Relation of plant species to substrate, landscape position, and aspect in north central Massachusetts

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Vegetation–site relationships in the region about the Harvard Forest in north central Massachusetts were explored by means of contingency table and cluster analyses of presence–absence data. Most of the arboreal species, the shrubs, and the ferns were strongly associated with segments of a microclimate – soil moisture gradient determined by landscape position and substrate. Cluster analysis of the species suggested the existence of a fertility gradient, with the more nutrient demanding white ash (*Fraxinus americana* L.), sugar maple (*Acer saccharum* L.) and basswood (*Tilia americana* L.) on one end of the gradient and pitch pine (*Pinus rigida* Mill.), scrub oak (*Quercus ilicifolia* Wangenh.), and aspen (*Populus* sp.) on the more impoverished sites. An analysis of the feasibility of determining vegetation–site relationships in an area with a long history of human disturbances concludes the report.

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Les relations entre la station et la végétation dans la région de la forêt de Harvard dans le centre-nord du Massachusetts ont été étudiées à l'aide de tableaux de contingence et d'analyses typologiques sur des données de présence–absence. La plupart des espèces arborescentes, des arbustes et des fougères étaient fortement associés avec les segments d'un gradient d'humidité sol – microclimat relié à la position topographique et au substrat. L'analyse typologique des espèces suggère qu'il existe un gradient de fertilité; le frêne blanc (*Fraxinus americana* L.), l'érable à sucre (*Acer saccharum* L.) et le tilleul (*Tilia americana* L.), les espèces plus exigeantes, se retrouvent à une extrémité du gradient alors que le pin rigide (*Pinus rigida* Mill.), le chêne à feuilles de houx (*Quercus ilicifolia* Wangenh.) et le peuplier (*Populus* sp.) apparaissent sur les stations plus pauvres. Une analyse de faisabilité sur la détermination des relations entre la station et la végétation dans une région qui possède une longue histoire de perturbations dues à l'activité de l'homme sert de conclusion à cette étude.

[Traduit par la rédaction]

Introduction

Plants have long been known as effective integrators of their environment. The strong relationship between plants and their physical environment is a major principle of several ecologically based forest site and ecosystem classification systems. Close relationships are often observed and quantitatively demonstrated between the vegetation, particularly the ground-cover vegetation, and the geology, the physiography, the soil, and the microclimate of the site (Hills and Pierpoint 1960; Barnes *et al.* 1982; Jones *et al.* 1983). Cutting, grazing, land clearing and other human activities can complicate our understanding of predisturbance vegetation–site relationships. As a result, it is not surprising that many of the more successful vegetation–site studies and classification systems in eastern North America have been initiated in areas relatively free of human disturbance (Heimburger 1934; Pregitzer and Barnes 1982, 1984; Spies and Barnes 1985*a*, 1985*b*; Simpson *et al.* 1990). The approach, however, has also been applied with success to cutover and grazed forest ecosystems in southern Michigan (Archambault *et al.* 1990) and Wisconsin (Hix 1988). Shrubs, herbs, and ferns have been utilized extensively as indicators of the nutrient and moisture status of the site because ground-cover species are typically less affected by disturbances than overstory trees. Many ground-cover species are clonal species or perennials that typically are not eliminated from sites following cutting, windstorms, fire, or grazing (Westveldt 1951; Archambault *et al.* 1990).

Central New England represents a good test case of the degree to which disturbances have affected vegetation–site relationships. Previous work at the Harvard Forest has shown that much of the diversity of forest types is due to past disturbances (Raup and Carlson 1941; Cline and Spurr 1942; Henry and Swan 1974; Foster 1988). Fires, hurricanes, and several centuries of European habitation have kept New England's forests in a continual state of flux. Over 70% of the forests of central Massachusetts today are secondary forests dating back to the widespread farm abandonment of the late 19th and early 20th centuries. Most of the woods were constructed de novo from old-field conditions. The result has been a "kaleidoscopic patchwork of species combinations scattered over [the] landscape" (Raup 1957).

One can also, however, find a certain degree of order in the distribution of New England's plant species. As Spurr (1956*a*) noted in his study of forest associations in the Harvard Forest, soil moisture and drainage are major determinants of the arboreal vegetation of the region. The experienced observer knows, for instance, that red maple and spruce are likely to be found on poorly drained sites, while white pine is a major component of the forests of very well drained sites (Spurr 1956).

Unfortunately we still have a fragmentary understanding of the nature of the vegetation in the middle of the soil moisture continuum or of the effects of landscape position and aspect on the species composition of the forest. To what degree has 250 years of human history obscured the control of the vegetation by site factors? In 1954, J. Goodlett, the forest geographer at the Harvard Forest, initiated a study of the factors affecting the distribution of woody plant

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species in central Massachusetts. Goodlett felt that topography, bedrock geology, and soil materials were the major determinants of the vegetation of the region. He collected a large amount of data on the vegetation and site conditions of upland areas in north central Massachusetts. Unfortunately Dr. Goodlett died before his study was completed. The present study is an extension of Goodlett's data base to a larger range of sites in north central Massachusetts. It represents an attempt to (*i*) determine the strength of species–site relationships in an area that has been heavily modified by human activity and (*ii*) describe the site-indicator value of trees, shrubs, and ferns in forest ecosystems in north central Massachusetts.

Study area

The study area (42°30′N, 72°10′W) encompassed approximately 40 000 ha of land in the northwestern portion of Worcester County and the adjacent northeastern corner of Franklin County, Massachusetts. Relief ranges from 150 to 400 m. The north–south trending ridges and valleys are characteristic of the Central Highlands region of Massachusetts, the larger physiographic region within which the study area lies. Bedrock exposures are common on the summits and upper slopes of the region. Coarse-textured tills (40–60% sand derived from gneiss, schist, and tonalite) dominate most of the uplands, while poorly to well-stratified ice-contact deposits of sands and gravels cover the intervening valleys and isolated basins in the uplands (Eschman 1966). The soils are predominately low base saturation Inceptisols and Spodosols with and without the occurrence of a fragipan.

The climate is of the humid continental type, with 110 cm of precipitation equitably distributed throughout the year. The frost-free season is approximately 140 days (United States Department of Agriculture 1978).

North central Massachusetts lies in the transition hardwoods – white pine – hemlock forest region (Westveld 1956). It contains elements of the central hardwoods region of southern New England as well as representatives of the spruce – fir – northern hardwood region to the north. White oak (*Quercus alba* L.), black oak (*Quercus velutina* Lam.), chestnut oak (*Quercus prinus* L.), and dogwood (*Cornus florida* L.) can be found on some of the drier hilltops and south-facing slopes of the region (Smith 1948), while red spruce (*Picea rubens* Sarg.) and balsam fir (*Abies balsamea* (L.) Mill.) are characteristic of many of the wetlands of the higher elevations (Stransky 1953).

Methods

Field procedures

Most of the fieldwork was carried out from 1953 to 1955 as part of an informal collaboration with D. F. Eschman of the United States Geological Survey. Dr. Goodlett accompanied Dr. Eschman on many of his trips about the Harvard Forest area as he mapped the bedrock and the surficial geology of the region. Goodlett recorded the location, the landscape position, the aspect, the parent material, the drainage conditions (see Table 1), and the tree, the shrub, and the herbaceous flora present on three hundred forty-five 0.1- to 0.25-acre (0.04- to 0.10-ha) plots distributed throughout the Athol quadrangle. Often this involved excavating a soil pit on the plot. A tree species was considered present on a plot if the plot possessed a ≥3 m tall sapling of the species in question. The plots were selected to show a range of flora and substrate, i.e., parent material and drainage, conditions. Goodlett's study, however, focused predominately on the upland areas. Eighty-four more plots were added to the study in 1989 and 1990. Particular emphasis was placed on increasing the data base with respect to lowland and cove sites and sites possessing red spruce, pitch pine (*Pinus rigida* Mill.), and basswood (*Tilia americana* L.), species poorly represented in Goodlett's earlier study. The nomenclature of this study follows Little (1979) for the trees and Fernald (1950) for the remainder of the flora.

TABLE 1. Site factor categories

Landscape position
  Ridgetops and upper slopes
  Midslopes
  Lower slopes
  Flats
  Cove; topographic contours concave outward
Substrate
  Well to excessively drained sands and gravels or "washed till"
  Rock outcrop; soil <30 cm deep
  Well to excessively drained till
  Moderately well drained to very poorly drained sands and gravels
  Moderately well drained to very poorly drained till
Aspect
  North, northeast 338°–67°
  East, southeast 68°–157°
  South, southwest 158°–247°
  West, northwest 248°–337°

Numerical analysis

Quantitative analysis followed standard contingency table analysis procedures (Strahler 1978). The presence (p) and absence (a) of each tree, shrub, and fern species was tabulated across the categories (C) of each site factor to form a 2 (p or a) × C contingency table. Cell values represented the number of plots in which the species was present or absent. A significant G-statistic indicated that the species occurrence was related to the factor. The cell frequencies of tables possessing a significant G-statistic were then converted to standardized residuals (Haberman 1973) to express the degree of association of the species with each of the categories, i.e., ridgetops and upper slopes, coves, etc. Species occurring at less than 5% of the sites were omitted from the analysis to minimize errors associated with small sample sizes (Sokal and Rohlf 1981, p. 709).

Analyzing the association or the co-occurrence of various species, particularly species with similar habitat requirements, provides another means of deciphering species–site relationships. Species associations were explored by treating each of the 450 plots as a stand and then analyzing the co-occurrence of pairs of species across all of the stands. Dissimilarity values were based upon the presence or absence equivalent of the Manhattan metric (Orloci 1974). The metric was standardized by the species totals to give more weight to the rarer species. The resulting dissimilarity matrix was then converted to a dendrogram utilizing a median fusion strategy (Greig-Smith 1983, pp. 195–203).

Results

Table 2 is indicative of the frequency of the various species in the 430 sample plots. Three species, red maple (*Acer rubrum* L.), white pine (*Pinus strobus* L.), and red oak (*Quercus rubra* L.), are very abundant, each occurring at over 85% of the sites. All are species that reach their highest abundance in the transition hardwoods – white pine – hemlock zone of central New England (Spurr 1956*a*; Westveld 1956).

With the exception of red maple and the opportunistic black cherry (*Prunus serotina* Ehrh.), most species appeared to be strongly influenced by site conditions (Table 3). Few species were significantly associated with one of the four

TABLE 2. Frequency of more common species in 430 sample plots

Trees	%	Shrubs	%	Ferns	%
Acer rubrum	95.6	*Vaccinium angustifolium*	55.8	*Pteridium aquilinum*	55.8
Pinus strobus	88.6	*Vaccinium corymbosum*	33.2	*Dennstaedtia punctilobula*	29.1
Quercus rubra	83.7	*Viburnum cassinoides*	32.6	*Osmunda cinnamomea*	22.6
Tsuga canadensis	62.3	*Comptonia peregrina*	24.2	*Dryopteris spinulosa*	11.6
Quercus alba	59.3	*Viburnum acerifolium*	21.4	*Thelypteris noveboracensis*	11.2
Castanea dentata	54.0	*Kalmia latifolia*	19.5	*Dryopteris marginalis*	10.7
Betula populifolia	53.7	*Hamamelis virginiana*	18.6	*Onoclea sensibilis*	8.4
Quercus velutina	47.2	*Vaccinium vacillans*	17.9	*Polystichum acrostichoides*	7.9
Betula alleghaniensis	46.7	*Juniperus communis*	11.6	*Athyrium Filix-femina*	7.4
Betula papyrifera	46.7	*Ilex* spp.[a]	10.7	*Polypodium vulgare*	7.2
Fraxinus americana	32.8	*Nemopanthus mucronata*	8.8	*Thelypteris simulata*	6.3
Prunus serotina	26.7	*Kalmia angustifolia*	8.4		
Fagus grandifolia	26.5	*Viburnum dentatum*	7.4		
Betula lutea	25.8	*Gaylussacia* spp.[b]	6.5		
Acer saccharum	21.4	*Corylus* sp.[c]	6.3		
Acer pensylvanicum	14.4	*Viburnum alnifolium*	5.6		
Amelanchier sp.[d]	14.4	*Taxus canadensis*	5.0		
Carya spp.[e]	10.9				
Ostrya virginiana	10.9				
Picea rubens	10.9				
Pinus rigida	9.5				
Populus grandidentata	9.3				
Populus tremuloides	6.5				
Tilia americana	5.1				
Quercus ilicifolia	5.0				

[a] *Ilex verticillata* and *Ilex laevigata*.
[b] *Gaylussacia baccata* and *Gaylussacia frondosa*.
[c] *Corylus americana* and *Corylus cornuta*.
[d] Predominantly *Amelanchier canadensis*.
[e] Mostly *Carya ovata*, some *Carya glabra* on midslopes.

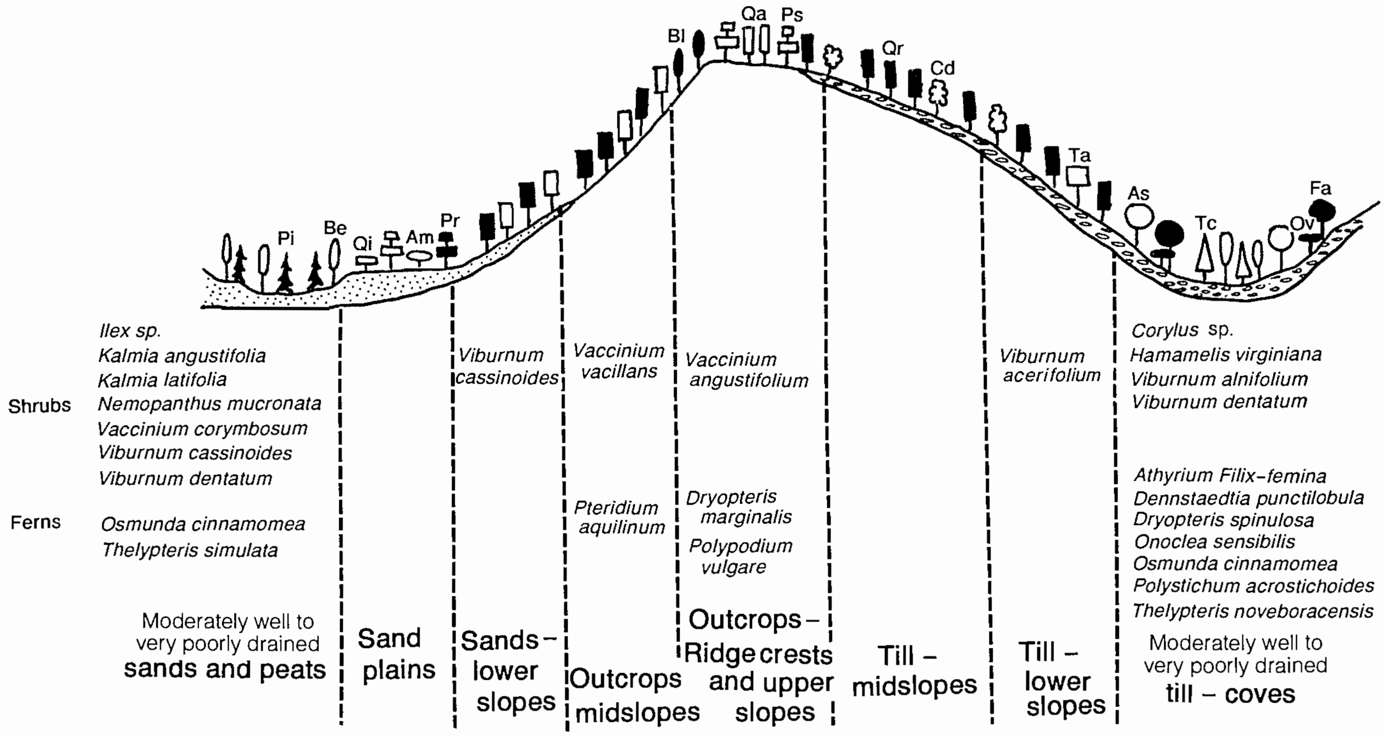

FIG. 1. Diagrammatic representation showing relationship of species to landforms and substrate conditions. Sites without a drainage designation are well to excessively drained. Tree species abbreviations are as follows: Pi, *Picea rubens*; Be, *Betula alleghaniensis*; Qi, *Quercus ilicifolia*; Am, *Amelanchier* sp.; Pr, *Pinus rigida*; Bl, *Betula lenta*; Qa, *Quercus alba* and *Quercus velutina*; Ps, *Pinus strobus*; Qr, *Quercus rubra*; Cd, *Castanea dentata* sprouts; Ta, *Tilia americana*; As, *Acer saccharum*; Tc, *Tsuga canadensis*; Ov, *Ostrya virginiana*; Fa, *Fraxinus americana*. Stippling indicates sands and gravels, ellipses indicate till, and unshaded areas indicate bedrock.

TABLE 3. Standardized residuals showing response of more common species to site factors

	Landscape position						Substrate					
	Ridgetops and upper slopes	Midslopes	Lower slopes	Flats	Coves	*G*-statistic	Sand and gravel	Rock outcrop	Till	Moderately well to very poorly drained sand	Moderately well to very poorly drained till	*G*-statistic
Trees												
Acer rubrum	−0.42	2.37	−1.49	0.16	−1.27	8.77	−0.67	0.52	−0.01	0.68	−0.42	1.21
Acer saccharum	−2.80	−1.08	1.48	−4.15	8.40	75.73**	−3.35	−2.57	2.24	−3.16	5.56	56.10**
Amelanchier sp.	−1.38	−3.40	1.93	3.95	−1.00	25.78**	5.05	−1.26	−2.79	0.90	−0.66	24.69**
Betula lenta	3.30	4.37	−0.10	−7.48	−0.25	71.79**	−4.62	4.04	4.44	−5.74	−1.03	83.22**
Betula alleghaniensis	−3.30	−4.30	−2.17	3.15	8.46	90.11**	−4.34	−5.11	−3.84	3.03	12.09	169.44**
Betula papyrifera	1.51	0.56	1.14	−2.62	−0.55	8.87	−1.42	−1.95	2.43	−0.86	1.00	10.02*
Betula populifolia	1.71	1.01	1.75	0.44	−6.10	41.54**	4.80	1.37	0.43	−2.14	−4.92	47.33**
Carya sp.	1.14	−0.98	0.50	−2.81	3.07	16.68**	−0.56	−0.24	1.84	−1.87	−0.08	6.76
Castanea dentata[a]	−0.63	4.98	2.45	−4.71	−3.15	49.68**	1.29	1.32	2.96	−5.10	−2.41	38.34**
Fagus grandifolia	−1.41	1.52	0.78	−2.02	1.18	8.34	−1.74	−1.44	2.06	−2.26	2.34	16.70**
Fraxinus americana	−2.60	2.33	−1.38	−4.13	6.76	63.62**	−4.81	0.80	1.75	−3.73	4.44	58.44**
Ostrya virginiana	−0.90	−0.30	0.90	−3.55	4.98	32.40**	−1.84	0.15	1.52	−2.39	1.55	16.45**
Pinus rigida	−0.07	−0.76	−1.11	3.83	−2.47	20.76**	7.97	−0.16	−2.07	−2.21	−3.09	60.59**
Pinus strobus	1.82	1.49	−0.34	1.83	−6.19	31.14**	2.36	3.40	0.32	0.40	−6.58	46.32**
Populus grandidentata	−0.43	1.89	0.66	−0.41	−2.44	12.83*	2.18	−1.31	1.83	−1.63	−1.74	13.25*
Populus tremuloides	−1.49	−2.26	3.91	0.79	−0.80	17.13**	4.12	−1.32	−0.93	0.17	−1.49	14.57**
Prunus serotina	−0.88	0.01	1.29	−1.03	0.80	3.34	2.13	−0.41	−0.74	−1.19	0.27	5.47
Picea rubens	−2.12	−4.70	−1.88	10.87	−2.66	103.32**	−0.99	−3.30	−5.22	15.31	−0.90	155.40**
Quercus alba	2.46	4.45	2.16	−4.35	−6.15	72.09**	4.40	3.85	1.69	−6.91	−5.04	99.63**
Quercus ilicifolia	−0.98	−1.57	−1.67	5.49	−1.72	26.62**	7.85	−1.27	−2.19	−1.55	−2.16	45.29**
Quercus rubra	2.83	4.20	2.69	−9.13	−0.69	80.64**	2.13	2.05	3.45	−9.75	−0.96	76.01**
Quercus velutina	3.46	4.24	−1.18	−2.96	−4.80	53.54**	5.24	5.93	−1.26	−5.87	−5.12	123.10**
Tsuga canadensis	−2.03	−1.34	0.55	0.84	2.53	11.48*	−2.13	−3.42	−0.51	3.63	3.48	37.87**
Shrubs												
Acer pensylvanicum	0.43	1.41	−0.89	−3.61	3.25	23.80**	−2.14	1.13	1.20	−2.34	1.15	14.83**
Comptonia peregrina	0.55	0.56	1.35	0.15	−3.25	14.16**	3.66	2.15	0.88	−2.72	−4.79	50.10**
Corylus sp.	−2.47	−3.04	1.01	1.86	3.56	30.68**	1.53	−2.72	−0.38	−0.43	2.25	16.70**
Gaylussacia sp.	1.09	−0.97	0.90	0.79	−2.01	9.51*	1.96	1.10	−0.93	0.17	−2.00	8.92
Hamamelis virginiana	−4.56	−2.07	0.99	1.17	5.56	57.30**	−0.16	−4.41	−0.87	0.50	5.57	44.45**
Ilex sp.	−3.30	−4.30	−2.63	8.07	2.68	85.94**	−1.79	−3.64	−5.15	11.83	2.87	126.10**
Juniperus communis	1.30	0.74	−0.89	0.62	−2.29	9.44	−0.74	4.39	0.20	−2.47	−2.27	28.45**
Kalmia angustifolia	−1.05	−2.91	−0.76	6.61	−2.30	41.90**	−0.29	−1.45	−3.33	9.08	−1.05	52.98**
Kalmia latifolia	−1.49	−0.48	−0.82	3.80	−1.49	14.71**	−1.71	−2.17	0.03	4.01	0.75	19.32**
Nemopanthus mucronata	−2.52	−4.18	−3.09	11.15	−1.84	108.51**	−2.31	−3.27	−4.92	15.04	0.17	149.75**
Vaccinium angustifolium	4.64	1.30	−0.91	−1.19	−4.64	41.73**	4.18	2.86	0.37	−4.07	−4.31	53.34**
Vaccinium corymbosum	0.29	−4.32	−0.69	6.06	−1.25	42.86**	−1.49	−2.35	−2.45	7.94	0.82	66.02**
Vaccinium vacillans	1.51	2.00	−0.11	−1.01	−3.16	18.55**	3.12	1.95	0.45	−2.34	−3.79	33.77**
Viburnum acerifolium	−0.63	1.76	2.38	−3.31	−0.33	16.91**	0.22	0.63	1.51	−3.16	−0.32	15.20**
Viburnum alnifolium	−2.32	−2.34	−0.25	0.80	5.30	29.35**	−1.01	−2.04	−0.36	0.46	3.22	12.38*
Viburnum cassinoides	−3.10	−5.04	2.10	7.49	−1.47	74.70**	2.89	−4.50	−3.72	7.74	0.70	86.58**
Viburnum dentatum	−2.22	−3.00	−1.87	4.74	2.96	37.33**	−2.02	−2.98	−2.58	6.73	3.11	53.65**

TABLE 3 (*concluded*)

	Landscape position						Substrate					
	Ridgetops and upper slopes	Midslopes	Lower slopes	Flats	Coves	*G*-statistic	Sand and gravel	Rock outcrop	Till	Moderately well to very poorly drained sand	Moderately well to very poorly drained till	*G*-statistic
Ferns												
Athyrium Filix-femina	−2.70	−3.40	−0.92	−1.41	10.91	80.84**	−1.01	−2.98	−1.43	−0.08	6.01	35.74**
Dennstaedtia punctilobula	0.62	1.18	−2.80	−3.10	4.98	36.16**	−3.07	−0.68	1.56	−3.29	4.25	37.24**
Dryopteris marginalis	2.05	−1.91	0.18	−3.87	5.09	43.91**	−2.65	2.93	1.00	−2.36	−0.01	24.80**
Dryopteris spinulosa	−3.46	−3.22	−1.66	0.26	10.27	86.75**	−1.16	−3.44	−1.99	1.58	6.06	42.75**
Onoclea sensibilis	−2.88	−3.68	−1.65	2.03	7.93	66.43**	−1.25	−3.18	−4.03	3.80	6.75	66.48**
Osmunda cinnamomea	−4.54	−5.98	−2.98	6.93	8.38	148.71**	−4.49	−5.39	−5.18	10.70	8.23	210.85**
Polypodium vulgare	3.73	−2.11	−0.85	−1.78	1.92	18.73**	−1.97	4.92	−1.70	−1.27	−0.20	22.47**
Polystichum acrostichoides	−2.79	−2.37	3.07	−2.42	6.06	49.96**	−1.13	−2.20	1.67	−2.00	2.86	20.34**
Pteridium aquilinum	1.32	3.22	1.58	−2.59	−4.64	35.51**	3.64	2.62	1.57	−5.05	−4.13	58.49**
Thelypteris noveboracensis	−2.57	−3.08	−0.76	0.06	8.20	54.05**	−3.16	−3.73	0.12	1.71	5.50	57.18**
Thelypteris simulata	−2.47	−3.47	−2.57	9.94	−1.97	87.01**	−2.31	−2.72	−4.09	12.97	0.15	106.87**

[a] *Castanea* persists only as sprouts.
*$P < 0.05$.
**$P < 0.01$.

aspect categories. The lack of an aspect response may be due to the predominance of north–south trending ridges with east- and west-facing slopes. Sites with a northern or a southern exposure were poorly represented.

Landscape position and substrate were two of the more important determinants of the vegetation. Substrate was related to landscape position (Table 4). Sands and gravels were concentrated on foot slopes and flats, while outcrop exposures dominated the ridgetops and upper slopes. The standardized residuals shown in Table 3 provide an estimate of the degree to which species are associated with unique site conditions. A high positive residual value (≥ 2.0) indicates that the species was more common on that site category than might have been anticipated by chance. Most species indicated a preference for certain substrates and landscape positions (Fig. 1). The shift from the black birch (*Betula lenta* L.), white pine, oak, and low sweet blueberry (*Vaccinium angustifolium* Ait.) communities of the rocky ridgetops to the red oak, chestnut (*Castanea dentata* (Marsh.) Borkh.), maple-leaved viburnum (*Viburnum acerifolium* L.) communities of the lower slopes or the contrast between the pitch pine, scrub oak (*Quercus ilicifolia* Wangenh.), shadbush (*Amelanchier* sp.) communities of drier sand plain sites and the red spruce - yellow birch (*Betula alleghaniensis* Britton) communities of the poorly to very poorly drained sand plain sites probably reflects a soil moisture gradient. Species preferring mesic site conditions, e.g., sugar maple (*Acer saccharum* Marsh.), white ash (*Fraxinus americana* L.), hemlock (*Tsuga canadensis* (L.) Carr.), beech (*Fagus grandifolia* Ehrh.) and witch hazel (*Hamamelis virginiana* L.), were concentrated on moderately well to poorly drained sites where the landscape position increased the supply of moisture (coves) or the existence of an impermeable fragipan layer near the surface retarded the drainage (Stout 1952). The additional supply of moisture was probably responsible for the rich fern flora of the cove sites (Table 3).

Some of the differences in the species occurrences associated with landscape position may be due to microclimatic effects. Studies in the Harvard Forest by Spurr (1956*b*) and Rache (1958), for instance, have shown that the length of the growing season varies significantly with landscape position. Enclosed basins or low-lying areas, e.g., peat bogs, subjected to cold air drainage may have a frost-free season as short as 77 days, while summits and ridgetops experience a frost-free period of 161 days. Local climatic differences may explain the occurrence of red spruce and yellow birch in the low-lying flats and basins and the occurrence of black oak and white oak, species more characteristic of southern New England, on the uplands.

The cluster analysis of the species (Fig. 2) shows a similar pattern of association. There is the hemlock - yellow birch spinulose wood-fern (*Dryopteris spinulosa* (O. F. Muell.)) community of the cooler ravines, the red spruce community of the lower lying flats, and the white pine - red maple - oak community of the till covered uplands. The species associations in the dendrogram also appear to reflect a fertility gradient. The species on the upper portion of the dendrogram, e.g., the pitch pine, the scrub oak, the aspens, the huckleberry, the shadbush, and the two *Kalmia* of the sand plains, are characteristic of the nutrient-impoverished end of the fertility gradient. At the opposite extreme are the sugar

TABLE 4. Association of substrate and landscape position (number of plots falling into each dual-factor site category)

	Landscape position				
Substrate	Ridgetops and upper slopes	Midslopes	Lower slopes	Flats	Coves
Sands and gravels	3 (4)	13 (10)	26 (32)	23 (24)	2 (4)
Rock outcrop	34 (45)	36 (29)	8 (10)	9 (9)	1 (2)
Till	31 (41)	65 (52)	40 (49)	7 (7)	15 (29)
Moderately well to very poorly drained sands and gravels	—	—	2 (2)	40 (41)	—
Moderately well to very poorly drained till	7 (9)	11 (9)	6 (7)	18 (18)	33 (65)
Total	75	125	82	97	51

NOTE: Values in parentheses are percentages of each landscape position falling into a specific substrate category.

maple – white ash – basswood – ironwood (*Ostrya virginiana* (Mill.) K. Koch) communities of the lower slopes and coves. Although they cover a limited area (most are less than 1 ha in size), they contain a number of herbaceous species (*Trillium erectum*, *Caulophyllum thalictroides*, *Hepatica americana*, *Arisamea atrorubens*, *Viola pubescens*, *Adiantum pedatum*, and *Polystichum acrostichoides*) characteristic of enriched sites throughout northeastern United States and adjacent Canada (Heimburger 1934; Damman and Kershner 1977; Gauthier and Gagnon 1990). They bear a striking resemblance to the enriched sugar maple – white ash communities of the White Mountains of New Hampshire (Leak 1976, 1980). Additional inputs of nutrients to these sites may be due to the flow of nutrient-rich water (several stands were associated with seepages) or to the accumulation of fine materials from the surrounding uplands (Leak 1976, 1980).

Discussion

With respect to the Harvard Forest, research designed to explain distribution of tree species has really gone in two different directions over the last 70 years. One approach has emphasized the control of the vegetation by human activities and natural disturbances: farm abandonment in the 19th century, the spread of old-field white pine across the landscape, and the eventual loss of the white pine owing to harvesting and the 1938 hurricane (Raup and Carlson 1941; Foster 1988). The result was often a "huge number of species combinations scattered patchwise over the landscape... without any apparent relation to slope, exposure, or...soil" (Raup 1957). Other researchers have focused on the control of the vegetation by site factors. The persistence of pure stands of white pine on the sand plains of the region, for instance, was attributed to the slower rate of height growth of hardwoods relative to pine (Lutz and Cline 1947; Goodlett 1960). The distribution of white ash, likewise, was tied to the occurrence of a fragipan layer within 50 cm of the surface, whereas the occurrence of the oaks was associated with more friable deposits of till (Stout 1952).

Attempts to assess the vegetation–site relationships of heavily modified regions of eastern United States have met with varying degrees of success. Hix (1988) and Archambault *et al.* (1989) found that select groups of ground-cover species were useful in identifying site conditions in the repeatedly grazed and cutover oak ecosystems of southern Wisconsin and southern Michigan. The use of ground-cover species is more problematical in the case of central New England's forests. The herbaceous flora is not as rich as that of the Midwest. Much of central New England is dominated by secondary (old-field) forests less than 150 years old. Owing to their poor colonizing ability, some herbaceous species may not be as well represented or as abundant in secondary woodlands as they are in primary woodlands (Whitney and Foster 1988).

Walker (1975) had little success relating the woody plant species of the overstory and the understory of 44 sites in the Harvard Forest to the physiography and the soils of the sites. He reported that much of the variation in the species composition of the sites was due to disturbance and chance events. His principal component analysis of the woody vegetation, however, was based on abundance data. The success of the present study in identifying key vegetation–site relationships may be due to the use of a larger number of species and sites (50 versus 23 species and 429 versus 44 sites), the omission of recently disturbed sites, and the use of presence–absence data as opposed to abundance data. There is little debate that disturbances can alter the proportional representation of species in the overstory. By encouraging a large influx of intolerant, opportunistic species, disturbances may at first appear to "homogenize" the sites, at least in terms of the abundances of the tree species represented. It is much more difficult, however, to envision a change in the species present on the sites. Many species will persist on the site in low numbers throughout the disturbance or will slowly reinvade following the cessation of disturbances. Presence–absence data will pick up the rarer overstory and understory species discounted by the abundance data.

Recent work on the habitat requirements, particularly the nutrient, substrate, and topographic requirements of the various tree species (Leak 1982; St-Jacques and Gagnon 1988; Gauthier and Gagnon 1990), has increased our understanding of the way site factors influence the vegetation and our ability to identify the more critical site factors. Goodlett, for instance, failed to identify coves or separate them from other middle and lower slope sites in his initial landscape

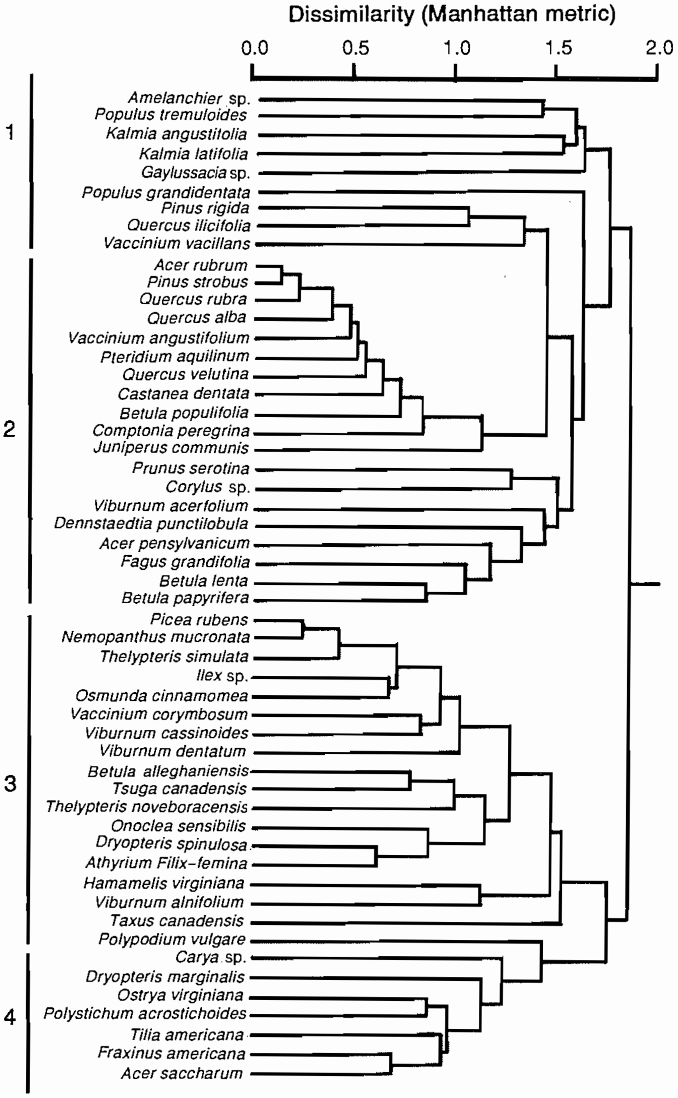

FIG. 2. Cluster analysis of species co-occurrences in plots. Species occurring in roughly the same plots have a low dissimilarity value. Clusters are based upon a median fusion strategy. Major clusters are roughly defined as follows: (1) species of nutrient-poor sands and gravels; (2) species of till uplands; (3) species of swamps and moist ravines; (4) species of rich coves.

position typology. Subsequent work by Hack and Goodlett (1960) in the central Appalachians demonstrated the importance of the concave cove position in channeling water to the site. Following the lead of Hack and Goodlett, many midslope and lower slope study sites of the 1953–1954 study were reclassified and analyzed as coves in the present study. Coves supported a unique flora more characteristic of the hemlock - northern hardwoods region to the north.

Time has also favored the reestablishment of predisturbance overstory vegetation - site relationships. Earlier workers at the Harvard Forest emphasized the control of the vegetation by land-use factors because they were familiar with the pioneer old-field forest types that temporarily occupied a wide range of sites (Goodlett 1960). They also, however, noted that the understory hardwoods of the old-field white pine stands varied with the nature of the site: white ash, sugar maple, and beech on the heavier soils and oaks and red maple on the coarser textured sites (Cline and Lockard 1925). Logging and the 1938 hurricane subsequently eliminated most of the overstory white pine and released the understory hardwoods. The passage of time relegated pure stands of white pine to the lighter soils. Spurr's (1956*a*) statement that forest communities at the Harvard Forest never really fit the concept of "a hodgepodge of species scattered indeterminately over the area" is even more valid today. We have a better idea of some of the substrate and physiographic factors underlying the observed order. Silvicultural prescriptions should consider these longer term trends and give more weight to the ultimate adjustment of the species to site conditions.

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