

Herb and shrub dynamics in a mature oak forest: a thirty-year study

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DAVISON, S.E., and R.T.T. FORMAN (Dept. Botany, Rutgers Univ., New Brunswick, NJ 08903). Herb and shrub dynamics in a mature oak forest: a thirty-year study. *Bull. Torrey Bot. Club* 109: 64-73. 1982—Cover and frequency of forest herbs and shrubs were measured in permanent plots of a mature mixed-oak woods (Hutcheson Memorial Forest, New Jersey). Plots previously measured in 1950 and 1969 were remeasured in 1979. During this 30-year period, herb layer cover increased seven fold with all predominant species increasing in cover and frequency. Meanwhile herb species diversity declined, with rare herbs decreasing or disappearing. In contrast, shrub layer cover remained about constant, and shrub diversity increased. A major increase in vine cover occurred in both the herb and shrub layers. These changes correlate with an increase in understory light intensity during the 30-year period. Therefore, herb and shrub layer changes are dramatic in this mature uncut forest, indicating that relatively stable or climax communities may have highly dynamic subcommunities.

Key words: Hutcheson Memorial Forest; oak forest; climax community; shrub layer; herb layer.

Long-term vegetational studies have been useful in understanding tree canopy dominants and successional trends in many forest types (Stearns 1949; Monk 1961; Collins 1962; Reiners and Reiners 1965; Olson 1965; Stephens and Waggoner 1970; Sulser 1971; Henry and Swan 1974; Christensen 1977). Forest understory species such as shrubs and herbs, have received little attention in long-term studies.

The only long-term study on a forest herb community known to us is of an uncut *Fagus-Acer* forest in southern Michigan (Brewer 1980). Samples taken over 55 years in the same general area within the forest showed a decline in abundance of a number of herb species and an increase in a few of the abundant species. Decreased light was considered the major cause and it was concluded that the forest might be ap-

proaching a steady state in herbaceous composition, with a rather low species diversity. A 30-year study of orchids in a partly-wooded meadow found large population changes during a period of varying shade, grazing, trampling and water table level (Tamm 1972). Other herb layer studies are short-term; for example, herb layer productivity has been measured in deciduous forests (Siccama *et al.* 1970; Bazzaz and Bliss 1971; Puszkas *et al.* 1972) and environmental factors controlling herb distribution within forests determined (Reid 1964; Anderson *et al.* 1969, Bratton 1976a, 1976b; Falinski 1978; Maguire 1979). The distribution and interspecific associations among perennial forest herb patches have been analyzed in several forest types (Whitford 1949; Bray 1956; McIntosh 1962; Struick and Curtis 1962; Smith and Cottam 1967; Maguire 1979). Whitford hypothesized that the degree of contagiousness (clumping) of perennial herbs decreased with stand age, resulting in mature stands exhibiting the most uniform herb distribution.

Shrub dynamics have received less attention than herbs. Shrub biomass and density increase with more light availability in hardwood forests (Keever 1953; Woods and Shanks 1959; Good and Good 1972; Crawford 1976). Gysel (1951) found an increase in pioneer shrubs and vines in forest

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Received for publication May 18, 1981.

gaps in southern Michigan. Similarly, pioneer shrubs (*Rubus* spp. and *Rosa* spp.) replaced characteristic understory shrubs in some New Jersey deciduous forest gaps (Ehrenfeld 1980).

Herbs and shrubs, in turn, influence future tree canopy composition. Wardle (1959) and Maguire (1979) demonstrated a direct effect of herb cover on tree seedling establishment. Slezak (1976) and Siccama *et al.* (1976) showed the ability of vines to alter community characteristics. Auclair and Cottam (1971) found no increase in seedling density in forest sites with higher light intensity, and attributed this to higher shrub density.

Long-term studies provide the time dimension to aid in interpreting the types of spatial differences described above. The William L. Hutcheson Memorial Forest (HMF) in New Jersey is an especially appropriate woods for long-term studies because of the available historical records and its protection by Rutgers University.

The stability, or climax status, of a forest is commonly measured by the relative abundances of trees of varying age. But would one expect the herb and shrub layer communities of a forest to be stable if the tree populations are changing little or slowly? We would like to examine this using HMF, a mature uncut mixed-oak woods.

The two primary objectives, therefore, are to (1) determine whether herb and shrub layer community characteristics change significantly in a 30-year period in the old woods, and (2) determine whether there are additional patterns of change in species composition for herbs and shrubs, which in turn may be responsible for any community patterns observed.

Methods. The vegetation of the William L. Hutcheson Memorial Forest in East Millstone, New Jersey, USA is well documented (Bard 1952; Buell 1957; Monk 1961; Frei and Fairbrothers 1963; Sulser 1971; Forman and Elfstrom 1975). The dominant overstory trees are *Quercus alba* (white oak), *Q. borealis* (red oak), *Q. velutina* (black oak), *Carya ovalis* (pignut hickory) and *C. ovata* (shagbark hickory).

Cornus florida (flowering dogwood) is the principal understory tree. *Viburnum acerifolium* (maple-leaved viburnum) is the dominant shrub in the well-developed shrub layer. The herb layer is the most diverse layer, and in spring is dominated by *Podophyllum peltatum* (mayapple).

The forest is uncut. Yet human disturbance in the form of regional air pollution, introduction of non-native species, and surrounding farmland has had diffuse effects. There is much evidence of natural disturbance, including fire in the seventeenth century (Buell *et al.* 1954), hurricanes in the 1950's and strong windstorms resulting in wind-throw and wind snaps (Reiners and Reiners 1965), drought in the 1950's and 1960's (Small 1961), and caterpillar outbreaks (Moulding 1977). Most of these factors continue to influence vegetation processes at HMF.

Hutcheson Memorial Forest is a 26-hectare forest patch in a matrix of agricultural fields, old fields and woodlots on the Piedmont of New Jersey. Annual precipitation averages approximately 112 cm and is distributed fairly evenly throughout the year (Biel 1958). Occasional summer droughts have been recorded (Small 1961). The average annual temperature is 11.7 C, with the mean monthly temperature ranging from 0.0 C in January to 24.0 C in July (United States Weather Bureau 1959). The silty-loam soils have developed from the underlying Triassic red shale of the Brunswick formation. The soils of the study area are well drained (Ugolini 1964) with a thin, but heterogeneous and nutrient-rich, detritus layer (Lang and Forman 1978).

In 1950, permanent quadrats were established to study vegetational change in the upland forest. In 1969, these quadrats were relocated as precisely as possible using the notebook and aid of the original researchers (Murray Buell, Helen Buell and John Small), and sampled according to the methods prescribed in 1950 (Sulser 1971). In 1979 we resampled these quadrats to determine the 30-year patterns. Minor discrepancies in the data indicate that several quadrats were not relocated in the exact spot for all 3 years. While the locations of a few quadrats appear to have varied by up

to several decimeters or meters, the overall area sampled in 1969 and 1979 is representative of the original area designated in 1950.

The quadrats were set up in the following manner: twenty-five 10 × 10 m quadrats were located on alternating sides of four compass lines, and spaced 10 m apart. These quadrats were for tree sampling (Davison 1980). Within each quadrat, four 0.5 × 2 m subplots (100 total) were located at each corner. The herb layer, which consisted of all herbaceous species and decumbent vines was sampled in the 100 subplots. Vines were considered decumbent if growing on the ground or on herbaceous species; vines were classified as climbing if growing on shrubs or trees. Percent cover was estimated for each species as the amount of ground surface covered by leaves and stems. The shrub layer was sampled using the line intercept method (Canfield 1941) along a 20 m line running diagonally through two opposite corners of each quadrat. The shrub layer consisted of all shrub species (any woody, multi-stemmed species) and climbing vines at any height. Cover of the shrub layer was estimated as the length along the line which was covered by leaves, stems and space within the outline of shrubs. Percent cover for each species was expressed as cover in decimeters over the total length of the 25 lines (5000 dm). Frequency data were calculated for all species in the herb and shrub layers.

Light readings were taken on a 100 m line which was established along part of a compass line in 1950. Light was measured in foot-candles with a Weston light meter (Model 756) at one-meter intervals along this line. Readings were taken at 15 cm and 1.8 m above the forest floor, and were restricted to clear, sunny days between 11:00 a.m. and 1:00 p.m. Full sunlight was calculated by averaging ten readings taken in open fields adjacent to the woods before and after each set of forest readings. The 100 readings for 15 cm and 1.8 m were averaged and divided by the illuminance of full sunlight. Thus light reaching 15 cm and 1.8 m above the forest floor was expressed as the percentage of full sunlight for that

particular day. Readings were taken on 14 days from mid-April to mid-November in 1950, 1969 and 1979.

Statistical significance ($\alpha = 0.05$) for totals and predominant species was calculated using one-way analysis of variance (ANOVA), and Fisher's Least Significant Difference (LSD) (Ott 1977) to determine which years were responsible for significant changes noted.

Vegetation sampling was initiated and completed in June in all three study years. Voucher specimens are deposited in the Chrysler Herbarium at Rutgers University. Nomenclature follows Gleason (1968) except where otherwise noted.

Results. Total cover of the shrub layer increased slightly, but nonsignificantly, from 45% in 1950 to 51% in 1969 and 1979 (Fig. 1). In contrast, the number of species in the shrub layer doubled in the 30-year period. Seven species were recorded in 1950 (Shannon-Wiener diversity index $H' = 0.06$), which increased to 11 in 1969 ($H' = 0.51$) and 14 in 1979 ($H' = 0.71$).

The most common shrub, *Viburnum acerifolium* (maple-leaved viburnum), though widely distributed throughout the forest based on the frequency data, decreased in cover from 43% in 1950 to 24% in 1979 (Table 1). In contrast, the shrubs, *Lindera benzoin* (spicebush) and *Rubus* spp., increased significantly in the past decade. Total vine cover also increased significantly in the shrub layer since 1950. In 1969 *Lonicera japonica* (Japanese honeysuckle) showed significantly greater cover than in 1950 or 1979. *Vitis aestivalis* (grape) and *Lindera*, two important species in the shrub layer today, were not recorded in the 1950 survey (Table 1). The shrub-layer species composition thus has been dynamic in the 30 years.

An increasing prevalence of shade-intolerant shrubs, such as *Rubus*, and woody vines is the most marked change. In 1950 vines only comprised 0.4% of the total shrub cover; this increased to 19.6% in 1969 and tapered to 11.5% in 1979 (Table 1). This overall increase in vines represents a distinctive shift in life-form in the shrub layer. Unoccupied space in the shrub layer

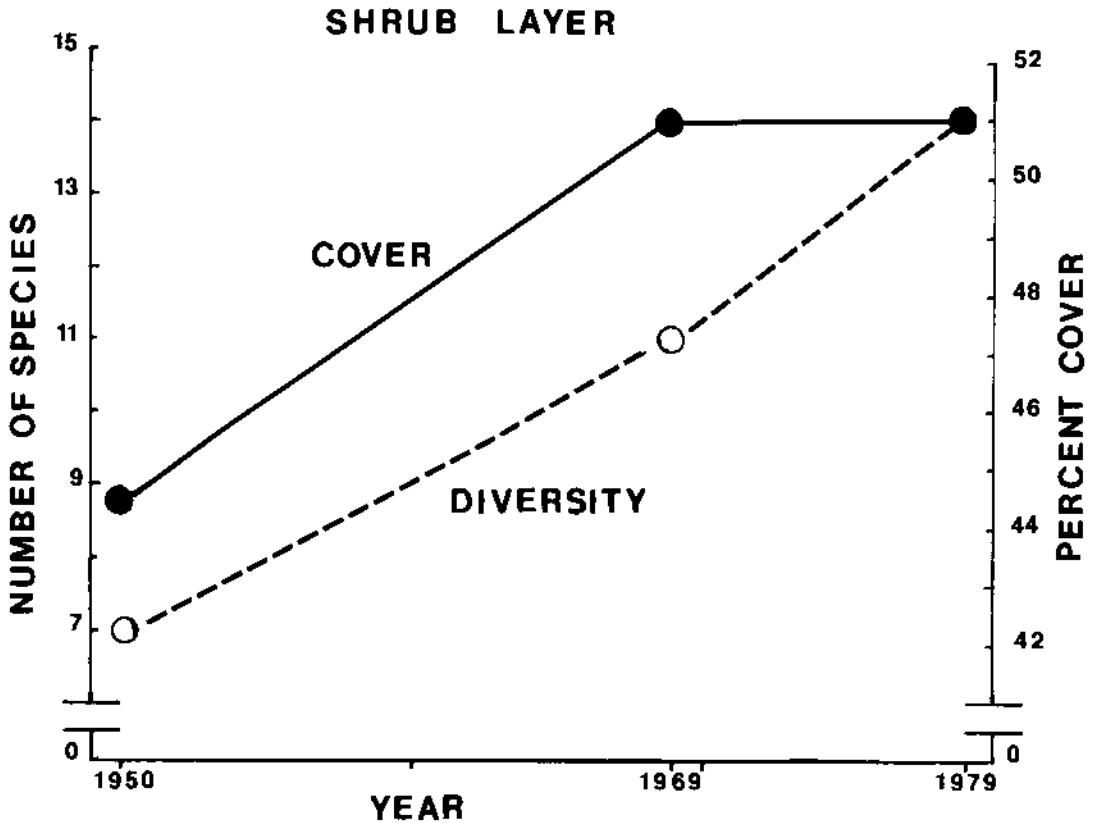


Fig. 1. Percent cover and species diversity in the shrub layer. The total number of species and the average percent cover in twenty-five 20 m line intercepts at Hutcheson Memorial Forest, New Jersey is plotted.

remained remarkably stable. An increase in shrub layer overlap is hypothesized, resulting largely from a significant increase in vines. In 1969 *Lonicera japonica* presumably was responsible for most of the overlap (Table 1), while in 1979, canopies of *Vitis* on vegetation were responsible for much of the shrub layer overlap. In short, the structure of the shrub layer has also been dynamic in the 30-year period.

In the herb layer the total number of species has declined from 33 species in 1950 ($H' = 0.76$) to 24 in 1969 ($H' = 0.66$) and 26 in 1979 ($H' = 0.81$) (Fig. 2). In contrast, herb layer cover rose dramatically from 8% to 60%.

These community changes in the herb layer differ markedly from those in the shrub layer during the three decades. In the shrub layer, cover remained about constant while diversity doubled. Yet in the herb

layer, cover rose sharply while diversity dropped.

The herb species composition pattern aids in interpretation. *Podophyllum peltatum* (mayapple) and *Circaea quadrisculcata* (enchanters nightshade) both increased significantly in cover (Table 2). *Podophyllum* cover increased seven-fold, from 2.5% (1950) to 18.7% (1979), while *Circaea* cover increased five-fold, from 1.1% (1950) to 5.8% (1979). The frequency for both species has doubled since 1950 (Table 2).

Vine species were counted as part of the herb layer if they were decumbent, and were usually encountered in this layer as runners or seedlings. All vine species increased in cover (Table 2). *Lonicera* and *Parthenocissus* increased markedly during the 30-year period.

Thirteen species have disappeared from the herb layer since 1950 (Table 2). Many

Table 1. Shrub layer cover and frequency for 1950, 1969 and 1979. Percent cover is expressed as the total cover of a species in decimeters divided by the total length (5000 dm) of the lines sampled. Frequency is on the basis of twenty-five (20 m) lines. Tr = trace (<0.05% cover). V = vine; all other species are shrubs.

Species	Percent Cover			Frequency		
	1950	1969	1979	1950	1969	1979
<i>Viburnum acerifolium</i>	43.4	27.2	24.8	25	24	25
<i>Lonicera japonica</i> V	0.3	17.8	5.2	1	17	15
<i>Lindera benzoin</i>	0.0	2.0	5.8	0	7	15
<i>Rubus</i> spp.	0.1	0.1	6.4	1	1	11
<i>Vitis aestivalis</i> V	0.0	0.1	4.9	0	1	10
<i>Rosa multiflora</i>	Tr	0.5	1.0	1	1	10
<i>Viburnum prunifolium</i>	0.6	1.1	1.0	4	5	6
<i>Parthenocissus quinquefolia</i> V	0.1	1.1	1.3	1	12	9
<i>Toxicodendron radicans</i> * V	Tr	0.6	Tr	1	5	1
<i>Viburnum dentatum</i>	0.0	0.6	0.1	0	3	3
<i>Lonicera maackii</i> **	0.0	0.0	0.5	0	0	1
<i>Sambucus canadensis</i>	0.0	0.2	0.1	0	2	2
<i>Berberis thunbergii</i>	0.0	0.0	Tr	0	0	1
<i>Ligustrum vulgare</i>	0.0	0.0	Tr	0	0	1
Unoccupied space	45.6	47.4	44.5	25	25	24
Total vines	0.4	19.6	11.5	—	—	—
Total shrub species	44.2	31.7	39.9	—	—	—

* Nomenclature follows Gillis 1971.

** Nomenclature follows Gleason and Cronquist 1963.

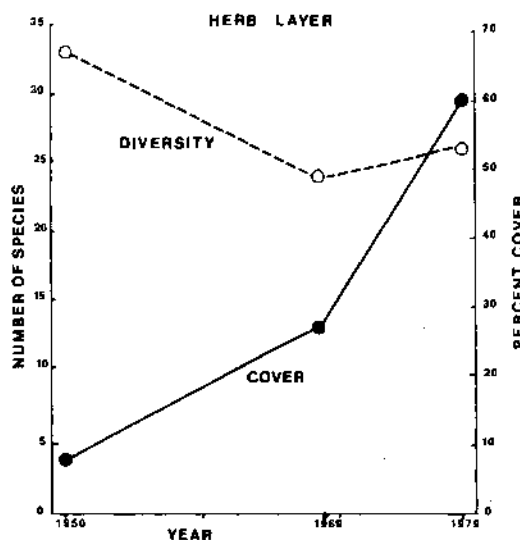


Fig. 2. Percent cover and species diversity in the herb layer. The total number of species and the average percent cover in one hundred 2×0.5 m quadrats at Hutcheson Memorial Forest, New Jersey is plotted.

of these species are rare in the forest, or at least were rare in the well-drained portion of the forest in 1962 when the flora was studied (Frei and Fairbrothers 1963). Since 1969, seven new herb species have appeared. Several of these species are shade-intolerant pioneer species (*Fragaria virginiana* and *Solidago* sp.)

Podophyllum has long been recognized as the dominant herb in the forest (Buell 1957; Monk 1957, 1961; Sulser 1971). Recently, however, *Lonicera* has become increasingly prominent (Slezak 1976). Since observations in the forest suggested a negative relationship between these two species, i.e., where *Podophyllum* occurred *Lonicera* did not and vice versa, a correlation coefficient (Sokal and Rohlf 1969) was used to compare cover of *Podophyllum* and *Lonicera* for all three study years. In addition, a correlation coefficient was calculated between *Podophyllum* and the total cover of other species in the herb layer, and between *Lonicera* and the total cover of other herb layer species. No significant correlations were found between any of the 3 groups in 1950 or 1969. Similarly, in 1979, *Lonicera* did not show a significant negative correlation with other species of the

Table 2. Herb layer cover and frequency for 1950, 1969 and 1979. Percent cover and frequency are on the basis of one hundred 2 × 0.5 m plots. Tr = trace (<0.05% cover). V = vine; all other species are herbaceous.

Species	Percent Cover			Frequency		
	1950	1969	1979	1950	1969	1979
<i>Lonicera japonica</i> V	1.8	13.0	18.1	8	44	52
<i>Podophyllum peltatum</i>	2.5	8.6	18.7	39	73	84
<i>Parthenocissus quinquefolia</i> V	0.2	1.0	9.0	13	28	75
<i>Circaea quadrisculcata</i>	1.1	1.2	5.8	19	25	54
<i>Smilacina racemosa</i>	0.6	0.8	1.4	17	16	27
<i>Pilea pumila</i>	Tr	1.3	1.1	1	6	12
<i>Impatiens biflora</i>	0.5	Tr	1.5	7	1	18
<i>Polygonatum biflorum</i>	0.3	0.4	0.9	9	11	15
<i>Arisaema triphyllum</i>	0.3	0.8	0.5	15	8	10
<i>Toxicodendron radicans</i> V	0.3	0.2	1.0	27	6	45
<i>Phytolacca americana</i>	0.3	0.2	0.5	27	6	25
<i>Vitis aestivalis</i> V	Tr	Tr	0.9	1	1	62
Other species*	0.9	0.2	1.0	—	—	—
Total vines	2.3	14.2	28.9	—	—	—
Total herbaceous species	12.4	13.8	30.6	—	—	—

* C = cover and F = frequency for 1950, 1969 and 1979 respectively. *Geranium maculatum* (C = 0.2/Tr/Tr; F = 7/1/1); *Carex abscondita* (C = Tr/Tr/0.2; F = 2/1/4); *Galium triflorum* (C = Tr/Tr/0.1; F = 1/1/1); *Viola sagittata* (C = Tr/0.1/Tr; F = 2/4/1); *Anemone thalictroides* (C = Tr/0.1/Tr; F = 3/1/1); *Smilax rotundifolia* V (C = 0.1/Tr/Tr; F = 5/1/1); *Oxalis stricta* (C = Tr/Tr/Tr; F = 2/3/3); *Botrychium virginianum* (C = Tr/Tr/0; F = 2/1/0); *Galium circaeans* (C = 0.2/Tr/0; F = 12/1/0); *Mitchella repens* (C = Tr/Tr/0; F = 2/1/0); *Ranunculus abortivus* (C = 0.1/0/0; F = 2/0/0); *Oakesia (Uvularia) sessilifolia* (C = 0.1/0/0; F = 5/0/0); *Amphicarpa bracteata* (C = 0.1/0/0; F = 1/0/0); *Sanicula trifoliata* (C = 0.1/0/0; F = 4/0/0); *Uvularia perfoliata* (C = Tr/0/0; F = 1/0/0); *Geum canadense* (C = Tr/0/0; F = 1/0/0); *Symplocarpus foetidus* (C = Tr/0/0; F = 2/0/0); *Galium aparine* (C = Tr/0/0; F = 1/0/0); *Berberis thunbergii* (C = Tr/0/0; F = 1/0/0); *Asclepias quadrifolia* (C = Tr/0/0; F = 1/0/0); *Maianthemum canadense* (C = Tr/0/0.1; F = 3/0/1); *Boehmeria cylindrica* (C = 0/Tr/0; F = 0/1/0); *Fragaria virginiana* (C = 0/Tr/Tr; F = 0/1/1); *Festuca obtusa* (C = 0/0/0.1; F = 0/0/1); *Eupatorium rugosum* (C = 0/0/0.5; F = 0/0/6); *Solidago* sp. (C = 0/0/Tr; F = 0/0/2); *Polygonum caespitosum* (C = 0/0/Tr; F = 0/0/1); *Osmorrhiza longistylus* (C = 0/0/Tr; F = 0/0/1).

herb layer summed. However, in 1979 a significant negative correlation was found between *Podophyllum* cover and *Lonicera* cover ($r = -0.42$, $P < .01$), and between *Podophyllum* cover and total cover of other herb-layer species ($r = -0.47$, $P < .01$).

The light measurements show that light reaching 1.8 m and 15 cm above the ground has increased markedly since 1950. The summer (June-August) average percent light penetration during the 30-year period is as follows:

	1950	1969	1979
15 cm	3.7%	1.1%	13.2%
1.8 m	3.4%	1.8%	16.2%

Thus several striking changes in community structure and species composition of the forest understory correlate with an overall increase in light. In the shrub layer, total cover remained about constant, species diversity increased, cover of the predominant species dropped, and vines

increased. Yet in the herb layer, cover increased, species diversity dropped, the predominant species spread widely, and vines again increased.

Discussion. The dynamic changes in the shrub and herb layers at HMF during this 30-year study indicate that they are not stable components of this uncut mature forest. The use of the climax community concept for HMF has been troublesome based on the tree community (Bard 1952; Monk 1961; Sulser 1971; Lang and Forman 1978), and now it becomes particularly difficult to apply to the shrub and herb communities of the forest.

Three types of factors should be examined as possible causes of these herb and shrub layer dynamics: (1) change in the light regime resulting from changes in canopy structure, particularly gaps; (2) change in the species composition and abundance of the canopy trees; and (3)

other environmental factors such as changes in fire frequency or human activities. A causative factor must operate at the scale of three decades. We have seen above that the first factor, light, has indeed changed markedly over 30 years.

Davison (1980) reported no significant change in total tree basal area over the 30-year period in the same area as the shrub and herb samples. The studies by Sulser (1971) and Forman and Elfstrom (1975) indicating very slow canopy species change tend to support this result. Davison also found a significant drop in total tree density, and qualitative observations indicate a plethora of fallen major limbs of canopy trees in 1979. (The cause of this tree and limb mortality is unknown, though wind, canker worms, gypsy moths and air pollutants may all play a role). These results are consistent with the conclusion that herb and shrub changes result from increased light due to canopy structure changes, not changes in canopy species composition. The third possibility, other environmental factors, is discussed below.

In a 20-year record of understory changes in a hemlock-hardwood virgin forest in Pennsylvania, Hough (1965) found a pronounced decrease in understory vegetation, chiefly as a result of deer browsing. Since the reverse trend, a vegetation increase, was found at HMF, the small deer population here does not appear to play a major role in the understory dynamics. Buell *et al.* (1954) reported evidence of fire in the forest in precolonial times, but since fires have been absent in the past 30 years (and much longer), it cannot be responsible for the observed changes. It should, however, be noted that though fire is not directly related to the patterns of change observed, indirectly a decrease in fire frequency this century in New Jersey may play a major role in the type of forest understory present today (Buell *et al.* 1954; Forman and Elfstrom 1975; Forman and Boerner 1981). Forman and Elfstrom (1975) found HMF to be broadly representative of the forests on the New Jersey Piedmont, but found the percent understory species, percent shrub layer species, and percent non-native species to be higher at HMF. *Lonicera*, a

non-native species, has contributed substantially to the observed changes (Tables 1 and 2).

The most likely cause for the observed changes in the understory is the high frequency of canopy gaps in the forest (Sulser 1971; Forman and Elfstrom 1975; Slezak 1976). Both herbs and shrubs respond to the liberation of resources such as light and moisture in canopy gaps. Minckler and Woerheid (1965) found soil moisture was higher beneath gaps than beneath a closed canopy. *Lindera*, *Pilea pumila* (clearweed), *Impatiens bilflora* (touch-me not) and *Circaea* are examples of species that would probably flourish under increased moisture conditions (Monk 1957; Sulser 1971). Smith and Cottam (1967), McIntosh (1962) and Struick and Curtis (1962) using Cole's Index (Cole 1949) all found a positive association between *Circaea*, *Impatiens* and *Pilea*. This suggests the similar microenvironmental requirements of these species, and probable gap response.

Light is an important available resource in gaps. In 1950 gaps were scarce in this part of HMF (Helen Buell, pers. comm.); by 1969 gaps were present, even though average overall light intensity had dropped (Sulser 1971). During this 20-year period, shrub and herb cover did not increase significantly, while *Lonicera*, which is sensitive to gaps (Slezak 1976), increased sharply (Tables 1 and 2). Shade-intolerant species such as *Lonicera*, *Parthenocissus*, and *Vitis* (Gill and Healy 1974; Slezak 1976) have increased most likely because of canopy gaps. All three vines thrive in gaps in the forest and, in the case of *Vitis*, appear to help create gaps (Siccama *et al.* 1976). However, a study in Wisconsin woods showed no correlation between gross light conditions and the number of vines (as cited in Reid 1964). In an uncut white oak forest on Gardiners Island, New York, Hehre (1977) found vines such as *Smilax*, *Toxicodendron* and *Vitis* dominating the understory. Thus, dense vine cover may be a characteristic of mature uncut oak forests.

In the shrub layer (50% cover), the overlap caused by vines growing over other vegetation resulted in no appreciable de-

crease in unoccupied space (Table 1). Unoccupied space was not measured in the herb layer (60% cover), but since stratification was not pronounced, it is hypothesized that the increase in herb layer cover encroached on previously unoccupied space. The herb layer thus may limit the distribution of the shrub layer.

When compared with many other forests, the herb layer cover at HMF today is considerably greater. In hemlock-hardwood forests Maguire (1979) found the average total herb cover in a West Virginia mature forest to be 36.8%, and Siccama *et al.* (1970) found the herb cover in a younger New Hampshire forest to be 36%. This is higher than the cover found at HMF in 1950 and 1969, but lower than the 60% cover in 1979.

Podophyllum and *Lonicera* are currently the two predominant species of the herb layer. Competition most likely is responsible for the negative correlation found between these two species in 1979. They both are distributed throughout the forest, mainly by vegetative reproduction (Slezak 1976; Frye 1977), and suffer a minimum amount of herbivory in the forest. *Podophyllum* is reported to have a resin, podophyllotoxin, which has a cytotoxic action (E. L. Rice, pers. comm.; Frye 1977), and *Lonicera*, an introduced species, is known to have few pests in the United States (Slezak 1976), though in some areas is browsed by deer (Sheldon and Caisy 1974). Bratton (1974, 1975) showed several spring ephemerals in the Great Smoky Mountains National Park suffered predation but *Podophyllum* did not. At HMF, with increasing herb density, a negative correlation was found between *Podophyllum* and all other species in the herb layer, but not for *Lonicera* and all other species in the herb layer. If shading is the proximal cause of the negative correlation between *Podophyllum* and other herb-layer species, the lack of a significant negative correlation between *Lonicera* and other herb-layer species might indicate *Podophyllum* more effectively excludes light from the forest floor than *Lonicera*. Horn (1971) suggests that *Podophyllum* has a very effective monolayer structure which causes intense

shading beneath, and the production of podophyllotoxin mentioned above may be an allelopathic mechanism enhancing the competitive ability of the species.

The overall 30-year pattern of herb and shrub change at HMF contrasts sharply with the slight change at the Warren Woods, Michigan *Fagus-Acer* site (Brewer 1980). Decreased shade at HMF and increased shade at Warren Woods appears to be the major overall reason. However, with more light available, herb and shrub species interactions appear to play a greater role as the community changes.

Conclusions from such long-term studies must be tempered by the possible effects of year-to-year variations in climate and herbivory, or by possible regular periodicities with intervals much longer than three decades. Nevertheless, the concepts of climax or steady state appear of limited use when applied to these shrub and herb communities, since their destiny is so dependent upon change in the forest canopy.

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