Groundlayer Vegetation Ordination and Site-Factor Analysis of the Wright State University Woods (Greene County, Ohio)[1]

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ABSTRACT. Detrended correspondence analysis (DECORANA) was used to examine groundlayer vegetation variation among seven locations of differing topography and successional age in the Wright State University woods (Greene County, OH). Two young sites (60 and 40 years since agricultural abandonment) and five older sites (one floodplain, one slope, and three uplands) were selected *a priori* and sampled four times in 1987. Taxon presences were recorded in 100 plots per location, and 12 environmental variables were measured from a subset of these plots. DECORANA ordination revealed that site age was the most important large scale factor affecting groundlayer vegetation. Topography was shown to be an important factor in the old growth sites. Stepwise linear regression with DECORANA plot scores as dependent variables and environmental factors as independent variables indicated that soil moisture content was the most important measured site factor associated with vegetation variation. This relationship was significant for vegetation along the overall successional gradient ($r^2 = 0.49$) with soil moisture content positively correlated with site age. It was also significant along the old growth topographic gradient ($r^2 = 0.46$) with soil moisture content negatively correlated with topographic elevation.

Species richness ($N = 75$) and diversity were greatest in the floodplain site and least in the 40 year old upland site ($N = 58$). Successional species differences were manifest in part by the relative contributions of various taxon life history characteristics. The younger sites had lower frequencies of annuals and some perennials, especially spring ephemerals. They also had higher frequencies of woody seedlings, especially *Lonicera maackii*, *Prunus serotina*, and *Rosa multiflora*.

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INTRODUCTION

Forest vegetation is influenced by a number of scale-related abiotic and biotic environmental factors. Within a forest, topographic relief is one higher scale factor that has been shown to be a major determinant of canopy and groundlayer species composition (Whittaker 1956, Davidson and Buell 1967, Runkle and Whitney 1987). Topography effects both water and nutrient pools. For instance, lowland areas within a forest tend to have greater water availability and higher concentrations of some nutrients, while upland areas have less water availability and lower concentrations of nutrients (Dickson et al. 1965, Franzmeier et al. 1969).

On a more local scale, community composition is affected by numerous microsite characteristics. For instance microtopographic relief influences species distributions by altering water and nutrient availability (Bratton 1976, Hicks 1980, Beatty 1984). Mound/pit relief and decaying treefalls are common examples of microtopographic variation that influence distributions (Peterson et al. 1990). The species and distance of the nearest living canopy tree may affect species distributions by altering water and nutrient availability (Crozier and Boerner 1984). Light penetration is also known to influence groundlayer species distributions (Anderson et al. 1969). The presence of a canopy gap greatly increases light availability and affects local water and nutrient relations (Moore and Vankat 1986).

Another major factor affecting forest vegetation is site history which encompasses aspects of human disturbance and stochastic natural events. Release of lands from anthropogenic uses such as agriculture or grazing results in stands of different successional ages.

In the present study, we examined the effects of two major factors, topography and successional age, on groundlayer community composition and components of the abiotic environment among stands within a large (80 ha) forest island. More specifically, we attempted to answer the following three ecological questions: 1) how does the groundlayer vegetation vary among stands differing in topography and successional age, 2) do environments vary among these stands, and 3) what environmental factors are most important in affecting groundlayer vegetation overall?

DESCRIPTION OF STUDY AREA

The study was conducted in the Wright State University (WSU) woods in Bath Township, Greene County, in southwestern Ohio (longitude 84°3' W and latitude 39°45' N). The climate of Greene County is considered continental (Miller 1969). Mean annual precipitation from 1951 to 1980 was 97 cm (NOAA 1987). In 1987 (sampling year), mean annual precipitation was 74 cm (NOAA 1987). Mean January and June temperatures from 1951 to 1980 were -2.3° C and 22.8° C, respectively (NOAA 1987). Mean January and June temperatures for 1987 were -1.4° C and 23.8° C, respectively.

The WSU woods encompasses approximately 80 ha and is composed of three major stands. Two stands are secondary, being derived from abandoned agricultural fields. One secondary stand is 40 years old, the other is 60 years old (determined from aerial photographs dating

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back to 1940). The other major stand is older growth; it has never been clear-cut but probably experienced selective cutting and livestock grazing up to 1950 (as evidenced by aerial photographs, tree diameter measurements, and dendrochronologic measurements). Additionally, minor disturbances resulting from foot paths and drainage from nearby parking lots is visible.

Topography varies among stands. Both secondary stands are on uplands while the older growth stand contains upland, slope, and floodplain sites. Soils throughout the WSU woods are relatively homogeneous and are classified as Miamian silt-loams (Garner et al. 1978). Bedrock is primarily shale and limestone. Soil depth to the bed rock ranges from 43 m to 91 m (Riggle and Kidd 1980); hence, soil properties are not influenced greatly by parent rock strata.

The canopy vegetation fits Gordon's (1969) classification as an oak-sugar maple forest. *Acer saccharum* L. dominates the canopy in all sites (DeMars 1988). Its greatest relative density occurs in the 40 year old stand. Other common older growth canopy species include *Quercus alba* L., *Quercus rubra* L., *Ulmus americana* L., and *Carya* spp. in uplands and slopes, and *Juglans nigra* L. in floodplains. *Fraxinus americana* L. is common to slopes and floodplains and is occasionally represented in uplands. Other common canopy species in the 60 year old stand include *Robinia pseudo-acacia* L., *Juglans nigra*, and *Ulmus* spp. Occasional species include *Prunus serotina* Ehrh., *Gleditsia triacanthos* L., and *Ailanthus altissima* (Mill.) Swingle. Other common canopy species in the 40 year old stand include *Robinia pseudo-acacia, Fraxinus americana,* and *Ulmus americana.* Occasional species include *Prunus serotina, Gleditsia triacanthos,* and *Populus deltoides* Marsh.

MATERIALS AND METHODS

Seven study sites were selected *a priori* for sampling. Each site represented an area homogeneous in topography and stand age. These areas included five upland sites (2 secondary and 3 older growth sites), one older growth slope, and one older growth floodplain (Fig. 1). Specific attributes of each sampling site are described below.

SEC40 – a 100 m x 100 m plot in the central portion of the 40 year old stand. Elevation varies between 268 to 274 m with a NE slope of 1% to 2%.

SEC60 – a 100 m x 100 m plot in the central portion of the 60 year old stand. Elevation varies between 271 to 277 m with a NNE-NE slope of 1% to 2%.

OLD-W – a 100 m x 100 m plot in the western portion of the older growth stand. Elevation varies between 280 and 282 m.

OLD-S – a 100 m x 100 m plot in the southern portion of the older growth stand. Elevation varies between 274 to 277 m.

OLD-N – a 100 m x 100 m plot in the northern portion of the older growth stand and adjacent to the southern boundary of the 60 year old stand. Elevation is relatively constant at 282 m.

SLOPE – a 125 m x 50 m plot located in the older growth stand and contiguous with the OLD-W site. Ridge elevation is 280 m and lowland elevation is 260 m. The site aspect ranges from NE to SE with a slope of 15 to 20°.

FLOOD – a 60 m x 45 m plot located in the older growth stand and contiguous with the SLOPE site. Its elevation is constant at 260 m and is approximately 1.5 m above the normal flow level of the bordering stream.

For each site 100 randomly selected grid coordinates were generated. These coordinates served as the center of 1.0 m^2 sampling plots. Plots were marked with flags and sampled four times during the 1987 growing season. Multiple sampling dates were utilized to account for differences in species phenology. No plots were established within 12 m of any forest edge. Plots were sampled the second and third weeks of April, the third week of May through the first week of June, the third and fourth weeks of July, and mid-September through early October.

The presence of each herbaceous plant and groundlayer woody stem (<1.0 m in height) within each plot was determined. Taxa presences were recorded regardless of developmental stage. Hence, recognizable seedlings were recorded whether or not they reached maturity. Presence/absence data were selected to save time in the field. The use of such binary data is comparable to continuous measures such as relative cover and frequency in terms of information content (Strahler 1978). The inverse of Simpson's Dominance index (Peet 1974) was calculated as a measure of diversity using the presence/absence data. Nomenclature follows Weishaupt (1971).

Detrended correspondence analysis (DECORANA) was used to examine the major gradients in vegetation among stands (Hill 1979). To reduce chance correlations caused by rare species, all taxa with an overall frequency <3% were excluded from DECORANA. Two ordinations were computed: one for all study sites and one for the older growth stands only.

Environmental measures were examined subsequent to DECORANA to assess vegetation variation in relation to smaller scale site factors. The following environmental data were included: soil moisture, soil structure and chemistry, a relative light measure, and the distance to nearest canopy tree. Environmental samples were taken from a subset of randomly selected plots per site (N = 10 for nutrients/soil chemistry, N = 20 for soil water content and relative light measures, N = 100 for nearest canopy tree). Soil sampling was performed by removing leaves and collecting two soil cores from the top 18 cm. Soil cores were collected during the first week of August, three days after a saturating rainstorm. By sampling on such a date, samples will differ most in soil moisture content (Cid-Benevento and Schaal 1986).

Percent soil moisture was determined gravimetrically. Soil samples were weighed wet and then oven-dried at 105° C for 48 hr. Percent organic content was also obtained gravimetrically by heating the same samples at 800° C for 30 min. Soil particle distribution was estimated by passing the dry, organic-free samples through sieves which collected their representative size particles (gravel, sand, and silt/clay). Soil pH, CEC (cation exchange capacity), and available K, P, Mg, and Ca measurements (North Dakota Agricultural Experiment Station 1980) were performed by the Ohio Agricultural Research and Development Center in Wooster, OH. A measure of light penetration to the forest floor was made using stacks of

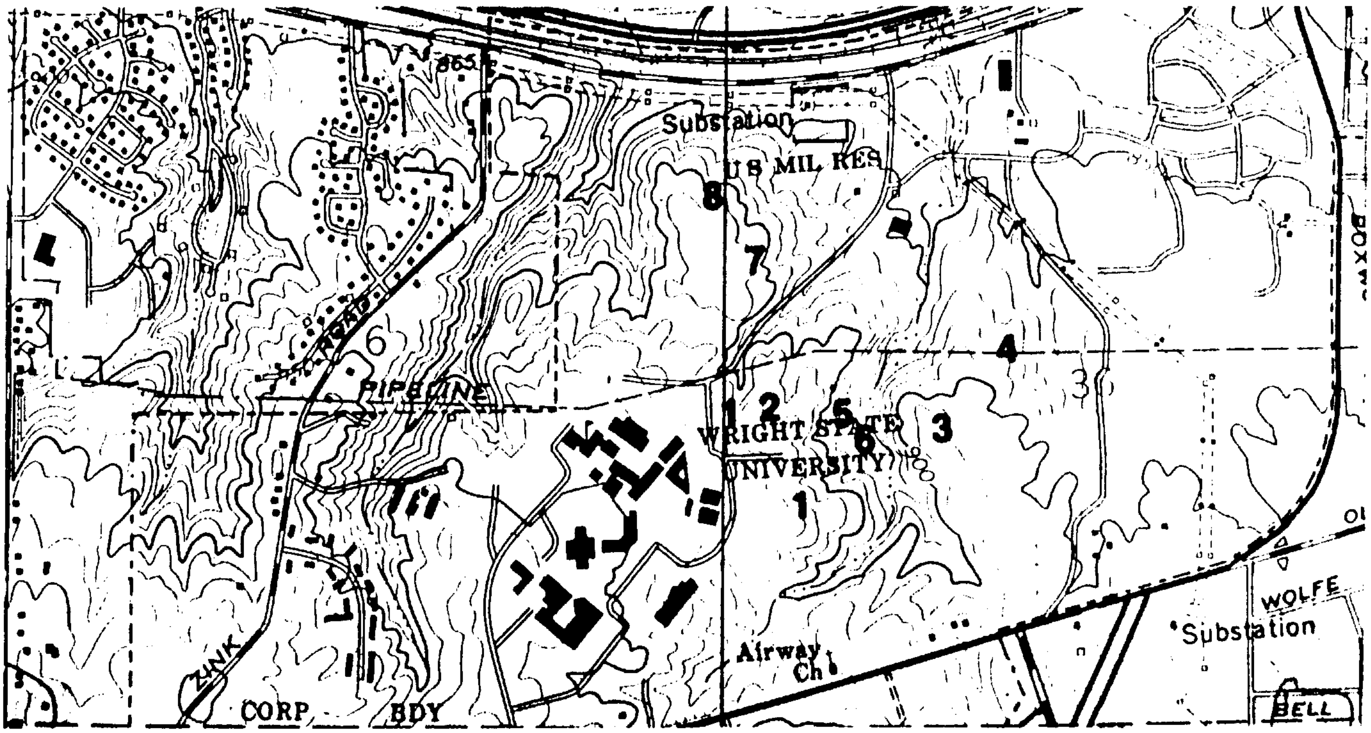

FIGURE 1. U.S.G.S. topographic map of WSU woods and surrounding area. Numbers 2-8 represent study sampling sites: 2 = OLD-W, 3 = OLD-S, 4 = SEC40, 5 = SLOPE, 6 = FLOOD, 7 = OLD-N, 8 = SEC60.

photosensitive paper (Friend 1962). Diazo paper meters were placed in the field on 4 July 1987 and left in place for 24 hr. The ratio (RELIGHT) of exposed sheets in sampled plots to those in 100% sunlight was calculated. Although this method does not directly measure photosynthetically active radiation, the ratio can be used as a relative measure to compare light penetration differences among sites. Distance to nearest canopy tree (DIST) was measured from the center of each plot.

Analysis of variance (ANOVA) was used to compare sites for all environmental factors. Tukey's honestly significant difference (HSD) multiple range test (SAS 1985) was employed to determine statistical differences among sites. Regression analysis with DECORANA axes scores as dependent variables and environmental factors as independent variables was performed with the Stepwise procedure of SAS (SAS 1985) to identify the site factors most highly correlated to community composition at the plot level.

RESULTS

Vegetation-site Relationships

Overall, 126 groundlayer taxa were encountered in the study (Table 1). Of these, 47 were found at an overall frequency greater than 3% and thus were entered into a 47 by 700 binary matrix (taxon by plot) for DECORANA. The first axis of the ordination separated the secondary sites (on the right) from the older growth sites (on the left, Fig. 2). The second axis separated older growth sites by topographic position; however, variation from the secondary stands confounds this interpretation.

The Stepwise regression procedure produced the following interpretations of the ordination axes. Percent moisture content was the most strongly correlated variable with DECORANA axis one scores ($r^2 = 0.47$; $P < 0.001$). DECORANA axis one scores were also significantly correlated with RELIGHT, pH, and available K (increasing r^2 to 0.70; $P < 0.01$). In the above model, all variables were negatively correlated with axis one scores except available K. These results suggest that percent moisture content, RELIGHT, and pH all decrease along the vegetation gradient represented by DECORANA axis one. However, the 60 year old site was not statistically different from older growth, upland stands in percent moisture content (Table 2). The second DECORANA axis was negatively correlated with available Ca ($r^2 = 0.51$; $P < 0.001$). This effect primarily distinguished upland older growth sites from the floodplain site.

To examine the relationship of topography to vegetation in the older growth sites without the confounding effects of successional vegetation variation, a separate DECORANA was performed excluding the secondary sites (Fig. 3). The first DECORANA axis displays a topographic gradient and separates upland older growth sites on the left and the floodplain on the right. The SLOPE site is transitional with an intermediate DECORANA axis one score. The stepwise regression procedure indicated that percent moisture content was the most highly correlated variable with these DECORANA axis one scores ($r^2 = 0.46$; $P < 0.001$). This correlation was negative with topographic elevation (uplands had lower percent moisture content than the floodplain).

Species-site Relationships

Overall, the ten most dominant taxa were *Alliaria officinalis, Dentaria laciniata, Impatiens* spp., *Galium*

TABLE 1

Taxon frequencies by site in descending order of overall importance and species richness and diversity

TAXON	TOTAL	FLOOD	SLOPE	OLD-W	OLD-S	OLD-N	SEC60	SEC40
Alliaria officinalis Andrz.†	450	65	74	39	72	76	69	55
Dentaria laciniata Muhl.	438	86	81	97	93	73	7	1
Impatiens spp.*	419	85	85	42	33	84	78	33
Galium aparine L.	414	71	54	71	68	81	64	5
Acer saccharum Marsh.	408	30	64	78	72	66	84	14
Ulmus americana L.	339	32	44	49	49	70	59	36
Viola pubescens Ait.	288	38	30	39	46	80	49	6
Claytonia virginica L.	281	15	33	58	12	89	69	5
Sanicula gregaria Bickn.	273	73	19	5	30	47	54	45
Asarum canadense L.	236	88	68	14	4	59	2	1
Osmorhiza longistylis (Torr.) DC.	233	65	6	2	7	51	81	21
Allium tricoccum Ait.	224	56	35	21	39	48	15	10
Geum canadense Jacq.	220	37	23	2	22	41	67	28
Smilacina racemosa (L.) Desf.	220	65	66	27	33	24	1	4
Lonicera maackii Maxim.†	202	10	7	11	3	11	69	91
Parthenocissus quinquefolia (L.) Planch.	197	23	34	21	10	21	77	11
Polygonum virginianum L.	148	65	18	5	6	9	39	6
Prunus serotina Ehrh.	128	0	0	7	4	33	31	53
Viola papilionacea Pursh	125	28	15	21	16	19	22	4
Agrostis perennans Walt. Tukerm.	120	29	17	10	8	13	34	9
Pilea pumila (L.) Gray	117	55	29	4	0	13	16	0
Trillium flexipes Raf.	96	61	28	0	0	5	1	1
Circaea quadrisculata (Maxim.) Franch. & Sav.	85	13	27	21	8	16	0	0
Podophyllum peltatum L.	80	2	21	5	27	12	8	5
Arisaema atrorubens (Ait.) Blume	79	19	18	22	0	14	6	0
Osmorhiza claytonii (Michx.) Clarke	77	1	17	10	31	4	7	7
Sanguinaria canadense L.	69	2	13	16	20	17	0	1
Cardamine douglassii (Torr.) Britt.	60	52	2	6	0	0	0	0
Ranunculus abortivus L.	55	10	2	1	0	4	38	0
Carex spp.	53	10	15	6	2	4	9	7
Laportea canadensis (L.) Wedd.	47	34	9	0	1	0	0	3
Hydrophyllum spp.	41	3	5	7	3	22	1	0
Celtis occidentalis L.	40	3	2	11	4	5	11	4
Aesculus glabra Willd.	37	8	1	13	10	5	0	0
Fraxinus americana L.	37	0	2	16	12	6	0	1
Trillium sessile L.	37	0	4	24	0	9	0	0
Ornithogalum umbellatum L.†	33	0	1	7	2	0	0	23
Phyrma leptostachya L.	32	7	0	10	2	7	0	6
Boehmeria cylindrica (L.) Sw.	28	1	2	10	3	6	5	1
Sanicula trifoliata Bickn.	27	0	0	15	8	1	3	0
Carya spp.	26	2	0	6	7	7	0	4
Lindera benzoin (L.) Blume	26	6	13	0	1	6	0	0
Polygonatum biflorum (Walt.) Ell.	24	20	4	0	0	0	0	0
Smilax tamnoides L.	24	1	2	3	2	3	8	5
Prenanthes spp.	23	13	2	0	0	6	2	0
Phlox divaricata L.	23	9	1	3	1	9	0	0
Sambucus canadensis L.	22	8	0	0	2	6	5	1
Eupatorium rugosum Houtt.	20	0	0	3	7	5	1	4
Rosa multiflora Thunb.†	20	0	1	0	0	1	1	17
Actaea pachypoda Ell.	19	11	2	0	1	5	0	0
Cystopteris fragilis (L.) Bernh.	18	5	13	0	0	0	0	0
Asimina triloba (L.) Dunal	17	0	3	0	0	14	0	0
Fraxinus quadrangulata Michx.	17	2	4	9	1	0	1	0
Rhus radicans L.	17	0	6	2	2	0	0	7
Allium canadense L.	16	8	1	0	0	0	6	1
Caulophyllum thalictroides (L.) Michx.	16	8	2	2	3	1	0	0
Hydrastis canadensis L.	16	13	1	0	0	0	2	0
Oxalis grandis Small	16	5	0	5	2	0	0	4
Hysterix patula Moench	15	0	0	1	3	3	6	2
Menispermum canadense L.	15	0	0	3	11	0	0	1
Uvularia perfoliata L.	15	0	1	5	5	3	1	0

Table 1 (continued)

TAXON	TOTAL	FLOOD	SLOPE	OLD-W	OLD-S	OLD-N	SEC60	SEC40
Vitis spp.	13	1	6	1	2	1	0	2
Panicum clandestinum L.	12	4	5	0	0	2	1	0
Elymus villosus Muhl.	11	0	3	4	4	0	0	0
Euonymus atropurpureus Jacq.	11	2	3	1	3	0	0	2
Hybanthus concolor (T. F. Forst.) Spreng.	11	1	10	0	0	0	0	0
Geum vernum (Raf.) T. & G.	10	1	0	0	1	1	7	0
Botrychium virginianum (L.) Sw.	9	2	4	0	0	0	0	3
Brachylectrum erectum (Schreb.) Beauv.	9	6	2	0	0	0	1	0
Quercus muehlenbergii Engelm.	9	3	0	0	3	0	0	3
Viburnum prunifolium L.	9	2	6	1	0	0	0	0
Ailanthus altissima (Mill.) Swingle†	8	0	0	2	0	4	2	0
Diarrhena americana Beauv.	8	3	3	1	1	0	0	0
Polemonium reptans L.	8	8	0	0	0	0	0	0
Quercus rubra L.	7	0	0	1	2	1	3	0
SPECIES RICHNESS#	126	75	66	69	67	66	60	58
DIVERSITY**	30.3	30.3	25.6	23.3	20.0	23.8	20.8	15.4

*We were unable to classify *Impatiens biflora* and *I. pallida* seedlings; however, all flowering individuals observed in plots were *I. pallida*.

**This value is the inverse of Simpson's Index based on presence frequencies.

#Taxa with an overall frequency <1% included: *Acer nigrum* Michx. f., *Acer rubrum* L., *Agrimonia pubescens* Wallr., *Anemone virginiana* L., *Anemonella thalictroides* (L.) Spach, *Aplectrum hyemale* (Nutt.) Torr., *Asplenium trichomanes* L., *Aster shortii* Lindl., *Bidens vulgata* Greene, *Botrychium dissectum* Spreng., *Bromus commutatus* Schrad.†, *Bromus inermis* L.†, *Bromus purgans* L., *Cacalia muhlenbergii* (Sch. Bip.) Fern., *Chaerophyllum procumbens* (L.) Crantz, *Conophilis americana* (L.) Wallr., *Convolvulus sepium* L., *Cryptotaenia canadense* (L.) DC., *Desmodium nudiflorum* DC., *Erigeron strigosus* Muhl., *Erythronium albidum* Nutt., *Eupatorium purpureum* L., *Festuca arundinacea* (Schreb.) Wimmer†, *Festuca obtusa* Spreng., *Fraxinus pennsylvanica* Marsh., *Galium asprellum* Michx., *Galium pilosum* Ait., *Galium triflorum* Michx., *Geranium maculatum* L., *Glechoma hederaca* L.†, *Gleditsia triacanthos* L., *Ipomea pandurata* (L.) G. F. W. Meyer, *Ligustrum vulgare* L.†, *Liparis lilifolia* (L.) Rich., *Lonicera japonica* Thunb.†, *Muscari botryoides* (L.) Mill.†, *Phytolacca americana* L., *Polygonatum canaliculatum* (Muhl.) Pursh, *Polygonum persicaria* L.†, *Quercus alba* L., *Ribes cynosbati* L., *Robinia pseudo-acacia* L., *Rubus* spp., *Rudbeckia laciniata* L., *Senecio vulgaris* L.†, *Setaria faberii* Herrm.†, *Smilax herbacea* L., *Solidago canadensis* L., *Solidago nemoralis* Ait., Gray G., *Staphylea trifolia* L., *Viburnum acerifolium* L.

†Indicates non-native taxon (Weishaupt 1971).

aparine, Acer saccharum, Ulmus americana, Viola pubescens, Claytonia virginica, Sanicula gregaria, and *Asarum canadense* (Table 1). Overall diversity (inverse of Simpson's dominance index) was 30.3.

The FLOOD site had the greatest species richness of all sites (75 taxa). Diversity of this site was the same as the overall diversity measure, 30.3. *Asarum canadense* (frequency = 88% of plots) dominated its groundlayer vegetation. Other important taxa at this site were *Dentaria laciniata* (86), *Impatiens* spp. (85), *Sanicula gregaria* (73), *Smilacina racemosa* (65), *Osmorhiza longistylis* (65), and *Polygonum virginianum* (65). Taxa reaching maximum importance (among all sites) included *Asarum canadense, Impatiens* spp. (85), *Sanicula gregaria* (73), *Allium tricoccum* (56), *Polygonum virginianum* (65), *Trillium flexipes* (61), *Pilea pumila* (55), *Cardamine douglassii* (52), *Laportea canadensis* (34), and *Polygonatum biflorum* (24).

The species richness of the SLOPE site was 66 and its diversity was 25.6. The site was dominated by *Impatiens* spp. (85) and *Dentaria laciniata* (81). Since upper and lower slope plots were not distinguished in the analyses, the SLOPE site shows much variation which may be attributable to the topographic positions of upper, middle, and lower SLOPE plots. *Smilacina racemosa* (66), *Circaea quadrisculata* (27), *Carex* spp. (15), and *Lindera benzoin* (13) reached maximum importance in this site.

The OLD-W had a species richness of 69 and diversity index of 23.2. *Dentaria laciniata* (97) dominated the groundlayer in this site. *Acer saccharum* (78), *Galium aparine* (71), and *Claytonia virginica* (58) were the only other taxa occurring at a frequency of >50. Taxa reaching maximum importance in this site were *Dentaria laciniata* (97), *Trillium sessile* (24), and *Arisaema atrorubens* (22).

The OLD-S site had a species richness of 67 and a diversity index of 20.0. Like the OLD-W, the groundlayer was dominated by *Dentaria laciniata* (93). Other taxa occurring at a frequency of >50 were *Acer saccharum* (72), *Alliaria officinalis* (72), and *Galium aparine* (68). *Podophyllum peltatum* (27) and *Osmorhiza claytonii* (31) reached maximum importance in this site.

The OLD-N site had a species richness of 66 and a diversity index of 23.8. *Claytonia virginica* (89) dominated the groundlayer. Nine other taxa were present at a frequency >50, including *Impatiens* spp. (84), *Galium aparine* (81), *Viola pubescens* (80), and *Alliaria officinalis* (76). Taxa reaching maximum importance in this site were *Claytonia virginica, Impatiens* spp., *Galium aparine,*

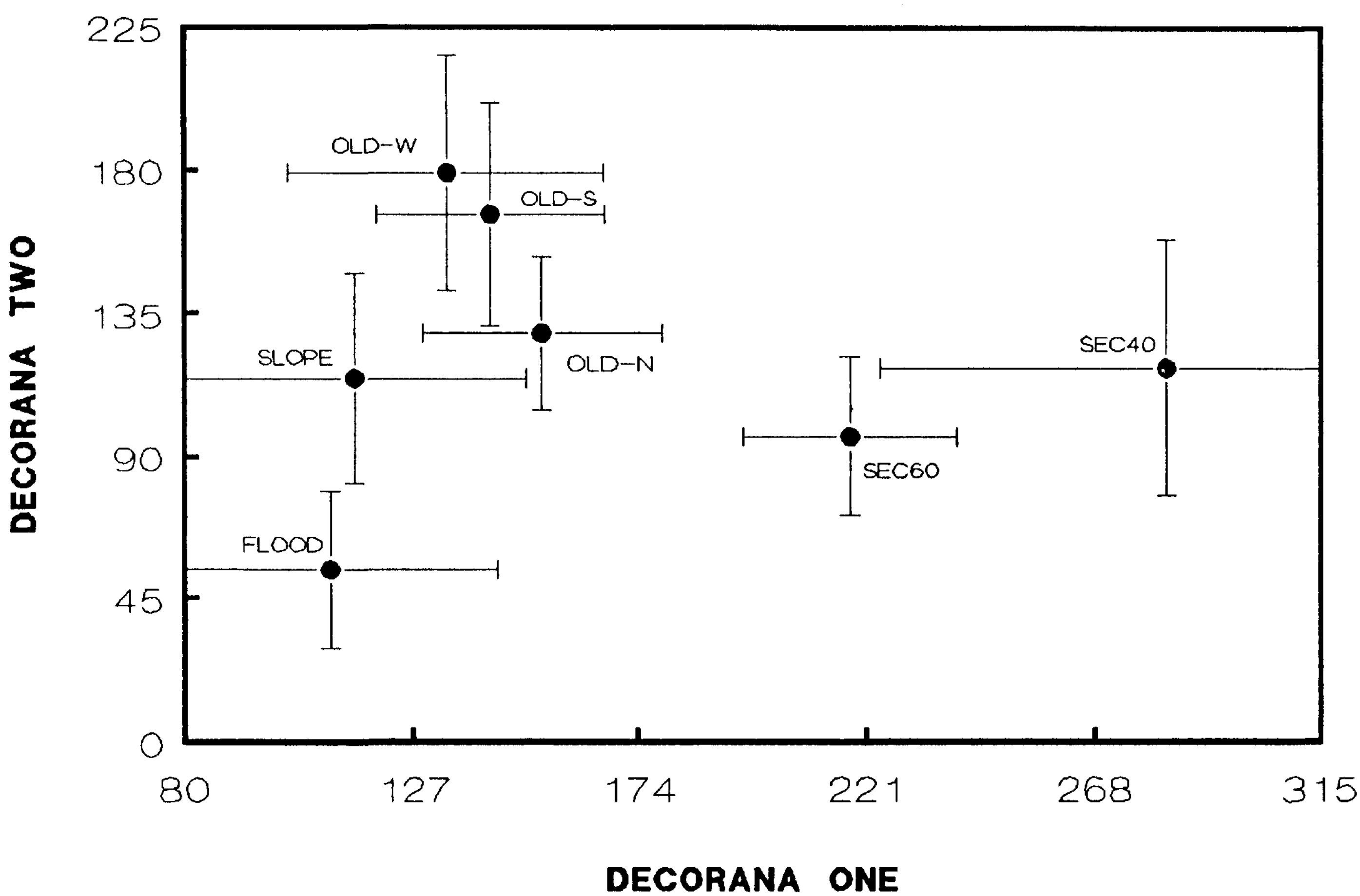

FIGURE 2. DECORANA ordination of all sites. Circles represent mean DCA plot scores; bars represent standard deviations.

TABLE 2

ANOVA on measured environmental factors.

	FLOOD	SLOPE	OLD-W	OLD-S	OLD-N	SEC60	SEC40
% water content*	25A	22B	21B	21B	21B	20BC	18C
% organics*	8AB	6C	10A	5CD	5CD	4D	5CD
% gravel*	IBC	0C	4AB	IBC	0C	2BC	7A
% sand*	70A	57CD	60ABC	48CD	45D	60AB	63AB
% silt-clay*	29C	41C	36C	51AB	55A	38BC	30C
pH	6.8A	6.6A	6.0AB	6.0AB	5.9AB	5.5B	5.9AB
P (ppm)	5.2B	15.8A	10.8AB	15.9A	10.6AB	8.2AB	6.4AB
K (ppm)	133.8A	106.7AB	65.8C	87.8BC	78.3BC	101.5ABC	131.6A
Ca (ppm)	3117A	1895B	1371BC	1421BC	1135C	1148C	1699BC
Mg (ppm)	504A	328BC	199CD	159BC	134D	199CD	374AB
CEC (meq/100mg)	21.2A	13.4BC	12.4BC	11.5BC	9.8C	12.7BC	15.5B
RELIGHT*	0.35A	0.31AB	0.30AB	0.33A	0.33AB	0.29B	0.25C
DISTANCE** (cm)	331AB	408AB	341AB	429A	402AB	301AB	293B

*N = 20; **N = 100; all others N = 10

Letters represent significant differences (P <0.05)

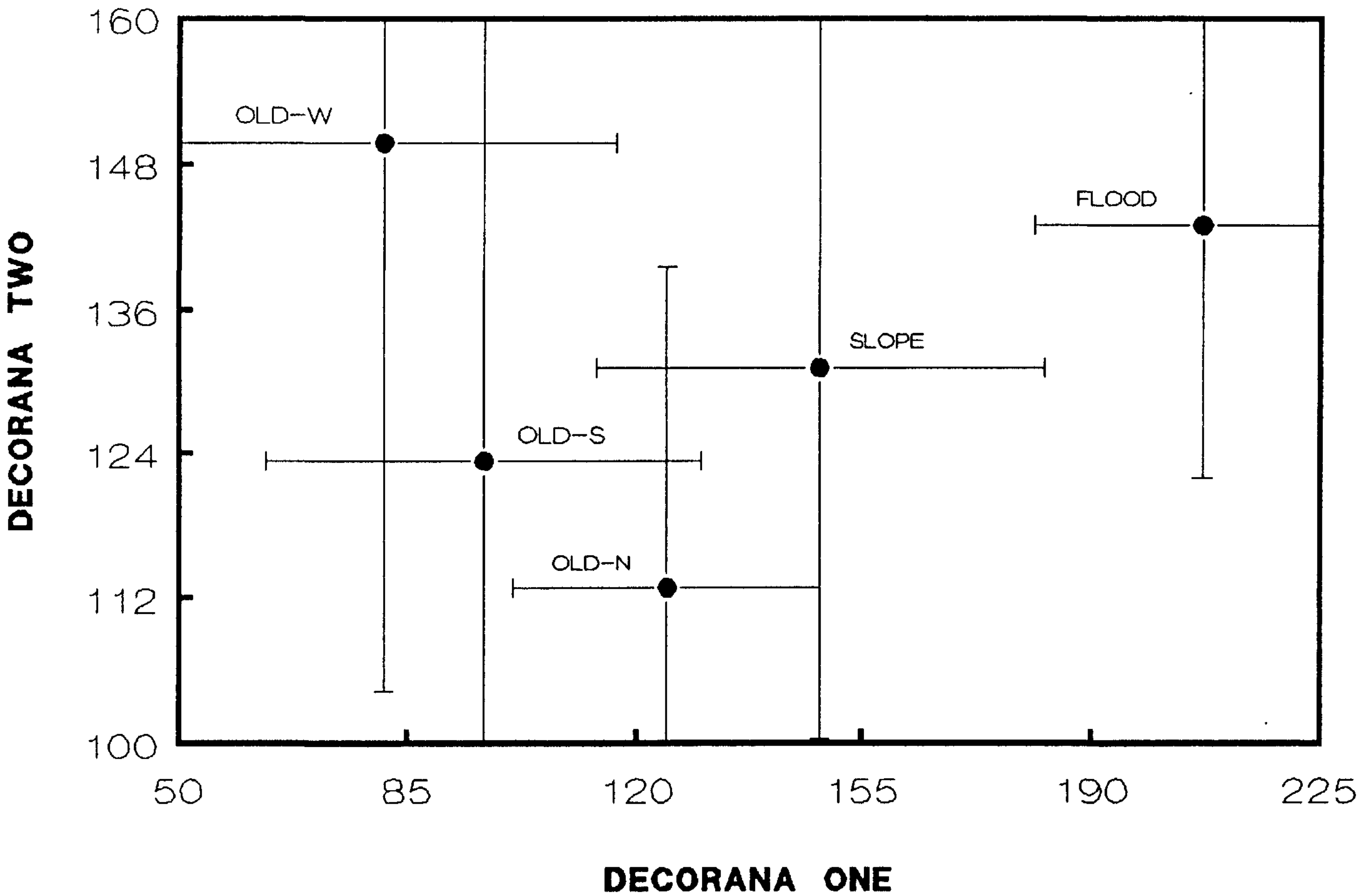

FIGURE 3. DECORANA ordination of old growth sampling locations only. Circles represent mean DCA plot scores; bars represent standard deviations.

Viola pubescens, Alliaria officinalis, and *Ulmus americana* (70).

The secondary sites varied considerably between themselves and among other sites. These sites had more woody taxa contributing to their overall vegetation than older growth sites. Species richness in the SEC60 and SEC40 sites were 60 and 58, respectively. The diversity index was 20.8 and 15.4, respectively.

The SEC60 site was dominated by *Acer saccharum* (84). Other important taxa included *Osmorhiza longistylis* (81), *Impatiens* spp. (78), *Parthenocissus quinquefolia* (77), *Alliaria officinalis* (69), *Claytonia virginica* (69), and *Lonicera maackii* (69). *Acer saccharum* (84), *Osmorhiza longistylis* (81), *Geum canadense* (67), *Parthenocissus quinquefolia, Agrostis perennans* (34), and *Ranunculus abortivus* (38) reached maximum importance in this site.

The SEC40 site was dominated by *Lonicera maackii* (91). *Alliaria officinalis* (55), *Prunus serotina* (53), *Sanicula gregaria* (54), and *Ulmus americana* (36) were also important in this site. Taxa reaching maximum importance in this site were *Lonicera maackii, Prunus serotina, Ornithogalum umbellatum* (23), and *Rosa multiflora* (17).

DISCUSSION

Successional age is the major large scale factor affecting groundlayer vegetation within the WSU woods. This conclusion is based on the separation of the secondary sites from the old growth sites along DECORANA axis one (Fig. 2). Several investigators have examined forest canopy change through succession (e.g., Potzger and Friesner 1934, Hosner and Minckler 1963, Bell and del Moral 1977, Peet and Christensen 1980); however, few have examined groundlayer successional change.

Groundlayer vegetation is affected by canopy dynamics. Young *Acer saccharum*-dominated forests in the eastern United States usually develop a tightly closed canopy (Nyland et al. 1986) which subjects the groundlayer to low light levels (Nicholson and Monk 1975). Relatively few groundlayer species can survive under these low light conditions. However, as the forest matures, the canopy layer self-thins (Christensen and Peet 1984) and gaps are created. This process increases the heterogeneity of the light and soil environment (Moore and Vankat 1986) allowing for the establishment of groundlayer species with differing environmental requirements. Further maturation of the forest results in ongoing gap-phase dynamics which maintains a heterogeneous environment and "safe sites" (Harper 1977) for the germination of local and arriving propagules.

The general result of the foregoing process is that species richness and diversity gradually increase throughout forest succession and then level off as the system becomes more stable. This general trend has been reported in several studies which examined groundlayer vegetation (Nicholson and Monk 1975, Scheiner and Teeri 1981, Taylor et al. 1987). The results of the present study also show increasing species richness and diversity with increasing site age. However, others have shown that richness and diversity peak at an intermediate stage and then decrease slightly (Auclair and Goff 1971, Shafi and Yarranton 1973). Groundlayer vegetation may continue to change during the climax in response to subtle changes in canopy structure and composition (Brewer 1980, Davison and Forman 1982).

In this study, successional differences were manifest in part by the relative contributions of various taxon life history characteristics (Vankat and Snyder 1991). The lower diversity in the SEC40 site reflected lower numbers of some perennials such as *Asarum canadense*, *Viola* spp., *Smilacina racemosa* and, especially, the spring ephemerals *Dentaria laciniata* and *Claytonia virginica*. It also reflected lower numbers of annuals such as *Impatiens* spp., *Galium aparine*, *Pilea pumila*, and *Circaea quadrisculata*. Their relative absence was offset by higher frequencies of woody stems such as *Lonicera maackii*, *Prunus serotina*, and *Rosa multiflora*. These trends were not as pronounced in the SEC60 site which approached the vegetation patterns found in the older growth upland stands. In the secondary sites, canopy structure may indirectly influence the groundlayer by affecting their light and soil environments. For instance, the lack of annuals in SEC40 may result from significantly less light there (if we assume that annuals as a group are relatively light demanding). The lower importance of annuals in this site may also reflect the lower soil moisture content (Struik and Curtis 1962). Propagule availability is another factor which may have contributed to successional differences. Many species characteristic of older growth and virgin stands have poor colonizing ability (Peterken 1981, Whitney and Foster 1988). This may explain the increased importance of *Lonicera maackii*, *Ornithogalum umbellatum*, and *Rosa multiflora* in the SEC40 site. All these taxa are bird dispersed and non-native.

In the DECORANA ordination of the older growth sites only (Fig. 3), the first axis represented a topographic gradient. Studies examining vegetation variation in sites of differing topography have shown that relief (topographic position) is a major factor affecting species distributions. The site factors which vary most with differences in topography are soil moisture, pH, and some nutrients (Whittaker 1956). Runkle and Whitney (1987) concluded that topography was the major factor affecting canopy vegetation composition in a Jackson County, OH, forest. They suggested that soil moisture was the primary site-factor responsible for species distribution patterns. Other studies have demonstrated that canopy vegetation responds to the underlying moisture gradient associated with topographic differences (Peet and Loucks 1977, Muller 1982, Seischab 1985). Groundlayer species have also been shown to respond to moisture availability along microtopographic gradients (Struik and Curtis 1962, Hicks 1980). The stepwise regression procedure showed that percent water content was the most highly correlated environmental factor with both overall and older growth DECORANA axis one scores.

The effects of moisture availability on canopy and groundlayer vegetation are well documented (e.g., Beals and Cope 1964) as is the relationship between topography and soil moisture (Whittaker 1956, Hack and Goodlet 1960). However, the relationship between soil moisture and site age is less recognized in the literature. The lower percent water content in the SEC40 site may be related to the dense canopy (DeMars, personal observation) common in young stands dominated by *Acer saccharum* (Nyland et al. 1986). A dense canopy serves to intercept more rainfall and hasten evaporation losses (Minkler and Woerheide 1965), and it may increase stem flow thus localizing water nearer to canopy stems.

Christensen and Peet (1984) showed that the understory vegetation in *Pinus taeda* stands was highly responsive to canopy stem density and that soil moisture increased with stand thinning over time. Taylor et al. (1987) showed that soil moisture significantly increased with increasing stand age in a forest chronosequence. They found that soil moisture was the variable most highly correlated with groundlayer vegetation along the successional gradient. Increasing water availability along a forest successional gradient has also been demonstrated by Kell (1938) and by Scheiner and Teeri (1986).

Although percent soil moisture was the most highly correlated site factor associated with groundlayer vegetation, community composition is influenced by a complex of environmental factors (Muller 1982). Gauch and Stone (1979) suggest that although groundlayer vegetation responds primarily to an underlying moisture gradient, this gradient is complex and is accompanied by gradients in soil nutrients and pH. In the present study, measures of water availability, light availability, soil chemistry, and nutritional status interact to best explain the composition of groundlayer vegetation. Since the coefficient of determination (r^2) was only 0.70 for the overall regression, other combinations of unmeasured and measured variables may lead to a better explanation of the vegetation. Additionally, higher scale site factors within and among sites such as stochastic and historical events, differential disturbance, microrelief, canopy composition, dynamics and landscape features probably play a role in the determination of the groundlayer vegetation in the WSU woods.

In conclusion, our data suggest that the groundlayer vegetation of the WSU woods is determined primarily by soil moisture relationships. This result, however, does not prove that soil moisture is the most important factor responsible for vegetation variation. Other unmeasured factors may vary and covary with soil moisture measures. It appears that the overall groundlayer vegetation of the WSU woods responds primarily to a moisture gradient established among successional stands and secondarily to the moisture gradient associated with topographic elevation within the older growth stand. Future studies on the groundlayer vegetation of the WSU woods should attempt to confirm this putative effect of soil moisture. These studies should make use of more accurate means of measuring soil moisture availability or utilize a direct gradient approach.

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