
Do Appalachian Herbaceous Understories Ever Recover from Clearcutting?

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Abstract: *Life history characteristics of many herbaceous understory plants suggest that such species recover slowly from major perturbations such as clear cutting. We examined herbaceous cover and richness in the understories of nine primary ("old-growth") forests in the southern Appalachian Mountains and of nine comparable secondary forests, ranging in age from 45 to 87 years since clear cutting. Neither cover nor richness increased with age in the secondary forests. This suggests three possibilities: (1) that recovery is so slow or variable among sites that 87 years is insufficient time to detect it; (2) that such forests will never recover to match remnant primary forests because climatic conditions are different today than when the forests became established; or (3) that herbaceous plants colonize pit and mound microtopography caused by the death of trees, so that recovery must await the growth, death, and decomposition of the trees of the secondary forest. Whatever the mechanism, herbaceous understory communities in the mixed-mesophytic forests of the Appalachians appear unlikely to recover within the present planned logging cycles of 40–150 years, suggesting a future loss of diversity of understory herbaceous plants.*

Resumen: *Las características del período de vida de numerosas plantas herbáceas, sugiere que estas especies se recuperan lentamente de grandes perturbaciones como la tala debosques. Nosotros examinamos la cubierta herbácea y abundancia en el sotobosque de nueve bosques primarios (antiguo crecimiento) en los Montes Apalaches del Sur, y los comparamos con nueve bosques secundarios que no han sido talados por periodos que van de 45 a 87 años. La riqueza y la abundancia no han aumentado con el tiempo en el bosque secundario. Esto sugiere tres posibilidades: (1) que la recuperación es tan lenta o variable entre sitios, que 87 años resultan insuficientes para detectarla, (2) que este tipo de bosques nunca se recuperará al nivel de los bosques primarios originales, ya que las condiciones climáticas actuales son diferentes a las existentes cuando los bosques fueron originariamente establecidos, o (3) que plantas herbáceas colonizan la microtopografía del suelo que ha sido removido a causa de la descomposición de los árboles muertos, y por consiguiente la recuperación debe esperar el crecimiento, muerte y descomposición de los bosques secundarios. Cualquiera sea el mecanismo, la cubierta herbácea de las comunidades de bosques mesofíticos mixtos en los Apalaches, no parece estar recuperándose dentro del ciclo previsto para la tala de árboles que es de 40 a 150 años. Esto sugiere una pérdida futura en la diversidad de las plantas que conforman la cubierta herbácea.*

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Paper submitted September 11, 1991; revised manuscript accepted March 11, 1992.

Introduction

“Old growth,” “virgin,” or primary forests in the United States have attracted scientific and cultural interest as examples of communities with high biological diversity (Whitney 1987). These forests have been much reduced in extent through clearing for wood products, farming, and urbanization; the fate of the remainder has generated considerable controversy (Norse 1989; Williams 1989).

Preservationists argue that once primary forests are harvested the resulting secondary forests lack the biodiversity of primary forests, while harvesters argue that sustainable yields of timber are compatible with maintenance of biodiversity and that sufficient areas of primary forest will remain following exploitation (Norse et al. 1986; Nyberg et al. 1987).

Most research on the effects of the exploitation of forests has focused on trees and wildlife (Wilderness Society 1986; Jackson 1989), but herbaceous understory plants of primary forests may be among the forest organisms most sensitive to clear-cutting or other forms of massive disturbance.

Recolonization of secondary forests by herbaceous species is likely to be slow (Thompson 1980). Sexual reproduction is often limited by small crops of seeds with poor dispersal by gravity or ants (Handel 1976; Beattie & Culver 1981) and low germination (Struik 1965). Herbaceous plants of primary forests typically have vegetative extension growth rates of less than 1.0 meter per decade (Whitford 1951; Sobey & Barkhouse 1977). Growth to first reproduction can take up to a decade (Bierzychudek 1982). Also, at least in the initial stages of forest regrowth, browsing by herbivores such as white-tailed deer (*Odocoileus virginianus*) may prevent seedling establishment (Alverson et al. 1988).

Studies of individual forests indicate slow recovery by herbaceous species. Hardwood forests in New Brunswick showed little evidence of recovery of late-successional herbaceous species several decades after disturbance (MacLean & Wein 1977). Following landslides in the White Mountains of New Hampshire, 72-year-old herbaceous communities had only 78% species overlap with communities in adjacent 200-plus-year-old forest (Flaccus 1959). An herbaceous community in Michigan was still recovering from a major disturbance event that had occurred 150 years earlier (Brewer 1980).

These studies suggest that the 40–150 year harvesting cycles used in southeastern deciduous forests (U.S. Department of Agriculture/Forest Service [U.S.D.A./F.S.] 1986) may not allow sufficient time for the recovery of herbaceous communities. If recovery is occurring, we predict that herbaceous communities in secondary forests should show increasing species richness and cover with age, becoming more similar to primary communi-

ties. We tested this prediction by examining one-square-meter plots of herbaceous understory plants at nine primary forest sites in the southern Appalachian Mountains and comparing them with plots in nine secondary-successional sites with similar latitudes, elevations, exposures, slopes, soil types, and geologies. We present several scenarios for forest recovery, suggested by our findings.

Methods

Terminology

Numerous terms have been used to describe forests such as *ancient*, *old*, *old-growth*, *over-mature*, *original*, *primary*, *primeval*, and *virgin*, on the one hand, and *recent*, *secondary*, and *second-growth*, on the other. Older secondary forests have been called *mature*, *over-mature*, and even *old-growth*. Unfortunately, several of these terms have opposite meanings when used by scientists of different disciplines or regions (see Rackham 1980; Norse 1989). Here, we use *primary* to describe forests that have never been clear cut and that have little or no evidence of past human activity. Such forests may have been grazed, they may have experienced limited exploitation of valuable tree species, and their floors may have been burned by Amerinds and European pioneers. Primary forests contain abundant downed timber in varying states of decay, standing dead trees, and live trees in a range of sizes. *Secondary* forests are those that have developed after the previous forest was extensively logged or clear cut. We use *mature* to refer to secondary forests that have existed longer than the normal harvesting rotation practiced by foresters on that particular forest type. A *mature secondary* forest may have the large trees of a primary forest but does not necessarily have the same species composition, age distribution, or community processes.

Study Sites

We examined nine sets of primary and matching secondary mixed-mesophytic forest, an ecosystem described by Braun (1950) as structurally complex, with a highly diverse species composition. The characteristic trees are *Liriodendron tulipifera*, *Tsuga canadensis*, *Fagus grandifolia*, *Quercus alba*, *Q. velutina*, and *Q. prinus* in the overstory, with *Cornus florida*, *Tilia heterophylla*, *Fraxinus americana*, *Ostrya virginiana*, and *Aesculus octandra* in the understory. The sites were as follows:

1. *Joyce Kilmer–Slickrock Wilderness Area*, Graham County, North Carolina. The wilderness area includes a primary stand, the Joyce Kilmer Memorial Forest on Little Santeetlah Creek, and a secondary forest on adjacent Horse Creek, dating from 1938

- (U.S. Forest Service, unpublished data). Both areas are on moist, north-facing slopes at approximately 1000 m elevation. Kilmer has apparently never been cut and there is no evidence of fire scars on trees or of charcoal in the soil within the cove (Lorimer 1980).
2. *Porter's Flat*, Greenbriar Cove area, Great Smoky Mountains National Park (GSMNP), Tennessee. The primary forest, at approximately 750 m elevation on a southwest-facing slope, has never been logged, but grazing may have occurred prior to the mid-1930s (Hicks 1980). The forest has been described by Whittaker (1956, 1966) and the herbaceous community by Bratton (1976) and Hicks (1980). The secondary forest site, on the east bank of the Little River near Elkmont, GSMNP, at 800 m elevation, was established after 1926 (R. S. Lambert 1958, GSMNP, unpublished report).
 3. *Upper Porter's Creek*, Greenbriar Cove area, GSMNP, Tennessee. The primary forest site is located on a southwest-facing slope at 1000 m elevation along Porter's Creek. The secondary forest site is located on Sweet Ridge, at one thousand meters elevation, on the eastern bank of the Little River near Elkmont, GSMNP; it was established after 1926 (Lambert report).
 4. *Ramsey Cascade*, Greenbriar Cove area, GSMNP, Tennessee. A primary forest on a north-facing slope at 950 m elevation, this may be one of the least anthropogenically disturbed areas in the entire park (S. P. Bratton, personal communication), and the stand falls within the region described by Pyle (1986) as "high in virgin forest attributes." The secondary forest site is located at Timber Ridge, at 950 m, on the Middle Prong of the Little River. After clear cutting in the 1930s, the forest began to re-grow in 1939 (Lambert report).
 5. *Sosebee Cove Scenic Area*, Union County, Georgia. A primary forest of only 10 ha, the stand was "sanitized" in the 1950s by removal of snags and downed or poorly-formed trees (U.S. Forest Service records, Blairsville, Georgia). The secondary forest site is immediately adjacent to the primary forest and was established after 1903 (U.S. Forest Service, unpublished data).
 6. *Lilley Cornett Woods*, Letcher County, Kentucky. This site is located in the eastern portion of the Cumberland Plateau in the center of the mixed-mesophytic forest described by Braun (1950). The primary forest site, Big Everidge Hollow, 52 ha, is described as "near-virgin," with some removal of dead trees and grazing of cattle but without logging of live trees (Martin 1975). An adjacent cove, Pollbranch Hollow, 89 ha, was harvested in 1945 (Muller 1982).
 7. *Walker Cove*, Buncombe County, North Carolina.

This is an upper cove site at 1300 m with numerous large sugar maples (*Acer saccharum*) and some buckeyes (*Aesculus octandra*). The date of clear cutting of the adjacent second-growth site was 1932 (U.S. Forest Service, unpublished data). This date was confirmed by coring a sugar maple of about 55 years of age.

8. *Ramp Cove*, Townes County, Georgia. This is also an upper cove (1000 m) with large, old-growth buckeyes; it is named for its population of ramps (*Allium tricoccum*). The second-growth site in Dis-mal Cove became reestablished during 1915–22 (Brasstown Ranger District, U.S.D.A./F.S., unpublished data).
9. *Thumpin' Dick Cove*, University of the South, Sewanee, Franklin County, Tennessee. At 460–500 m elevation, this 40 ha cove is located on the western slope of the Cumberland Plateau (Cameron & MacCrary 1967). There is no evidence of logging, and the only apparent disturbance is a dirt road constructed through the forest in 1965 (McGee 1986). The secondary site, Bennett Cove, appears, based on tree diameters, to be a two-aged stand with cutting around 1920 and 1980. Since we were unable to determine the chronology of exploitation, we excluded this site from analyses involving time.

Sampling Methods

Primary and matching secondary sites (100 m × 100 m, except Upper Porter's Creek, which was 100 m × 50 m) were sampled within thirty hours of each other at each location. We used random samples consisting of 10 to 24 one-m² quadrats in each of the primary and secondary sites, based on the size of the sample area (Table 1). We also avoided sampling in areas with *Rhododendron maximum* understories, as they have little groundcover and verge on the impenetrable. A modification of the Daubenmire cover-scale that separates the 0%–5% cover class into 0%–1% and 1%–5% cover classes (Bailey & Poulton 1968) was used to estimate cover for each species within the quadrats. We excluded woody shrubs from our cover measurements because many woody species still had only bare stems at the time of sampling.

Ages of secondary succession sites ranged from 45 to 87 years. We used number of species per 1 m² plot as an index of the species richness at each site, and total herbaceous cover as an index of abundance.

Analysis

Cover and number of species per quadrat for each pair of matching sites were compared using one-tailed, unpaired *t*-tests. We plotted mean cover and species rich-

Table 1. Means and standard errors for species richness of primary and matching secondary sites.

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

* See text for details.

ness per quadrat against stand age of the secondary sites in an effort to detect any trends toward primary forest values. When comparing average cover and species-richness values, we used one-tailed paired *t*-tests.

The second-growth cove sites occurred at different latitudes, elevations, exposures, and slopes, so that the spring flowering season occurred earlier at some sites than at others. Earlier-flowering sites might appear more diverse than later-flowering sites sampled at the same time. Similarly, sites measured late in the season would appear to have greater cover values than sites sampled earlier, before full emergence of leaves. To adjust for these problems, we developed a similarity ratio where the cover and species-richness values for each second-growth site were divided by the matching values for the corresponding primary site.

Results

Mean species richness in primary forest ranged from 9.0 to 14.5 species per m², all significantly greater than in secondary sites with a range of 2.5–8.75 species per m² (Table 1). The average in primary forest was 10.9 species per m², and in secondary forest 6.6 species per m² ($P = 0.0011$, $DF = 8$, one-tailed paired *t*-test). Total cover values in primary forest ranged from 22.5% to 87%, whereas in secondary forests cover ranged from 10.5% to 42.5% (Table 2). Average cover in primary forest was 53% but only 21% in secondary sites ($P = 0.0001$; $DF = 8$; one-tailed paired *t*-test). Areas of extensive cover in secondary forests tended to be restricted to more mesic sites. Secondary forest also appeared to have more woody brush than primary sites.

We found a negative, but not significant relationship ($r^2 = 0.314$; $p = 0.148$) between the age of secondary forest stands and total herbaceous cover. In part, this was influenced by the high cover value of the youngest second-growth stand, Pollbranch Hollow, the match for Lilley Cornett Woods, which was measured late in the growing season. Species richness ($r^2 = 0.009$) and the ratios for cover ($r^2 = 0.013$) and richness ($r^2 = 0.002$)

showed no trend toward recovery with age. These data provide no support at all for the hypothesis that cover and species richness of herbaceous communities in secondary forests increase with age.

Discussion

Our results suggest that even 50 to 85 years following deforestation, succession of herbaceous understory plants in secondary mixed-mesophytic forests of the southern Appalachian Mountains resulted in only half the species richness and one-third the total cover measured in primary forests. Neither community characteristic showed any trend toward recovery with age; if anything, both richness and cover appeared to be decreasing. Such decreases might be caused by the gradual loss of early-succession herbs as the tree canopy closes, reducing available light (Horn 1974).

While our data are sufficient to discount any rapid, isotonic return of secondary herbaceous communities to primary-like conditions, the period of successional time sampled (up to 87 years after perturbation) may simply be too short to distinguish between three longer term scenarios.

Table 2. Means and standard errors for cover of primary and matching secondary sites.*

	Primary	Secondary	P
Thumpin' Dick Cove	38.0 ± 3.2	10.5 ± 1.7	<0.0001
Lilley Cornett	66.6 ± 3.8	42.5 ± 2.9	<0.0001
Ramsay Cascade	66.0 ± 3.9	23.0 ± 3.1	<0.0001
Kilmer Memorial	53.0 ± 4.2	15.7 ± 2.6	<0.0001
Walker Cove	42.5 ± 3.5	12.25 ± 3.5	<0.0001
Porter's Flat	87.0 ± 1.9	27.6 ± 5.0	<0.0001
Upper Porter's Creek	62.0 ± 7.8	21.5 ± 7.7	0.0008
Ramp Cove	42.5 ± 2.9	21.3 ± 2.4	<0.0001
Sosebee Cove	22.5 ± 1.9	11.7 ± 1.2	<0.0001

* Sites are arranged by increasing age of the secondary sites (Table 1).

First, the rate of recovery may depend more on the type and severity of initial disturbance and on the ecological characteristics of each site than on time since disturbance. Our nine sites, despite all being in mixed mesophytic forest, may simply have too disparate histories to allow analysis of temporal trends.

Second, herbaceous cover and species richness may continue to decline with time until trees become large and old enough to die, fall, and decay. The resulting pit and mound micro-topography of fallen tree trunks and bare soil would provide a continual source of unvegetated areas for colonization. Gaps and pit and mound effects maintain herb diversity in primary forest (Struik & Curtis 1962; Falinski 1978; Beatty 1984; Moore & Vankat 1986); they may also initiate it. This pattern would be similar to that already proposed for trees in secondary-succession forests (Bormann & Likens 1979; Peet & Christensen 1980) only on a much longer time scale: an initial increase in species richness and cover during early succession, a decrease during mid-succession, followed by an increase once again during late succession to a mature secondary equilibrium.

Finally, there is the possibility that secondary herbaceous communities in mature secondary Appalachian forests will never return to primary conditions. This appears to be the case in British mature secondary woodlands originating as early as 1600 B.P. (Peterken & Game 1984). The original Appalachian forests may have become established under cooler and moister conditions than occur at present (Delcourt & Delcourt 1987). In addition, conditions during future climate change, even several centuries into the future, might become sufficiently unfavorable to prevent complete secondary succession following present-day clear cutting (Solomon 1986).

Conclusion

Whatever the long term dynamics of herbaceous understory communities in mixed-mesophytic forests following logging or other massive disturbances, the data presented here strongly suggest that recovery requires at least several centuries, longer than the present logging cycles of 40–150 years for Appalachian cove hardwoods. Management of fully-functioning forest herbaceous communities to maintain biological diversity as mandated by the 1976 National Forest Management Act may require greatly lengthened tree harvest cycles, extraction methods less damaging to herbs, intensive management and planting of herbaceous species to speed up secondary succession, and the maintenance of sufficient primary forest to sustain intact herbaceous communities and to serve as sources for recolonization. Research is needed to address the relative ecological and economic efficiencies of these three strategies.

Acknowledgments

This study benefited from support by the University of Georgia Research Fund, the Seatuck Foundation, and the Cooperative Unit of the National Park Service at the University of Georgia. Permission to work in the study areas was granted by Eastern Kentucky University, the U.S. Park Service, and the U.S. Forest Service. We thank D. Berg, M. Botzge, B. Dahl, F. Finley, W. H. Martin, and R. Watts for assistance with logistics. S. Bratton, F. Golley, H. Horn, W. H. Martin, and D. Waller provided valuable discussion and encouragement. This is Contribution 14 from Lilley Cornett Woods, Appalachian Ecological Research Station, Eastern Kentucky University, Richmond, Kentucky.

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