA Fish and Boat Commission, Harrisburg, PA. pp. 60.

Tilghman, N.G., 1989. Impacts of white-tailed deer on regeneration in northwestern Pennsylvania. J. Wildl. Manage. 53, 524–532.

Whitney, G.G., 1990. The history and status of the hemlock-hardwood forests of the Allegheny Plateau. J. Ecol. 78, 443–458.

Widmann, R.H., 1995. Forest Resources of Pennsylvania, Resource Bulletin NE-131. USDA Forest Service Northeast Forest Experiment Station, Radnor, PA. pp. 41.

f

r.