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OVERSTOREY COMPOSITION AND AGE AS DETERMINANTS OF THE UNDERSTOREY FLORA OF WOODS OF CENTRAL NEW ENGLAND

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SUMMARY

(1) The vascular plant species composition of 190 woodland sites in central New England was analysed to determine the effects of overstorey composition and age on the understorey flora.

(2) Multiway contingency table analysis suggested there were significant differences in the understorey flora of primary (old-growth) versus secondary (old-field) woods. Differences in the flora of conifer versus broadleaved woods were less pronounced.

(3) A variety of factors, e.g. microclimatic conditions and the low seed production and poor colonizing ability of many species are probably responsible for the distinctive flora of central New England's primary woodlands.

INTRODUCTION

Henry David Thoreau (1864) once wrote of New England's woods, 'no one has yet described for me the difference between the wild forest which once occupied our oldest townships, and the tame one which I find there today. It is a difference which would be worth attending to. The civilized man not only clears the land permanently to a great extent, and cultivates open fields, but he tames and cultivates to a certain extent the forest itself.' Human history, site, and cover type are all factors ecologists have considered important in the determination of the understorey flora of woodland areas. The field layer reflects the microclimate, the soils, the slope, the aspect, and the topographic position of the site. Since Cajander's (1926) early work in Finland, foresters have utilized the herbaceous flora of woods as an indicator of the site's physical conditions and potential productivity. The herbaceous flora also epitomizes the direct influence of the overstorey species on the chemical and physical properties of the litter and the soil. Leaf litter, stemflow, and throughfall can alter the nutrient levels and pH of the forest floor, creating unique microhabitats for certain herbaceous species (Sydes & Grime 1981; Crozier & Boerner 1984). As Thoreau noted, the history or age of a wood can also have an important bearing on the composition of its herbaceous flora. In Europe, for instance, many woodland areas contain a unique suite of species that is indicative of the original forest, the 'Urwald', or the wildwood (Peterken 1974; Rackham 1980; Bunce 1982). Due to their poor colonizing ability, these species are limited to primary or 'ancient' woodland areas, i.e. areas that have been continuously wooded throughout the historical period or the last 300–400 years (Peterken 1981).

The history and character of central New England's woodlands are unique in several respects. Central New England represents a transition zone between the mixed conifer

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and hardwood forests of northern New England and the broadleaved forests of southern New England (Westveld *et al.* 1956). The presettlement forest contained a variety of deciduous species (*Quercus alba*, *Q. rubra*, *Castanea dentata*, *Acer saccharum*, *A. rubrum*, *Fagus grandifolia*, *Fraxinus americana*, *Betula lenta*, and *B. lutea*)* as well as an admixture of conifers (*Pinus strobus* and *Tsuga canadensis*) (Cline & Spurr 1942; Foster 1988). Large segments (up to 75%) of central New England's forest were cleared for agricultural purposes in the eighteenth and nineteenth centuries (McKinnon, Hyde & Cline 1935; Raup & Carlson 1941). Unable to compete economically with the more fertile, recently settled regions to the west, farmers abandoned much of New England's uplands in the mid-nineteenth to early twentieth centuries. Farm abandonment favoured the establishment of extensive forests of old-field white pine (*P. strobus*), birch and maple. Logging of much of the white pine at the turn of the century resulted in the formation of second- and third-growth hardwood forests of red oak, red maple, and hemlock (Spurr 1956a). Central New England today contains a mosaic of woodlands in various stages of recovery since the last human-imposed disturbance. Both the diversity of overstorey species and the variety of age-classes present suggest that central New England is an excellent area for determining the influence of overstorey composition and age on the understorey flora of eastern North America's woodlands.

Forest biologists have traditionally focused most of their attention on the use of herbaceous species as indicators of site or habitat conditions in New England's woodlands (Hazard 1937; Stanley 1938). This study compares the understorey flora of central New England's natural primary, i.e. old-growth, and secondary, i.e. old-field, woodlands as well as its coniferous and broadleaved woodlands. The analysis is based on data collected by the staff of the Harvard Forest on a series of old-field pine and hardwood sites in central New England (Griffith, Hartwell & Shaw 1930) and a number of old-growth forest sites distributed throughout the Pisgah Forest region (Branch, Daley & Lotti 1930; Griffith, Hartwell & Shaw 1930). The 2000-ha Pisgah Forest contained one of the last extensive remaining tracts of primeval or virgin forest in central New England in the 1920s. Much of it was subsequently damaged by cutting and the 1938 hurricane (Cline & Spurr 1942; Foster 1988).

STUDY AREA

The study was confined to northern Worcester County, Massachusetts and the adjacent portions of southern Cheshire County, New Hampshire (42°40′N, 72°20′W). The climate is of the humid continental, cool summer type. Approximately 100 cm of precipitation are evenly distributed throughout the year. The growing season averages 120 days (Kingsley 1985).

The area is dominated by a series of north–south trending hills, ridges, and valleys, 200–400 m above sea level. The substratum consists of medium- to course-textured Wisconsin till derived from schist, granite, and gneiss (Goodlett 1960; Foster 1987). Braun (1950) considered the area part of the New England section of the hemlock–white pine–northern hardwoods region.

METHODS

In the 1920s and 1930s the staff of the Harvard Forest established a series of 0·10–0·25 acre (0·04–0·10 ha) plots on over 240 different woodland sites. Approximately half of the

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* Nomenclature follows Fernald (1970).

plots were located in secondary woodlands in northern Worcester County, Massachusetts. The pine plots and the hardwood plots were part of a study on the effects of old-field white pine–mixed hardwood succession on soils (Griffith, Hartwell & Shaw 1930). Most of the hardwood plots originated after the cutting of the white pine. A few were hardwood stands from which the merchantable hardwoods had been selectively removed. The remaining primary woodland plots were part of an analysis of the soils, the vegetation and the history of the Pisgah Forest of neighbouring Cheshire County, New Hampshire (Branch, Daley & Lotti 1930; Griffith, Hartwell & Shaw 1930). The two study sites are similar with respect to topography, soils, climate and natural vegetation and have been the focus of several other comparative studies in the past (Fisher 1915; Griffith, Hartwell & Shaw 1930; Spurr 1956b).

In each of the plots the trees were tallied by species and dbh. Shrubs and herbs were recorded according to species and three classes of abundance: few, many and abundant. Notes were also taken on the origin and age of the stand and on site conditions, i.e. soil texture and drainage, topography, aspect and slope. Both the Branch, Daley & Lotti (1930) and the Griffith, Hartwell & Shaw (1930) studies were supervised by the same individuals (A. Cline, P. Gast and N. Hosley). This ensured uniformity of approach, coverage and identification.

Although much of the old-growth Pisgah Forest tract was destroyed in the 1938 hurricane, the records of the earlier studies were maintained at the Harvard Forest in Petersham, Massachusetts. The raw data of the Branch, Daley & Lotti (1930) study and the Griffith, Hartwell & Shaw (1930) study formed the basis of the present work. In order to eliminate the confounding effect of site conditions, the study was limited to plots which had been established on dry to moist loams on the uplands. Xeric sites with shallow soils or plots on wet, poorly drained soils were automatically excluded from consideration. Forty-six of the ninety-two suitable secondary woodland plots were dominated by white pine. The remaining fifty-two plots were in areas of mixed hardwoods (predominately *Quercus rubra*, *Betula lenta* and *Acer rubrum*). Although the plots ranged from 10 to 105 years in age, the majority of the pine as well as the hardwood plots fell into the 50–90 year age category. Of the ninety-two primary forest plots, fifty-nine were on sites dominated by white pine and hemlock, while thirty-three were on hardwood (*Acer–Betula–Fagus–Quercus*) sites. Dominance in both cases refers to stem counts of individuals in the overstorey, i.e. individuals with a dbh >25 cm (10″).

More than seventy species of herbs and shrubs were recorded in the earlier studies, many of which had a very sporadic occurrence. Species which occurred in fewer than 5% of the plots were automatically omitted from further consideration. Although the rarer or the more infrequent species have often been among the better indicators of primary woodlands in England (Peterken 1974; Peterken & Game 1984), they frequently are not very amenable to statistical analyses. In contingency table analysis, for instance, the rarer species are often subject to the problem of bias resulting from the large number of cells with small fitted values (Sokal & Rohlf 1981, p. 709).

Most of the abundance data of the species analysed in the present study fell into the ‘few’ or, less frequently, the ‘many’ category. Because simple presence and absence data are often the best indicator of a wood’s age and continuity (Rackham 1986), the abundance data of the herbs and the shrubs were ultimately converted to simple presence and absence values.

Multiway contingency table analysis was used to determine the effects of the overstorey and the age of the woodland on the herb and shrub flora. For each of the more common herb and shrub species, the available data were arranged in a three-way table, the three variables being overstorey type (T) (conifer versus broadleaved), age of the woodland (A) (primary, i.e. old growth, versus secondary, i.e. old field), and a response variable (P) (species present or absent). The number of sites or plots falling into each of the categories was tabulated. A value of 0·5 was added to each of the observed cell frequency or category values in order to eliminate the problem of sampling zeros (Everitt 1977).

Although it is applied to categorical data, multiway contingency table analysis in many ways mirrors the standard analysis of variance design. According to the log–linear model, the logarithm of a cell probability in a contingency table can be expressed as the sum of a number of effects in a format equivalent to that of the value of a cell mean in an analysis of variance design (Shaffer 1973). Main effects and interaction effects in the present study were tested individually for significance by constructing a series of models that embodied the hypothesized effects. Expected cell frequency values were determined iteratively according to the procedure outlined by Wilkinson (1986). The fit of the observed to the expected cell frequency values was then tested with the log likelihood ratio chi-square statistic. Starting with the most complex model in a nested sequence of models, parameters, i.e. effects and interactions, were deleted one by one until the log likelihood ratio chi-square value was significant. The model was rejected if the ratio exceeded the 5% significance value. Where several models provided a reasonable fit to the data, the rival models were compared by determining the difference between the two log likelihood ratio

TABLE 1. Percentage occurrence of more common understorey species in major woodland types. Values are percentages of sites or woods representing specific age and overstorey combination.

	Primary woodlands		Secondary woodlands	
Species	Conifer	Broadleaf	Conifer	Broadleaf
Acer pensylvanicum	32	73	0	0
Aralia nudicaulis	36	30	0	2
Aster acuminatus	5	36	0	36
Chimaphila umbellata	20	12	0	0
Dennstaedtia punctilobula	0	0	0	42
Dryopteris spinulosa	25	18	22	17
Epigaea repens	12	3	2	0
Gaultheria procumbens	92	48	26	29
Lycopodium clavatum	0	0	22	27
Lycopodium obscurum	2	0	9	13
Maianthemum canadense	2	0	41	12
Medeola virginiana	12	12	0	0
Mitchella repens	56	30	37	19
Polypodium virginianum	32	3	0	0
Polytrichum commune	0	0	17	8
Pteridium aquilinum	2	3	17	19
Pyrola sp., predominantly *elliptica* and *rotundifolia*	0	0	35	17
Rubus sp., predominantly *fragillaris*	0	0	36	38
Vaccinum angustifolium	39	24	39	23
Viburnum acerfolium	10	52	4	2
Viburnum alnifolium	76	48	2	0
Total no. of sites or woods analysed	59	33	46	52

chi-square values. The resulting difference statistic has an approximate chi-square distribution and was used to assess the change in goodness-of-fit that resulted from adding terms. Only a significant improvement in fit warranted the acceptance of the more complex model (Everitt 1977). For a more detailed account of the methodology and its use in the field of ecology, the reader should consult Fienberg (1970), Bishop, Fienberg & Holland (1975), Jenkins (1975), and Everitt (1977).

RESULTS

Relatively few species were confined *solely* to one overstorey type or age category (Table 1). Conversely, only the spinulose wood fern (*Dryopteris spinulosa*) showed a complete lack of association with either the age or type of woods. Neither the $P\times T$ nor the $P\times A$ model was required (Table 2). *Dryopteris spinulosa* was ubiquitous in all of the woods (Table 1). Most species demonstrated a quantifiable association or an affinity with specific types of woodlands (Table 2). They reached their highest frequency or abundance in either primary or secondary woodlands under either conifers or broadleaved species or various combinations thereof. These relationships are summarized in Table 3.

Table 2. Multiway contingency table analysis of the effects of overstorey type (T) and age of woodland (A) on the occurrence (P) of the more common understorey species. Numbers are likelihood ratio chi-square values showing fit of proposed model to observed data.

Model	$P\times A\times T$	$P\times A+P\times T+T\times A$	$P\times A+T\times A$	$P\times T+T\times A$	$P+T\times A$
(Interpretation)	(important interaction between age and type)	(both age and type are important)	(only age is important)	(only type is important)	(species is ubiquitous)
d.f.	0	1	2	2	3
Species					
Acer pensylvanicum	0·00	0·69*	13·98	68·29	83·00
Aralia nudicaulis	0·00	0·58	0·66*	39·02	40·56
Aster acuminatus	0·00	1·48	39·18	1·95*	7·53
Chimaphila umbellata	0·00	0·04	0·88*	18·25	20·68
Dennstaedtia punctilobula	0·00	1·95*	30·14	23·04	56·42
Dryopteris spinulosa	0·00	0·02	0·86	0·20	1·19*
Epigaea repens	0·00	0·00	2·49*	4·37	8·05
Gaultheria procumbens	0·00*	12·86	20·82	53·53	66·48
Lycopodium clavatum	0·00	0·02	0·42*	27·74	29·73
Lycopodium obscurum	0·00	0·34	0·62*	7·53	8·45
Maianthemum canadense	0·00	0·33*	11·49	32·19	37·67
Medeola virginiana	0·00	0·01	0·01*	12·17	12·40
Mitchella repens	0·00	0·06*	9·30	5·05	16·69
Polypodium virginianum	0·00	0·93*	11·90	22·97	38·02
Polytrichum commune	0·00	0·44	2·12*	13·82	14·34
Pteridium aquilinum	0·00	0·14	0·30*	12·73	13·66
Pyrola sp. predominantly *elliptica* and *rotundifolia*	0·00	0·48	3·92*	34·00	34·78
Rubus sp. predominantly *fragillaris*	0·00	0·04	0·22*	47·20	49·27
Vaccinium angustifolium	0·00	0·02	4·90	0·02*	5·10
Viburnum acerfolium	0·00*	5·73	18·94	31·66	38·69
Viburnum alnifolium	0·00	0·00*	7·77	100·29	113·62

* Indicates best fitting model.

TABLE 3. Results of multiway contingency table analysis showing relationship of understorey species to specific woodland types.

	Species showing affinity for:					
All woodlands (species is ubiquitous)	Type of woods		Age of woods		Both of age and type of woods	
	Conifer	Broadleaf	Primary	Secondary	Primary conifer	Primary broadleaf
Dryopteris spinulosa	*Vaccinium angustifolium*	*Aster acuminatus*	*Aralia nudicaulis*	*Lycopodium clavatum*	*Mitchella repens*	*Acer pensylvanicum*
			Chimaphila umbellata	*Lycopodium obscurum*	*Polypodium virginianum*	
			Epigaea repens	*Polytrichum commune*	*Viburnum alnifolium*	
			Medeola virginiana	*Pteridium aquilinum*	Secondary conifers	Secondary broadleaved
				Rubus fragillaris	*Maianthemum canadense*	*Dennstaedtia punctilobula*
					Conifers in primary, broadleaved in secondary woods: *Gaultheria procumbens*	
					Broadleaved in primary, conifers in secondary woods *Viburnum acerifolium*	

Cover type or overstorey influenced the occurrence of two species (Table 2). *Aster acuminatus* was largely limited to hardwood sites whereas *Vaccinium angustifolium* was more strongly associated with conifer sites (Tables 1 and 3). Age was a critical variable for approximately half of the species (Table 2). *Aralia nudicaulis*, *Chimaphila umbellata*, *Epigaea repens* and *Medeola virginiana* were more indicative of primary woodlands whereas an even larger number of species was associated with secondary woodland sites (Tables 1 and 3).

Occasionally both the composition of the overstorey and the age of the woods were important determinants of the herb and shrub strata (Tables 2 and 3). *Dennstaedtia punctilobula* reached its highest frequency in secondary woodlands of a broadleaved character (Table 1). *Maianthemum canadense* occurred preferentially in old-field white pine sites, whereas *Acer pensylvanicum* was more representative of old-growth hardwood sites and *Mitchella repens*, *Polypodium virginianum* and *Viburnum alnifolium* demonstrated an affinity for primary white pine and hemlock sites (Tables 1 and 3). Significant interactions between the two major factors, i.e. the $P \times A \times T$ model, were limited to *Gaultheria procumbens* and *Viburnum acerfolium* (Tables 2 and 3). For both species, frequency of occurrence in the primary and secondary woodlands varied with the nature of the overstorey.

DISCUSSION

The chemical and physical characteristics of the litter, and the soil moisture and light regimes of conifer and broadleaved stands often differ significantly (Anderson, Loucks & Swain 1969; Miles 1985). Hemlock and white pine, for instance, are noted for the low pH, high C/N ratios, high Al and Fe concentrations, and podzolizing tendencies of their litter

(Hole 1975; Messenber 1975; Johnson & Siccama 1979; Beatty 1984). The chemical characteristics of their litter probably explains the high frequency of ericaceous species like *Vaccinium angustifolium* on the conifer-dominated sites as many ericaceous species have a high affinity for acid, iron-rich substrata (Brady 1984). The physical characteristics of the litter can also alter a site's flora (Sydes & Grime 1981). Prostrate or acaulescent herbs with evergreen leaves, e.g. *Mitchella repens* are particularly susceptible to coverage or innundation by a thick layer of hardwood leaves. The smaller leaves or needles of eastern hemlock favour the occurrence of *Mitchella repens* in the old-growth conifer sites (Griggs 1914).

A variety of factors probably contributed to the relatively small number of species that responded directly to the broadleaved–conifer overstorey dichotomy. The more acidic end of the hardwood soil continuum approaches the conifers in terms of its chemical properties. Since the soil reaction under oaks and pines is very similar (Griffith, Hartwell & Shaw 1930), understorey species responding simply to pH should be able to occupy either habitat. Unique microhabitats within a given overstorey type may also compensate for the broader limitations of the forest type. Prostrate evergreen species that are normally smothered by a thick layer of hardwood leaves may find a refuge on areas of limited litter accumulation, e.g. the occurrence of *Epigaea repens* on rocks and boulders in broadleaved forests (Griggs 1914). Finally there is the recognition of the persistence of a given overstorey type and its long-term influence on the field layer. Griffith, Hartwell & Shaw (1930) in their pioneering work on the evolution of soils as affected by overstorey types attributed the poor link between soils and overstorey vegetation in the Pisgah tract to overlapping phases of succession. They noted an apparent tendency over long periods for hardwoods and softwoods to occupy alternately a given site in central New England's disturbance-prone, old-growth forests. Disturbances maintained the mixed hardwood–hemlock–white pine forests of the presettlement period (Cline & Spurr 1942). Blowdowns, fires and openings in the canopy favoured an influx of the copious seed producers: the pines, the birches and the maples. These relatively shade-intolerant species, in turn, were eventually replaced by the slower growing hardwoods and hemlock (Henry & Swan 1974; Hibbs 1982; Foster 1988).

The dynamic nature of the overstorey vegetation probably kept the understorey flora in a constant state of flux, preventing any long-term accommodation to a specific overstorey type. The destruction of the canopy, attendant changes in the microclimate and the establishment of a number of opportunistic competitors (notably *Rubus* and *Sambucus*) reduced the abundance of the more sensitive woodland herbs and shrubs. *Viburnum alnifolium*, *Aralia nudicaulis*, *Mitchella repens* and *Gaultheria procumbens* are among the better representatives of the more sensitive species (White 1929; Egler 1940; Dunn, Guntenspergen & Dorney 1983). However, because of the very patchy nature of the disturbance, a few individuals usually survived to slowly repopulate the affected area.

Differences in the understorey flora of eastern North America's primary and secondary woodlands have not been as fully assessed as understorey–canopy interactions. Scanlan's (1981) study of the vascular plants of natural and planted woods in the prairie–forest border area of southern Minnesota, is suggestive of at least a limited degree of specificity with respect to woodland habitats. The present study also substantiates some of Nichols (1913) and Egler's (1940) earlier observations on the flora of central New England's old-growth forests. Both noted that these forests were characterized by a unique assemblage of shrubs, seldom encountered in the region's second-growth forests. Hobblebush (*Viburnum alnifolium*), striped maple (*Acer pensylvanicum*), and yew (*Taxus canadensis*—

a species limited to two primary woodland sites in the present study) were the dominant representatives of Nichol's and Egler's old-growth shrub communities.

Several factors might account for the association of *Viburnum alnifolium*, *Acer pensylvanicum*, and *Taxus canadensis* with primary woodland sites. All are mesophytic species that reach their southern limits in central New England. In the cooler and more humid portions of northern New England they are common over a wide range of conditions. Both Nichols (1913) and Egler (1940), however, defined them as strictly forest species in central New England and felt they required the more mesophytic conditions of old-growth forests to germinate and grow. Few individuals survived the effects of lumbering or could tolerate the more xerophytic conditions of secondary woodlands (Nichols 1913; Egler 1940). Poor colonizing ability may also limit the spread of some of the old-growth indicator species. In the case of *Viburnum alnifolium*, for instance, invasion of new areas is by the chance, long-distance dispersal of seed by small mammals. Local spread by means of basal sprouting and the layering of prostrate branches eventually allows *Viburnum alnifolium* to dominate a site once it has been established. A variety of factors, including a paucity of flowers and fruit under closed-canopy conditions and frost damage in openings, however, limits hobblebush's production of seed and thus its potential for long-distance dispersal by seed (Rollins 1974).

The weedier, much more aggressive nature of the species characteristic of secondary woodlands provides a striking contrast with the poor seed production and colonizing ability of many primary woodland species. Most of the secondary species (*Lycopodium clavatum*, *L. obscurum*, *Polytrichum commune*, *Dennstaedtia punctilobula*, *Pteridium aquilinum*, and *Pyrola* spp.) produce large quantities of light, wind-dispersed spores or seeds known as dust diaspores (Van der Pijl 1972). Expanses of mineral soil in the early phases of the old-field successional process probably provided favourable conditions for the establishment of the gametophytes of many of these spore-bearing species (Eames 1942). The two remaining secondary species (*Rubus fragillaris* and *Maianthemum canadense*) bear conspicuous fleshy fruits that are dispersed over long distances by birds and mammals (Martin, Zim & Nelson 1951). A high rate of spread by means of rhizomes also encourages the local expansion of many of these species (*Dennstaedtia punctilobula*, *Pteridium aquilinum*, *Lycopodium clavatum*, *L. obscurum*, and *Maianthemum candense*) once long-distance dispersal has occurred. Rhizome growth rates are generally much lower in the case of the primary woodland species, e.g. *Medeola virginiana* and *Mitchella repens* (Cody, Hall & Crompton 1977; Sobey & Barkhouse 1977).

It would be hazardous to extrapolate the results of the present study to other areas of the eastern United States. The response of understorey species to woodland age in England has been shown to vary from region to region, depending upon climatic conditions and a host of other factors (Peterken 1974; Rackham 1980; Bunce 1982; Peterken & Game 1984). The results of the present study, however, do at least provide a first approximation of the more sensitive species, the species that are likely to be good indicators of primary woodland conditions in central New England. A better knowledge of these indicator species can then be used to evaluate the history and the suitability of various sites for inclusion in natural areas.

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