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## POSSIBLE ECOLOGICAL MECHANISMS FOR LOSS OF VERNAL-HERB DIVERSITY IN LOGGED EASTERN DECIDUOUS FORESTS<sup>1,2</sup>

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**Abstract.** The ecological literature on eastern forest-floor herbs and data collected in the southern Appalachians in Tennessee and North Carolina suggest five possible ecological mechanisms for reducing or limiting alpha diversity of vernal herbs in logged stands, three of which may also account for the slow recovery of some herbaceous species: (1) logging reduces populations of rarer herbs; (2) populations of forest-floor species are further reduced during the successional stages following logging, either by inability to adapt to changed microclimate or by competition with *r*-selected species that are better dispersers and better able to tolerate desiccation and increased radiation; (3) forest-floor herbs have slow growth and reproduction rates, thus population densities increase slowly; (4) many forest-floor herbs are clonal, ant-dispersed, or gravity-dispersed, thus they are slow to reoccupy suitable habitat once extirpated or greatly reduced in population numbers; and (5) logging results in less-than-optimal conditions for forest-floor herb reproduction by modifying microhabitats on the forest floor and by temporarily eliminating gap-phase succession. The data indicate some species of vernal herbs are far more tolerant of disturbance than others, and that sensitive species can be identified and utilized as indicators of community integrity and diversity.

**Key words:** *Appalachians; clearcut; community integrity; dispersal; diversity; forest management; gap dynamics; old growth; Panax trifolium; primary forest; Trillium; vernal herbs.*

### INTRODUCTION

One of the more conspicuous components of old-growth eastern deciduous forests is the understory herbaceous community, which provides rich wildflower displays in early spring before canopy closure (Braun 1950, Bormann and Buell 1964, Taylor 1972 in Muller 1978). These displays are widely appreciated by the public, who visit parks and forests to view the flowers. Early naturalists described wildflowers and other understory plants as abundant and widespread in uncut forest (e.g., Brickell 1737, Bartram 1792, Gray 1841). These profusely flowering spring herbs are termed "vernal herbs" by the public; however, we use the phrase "vernal herbs" to include all herbaceous species visible on the forest floor before canopy closure in late spring, regardless of the presence of flowers.

Recently, public controversy has arisen concerning the impact of logging on the species-rich, mixed, mesophytic cove forests of the southern United States (described by Braun 1950). Environmental concerns in-

clude the impact of both cutting of old-growth stands and repeated clear-cutting of forests on the diversity of forest-floor herbs. Duffy and Meier (1992) found primary ( $\approx$ old-growth) forest stands in the southern Appalachian and the Cumberland Mountains had more species of vernal-phase herbs in 1-m<sup>2</sup> plots than did similar stands that had been logged.

Previous studies indicate that recovery of forest understories may require a century or more after major disturbance. In hardwood stands in New Brunswick, Canada, MacLean and Wein (1977) found little evidence of recovery of late-successional herbaceous species several decades after canopy opening. Flaccus (1959) considered that, following landslides in the White Mountains of New Hampshire, 72-yr-old herb communities were similar to old growth (>200 yr), although his data showed that a number of old-growth species were still absent from the 72-yr site. Brewer (1980), working in old growth in Michigan, concluded that the herbaceous community was still recovering from a major disturbance event that occurred 150 yr prior. Recovery of forest herbs after an area has been used for agriculture may take centuries (Peterken and Game 1984). Duffy and Meier (1992) found no evidence of recovery of vernal herbs in secondary cove hardwood forests ranging from 45 to 87 yr old.

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<sup>2</sup> For reprints of this 67-page group of papers on plant diversity in managed forests, see footnote 1, page 911.

This paper investigates some of the factors that might account for lower alpha diversity of vernal herbs in logged and disturbed cove hardwood stands and for the slow recovery of native-herb species diversity after logging. We will limit the discussion to vernal herbs in forested habitats and alpha diversity (defined as "per plot species richness"). Scales used range from typical herb sampling plots (e.g., in square metres) to the scale of "stands" (e.g., 0.1-ha to 1-ha plots). First we present data from a recently cut primary cove hardwood forest in order to show the early influences of clear-cutting on vernal herbs. This will add to the temporal sequence presented by Duffy and Meier (1992), which examined only older secondary stands also in cove hardwood forests. We then present the following mechanisms to help explain the loss of diversity and lack of recovery observed after logging: (1) loss of diversity as a result of logging disturbance; (2) physiological stress and competition with weedy or exotic plant species soon after logging and during succession; (3) low rates of reproduction and slow growth of forest-floor herbs; (4) limited spread and slow dispersal due to clonal reproduction and ant-mediated dispersal of seeds; and (5) loss of suitable seedling habitat and disruption of gap-phase succession.

We develop our hypotheses explaining the loss of diversity and lack of recovery by utilizing seven sources of information: (1) the existing literature on the attributes of vernal herbs, including Duffy and Meier (1992); (2) a field sample of vernal herbs in a recently logged old-growth stand in North Carolina (field work done by A. Meier and S. Bratton); (3) sampling of vernal herb frequencies in forested and open successional areas in the Susquehanna River gorge and floodplain in Pennsylvania and Maryland (Bratton et al. 1994); (4) measurement of growth rates of vernal herbs (done by A. Meier and D. Duffy); (5) sampling of the distribution of *Trillium* species in the Great Smoky Mountains National Park relative to the disturbance history of different watersheds (done by S. Bratton and A. Meier); (6) measurement of drupe dispersal of *Panax trifolium* (done by A. Meier); and (7) sampling of the distribution of *Cimicifuga americana* relative to the presence of canopy gaps (done by A. Meier and S. Bratton). We remind the reader that we are developing a synthesis based on these sources of information. It is the intent of this paper to investigate rather than test each mechanism as a hypothesis applying to vernal herbs as a whole. Since the resulting synthesis is based upon results from several different studies, the methods for each study are presented with each data set under the appropriate mechanism. After investigating five possible mechanisms of diversity loss, or limitations on diversity recovery through the successional sere, we summarize the implications for forest management strategies to maintain regional biodiversity.

## MECHANISMS AFFECTING VERNAL-HERB DIVERSITY

### *Mechanism 1: Losses of diversity as a result of logging disturbance*

The first potential way for herbaceous alpha diversity to be reduced is as a direct result of the disturbance that accompanies logging. The harvesting systems, and the occurrence of associated disturbances such as erosion and accidental or purposeful slash fires, determine the degree to which the forest-floor flora is modified. The question is not, "Will herbaceous species be affected?" but rather, "Which species will eventually be sensitive, and are populations lost or reduced during cutting or as a result of subsequent successional processes?"

*Site and methods.*—In an attempt to determine the influences of forest management on vernal herbs soon after cutting, we found a small area of primary cove hardwood forest at Upper Ivy Creek (a portion of the area commonly referred to as Big Ivy), in the Toecane District of Pisgah National Forest, North Carolina, which the USDA Forest Service permitted to be logged in 1988. The site was logged with a skidder (Frank Roth [USDA Forest Service], *personal communication*). After an endangered species was found on the site, clear-cutting was terminated, but a few trees were selectively thinned from another section of the stand. This left a selectively thinned stand and a clearcut (each <3 ha and oblong with shaded edges) adjoining a 1-ha remnant of primary cove hardwood forest. We were not able to find another case where a portion of a primary cove hardwood stand was recently logged and a similar portion left unlogged. In April 1993 we established three 25 × 50 m plots at Upper Ivy Creek, one in the old growth, one in the selective cut, and one in the clearcut. Each plot was in the central portion of the "treated" area, and each was placed to make it as topographically similar to the others as possible: slope was measured at five points on each plot with a Suunto clinometer (Espoo, Finland) and aspect was measured with a compass. The percentage cover of each herbaceous species and total cover were estimated by eye in each of 15 randomly selected 1-m<sup>2</sup> quadrats. Methods were comparable to Duffy and Meier (1992), who reported species diversities and percentage covers for nine other pairs of primary and logged cove hardwood stands.

Herb sampling was conducted on 29 April 1993 and soil sampling was conducted on 15 October 1993. Twenty-five soil samples were randomly located within the primary stand, and 25 within the clearcut. For each soil sample, the top 5 cm of A horizon were collected and analyzed following the methods of MacLean (1982). Nomenclature here, and in the examples given below, follows Radford et al. (1968) and Wofford (1989). Statistical analysis, for this data set and those presented subsequently, was performed using the Sta-

TABLE 1. Means and one-way ANOVA results for species richness of vernal herbs in primary and matching sites by type of logging and rarity of species at Upper Ivy Creek, North Carolina, USA.  $N = 15$  1-m<sup>2</sup> quadrats in all cases.

| Species occurrence* | Means    |                     |           | ANOVA results |        |        |        |       |        |
|---------------------|----------|---------------------|-----------|---------------|--------|--------|--------|-------|--------|
|                     | Unlogged | Selectively thinned | Clear-cut | df            |        | MS     |        | F     | P      |
|                     |          |                     |           | Among         | Within | Among  | Within |       |        |
| Common              | 10.1     | 10.3                | 8.9       | 2             | 42     | 7.756  | 2.0666 | 3.75  | 0.0317 |
| Occasional          | 2.8      | 1.5                 | 0.9       | 2             | 42     | 14.689 | 0.9016 | 16.29 | 0.0001 |
| Rare                | 1.0      | 0.7                 | 0.3       | 2             | 42     | 1.688  | 0.7683 | 2.20  | 0.1236 |
| Total               | 13.9     | 12.5                | 10.1      | 2             | 42     | 53.336 | 3.3620 | 15.87 | 0.0001 |

\* Common = species found in >50% of the quadrats for at least one of the three 25 × 50 m plots; Occasional = species found in at least 4–7; Rare = species found in ≤3 quadrats.

tistical Analysis System for IBM-compatible microcomputers (SAS Institute 1985).

**Results.**—Application of non-parametric ANOVA (SAS procedure NPARIWAY) indicated the total herbaceous cover was not significantly different among the three sample plots within this small site. The selectively thinned stand had an average cover of forbs of 71.0%, as opposed to 68.3% for the clearcut and

TABLE 2. Vernal herbaceous species found in quadrats within primary, selectively thinned, and clear-cut stands at Upper Ivy Creek, North Carolina, USA. x = present.

| Species                           | Primary | Thinned | Clear-cut |
|-----------------------------------|---------|---------|-----------|
| <i>Actea pachypoda</i>            | x       | ...     | ...       |
| <i>Allium tricoccum</i>           | ...     | ...     | x         |
| <i>Anemone quinquefolia</i>       | x       | x       | ...       |
| <i>Anemone virginiana</i>         | ...     | x       | ...       |
| <i>Aplectrum hymenale</i>         | ...     | x       | ...       |
| <i>Arisaema triphyllum</i>        | x       | x       | x         |
| <i>Asarum canadense</i>           | x       | x       | x         |
| <i>Aster divaricata</i>           | x       | x       | x         |
| <i>Aster</i> sp.                  | x       | x       | ...       |
| <i>Botrychium</i> sp.             | ...     | x       | ...       |
| <i>Carex plantaginea</i>          | x       | ...     | ...       |
| <i>Caulophyllum thalictroides</i> | x       | x       | x         |
| <i>Cimicifuga americana</i>       | x       | x       | x         |
| <i>Claytonia caroliniana</i>      | x       | x       | x         |
| <i>Delphinium tricorne</i>        | x       | x       | x         |
| <i>Dentaria diphylla</i>          | x       | x       | x         |
| <i>Dicentra canadensis</i>        | x       | x       | x         |
| <i>Disporum lanuginosum</i>       | x       | ...     | x         |
| <i>Dryopteris</i> sp.             | x       | x       | x         |
| <i>Eupatorium</i> sp.             | ...     | x       | x         |
| <i>Gallium</i> sp.                | x       | ...     | ...       |
| <i>Geum</i> sp.                   | x       | ...     | ...       |
| <i>Hepatica acutiloba</i>         | x       | x       | x         |
| <i>Hydrastis canadensis</i>       | x       | ...     | ...       |
| <i>Hydrophyllum</i> sp.           | x       | x       | x         |
| <i>Impatiens pallida</i>          | x       | x       | x         |
| <i>Mitella diphylla</i>           | x       | x       | x         |
| <i>Osmorhiza</i> sp.              | x       | x       | x         |
| <i>Podophyllum peltatum</i>       | x       | x       | ...       |
| <i>Polygonatum biflorum</i>       | x       | x       | x         |
| <i>Polystichum acrostichoides</i> | x       | x       | x         |
| <i>Smilacina racemosa</i>         | x       | ...     | ...       |
| <i>Stellaria corei</i>            | x       | x       | x         |
| <i>Trillium erectum</i>           | x       | ...     | ...       |
| <i>Trillium rugelii</i>           | x       | x       | x         |
| <i>Uvularia grandiflora</i>       | x       | ...     | ...       |
| <i>Viola rostrata</i>             | x       | x       | x         |
| Total number of herbs present     | 32      | 27      | 23        |

57.0% for the remaining old-growth area. Mean herbaceous species numbers per square metre, however, were significantly different among the three sample plots ( $F_{2,42} = 15.87$ ,  $P > F = 0.0001$ ), with the clearcut having the lowest diversity. When species were categorized as “common”, those found in >50% of the quadrats for at least one of the plots, “occasional”, those found at most in 4–7 quadrats, and “rare”, those found at most in 3 quadrats, the differences among plots for common species and for occasional species were still significant (Table 1). The statistical comparison among plots for rare species alone was problematic because of the low numbers of these in the clearcut. Summing “occasional” and “rare” to form a single class for less-common species, the differences among the three plots gave a significant nonparametric ANOVA result ( $F_{2,42} = 13.68$ ,  $P > F = 0.0001$ ).

Species found in the quadrats in each stand are listed in Table 2. Thirty-two species were found in the quadrats in the primary stand, 27 in the selectively thinned stand, and 23 in the 5-yr-old clearcut. Eight species were unique to the quadrats in the primary stand, three in the selectively thinned stand, and one in the clearcut.

Application of SAS procedure UNIVARIATE indicates that the median soil pH in the clearcut was 6.4, with a range of 5.8–6.6. The primary stand median pH was 6.0, with a range of 5.0–7.0. Application of a Wilcoxon two-sample test (SAS procedure NPARIWAY) indicates that pH in the clearcut was significantly higher than in the primary stand ( $Z = 2.294$ ,  $P > |Z| = 0.218$ ;  $t$  test approximate significance = 0.0261). It has been suggested by R. Peet (*personal communication*) that herbaceous diversity should be higher in stands with higher pH; we report pH values here in order to demonstrate that our plots were not biased toward higher pH (and therefore higher diversity) in the primary stand, but rather the opposite.

Despite the decline in diversity, all species rated as “common” on the primary site appeared in the clearcut samples, except for *Anemone quinquefolia*. Species whose frequency was >25% on both the primary stand and the clearcut included *Dicentra canadensis*, *Viola rostrata*, *Stellaria corei*, *Hepatica acutiloba*, *Polygonatum* sp., *Polystichum acrostichoides*, *Dentaria diphylla*, *Osmorhiza* sp., and *Cimicifuga americana*. Two

TABLE 3. Species richness (mean  $\pm$  1 SE) of primary and matching secondary (logged) cove hardwood forest sites.\*

| Site                 | Primary          | Secondary       | df | P       | Age of second growth (yr) |
|----------------------|------------------|-----------------|----|---------|---------------------------|
| Upper Ivy Creek      | 13.9 $\pm$ 0.55  | 10.1 $\pm$ 0.36 | 28 | 0.0001  | 5                         |
| Thumpin' Dick Cove   | 11.20 $\pm$ 0.67 | 7.25 $\pm$ 0.49 | 38 | <0.0001 | 10,70                     |
| Lilley Cornett       | 9.00 $\pm$ 0.43  | 7.35 $\pm$ 0.42 | 37 | 0.0047  | 45                        |
| Ramsay Cascade       | 9.95 $\pm$ 0.30  | 8.75 $\pm$ 0.63 | 38 | 0.0475  | 51                        |
| Kilmer Memorial      | 14.53 $\pm$ 0.67 | 6.04 $\pm$ 0.59 | 37 | <0.0001 | 52                        |
| Walker Cove          | 10.40 $\pm$ 0.53 | 7.30 $\pm$ 0.50 | 38 | <0.0001 | 58                        |
| Porter's Flat        | 11.60 $\pm$ 0.43 | 4.94 $\pm$ 0.51 | 36 | <0.0001 | 64                        |
| Upper Porter's Creek | 11.36 $\pm$ 1.12 | 2.50 $\pm$ 0.67 | 19 | <0.0001 | 64                        |
| Ramp Cove            | 10.65 $\pm$ 0.39 | 7.45 $\pm$ 0.31 | 38 | <0.0001 | 68                        |
| Sosebee Cove         | 9.55 $\pm$ 0.41  | 7.55 $\pm$ 0.36 | 38 | 0.0003  | 87                        |

\* All values are from Duffy and Meier (1992) except those for upper Ivy Creek, North Carolina (this study).

species thought to be sensitive to disturbance, *Trillium rugelii* and *Dicentra canadensis*, were present in three or more clear-cut quadrats, and the latter was actually higher in cover and frequency in the clear-cut area. Less common species, such as *Disporum languinosum*, *Uvularia perfoliata*, *Trillium erectum*, and *Delphinium tricorne*, were absent from the clear-cut quadrats. Three taxa, *Hydrophyllum* sp., *Impatiens pallida*, and *Eupatorium* sp., were far more common on the clearcut. The increased cover of these more disturbance-tolerant species may be expected to decline after the canopy closes (Bormann and Likens 1979).

**Discussion.**—These results suggest that one of the reasons herbaceous alpha diversity is lower in logged than in unlogged cove forest is that logging disturbs or removes less-common species. Having few and small populations in scattered patches may place a species at risk, because it increases the probability that all the populations of a species will be damaged or extirpated. Less common species may also have more specific environmental requirements and may be less able to tolerate microclimatic changes initiated by logging. Persistence of herbs associated with mature forest, in some cases in reduced populations, on a small clearcut should not be surprising, considering their ability to adapt to gap-phase succession. *Dicentra canadensis* actually appeared to be doing well in the open area. Perhaps this is due to its having a high light-saturation point (Hicks and Chabot 1985). In this case, selective cutting resulted in less reduction in species number than clear-cutting and limited the population increase of species tolerant of open habitats, such as *Impatiens* and *Eupatorium*. It should be noted that we have no replicates of the selectively thinned primary stand. Therefore, we consider this result tentative.

The results from even the small, recent (5-yr-old) clearcut demonstrate early loss of vernal herbs after clear-cutting. If one includes the nine pairs of primary and secondary cove hardwood forest sites examined by Duffy and Meier (1992), this is the tenth secondary cove hardwood site where species richness per square metre was lower in the secondary than in the primary forest (Table 3). The Upper Ivy Creek site was by far the richest second-growth site of the ten. In all cases

pairs of sites were matched according to latitude, elevation, aspect, slope, and forest type. When we examine the temporal sequence presented in Table 3, we find an initial loss of vernal herbs soon after clear-cutting, followed by a lack of recovery, if not continuing losses, of vernal herbs through age 87 yr. The pattern described by these data agrees with the temporal sequence of changes in herb diversity after logging of second-growth stands predicted by Bormann and Likens (1979). However, unlike Bormann and Likens' prediction for herb diversity, we find that diversity of vernal herbs is higher in primary forest than in recently clear-cut stands.

*Mechanism 2: Physiological stress and competition with weedy or exotic plant species soon after logging and during succession*

If logging is carefully conducted and few herb populations are damaged in the process, logging still opens the forest canopy and initiates succession. In the eastern United States, "high-grading" (the removal of a few exceptionally valuable trees) or careful selective cutting may be similar to gap-phase succession in its impacts. Even in the two small cuts studied at Upper Ivy Creek, however, the more disturbance-tolerant genera increased in frequency and cover, especially on the clearcut. This phenomenon implies that more disturbance-tolerant genera may displace populations of more diverse, less disturbance-tolerant forest-floor herbs. Most logged areas in the southern Appalachians are larger than those studied at Upper Ivy Creek (Jackson 1989) and are soon invaded by old-field herbaceous species and shrubs, which should in turn cause even further losses of forest-floor specialists.

Community organization for spring ephemerals in relatively undisturbed forest is based on a mixture of biotic and abiotic factors, including competition for light, pollinators, and nutrients; species-specific microhabitat preferences; canopy species; and stand history (e.g., Bratton 1976, Muller 1978, Hicks 1980, Motten et al. 1981, Givnish 1982, Beatty 1984, Rogers 1985, Motten 1986). For many species, reproduction and growth must occur in the spring, after ambient

conditions permit growth, but before closure of the tree canopy reduces light (Taylor 1972, Rogers 1983). Species achieve this in a variety of ways. Some species have low, evergreen growth forms, allowing them to use near-ground heat to remain metabolically active during the winter and early spring (Givnish 1982). Early-flowering species require sufficient light for photosynthesis before the spring closure of the tree canopy but can experience limited access to pollinators because of inclement weather (Motten 1986). Later-flowering or later-growing species are adapted to more efficient photosynthesis at lower light levels (Sparling 1967) but still may be limited by light (Brewer 1980) or by local nutrients that have been depleted by earlier species (Rogers 1985). Although species differ slightly in habitat preferences, there may be considerable potential for overlap, and aestival and vernal species occupy the same microhabitats (Bratton 1976). The references suggest that vernal species may be eliminated by competition with taller herbs and shrubs for light, and are sensitive to nutrient competition. Further, some vernal herbs occupy very specific types of microhabitats on the forest floor, and if replaced by early-successional species, may not be able to survive on other, less suitable sites.

Other physical parameters that may change with clear-cutting are soil moisture and temperature. Following clear-cutting in a watershed in the southern Appalachians, moisture contents of the O1 and O2 layers were reduced by 30–50%; however, moisture in the A horizon increased (Swank and Vose 1988). Perhaps more harmful to vernal herbs, the mean monthly surface temperature was elevated by 8–11°C. Daily maximum temperatures frequently exceeded 54°C. Such temperatures can cause direct mortality of many shallow-rooted vernal herbs and can lead to further mortality as a result of increased metabolic rates.

Ash (1988) found an increase in bare soil in clearcuts, and Raphael (1988) found a decrease of litter in clearcuts. Loss of litter can lead to the exposure of shallow roots and thus to desiccation of vernal herbs (A. J. Meier, *personal observation*). With the removal of the canopy, many forest herbs are not able to make photosynthetic use of greater light availability (Hicks and Chabot 1985). Even without the additional physical stresses resulting from clear-cutting, many herbs may be energy limited. The annual energy budget of *Erythronium americanum*, a common vernal herb in the southern Appalachians, sometimes shows a net loss (Muller 1978). Increased temperatures, especially in summer, lead to increased metabolic costs. Many vernal herbs lack the ability to sustain such costs and may experience mortality or at least fail to reproduce (Nault and Gagnon 1993).

In the Susquehanna River gorge, Bratton et al. (1994) found that on 25 × 50 m plots early-successional stands had fewer vernal herb species than did pole-sized stands (where dominants are <20 cm in diameter at

breast height), which in turn had fewer species than mid-successional stands, which had fewer species than mature stands. The low frequencies of species such as *Trillium flexipes* and *Dicentra canadensis* in the pole-sized stands also indicate that some herbaceous species have been nearly extirpated either by the disturbance that opened the canopies or by successional processes. It is important to recognize that some herb species occur much less frequently in younger stands than do others, and that the ecological tolerances of the herbs may be important in this process.

Open successional sites and the initial stages of forest regrowth may also be more prone to browsing by white-tailed deer (*Odocoileus virginianus*) (Alverson et al. 1988). S. Bratton and J. Hapeman, for example, observed selective deer grazing of *Trillium flexipes* in several forest stands along the Susquehanna (S. Bratton, *personal observation*).

### *Mechanism 3: Low rates of reproduction and slow growth of forest-floor herbs*

A third reason that alpha diversity may remain low, even decades after logging, is that herbaceous plants of late-successional or mature forests grow slowly, some species requiring a decade or more from seed to first flowering (Curtis 1943, Bierzychudek 1982a). Upon reaching maturity, many vernal herb species produce few seeds. Nault and Gagnon (1993) estimated that sexual reproduction contributed <1.5% of the population growth rate ( $\lambda$ ) in a population of *Allium tricoccum*. Many species also demonstrate slow rates of growth. Growth as little as 1 cm/yr has been reported from a wide variety of late-successional forest herbs at sites in the northern United States and Canada. Sobey and Barkhouse (1977) investigated vegetative growth of 34 species in the New Brunswick–Nova Scotia border region and found that growth ranged from undetectable to 100 cm/yr, with later-successional species growing more slowly. Whitford (1951) reported growth rates of 0.66–3.50 cm/yr for eight late-succession understory herbs in Illinois. In Finland, Oinonen (1971) reported growth rates of 6.3 cm/yr for a fern (*Carpogymnia dryopteris*) and 6.1 cm/yr for *Maianthemum bifolium*. Martin (1965) reported growth rates of terminal shoots of *Geranium maculatum* in Indiana of 6.74 cm/yr in shade and 7.96 cm/yr in sun. Growth of *Trientalis borealis* in Wisconsin is highly variable, ranging from 5–6 cm/yr in dry soils to >100 cm/yr in mesic environments (Anderson and Loucks 1973). Growth of five species of *Lycopodium* in Massachusetts ranged from 17 to 70 cm/yr (Primack 1973). For *Medeola virginiana*, Bell (1974) reported a mean rhizomal growth of 11.0 cm/yr in Massachusetts, while Cook (1988) found that growth ranged from 14.9 to 15.7 cm/yr at the same site.

All of these studies have been done in northern areas, where severe winters, snow cover, and short growing seasons might limit growth. To confirm the applica-

TABLE 4. Rates of vegetative spread of forest herbs from the southern Appalachians and from conspecifics or congeners from northern locations (see *Mechanisms affecting vernal herb diversity: Mechanism 3*). Note that listings include multiple literature citations for some taxa.

| Species                           | Growth rate (cm/yr) |         | This study |             | $N_i$ ‡ | $N_m$ § |
|-----------------------------------|---------------------|---------|------------|-------------|---------|---------|
|                                   | From literature     | Source† | $\bar{X}$  | 1 SE        |         |         |
| <i>Lycopodium lucidulum</i>       | 1–3                 | a       | ...        | 2.31 ± 0.29 | 3       | 10      |
| <i>Lycopodium</i> spp.            | 17–70               | b       | ...        | ...         | ...     | ...     |
| <i>Dryopteris spinulosa</i>       | <1; <4              | a       | ...        | 1.50 ± 0.15 | 12      | 12      |
| <i>Polystichum acrostichoides</i> | <1                  | a       | ...        | 0.54 ± 0.11 | 3       | 3       |
| <i>Athyrium filix-femina</i>      | <1                  | a       | ...        | 1.13 ± 0.27 | 4       | 4       |
| <i>Athyrium filix-femina</i>      | 1.85                | c       | ...        | ...         | ...     | ...     |
| <i>Clintonia umbellulata</i>      | ...                 | ...     | ...        | 1.98 ± 0.10 | 4       | 18      |
| <i>Clintonia borealis</i>         | 6.0–10.0            | a       | *          | ...         | ...     | ...     |
| <i>Smilacina racemosa</i>         | 1–3                 | a       | ...        | 1.88 ± 0.08 | 4       | 41      |
| <i>Smilacina racemosa</i>         | 2.4                 | c       | ...        | ...         | ...     | ...     |
| <i>Polygonatum pubescens</i>      | 1–3                 | a       | ...        | 2.49 ± 0.05 | 81      | 209     |
| <i>Medeola virginiana</i>         | 2–8                 | a       | ...        | 4.69 ± 0.72 | 3       | 15      |
| <i>Medeola virginiana</i>         | 11.0                | d       | *          | ...         | ...     | ...     |
| <i>Medeola virginiana</i>         | 14.9–15.7           | e       | *          | ...         | ...     | ...     |
| <i>Trillium grandiflorum</i>      | ...                 | ...     | ...        | 0.11 ± 0.01 | 11      | 22      |
| <i>Trillium erectum</i>           | 0.4–0.6             | a       | *          | ...         | ...     | ...     |
| <i>Trillium undulatum</i>         | 0.4–0.5             | a       | *          | ...         | ...     | ...     |
| <i>Podophyllum peltatum</i>       | 13.7                | c       | *          | 8.32 ± 1.71 | 2       | 5       |
| <i>Mitchella repens</i>           | <10                 | a       | ...        | 7.22 ± 0.44 | 5       | 5       |

\* Significant differences between 95% confidence limits of southern Appalachian measurements and literature values; in some cases literature values only exist for congeners.

† Literature sources: a = Sobey and Barkhouse 1977, b = Primack 1973, c = Whitford 1951; d = Bell 1974, e = Cook 1988.

‡ Number of individuals, this study.

§ Number of growth measurements, this study.

bility of these data to the southern as well as northern forests, we collected specimens of seven species (*Adiantum pedatum*, *Polystichum acrostichoides*, *Athyrium filix-femina*, *Clintonia umbellulata*, *Smilacina racemosa*, *Podophyllum peltatum*, and *Trillium grandiflorum*) during the spring of 1990 from a second-growth stand at Sosebee Cove, Union County, Georgia. Four other species (*Lycopodium lucidulum*, *Dryopteris spinulosa*, *Medeola virginiana*, and *Mitchella repens*) were sampled during the same period in a second-growth cove hardwood forest above Avery Creek, Nantahala National Forest, Graham County, North Carolina. Additionally, we obtained wild-grown *Polygonatum pubescens*, collected in western Tennessee during the fall and winter of 1989–1990 by a commercial nursery.

Methods of estimating vegetative growth followed those of the authors of the northern studies as closely as possible, and are species-specific. We measured the distance between shoot scars on the rhizome (*Smilacina racemosa*, *Polygonatum pubescens*, *Clintonia umbellulata*, *Podophyllum peltatum*, and *Trillium grandiflorum*; Whitford 1951, Sobey and Barkhouse 1977), the distance between tubers along the rhizome (*Medeola virginiana*; Bell 1974, Cook 1988), or the microphyll compressions on tubers where growth stopped for the winter (*Lycopodium lucidulum*; Primack 1973). For *Mitchella repens*, with evergreen leaves, growth from the previous year is colored differently from the rest of the plant (Sobey and Barkhouse 1977). In ferns that

produce more than one frond per year (*Adiantum pedatum*, *Polystichum acrostichoides*, *Athyrium filix-femina*, and *Dryopteris spinulosa*), the number of stipes per year was measured on living plants and the distance from the first to the last stipe base on the rhizome was measured.

We measured 352 growth-increments of 135 individuals of 11 species (Table 4). Median growth for all species measured at southern Appalachian sites was 1.98 cm/yr. The slowest growing species was *Trillium grandiflorum*, which grew 0.11 cm/yr (Table 4); the fastest growing species was *Podophyllum peltatum*, at 8.3 cm/yr.

Using 95% confidence limits, a comparison of mean growth of nine of the southern Appalachian species with the means for the same species further north produced two statistically significant differences: (1) the growth of *Podophyllum peltatum* was 1.6 times greater in Illinois than in the southern Appalachians, while (2) the growth of *Medeola virginiana* did not differ between North Carolina and the New Brunswick–Nova Scotia border, but was 2.3–3.3 times greater in Massachusetts than at the two other sites. In the two intragenetic comparisons, northern *Clintonia borealis* grew 3.0–5.0 times faster than its southern congener *C. umbellulata*, and *Trillium erectum* and *T. undulatum* grew 3.6–5.45 times faster than Appalachian *T. grandiflorum*.

The data suggest that growth rates in the south may be similar to or slower than northern rates, rather than

faster. Second, slow vegetative growth of vernal herbs may reflect a *K*-strategy of restrained investment in reproduction and growth (Gadgil and Solbrig 1972, Bierzychudek 1982a) and increased allocation of resources to energy and nutrient storage (Newell and Tramer 1978) in an environment where competition is severe for soil nutrients (Rogers 1985) or for light at the herbal canopy layer (Givnish 1982). Such competition may be more a factor of successional state than of latitude. Annual or site-specific variations in climate, soil, or plant communities between sites, however, may be more important in determining plant growth than differences in growing season.

Given a time lag of up to a decade from seed to first flowering for many vernal species and limited seed production of these understory herbaceous plants, slow vegetative growth should contribute to slow recovery following population reductions such as those associated with logging. Further, although low-elevation southern forests often regain basal area faster than do northern stands, southern vernal herbs may be too limited by their short growing season to display a similar response.

*Mechanism 4: Limited spread and slow dispersal due to clonal reproduction and ant-mediated dispersal of seeds*

Understory herbaceous plants exhibit a variety of life-history strategies, but many are functionally clonal (Whitford 1949, Harper 1977) and long-lived (Whitford 1951, Cook 1983). Species that reproduce predominantly by vegetative means may be slow to reoccupy areas where the species has been recently extirpated. Spatial interactions are likely to be complex, influenced by the initial location of founding individuals and by the rate of clonal spread and extinction of individual ramets and genets. In forests at the prairie-forest border in Wisconsin, Whitford (1949) found that some herbaceous species became more evenly distributed in later successional stages. He also suggested, without direct measurement, that patches of herbaceous species are larger in later succession. He concluded that reproductive strategies determined distribution: clonally reproducing species became less patchy with apparent increases in stand age, whereas species with widely dispersed seeds showed no change in distribution. Primary-forest sites often contain networks of overlapping clonal patches of various herb species (cf. Whitford 1949). Parts of patches may die off or be invaded by other species so that remnants of the original clones become noncontiguous. Recolonization of disturbed sites is likely to be slow because vernal herbaceous species tend to spread by clonal growth or by gravity- or ant-dispersed seeds (Beattie and Culver 1981), limiting the range at which deforested areas can be colonized. In addition, some plant species may be dependent upon a single species of ant for seed dispersal (D. Waller, *personal communication*). Matlack

(1994) has found that rates of dispersal of some seeds can be extremely slow. In fact, he found that the rate of dispersal of *Cimicifuga racemosa* was effectively 0 m/yr.

Other species of vernal herbs are dispersed by gravity; for example, *Panax trifolium* (Philbrick 1983). In April and May of 1992 at Cucumber Gap in Great Smoky Mountains National Park, we chose seven widely separated female individuals of *Panax trifolium* in fruit. They bore a total of 43 drupes. At 3- to 5-d intervals we located all 43 drupes and marked the location of each drupe with a colored toothpick. We continued to follow the drupes until they were embedded under the leaf litter. We measured the distance from the base of the female plants to the embedded drupe. Twenty-five of the drupes embedded within 10 cm of the parent, 39 embedded within 15 cm of the parent, and all 43 embedded within 25 cm of the mother. Given the slow rates of dispersal and the short distances that propagules are dispersed from parent plants, many landscape features including high elevations, dry ridges, and agricultural fields would be expected to present impassable barriers to dispersal for these plants.

We hypothesized that if slow population growth or clonal growth were inhibiting recovery of herbs in logged watersheds in the southern Appalachians, their population densities where they did occur would be lower relative to those in primary forest. As part of a more extensive, ongoing study of distribution of vernal herbs relative to disturbance history in the southern Appalachians, we searched along backcountry trails in logged (secondary) and unlogged (primary) watersheds in Great Smoky Mountains National Park recording the presence and estimated density of *Trillium grandiflorum*, *T. erectum*, and *T. luteum* in 90 × 90 m plots, over a total of >800 plots. Searches of individual plots typically lasted about 15 min. The density of ramets was evaluated by scalars, on a log scale: 1 = 1–9 shoots, 2 = 10–99, 3 = 100–999, 4 = 1000–9999, and 5 ≥ 10 000 shoots. We assessed both accuracy and repeatability of the sampling method by using test plots where the plot was intensively examined in a gridded search, and by having multiple individuals search the same plots. We found no significant differences between observers or between search methods. We also recorded the forest type and the elevation of these populations. For purposes of analysis here, elevation was divided into three classes: <900 m, ≥900–<1200 m, and ≥1200 m. Trails through primary forest included seven in the Maddron Bald, Mount LeConte, and Cades Cove areas; those through second growth were in the Elkmont, Tremont, and Cades Cove areas of Great Smoky Mountains National Park. All trails are in north-facing watersheds in Tennessee.

We attempted to determine whether slow population growth was limiting densities of *Trillium*. We decided to reduce the influence of lack of initial dispersal to sites by using only sample plots where the species were

TABLE 5. Distribution of three *Trillium* species by elevation and successional status of forest, Great Smoky Mountains National Park, Tennessee, USA. Presented are the number of 90 × 90 m plot and percentage of plots in which ramets of each species occurred. Density of ramets was estimated by scalars, on a log scale: 1 = 1–9 ramets, 2 = 10–99, 3 = 100–999, 4 = 1000–9999, and 5 ≥ 10,000 ramets.

| Successional status,*<br>Elevation | Density scalar |    |    |     |    |    |     |     |     |     |
|------------------------------------|----------------|----|----|-----|----|----|-----|-----|-----|-----|
|                                    | 1              |    | 2  |     | 3  |    | 4   |     | 5   |     |
|                                    | N              | %  | N  | %   | N  | %  | N   | %   | N   | %   |
| <i>Trillium luteum</i>             |                |    |    |     |    |    |     |     |     |     |
| Secondary forest                   | 9              | 25 | 23 | 64  | 4  | 11 | ... | ... | ... | ... |
| Primary forest                     | 0              | 0  | 6  | 46  | 7  | 54 | ... | ... | ... | ... |
| <i>Trillium erectum</i>            |                |    |    |     |    |    |     |     |     |     |
| Secondary forest:                  |                |    |    |     |    |    |     |     |     |     |
| <900 m                             | 14             | 13 | 54 | 50  | 40 | 37 | 1   | 1   | ... | ... |
| ≥900 to <1200 m                    | 9              | 13 | 37 | 53  | 21 | 30 | 3   | 44  | ... | ... |
| ≥1200 m                            | 1              | 7  | 5  | 36  | 8  | 57 | 0   | 0   | ... | ... |
| Primary:                           |                |    |    |     |    |    |     |     |     |     |
| <900 m                             | 1              | 4  | 7  | 30  | 15 | 65 | 0   | 0   | ... | ... |
| ≥900 to <1200 m                    | 13             | 16 | 23 | 28  | 34 | 41 | 13  | 16  | ... | ... |
| ≥1200 m                            | 4              | 10 | 6  | 15  | 18 | 45 | 12  | 30  | ... | ... |
| <i>Trillium grandiflorum</i>       |                |    |    |     |    |    |     |     |     |     |
| Secondary forest:                  |                |    |    |     |    |    |     |     |     |     |
| <900 m                             | 16             | 28 | 27 | 47  | 13 | 23 | 1   | 2   | 0   | 0   |
| ≥900 to <1200 m                    | 3              | 20 | 7  | 47  | 5  | 33 | 0   | 0   | 0   | 0   |
| ≥1200 m                            | 0              | 0  | 0  | 0   | 0  | 0  | 0   | 0   | 0   | 0   |
| Primary forest                     |                |    |    |     |    |    |     |     |     |     |
| <900 m                             | 0              | 0  | 2  | 11  | 13 | 72 | 3   | 17  | 0   | 0   |
| ≥900 to <1200 m                    | 0              | 0  | 6  | 19  | 11 | 34 | 13  | 41  | 2   | 6   |
| ≥1200 m                            | 0              | 0  | 1  | 100 | 0  | 0  | 0   | 0   | 0   | 0   |

\* Primary = unlogged; secondary = logged.

already present. We found using SAS procedure CATMOD (categorical data modelling) that *T. luteum* population densities were significantly larger in primary forest than in second-growth forest ( $\chi^2 = 8.11$ ,  $P = 0.0167$ ) (Table 5). Few populations were found over 1200 m elevation. In the case of *Trillium erectum*, a model incorporating primary vs. secondary stands and elevation found significantly larger populations of *T. erectum* in primary forest (primary vs. secondary:  $\chi^2 = 18.45$ ,  $P = 0.0004$ ; elevation:  $\chi^2 = 12.52$ ,  $P = 0.0513$ , residual:  $\chi^2 = 3.11$ ,  $P = 0.7951$ ) (Table 5). Perhaps the greatest difference in densities between primary and secondary forest was found for *T. grandiflorum*. In a model that also incorporated elevation, *T. grandiflorum* population densities were greater in primary than secondary forest (primary vs. secondary:  $\chi^2 = 21.55$ ,  $P = 0.0002$ ; elevation:  $\chi^2 = 7.80$ ,  $P = 0.4531$ ) (Table 5). For all species of *Trillium* reported, populations in secondary forest, where they occurred, were significantly smaller in density than populations in primary forests. This suggests that slow population growth is a factor leading to low densities of *Trillium* in secondary forests. Bratton et al. (1994) found that *Trillium flexipes* and *Dicentra canadensis* were less likely to occur in stands in stream drainages where the forest had been highly fragmented, but where they did occur, their populations were equal in density to those in less-disturbed sites. *Mertensia virginica*, in contrast, was as likely to occur in disturbed as in undisturbed

areas, but its populations were smaller in disturbed areas.

#### *Mechanism 5: Loss of suitable habitat and disruption of gap-phase succession*

Differences in physical structure and cover between primary and second-growth understory herbaceous communities may affect the functioning of forest ecosystems. Maguire and Forman (1983) suggest that forest herbs restrict the survival of seedlings of shade-intolerant tree species. Bratton (1976) found that some species of vernal herbs root in deep pockets of organic matter or have higher covers at the base of trees or on fallen logs. This suggests that removal of organic materials, such as logs, may reduce microhabitat availability for some species.

A second modification caused by logging is the distribution of light on the forest floor. Clearcuts change from high light to very limited light as succession closes the canopy. Canopy gaps are actually rare in younger successional forests and probably continue to decline in the Appalachians until at least age 80 yr. Stands may have to be 150–200 yr old before gap-phase processes are completely reestablished. Canopy gaps produce not only pits and mounds and fallen logs that provide new microhabitats for herbs, but also supply small areas of elevated but not extreme radiation. Since canopy gaps are partially shaded, they are not as dry as open clear-

cuts, nor are they as likely to be invaded by *r*-selected species or exotics.

*Site and methods.*—In order to assess the potential importance of canopy gaps to herb establishment, we gathered data on *Cimicifuga americana* in the Toecane District of Pisgah National Forest in October 1993. Initially, 50  $2 \times 5$  m quadrats were established in a  $250 \times 100$  m plot in primary cove hardwood forest, at Walker Cove, and in a  $250 \times 100$  m plot in second-growth cove hardwood forest established in 1932 (Duffy and Meier 1992). All the *C. americana* were counted and recorded as fruiting or not fruiting. Since this sample did not provide enough plots in gaps with *Cimicifuga* for statistical purposes, additional quadrats were placed in randomly selected canopy gaps, bringing the sample to 22 gap quadrats and 50 closed-canopy quadrats in primary forest, and 7 gap and 50 closed-canopy quadrats in second growth. Gap boundaries were identified following the methods of Runkle (1981 and 1982).

*Results and discussion.*—The average number of *Cimicifuga* ramets per quadrat in closed canopy was 0.06 ramets/quadrat in second-growth closed canopy and 0.24 ramets/quadrat in primary forest. In canopy gaps it was 0.71 in second-growth and 1.68 in primary forest. Using SAS procedure GENMOD for Poisson regression analysis, *Cimicifuga* occurrence in gaps was significantly different from that in closed canopy, as was *Cimicifuga* occurrence in old-growth vs. second-growth forest (gap vs. closed:  $\chi^2 = 43.28$ ,  $P < 0.0001$ ,  $df = 1$ ; old growth vs. successional:  $\chi^2 = 8.05$ ,  $P = 0.0045$ ,  $df = 1$ ). Because the number of *C. americana* under the closed canopy was not sufficient to compare fruiting between gaps and the closed canopy, we established a 2 m wide stratified random-walk sample in Walker Cove, counting individuals of *C. americana* that were fruiting or not fruiting. Under the closed canopy we found 57 individuals not fruiting and 3 fruiting. Within canopy gaps we found 45 not fruiting and 15 fruiting. A chi-square test of independence was performed and showed that *C. americana* fruiting was significantly dependent on and positively associated with the presence of gaps ( $\chi^2 = 9.412$ ,  $P = 0.002$ ,  $df = 1$ ,  $\Phi$  coefficient = 0.280). This result suggests that canopy gaps are important for reproduction in *C. americana*. The reduction in gap formation prevalent in secondary forests may lead to a lack of recovery or even decline in populations of this species. This may also apply to other gap-dependent species. Moore and Vankat (1986) found that herb cover slowly increased in gaps. The need for adequate germination and reproduction niches should be taken into account when inferring rates of dispersal of propagules from the spread of a species over time.

#### IMPLICATIONS FOR MANAGEMENT

In an attempt to determine the influence of the area of primary stand on alpha diversity, we ranked, by

stand area, the nine primary stands studied by Duffy and Meier (1992) and the primary stand at Upper Ivy Creek reported here. The three primary stands in Great Smoky Mountains National Park were ranked as tied in area because they are part of a large, nearly contiguous block of primary forest. We performed a Spearman rank correlation analysis and found no correlation between area of primary stand and mean number of species per square metre ( $\rho = 0.178$ ,  $z = 0.534$ ,  $P = 0.593$ ,  $n = 10$ ). This result suggests that even small, remnant, primary-forest stands are important reserves of vernal-herb diversity. While preservation of small tracts of primary forest appear to be important in maintaining herb diversity, they may not be adequate to preserve diversity of herbs on regional and larger scales. The caveat for forest management here is that larger remaining blocks of primary forest should be protected as well as small stands: by leaving only small tracts, one could expect a reduction in beta (regional) and gamma (global) diversity. Furthermore, the evidence we now have suggests that vernal herbs would be slow to recolonize clear-cut areas from small, remnant, primary stands because of slow growth, low rates of reproduction, poor dispersal, loss of suitable habitat, and disruption of gap-phase dynamics.

Life-history characteristics of vernal herbs suggest that vernal-herb populations remaining in secondary forest may also be adversely impacted by clear-cutting, though the most vulnerable may have already been eliminated. Because vernal herbs demonstrate low rates of recovery (Duffy and Meier 1992), harvest methods that cause less mortality should be preferred. Logging methods that mimic natural gap-phase dynamics may be less damaging than clear-cutting for vernal herbs. Our findings in Upper Ivy Creek suggest that selective cutting is more appropriate than clear-cutting for the maintenance of vernal-herb populations in secondary, mixed, mesophytic forests. Reader and Ericker (1992) found that thinning small patches increased populations of some vernal herbs. However, our findings in Upper Ivy Creek suggest that even selective thinning can cause loss of diversity. Because of the poor dispersal characteristics of many vernal herbs, it is possible that transplantation of these species may help restore vernal-herb populations of secondary, mixed, mesophytic forest.

#### CONCLUSION

Based on our work in eastern deciduous forests, we offer the following working hypothesis of what happens when a forest is clear-cut. While the ecological effects of a clearcut may depend on many things, such as the extent and shape of the cut, the contour of the land, and the nature of the original forest, there are certain general trends that can be expected. When canopy trees are removed, nutrients in the ecosystems are removed with them (Bormann and Likens 1979). Log-

ging equipment causes direct damage to herbs (A. J. Meier, *personal observation*).

With the canopy removed, temperatures at the soil surface become greatly elevated during the summer (Swank and Vose 1988), causing direct mortality of shallow-rooted vernal herbs, and leading to further mortality as a result of metabolic processes. Many forest herbs cannot make full use of the greater light availability that results from canopy removal since they tend to have low values for maximum photosynthesis rate,  $P_{max}$  (Hicks and Chabot 1985), and when summer comes, increased temperatures lead to vastly increased metabolic cost. Vernal herbs often cannot afford such additional metabolic cost. Nault and Gagnon (1993) report that the population growth rate (intrinsic rates of increase) of *Allium tricoccum* and other vernal herbs tends to barely exceed the equilibrium value of 1.0. Other long-lived perennial herbs show similar slow population growth rate (Bierzychudek 1982b, Meagher 1982, Kinoshita 1987).

While total canopy removal is harmful to vernal herbs, so is the closed canopy of the young forest that begins to develop about 15 yr after clear-cutting (Bormann and Likens 1979). The closed canopy limits population growth for any surviving herbs that depend upon gaps for reproduction. This lack of canopy gaps will continue through age 80 yr, and the size and rate of canopy gap formation will not return to the levels found in primary forests before age 150–200 yr (Bormann and Likens 1979).

Some species benefit from the formation of canopy gaps, pits and mounds, and rotting logs (Bratton 1976). We do not know which environmental factors in canopy gaps are responsible for these benefits, but we understand that canopy gap formation increases light availability, soil moisture, and soil nutrient availability (Bormann and Likens 1979). It is worth noting that canopy gaps, unlike clearcuts, provide a gradient of light intensity increasing from the edge of the gap towards the center; that is, the process of clear-cutting forests leads to a decrease in both spatial and temporal heterogeneity of the environment within the stand.

By the time canopy gap formation has been reestablished to the levels found in primary forests, many species have been eliminated from the clearcuts. Most vernal species are not adapted for rapid dispersal. In the southern Appalachians there are many topographic barriers to dispersal. Once a species becomes established in an area, it is still likely to show low rates of clonal growth and sexual reproduction. Clear-cutting of primary, mixed, mesophytic forests causes mortality of many vernal herbs. Life-history characteristics of these species lead to very long recovery periods—if recovery occurs at all.

All of these factors combine to retard recovery of the vernal-herb diversity in southern Appalachian forests. If management of these forests for biodiversity is desirable, then a variety of strategies might be em-

ployed to reduce the effect of logging and to speed recovery. These include reducing the size of logging areas to mimic the natural pattern of canopy gap formation. Selective cutting would be superior to clear-cutting. Methods of removing logs that reduce damage to vegetation and limit soil compaction and erosion would be important. However, the low to non-existent recovery rates observed for vernal forest herbs suggest that even a landscape of hypothetically restored, old, secondary forest may not serve to conserve and restore vernal-herb populations. Management plans should therefore include protection of remaining primary, mixed, mesophytic forests.

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#### LITERATURE CITED

- Alverson, W. S., D. M. Waller, and S. L. Solheim. 1988. Forests too deer: edge effects in northern Wisconsin. *Conservation Biology* 2:348–358.
- Anderson, R. C., and O. L. Loucks. 1973. Aspects of the biology of *Trientalis borealis*. *Ecology* 54:798–808.
- Ash, A. N. 1988. Disappearance of salamanders from clear-cut plots. *The Journal of the Elisha Mitchell Scientific Society* 104:116–122.
- Bartram, W. 1792. *Travels through North and South Carolina, Georgia, east and west Florida*. A facsimile of the 1792 London edition embellished with its nine original plates, also seventeen additional illustrations and an introduction by Gordon DeWolf. 1973. Beehive Press, Savannah, Georgia, USA.
- Beattie, A. J., and D. C. Culver. 1981. The guild of myrmecochores in the herbaceous flora of West Virginia forests. *Ecology* 62:107–115.
- Beatty, S. W. 1984. Influence of microtopography and canopy species on spatial patterns of forest understory plants. *Ecology* 65:1406–1419.
- Bell, A. D. 1974. Rhizome organization in relation to vegetative spread in *Medeola virginiana*. *Journal of the Arnold Arboretum* 55:458–468.
- Bierzychudek, P. 1982a. Life histories and demography of shade-tolerant temperate forest herbs: a review. *New Phytologist* 90:757–776.
- . 1982b. The demography of jack-in-the-pulpit, a forest perennial that changes sex. *Ecological Monographs* 52:335–351.
- Bormann, F. H., and M. F. Buell. 1964. Old-age stand of hemlock–northern hardwood forest in central Vermont. *Bulletin of the Torrey Botanical Club* 91:451–465.
- Bormann, F. H., and G. E. Likens. 1979. *Pattern and process in a forested ecosystem*. Springer-Verlag, New York, New York, USA.
- Bratton, S. P. 1976. Resource division in an understory herb

- community: responses to temporal and microtopographic gradients. *American Naturalist* **110**:679–693.
- Bratton, S. P., J. R. Hapeman, and A. R. Mast. 1994. The lower Susquehanna River gorge and floodplain (U.S.A.) as a riparian refugium for vernal, forest floor herbs. *Conservation Biology* **8**:1069–1077.
- Braun, E. L. 1950. Deciduous forests of eastern North America. Hafner, New York, New York, USA.
- Brewer, R. 1980. A half-century of changes in the herb layer of a climax deciduous forest in Michigan. *Journal of Ecology* **68**:823–832.
- Brickell, J. 1737. The natural history of North Carolina. Series in American Studies Reprint, 1969. Johnson Reprint Corporation, New York, New York, USA.
- Cook, R. E. 1983. Clonal plant populations. *American Scientist* **71**:244–253.
- . 1988. Growth in *Medeola virginiana* clones. I. Field observations. *American Journal of Botany* **75**:725–731.
- Curtis, J. T. 1943. Germination and seedling development in five species of *Cypripedium* L. *American Journal of Botany* **30**:199–206.
- Duffy, D. C., and A. J. Meier. 1992. Do Appalachian herbaceous understories ever recover from clearcutting? *Conservation Biology* **6**:196–201.
- Flaccus, E. 1959. Revegetation of landslides in the White Mountains of New Hampshire. *Ecology* **40**:692–703.
- Gadgil, M., and O. Solbrig. 1972. The concept of *r*- and *K*-selection: evidence from wildflowers and some theoretical considerations. *American Naturalist* **106**:14–31.
- Givnish, T. J. 1982. On the adaptive significance of leaf height in forest herbs. *American Naturalist* **120**:353–381.
- Gray, A. 1841. Notes on a botanical excursion to the mountains of North Carolina & c; with some remarks on the botany of the higher Allegheny Mountains (in a letter to Sir Wm. J. Hooker). *American Journal of Science* **42**:1–49.
- Harper, J. L. 1977. The population biology of plants. Academic Press, London, England.
- Hicks, D. J. 1980. Intra-stand distribution patterns of southern Appalachian cove forest herbaceous species. *American Midland Naturalist* **104**:209–222.
- Hicks, D. J., and B. F. Chabot. 1985. Deciduous forest. Pages 257–277 in B. F. Chabot and H. A. Mooney, editors. Physiological ecology of North American plant communities. Chapman & Hall, London, England.
- Jackson, L. E. 1989. Mountain treasures at risk: the future of the southern Appalachian national forests. The Wilderness Society, Washington, D.C., and Global Printing, Alexandria, Virginia, USA.
- Kinoshita, E. 1987. Sex change and population dynamics in *Arisaema* (Araceae). I. *Arisaema serratum* (Thunb.) Schott. *Plant Species Biology* **2**:15–28.
- MacLean, D. A., and R. W. Wein. 1977. Changes in understory vegetation with increasing stand age in New Brunswick forests: species composition, cover, biomass, and nutrients. *Canadian Journal of Botany* **55**:2818–2831.
- MacLean, E. O. 1982. Soil pH and lime requirement. Pages 199–224 in: A. L. Page, R. H. Miller, and O. R. Keeney, editors. Methods of soil analysis. II. Chemical and microbiological properties. Second edition. Number 9 in the Agronomy series. American Society of Agronomy, Inc., Madison, Wisconsin, USA.
- Maguire, D. A., and R. T. T. Forman. 1983. Herb cover effects on tree seedling patterns in a mature hemlock–hardwood forest. *Ecology* **64**:1367–1380.
- Martin, M. C. 1965. An ecological history of *Geranium maculatum*. *American Midland Naturalist* **73**:111–149.
- Matlack, G. R. 1994. Plant species migration in a mixed-history forest landscape in eastern North America. *Ecology* **75**:1491–1502.
- Meagher, T. R. 1982. The population biology of *Chamaelirium luteum*, a dioecious member of the lily family: two-sex population projections and stable population structure. *Ecology* **63**:1701–1711.
- Moore, M. R., and J. L. Vankat. 1986. Response of the herb layer to the gap dynamics of a mature beech–maple forest. *American Midland Naturalist* **115**:336.
- Motten, A. F. 1986. Pollination ecology of the spring wildflower community of a temperate deciduous forest. *Ecological Monographs* **56**:21–42.
- Motten, A. F., D. R. Campbell, and D. E. Alexander. 1981. Pollination effectiveness of specialist and generalist visitors to a North Carolina population of *Claytonia virginica*. *Ecology* **62**:1278–1287.
- Muller, R. N. 1978. The phenology, growth and ecosystem dynamics of *Erythronium americanum* in the northern hardwood forest. *Ecological Monographs* **48**:1–20.
- Nault, A., and D. Gagnon. 1993. Ramet demography of *Alium tricoccum*, a spring ephemeral, perennial forest herb. *Journal of Ecology* **81**:101–119.
- Newell, S. J., and E. J. Tramer. 1978. Reproductive strategies in herbaceous plant communities during succession. *Ecology* **59**:228–234.
- Oinonen, E. 1971. The time table of vegetative spreading in oak fern (*Carpogymnia dryopteris* (L.) Löve and Löve) and may-lily (*Maianthemum bifolium* (L.) F. W. Schmidt) in southern Finland. *Acta Forestalia Fennica* **118**:1–36.
- Peterken, G. F., and M. Game. 1984. Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. *Journal of Ecology* **72**:155–182.
- Philbrick, C. T. 1983. Contributions to the reproductive biology of *Panax trifolium* L. (Araliaceae). *Rhodora* **85**:97–114.
- Primack, R. B. 1973. Growth patterns of five species of *Lycopodium*. *American Fern Journal* **63**:3–7.
- Radford, A. E., H. E. Ahles, and C. R. Bell. 1968. Manual of the vascular flora of the Carolinas. University of North Carolina Press, Chapel Hill, North Carolina, USA.
- Raphael, M. G. 1988. Long-term trends in abundance of amphibians, reptiles, and mammals in Douglas-fir forests of Northwestern California. Pages 23–31 in R. C. Szaro, K. E. Severson, and D. R. Patton, editors. Management of amphibians, reptiles, and mammals in North America. Technical Report RM-166. USDA Forest Service, Rocky Mountain Forest and Range Experimental Station, Fort Collins, Colorado, USA.
- Reader, R. J., and B. D. Bricker. 1992. Value of selectively cut deciduous forest for understory herb conservation: an experimental assessment. *Forest Ecology and Management* **51**:317–327.
- Rogers, R. S. 1983. Annual variability in community organization of forest herbs: effect of an extremely warm and dry early spring. *Ecology* **64**:1086–1091.
- . 1985. Local coexistence of deciduous-forest ground-layer species growing in different seasons. *Ecology* **66**:701–707.
- Runkle, J. R. 1981. Gap regeneration in some old-growth forests of the eastern United States. *Ecology* **62**:1041–1051.
- . 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology* **63**:1533–1546.
- Sobey, D. G., and P. Barkhouse. 1977. The structure and rate of growth of the rhizomes of some forest herbs and dwarf shrubs of the New Brunswick–Nova Scotia border region. *Canadian Field Naturalist* **91**:377–383.
- Sparling, J. H. 1967. Assimilation rates of some woodland herbs in Ontario. *Botanical Gazette* **128**:160–168.
- SAS [Statistical Analysis Systems Institute]. 1985. SAS

- user's guide: statistics. SAS Institute, Inc., Cary, North Carolina, USA.
- Swank, W. T., and J. M. Vose. 1988. Effects of cutting practices on microenvironment in relation to hardwood regeneration. Pages 71–88 *in* H. C. Smith, A. W. Perkey, and W. E. Kidd, Jr., editors. Guidelines for regenerating Appalachian hardwood stands. Proceedings of a workshop, 24–26 May 1988, Morgantown, West Virginia. Society of American Foresters Publication 88–03. West Virginia University Books, Office of Publications, Morgantown, West Virginia, USA.
- Taylor, F. G. 1972. Phenodynamics of production in a mesic deciduous forest. EDFB-IBP 72–8. Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA.
- Whitford, P. B. 1949. Distribution of woodland plants in relation to succession and clonal growth. *Ecology* **30**:199–208.
- . 1951. Estimation of the ages of forest stands in the prairie–forest border region. *Ecology* **32**:143–147.
- Wofford, B. E. 1989. A guide to the vascular plants of the Blue Ridge. University of Georgia Press, Athens, Georgia, USA.