VARIABILITY IN OAK FOREST HERB LAYER COMMUNITIES

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Abstract: This study evaluates forest herb-layer sensitivity to annual-scale environmental fluctuation. Specific objectives were to determine the between-year variation in herb-layer community biomass, and to contrast and evaluate the temporal stability of spatial relationships in herb-layer community structure and composition between successive years. Aboveground dry weights of herbs and of woody species <2.5 cm dbh were estimated in June of 1988 and 1989 in 13 ecologically analogous, oak-dominated stands along a 170-km east-west transect in north-central Pennsylvania. An approximately 50% reduction in total herb-layer biomass was measured from 1988 to 1989, presumably due to a residual or lagged effect of the early summer drought in 1988. Herb biomass reductions were inferred to largely result from reduced plant size rather than decreased spatial distribution. Smaller and (or) less-consistent biomass reductions for woody species may have resulted from high first-year seedling mortality in the case of *Acer rubrum* L., and possibly from intensified deer browsing of shrubs and saplings as a consequence of reduced herb forage resulting from the drought. Classification and ordination also indicated a 1989 reduction in importance of mesic-type species and an increase in similarity of herb-layer communities among stands. Conversely, greater spatial differences in species diversity measures were evident in 1989. Comparisons among herb layer communities based on single or infrequent measurements may be misleading due to large temporal variability and the spatially differential responses that broad-scale environmental factors such as climate may superimpose. Monitoring herb layer biomass in this oak forest ecosystem offers a sensitive means for detecting short-term environmental fluctuations such as annual climate variation, and additional data may enable identification of vegetation trends with statistical confidence.

INTRODUCTION

Eastern North American deciduous forests receive a multitude of natural and anthropogenic stresses, including climatic extremes, air pollution, and disease and insect outbreaks. These stresses can eventually alter ecosystem composition, structure and function (Graham et al., 1990; Hinrichsen, 1987). A national research priority is to identify and monitor sensitive forest ecosystem indicators that portend such changes.

The forest herb-layer can be a sensitive indicator of microsite (Pregitzer and Barnes, 1982), and is useful for classifying forest ecosystem types (Host and Pregitzer, 1991; Hix, 1988). An altered understory community is theorized to be an early response of forested landscapes to global change (Davis, 1989). However, most long-term studies involve measurement intervals of several years to decades (Rodenkirchen, 1992; Mueggler, 1992), thus masking any effects of climate or other high-frequency environmental fluctuation.

Few annual-scale studies of forest understory have been published. A six-year study of vegetation cover and frequency in a Pinyon-Juniper community demonstrated the high variability to be expected among both perennial and annual herbs, with little fluctuation among shrubs and trees (Treshow and Allan, 1979). It thus appears that spatial and temporal monitoring of herb-layer community dynamics may yield sensitive bioindication of both environmental fluctuations and trends. Further, with appropriate measurements of forest overstory, site, climate, atmospheric pollution and other intervening factors, the influence of these environmental variables can also be assessed.

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This paper focuses on evaluating the spatial and temporal variability of herb-layer biomass in mixed oak forests. Specific objectives were: (1) to determine the between-year variation in herb-layer community biomass and, (2) to contrast and evaluate the temporal stability of spatial relationships in herb-layer community biomass between successive years.

Background

Ecological monitoring can be a useful approach for investigating long-term processes such as effects of climate change and atmospheric pollution (Likens, 1989). Substitution of space for time is one technique employed to investigate long-term processes on shorter time scales (Pickett, 1989). We used a spatial gradient of wet sulfate and nitrate deposition across north central Pennsylvania to capitalize on an existing range of atmospheric inputs as a substitute of space for time (Likens, 1989). Data reported here were collected as part of the broader study of oak forest condition and response along this gradient (Nash et al., 1992).

Ecologically similar sites are often used to reduce experimental variation, but in studies such as ours where space is substituted for time, different site conditions or histories can lead to erroneous conclusions (Pickett, 1989). Therefore, initial emphasis was placed on selecting ecologically analogous sites. The selection process included ordination and classification analyses of candidate sites using preliminary data on soil physical properties, physiography, canopy stratum species abundances, and evaluation of disturbance history as determined from insect defoliation surveys, forest management records, and on-site evidence of fire and cutting (Long et al, 1991). Our rationale was to confine selection criteria to factors unlikely to have been influenced by chemical deposition. Subsequent intensive sampling of herb-layer biomass on the selected sites in 1988 and 1989 form the basis for this report.

METHODS

Study Area

The study region lies within the Appalachian Plateaus Physiographic Province (Ciolkosz et al., 1983). Soils of the study sites are derived from residual sandstone and are mostly Typic Dystrochrepts with small areas of Ultisols and Alfisols. Thirteen ecologically analogous sites (6-50 ha) were selected within four approximately equally-spaced core areas (clustered sites) across the 170-km gradient (Long et al., 1991). The core areas, from west to east and corresponding to the state forests in which they are located, are referred to as Clear Creek (C), Moshannon (M), Sproul (S) and Tiadaghton (T). The 13 sites occupied gently sloping, mostly broad uplands at a mean elevation of 576 m (range: 490-661).

Forest canopy trees on the sites were 70-80 yr old, even-aged, and dominated by *Quercus rubra* L). Common associated canopy species were *Acer rubrum* L., *Quercus alba* L., *Quercus prinus* L., and *Betula lenta* L.

Basal areas for canopy trees on the 13 sites averaged 25.1 (19.7-28.9) m^2/ha, with a mean overstory density of 291 (243-334) stems/ha. *Sassafras albidum* (Nutt.) Nees, *Hamamelis virginiana* L., *Amelanchier* spp, *Cornus florida* L., and in the Tiadaghton core area, *Acer pensylvanicum* L., were common understory trees.

Sampling

Herb-layer above-ground biomass was destructively sampled on the 13 sites in 1988 and 1989. Pairs of 3.1 m^2 (1-m-radius) plots were located 14 m north and south (1988) or east and west (1989) of permanent, randomly-established reference stakes. Depending on area of the site, 10 or 20 plots per site were sampled, for a total of 160 plots each year.

Sampling was conducted after the initial growth flush by clipping at the ground surface all herbaceous plants and all woody stems <2.5 cm dbh. In 1988 sampling was completed between June 6 and June 23, and in 1989 between June

5 and June 16. Clipped material was placed in paper bags by species. In the laboratory, samples were temporarily refrigerated, dried at 70° C to constant weight, and weighed to 0.01 g. A voucher collection was prepared. Species identification of *Carex*, *Viola* and other difficult genera was verified by consultation with personnel at The Ohio State University Herbarium.

Data Analysis

A split-plot ANOVA fixed effects model was one method used to evaluate spatial and temporal differences in herb layer biomass. Stands were tested as spatial (main) effects, and years and the years by species groups interaction terms were subunits used to test for temporal differences and possible interactions between species and years (Neter et al., 1985). Means of factors with significant F-values ($P \leq .05$) were separated by Student-Newman-Keuls' test. Species were combined into groups to avoid non-normality problems resulting from high frequencies of zero's for individual species. The groupings were based mostly on species abundances and taxonomic relationship. One analysis tested two groups consisting of total woody biomass and total herbaceous biomass. A second analysis used the following nine species groups: (1) *Dennstaedtia punctilobula*, (2) other fern species, (3) *Viola* spp., (4) *Gramineae* and *Carex* spp., (5) other herbaceous species, (6) *Vaccinium* spp. and *Gaylussacia* spp., (7) other *Ericaceae*, (8) other shrubs and, (9) tree seedlings. *Kalmia latifolia* was omitted from the second analysis due to its extreme variability in biomass, a result of the wide range in plant size and clumped spatial distribution.

The herb-layer communities were compared on the basis of species biomass by classification and ordination techniques to examine geographical and temporal trends. Plots were classified using Hill's (1979a) TWINSPAN algorithm, and ordinated by detrended correspondence analysis (DCA) using computer program DECORANA (Hill, 1979b).

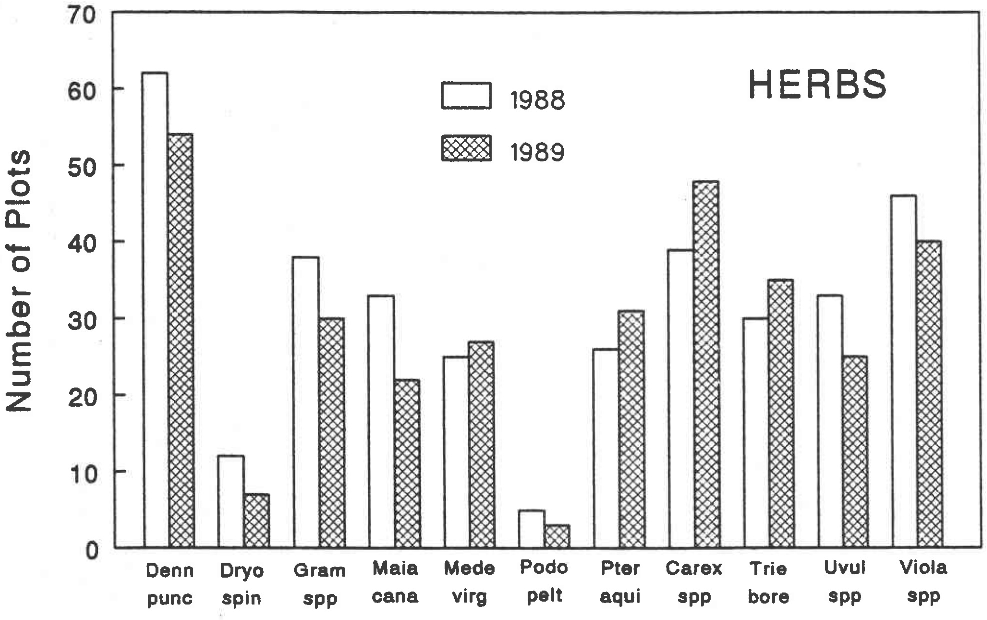
Species diversity was compared geographically (among core areas) on the basis of Hill's (1973) diversity numbers: N0, N, and N2 (Ludwig and Reynolds, 1988). N0 is the number of species. N1 is calculated as $e^{H'}$, where e is the base of natural logarithms and H' is Shannon's diversity index, yielding the biomass-weighted or *effective* number of relatively well-represented species. N2 is $1/\lambda$, where λ is Simpson's diversity index, which provides a biomass-weighted *effective* number of relatively dominant species. The modified Hill's ratio (Alatalo, 1981), a measure of evenness (E), was calculated for core areas as (N2 - 1)/(N1 - 1). Thus, E achieves a maximum of 1.0 when all species are equally abundant, whereas values of E approaching the minimum of 0 indicate increasing dominance by a single species.

Biomass distribution among species was also compared between years and among core areas on the basis of dominance-diversity curves (Bonham, 1989).

RESULTS

Biomass for each species sampled on plots is presented in Table 1. Analysis of variance detected no significant differences in biomass among the 13 sites ($P \leq .05$) on the basis of the nine species groups; nor were site differences found when total woody and total herbaceous biomass groupings were used.

However, there was a significant difference in biomass between years when the nine species groups were used in ANOVA, with mean biomass decreasing nearly 50% from 1988 (283.5 kg/ha) to 1989 (151.1 kg/ha). Between-year biomass reductions were consistent for the nine species groups. The relative decreases were close to 50% (40.4% - 56.6%) for all four herbaceous groups and the miscellaneous shrubs, while the smallest decrease (12.1%) occurred within the tree seedling group. A significant species group by year interaction resulted from the comparatively large biomass reduction of *Dennstaedtia punctilobula*. For other individual species, primarily those with low plot frequencies (e.g., *Dryopteris spinulosa*, *Podophyllum peltatum*, *Vaccinium vacillans*; Fig. 1) between-year biomass differences were less consistent (Table 1).



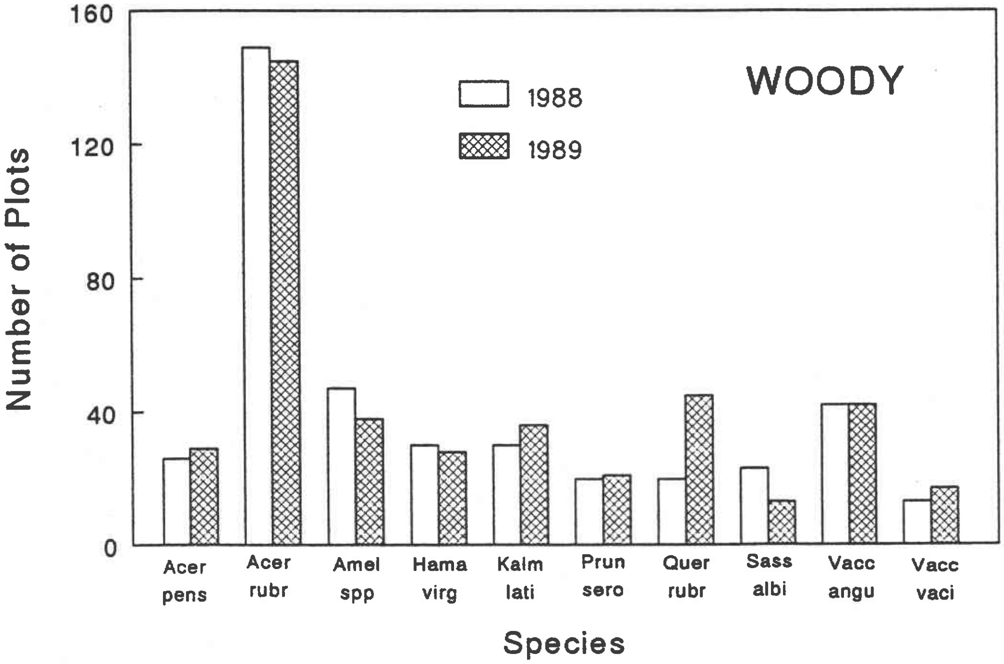


Figure 1. Plot frequencies of selected herbaceous and woody species. Complete species names are found in Table 1.

Table 1. Mean herb-layer species aboveground dry matter by core area and year. Core areas are Clear Creek (C; n=40), Moshannon (M; n=50), Sproul (S; n=40), and Tiadaghton (T; n=30).

		Core Area			
Species	Year	C	M	S	T
			-kg/ha-		
Acer pensylvanicum L.	1988	-	-	-	340.5
	1989	-	2.25	0.06	193.9
Acer rubrum L.	1988	1.84	9.94	5.66	1.91
	1989	1.07	7.24	0.86	1.95
Amelanchier spp.	1988	1.98	1.40	0.66	0.84
	1989	0.38	2.28	0.47	1.64
Aralia nudicaulis L.	1988	0.19	-	-	-
	1989	0.59	1.14	-	2.01
Aster spp.	1988	-	-	-	-
	1989	0.13	-	0.04	-
Azalea spp.	1988	5.14	0.25	-	-
	1989	0.73	0.57	-	-
Betula lenta L.	1988	-	2.88	0.11	0.10
	1989	-	2.73	0.10	2.01
Brachyeletrum erectum (Schreb.) Beauv.	1988	4.78	1.92	2.23	-
	1989	-	-	-	-
Carex debilis Michx.	1988	-	42.1	-	-
	1989	0.44	1.14	-	-
C. digitalis Willd.	1988	4.78	0.19	5.76	1.40
	1989	2.50	-	1.38	2.26
C. pensylvanica Lam.	1988	47.2	7.27	25.2	15.3
	1989	10.6	8.66	17.3	-
C. swanii (Fern.) MacKenz.	1988	-	-	0.03	5.82
	1989	-	-	-	-
Carex spp.	1988	5.14	1.54	-	3.85
	1988	0.06	-	-	4.31
Carya spp.	1988	-	-	-	0.38
	1989	-	-	-	0.01
Conopholis americana (L.) Wallr.	1988	23.0	-	-	-
	1989	-	-	-	-

Table 1 (continued)

Species	Year	C	M	S	T
			-kg/ha-		
Cornus florida L.	1988	-	0.41	-	-
	1989	-	-	-	-
Craetegus spp.	1988	1.46	-	0.35	-
Danthonia compressa Aust.	1988	-	41.0	55.1	-
	1989	-	3.44	3.08	-
Dennstaedtia punctilobula (Michx.) Moore	1988	112.2	200.6	239.0	504.8
	1989	58.3	67.3	89.1	398.2
Dryopteris spinulosa (O.F. Muell.) Watt	1988	5.15	6.22	0.16	28.1
	1989	1.61	12.5	0.13	7.64
Euonymous spp.	1988	-	-	-	0.16
	1989	-	-	-	-
Eupatorium rugosum Houtt.	1988	-	-	-	1.56
	1989	-	-	-	-
Fagus grandifolia Ehrh.	1988	0.22	26.7	-	8.50
	1989	-	104.4	-	4.96
Fraxinus americana L.	1988	-	-	-	0.84
	1989	0.03	0.08	-	0.30
Galium spp.	1988	0.52	-	-	-
	1989	0.03	0.32	-	-
Gaultheria procumbens L.	1988	2.83	29.7	1.31	2.70
	1989	3.86	6.22	1.28	2.26
Gaylussacia spp.	1988	50.2	-	-	-
	1989	244.	-	-	-
Hamamelis virginiana L.	1988	10.9	1.68	0.13	83.1
	1989	6.70	1.38	0.32	9.32
Hepatica acutiloba DC.	1988	-	-	-	-
	1989	-	0.06	-	-
Hypericum spp.	1988	-	0.03	-	-
	1989	-	-	-	-
Ilex verticillata (L.) Gray	1988	2.29	0.13	-	-
	1989	-	1.02	0.32	-

Table 1 (continued)

Species	Year	C	M	S	T
			-kg/ha-		
Kalmia latifolia L.	1988	0.89	3690	2120	2394
	1989	110.6	65.0	1091	2993
Liriodendron tulipifera L.	1988	0.03	-	-	-
	1989	-	-	-	-
Lycopodium obscurum Var. *dendroideum* (Michx.) D.C. Eat.	1988	-	-	-	-
	1989	0.35	-	-	-
Lysimachia quadrifolia L.	1988	2.96	0.11	0.06	0.60
	1989	0.89	0.48	-	0.70
Magnolia acuminata L.	1988	-	-	-	-
	1989	-	2.16	-	-
Maianthemum canadense Desf.	1988	0.90	1.00	0.06	0.29
	1989	0.70	0.20	-	0.48
Medeola virginiana L.	1988	2.38	3.21	0.21	0.23
	1989	0.78	2.96	0.34	1.05
Mitchella repens L.	1988	2.59	4.68	-	-
	1989	0.40	3.50	0.67	1.75
Monotropa uniflora L.	1988	-	1.92	1.95	-
	1989	-	-	-	-
Nyssa sylvatica marsh.	1988	0.83	-	1.53	-
	1989	0.53	5.57	0.10	-
Onoclea sensibilis L.	1988	1.59	-	-	-
	1989	-	-	-	-
Oryzopsis asperifolia Michx.	1988	3.41	15.2	17.7	-
	1989	-	5.51	2.51	-
Panax trifolius L.	1988	-	-	0.32	-
	1989	-	-	-	-
Panicum spp.	1988	0.64	0.16	-	-
	1989	0.06	8.54	-	-
Phlox spp.	1988	-	-	-	-
	1989	-	-	0.03	0.37

Table 1 (continued)

Species	Year	C	M	S	T
			-kg/ha-		
Pinus strobus L.	1988	0.16	-	0.03	-
	1989	-	-	-	-
Poa spp.	1988	-	-	-	1.37
	1989	-	-	-	-
Podophyllum peltatum L.	1988	6.12	-	-	-
	1989	24.4	-	-	-
Polygala paucifolia Willd.	1988	-	-	-	-
	1989	-	0.13	0.16	-
Populus grandidentata Michx.	1988	2.20	-	-	-
	1989	-	-	-	-
Potentilla spp.	1988	1.81	-	-	-
	1989	-	-	-	-
Prenanthes sp.	1988	0.60	0.09	-	0.42
	1989	0.03	0.14	0.17	0.95
Prunus serotina Ehrh.	1988	0.67	0.40	-	0.40
	1989	0.30	0.21	-	4.22
Pteridium aquilinum (L.) Kuhn	1988	8.59	111.7	-	-
	1989	1.02	66.5	-	-
Quercus alba L.	1988	-	0.58	-	-
	1989	0.29	0.53	0.10	0.80
Q. coccinea Muenchh.	1988	1.81	-	-	-
	1989	-	-	-	-
Q. prinus L.	1988	1.29	1.20	-	1.69
	1989	-	-	-	13.8
Q. rubra L.	1988	0.54	0.54	1.02	1.09
	1989	0.80	1.74	0.93	0.55
Q. velutina Lam.	1988	0.83	0.40	0.22	0.68
	1989	-	-	-	-
Rubus spp.	1988	0.38	0.57	-	-
	1989	-	0.10	-	0.06
Sassafras albidum (Nutt.) Nees	1988	0.44	4.51	2.65	-
	1989	-	0.66	0.37	-

Table 1 (continued)

Species	Year	C	M	S	T
			-kg/ha-		
Smilacina racemosa (L.) Desf.	1988	-	-	-	-
	1989	-	-	0.89	-
Smilax herbacea L.	1988	-	-	-	-
	1989	2.43	-	-	-
S. rotundifolia L.	1988	0.60	0.92	3.47	-
	1989	0.38	0.29	0.13	-
Solidago spp.	1988	-	-	-	-
	1989	0.32	0.04	-	-
Streptopus spp.	1988	-	0.06	-	0.10
	1989	0.21	0.43	-	0.76
Thelypteris noveboracensis (L.) Nieuwl.	1988	-	41.2	2.58	-
	1989	-	7.25	-	-
T. palustris Schott	1988	-	62.3	-	-
	1989	0.13	-	-	-
Trientalis borealis Raf.	1988	2.05	0.75	-	1.27
	1989	1.15	1.49	-	1.40
Trillium undulatum Willd.	1988	-	0.65	-	0.51
	1989	0.37	0.41	0.03	0.60
Uvularia perfoliata L.	1988	0.22	1.05	-	-
	1989	0.70	-	0.06	1.46
U. sessilifolia L.	1988	1.25	0.80	0.14	0.11
	1989	0.70	0.97	-	1.72
Vaccinium angustifolium Ait.	1988	127.1	133.4	28.3	24.1
	1989	103.9	100.2	14.2	10.3
V. vacillans Torr.	1988	62.3	48.2	-	6.68
	1989	23.8	73.5	2.39	-
Viburnum acerifolium L.	1988	5.49	-	-	2.10
	1989	-	-	-	20.2
Viola hastata Michx.	1988	0.46	0.13	-	-
	1989	0.32	1.24	-	1.24
V. pallens (Banks) Brainerd	1988	19.2	0.03	-	-
	1989	-	-	-	-

Table 1 (continued)

Species	Year	C	M	S	T
			-kg/ha-		
V. rotundifolia Michx.	1988	4.06	-	-	0.28
	1989	-	-	-	-
V. spp.	1988	1.29	0.48	0.06	0.76
	1989	1.74	-	-	-
Vitis spp.	1988	0.04	0.08	0.06	8.12
	1989	0.05	0.20	-	0.12
Total Woody	1988	279.2	3924.	2164.	2875.
	1989	496.0	372.0	1111.	3257.
Total Herbaceous	1988	266.3	576.7	351.9	569.5
	1989	112.4	200.7	117.2	429.2
TOTAL	1988	545.5	4500.	2516.	3445.
	1989	608.4	572.7	1228.	3686.

Spatial Relationships

Classification. TWINSPAN analysis revealed considerable overlap in species composition among core areas (Fig. 2). With the notable exception of Tiadaghton, plots were not strongly segregated by core areas in either year. The most important indicator species in both years were *K. latifolia, D. punctilobula* and *A. rubrum*, with high relative abundances of *K. latifolia* and *A. pensylvanicum* distinguishing most Tiadaghton plots from those of other core areas. *A. rubrum* and *Vaccinium angustifolium* were additional consistent indicator species between years.

Other indicators in 1988 were mostly representative of mesic sites, including *Viola pallens, Amelanchier* spp., *Trientalis borealis, Maianthemum canadense, D. spinulosa* and *Brachyeletrum erectum*. In contrast, additional indicators in 1989, *Carex pensylvanica* and *Gaultheria procumbens*, were typical of dry or acidic sites, except for the unique occurrence of *Podophyllum peltatum* as an indicator on two plots (Fig. 2).

The shift between years from mesic to xeric indicator types and associated species (preferentials) was also evident at more refined divisions (not shown). Mesic herbs (e.g., *Viola* spp.) in the 1988 analysis tended to be replaced by xeric shrubs and herbs (e.g., *Vaccinium pallens, V. angustifolium, Pteridium aquilinum, G. procumbens*) in 1989. Moreover, compared to 1989, the 1988 analysis identified more indicator species, and revealed more detailed vegetational trends.

Ordination. The 1988 DCA ordination generally confirmed the considerable overlap of plots from Clear Creek, Moshannon, and Sproul, and the distinction of most Tiadaghton plots as indicated by TWINSPAN (Fig. 3). The 1989 ordination reflected a more homogeneous vegetation structure than did that for 1988, especially regarding the Tiadaghton samples (Fig. 3). The three outlying Moshannon plots seen in the 1988 and 1989 ordinations and classifications are due to the presence of *Fagus grandifolia* Ehrh.

The 1988 species ordinations (Fig. 4) suggest a weak moisture gradient on the first axis. The gradient extends from species mostly associated with well-drained soils (*A. pensylvanicum, F. grandifolia, Fraxinus americana* L., *Carex swanii* (Fern.) MacKenz. and *K. latifolia*) to those associated with more mesic sites (*Viola* spp., *P. peltatum*) and finally to species typical of very moist sites (*Thelypteris noveboracensis* (L.) Nieuwl. and *Thelypteris palustris* Schott).

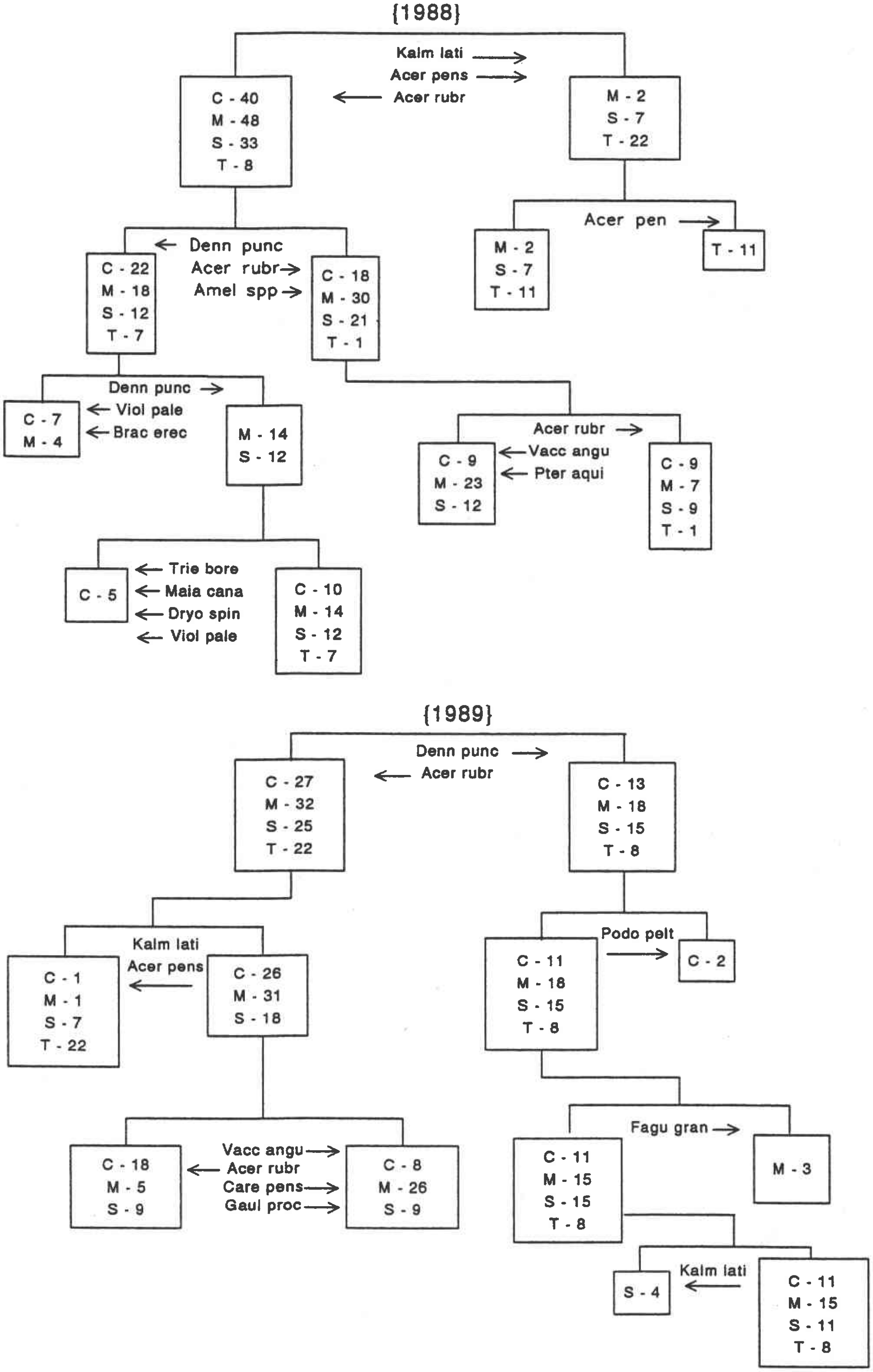


Figure 2. Hierarchal (TWINSPAN) classification of plots accoring to core areas in 1988 and 1989. Major indicator species and their directional indication are shown by arrows.

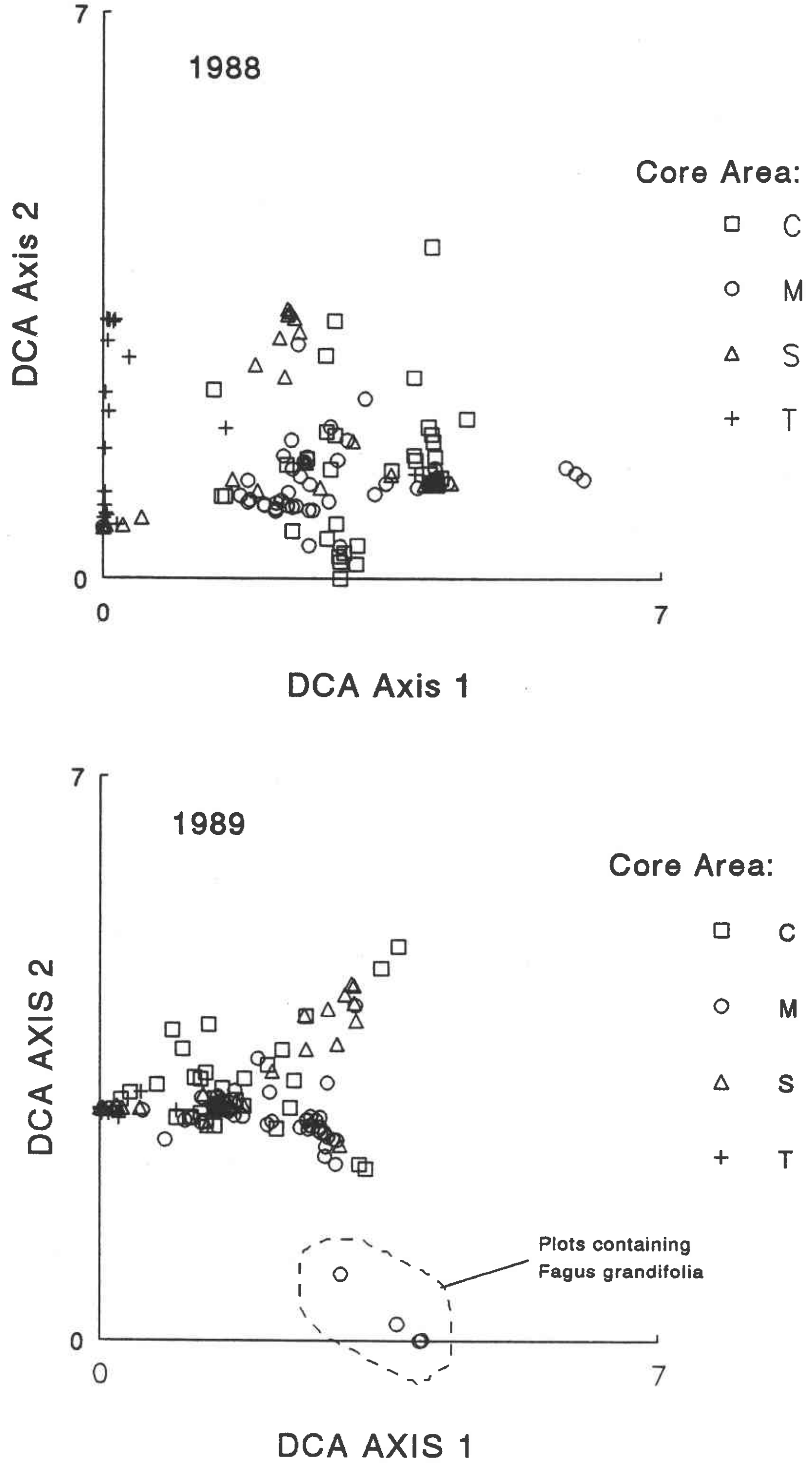


Figure 3. Detrended correspondence analysis (DCA) ordinations of plots in 1988 and 1989 in relation to core areas.

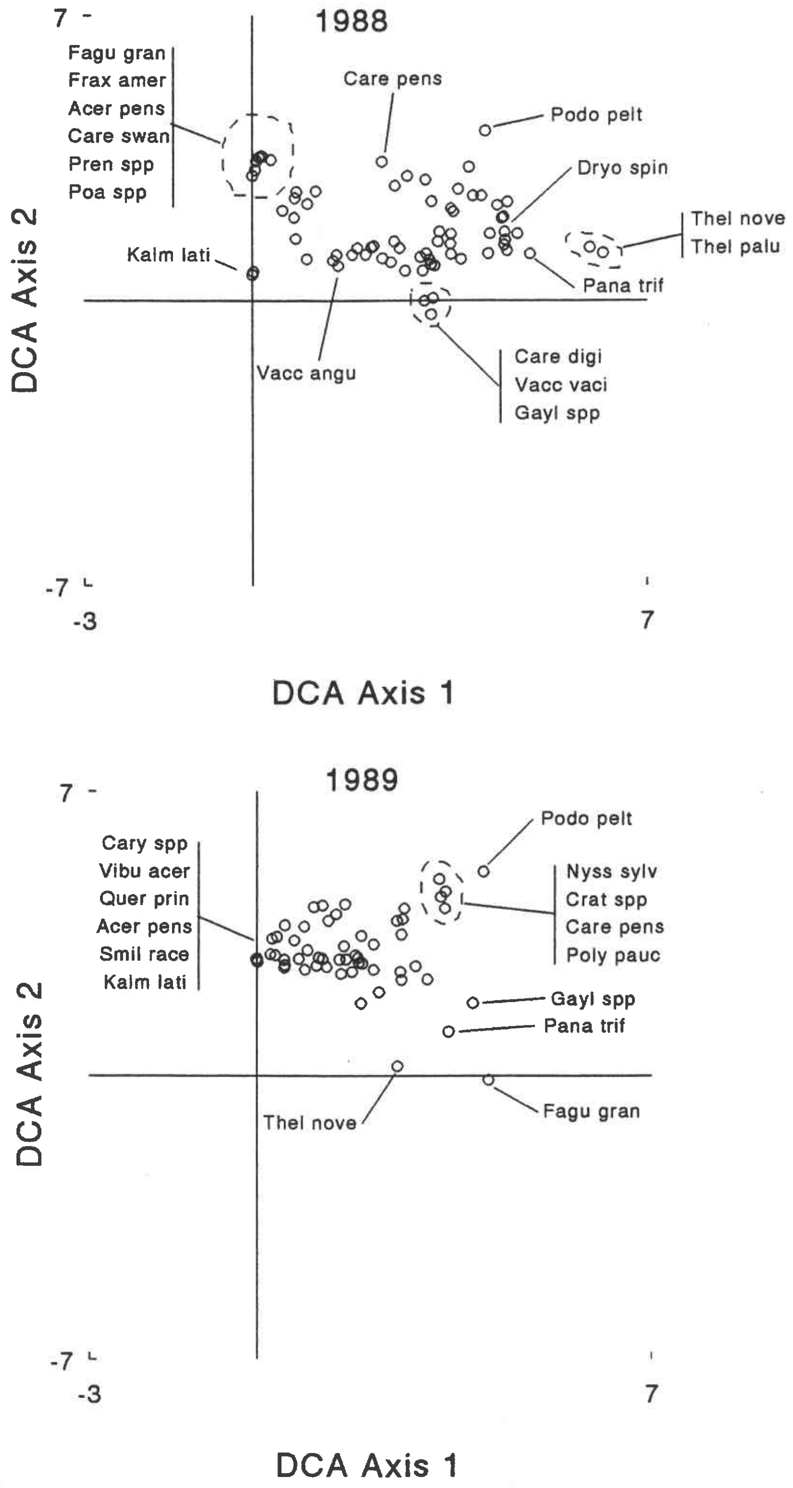


Figure 4. Detrended correspondence analysis (DCA) ordinations of species in 1988 and 1989 in relation to core areas. Species names are found in Table 1.

The second DCA axis revealed a slight trend from mostly ericaceous shrubs typical of infertile, acidic soils (e.g., *K. latifolia*, *Gaylussacia* spp., *Vaccinium* spp.) to more fertile, mesic site species such as *P. peltatum*, *C. swanii*, *Poa* spp., *A. pensylvanicum*, *F. grandifolia*, and *F. americana*. In 1989, these relationships were not evident and, as was the case for the plot ordinations, there was little differentiation except for a few outliers (Fig. 4).

Differences in herb-layer composition on the Tiadaghton core area suggested by classification and ordination are evident in the comparative species abundances (Table 1). Seven species were sampled almost exclusively at Tiadaghton in 1988, while four species sampled on most or all other core areas were absent at Tiadaghton. Particularly notable were the comparative abundances of *A. pensylvanicum* and *C. swanii* at Tiadaghton, and the absence of three species well-represented on other core areas: *S. albidum*, *Smilax rotundifolia* L., and *Oryzopsis asperifolia* Michx.

Species Diversity. On the basis of Hill's diversity numbers, the western pair of core areas (Clear Creek and Moshannon) had greater species richness (N0) and more abundant (N1) and very abundant (N2) species than the two eastern core areas in both years (Table 2). Conversely, evenness was similar among all four core areas in 1988; however, between 1988 and 1989 it increased at Clear Creek and Moshannon, but decreased at Sproul and Tiadaghton. This same temporally diverging pattern is evident for N1 and N2 between the western and eastern pairs of core areas. However, within the western and eastern pairs of core areas these diversity measures were consistently similar.

The dominance-diversity curves indicate a lognormal distribution typical of relatively complex, species-rich communities (Fig. 5). They clearly illustrate the distributional differences in species abundances between the western and eastern pairs of core areas noted above. A shift toward greater similarity in species distributions is also revealed between Clear Creek and Moshannon from 1988 to 1989, making each half of the gradient appear even more distinct in 1989. These spatial patterns reveal distinctly lower species diversity in the eastern half of the gradient.

DISCUSSION AND CONCLUSIONS

Lacking site-specific environmental monitoring data, reasons for the large between-year differences in herb-layer biomass cannot be definitely determined. However, a severe drought developed over the 1988 growing season. Palmer Drought Severity indices revealed mild drought conditions across the study area by the end of April (Figure 6). Drought conditions were rated moderate (-2.3 to -2.5) by mid-June, becoming severe (-3.3 to -3.5) in July. Despite increased rainfall in mid-July, drought conditions prevailed through August (Figure 6). There was little difference in drought severity across the study transect. In contrast, growing season precipitation in 1987 and 1989 was at or above normal.

We suggest that the 1988 drought could have produced a lagged decrease in herb layer production as measured in 1989. Such a lag might occur among perennial herbs with large belowground storage organs if initial growth flush is largely determined by stored reserves. For herbaceous plants, this decrease would likely have occurred primarily through a reduction in the size of individual plants and, for rhizomatous species, perhaps the numbers of stems as well. Both of these factors could have been operative in the case of *D. punctilobula*, the most abundant and widely distributed herbaceous species (Table 1, Fig. 1). The nearly 50% reduction in total biomass between years cannot be attributed entirely to the small reduction in distribution (Fig. 1). Mortality or decreased reproductivity probably contributed relatively little to the herbaceous biomass decrease, as suggested by the comparatively small reductions or even increases in plot frequencies. For example, there was a large between-year decrease in *Carex* spp. biomass (Table 1), yet plot frequency increased (Fig. 1). Thus, herb-layer biomass reductions between years are inferred to result more from reduced plant size rather than decreased spatial distribution.

The above hypothesis cannot, however, be directly invoked to explain the apparent 1989 woody biomass reduction. The large but non-significant decrease in *K. latifolia* biomass is evidently an artifact of extreme variability in plant size and patchy distribution. Seedlings of many tree species such as *Q. rubra*, *Amelanchier* spp., *H. virginiana*, and *Prunus serotina* Ehrh. also did not change perceptibly in frequency (Fig. 1), but were relatively uncommon and highly variable in individual plant size, all of which contributed to inconsistent between-year differences.

Table 2. Species diversity measures summarized for core areas and years.

Core Area	Year	n[1]	NO[2]	N1[2]	N2[2]	Evenness[3]
Clear Creek	1988	40	58	6.53	3.74	0.50
	1989	40	51	7.43	5.44	0.69
Moshannon	1988	50	55	4.95	3.24	0.57
	1989	50	49	7.65	5.28	0.63
Sproul	1988	40	31	1.83	1.41	0.49
	1989	40	33	1.66	1.31	0.47
Tiadaghton	1988	30	41	2.31	1.78	0.59
	1989	30	38	1.75	1.36	0.48

[1] Number of 3.1 m^2 plots
[2] Hill's diversity numbers (Hill, 1973); includes unidentified species.
[3] Modified Hill's ratio (Alatalo, 1981).

In contrast, *A. rubrum* seedling density can fluctuate markedly even within a growing season (McClenahen and Hutnik, 1979). This species was widely distributed (Fig. 1), but newly germinated seedlings predominated. Prolific seed production often results in large *A. rubrum* populations in late spring when the current seed crop is dispersed and germinates. Many of these seedlings disappear by autumn (McClenahen and Hutnik, 1979).

A. pensylvanicum was well-represented at Tiadaghton, but not elsewhere (Table 1), and significantly decreased by almost 50% in biomass between years. The most abundant and well-distributed shrub, *V. angustifolium*, also declined in biomass (by 27%) between years (Table 1). Plot frequency did not change (Fig. 1), but it is unclear from the data how this biomass reduction occurred. An interesting conjecture, however, is that deer browsing and drought may have interacted. Deer browsing has had a major, long-term impact on forest understory vegetation in northern Pennsylvania (Hough, 1965; Marquis, 1974). In order to compare deer browsing intensities on the study sites, we used the pellet group count method to estimate deer population densities for each site in 1992 (Eberhardt and Van Etten, 1956). Sampling was confined within the site boundaries, so deer densities reflect comparative deer use of the sites during the dormant season (October - April); they cannot be interpreted as actual population estimates. Densities averaged 9.4 deer per km^2 (range: 1.8 - 28.3). Except for one Sproul site, all density estimates were above levels believed to reduce understory richness and cover (D. deCalesta, personal communication).

Thus, intensive deer browsing has probably altered the herb-layer over the long term at virtually all sites and may have exacerbated the impact of other stresses on existing vegetation. As a result of drought-reduced herbage by early summer of 1988, deer may have more intensively browsed woody vegetation. Woody species most clearly reduced in biomass were *V. angustifolium* and, at Tiadaghton, *A. pensylvanicum*. These two species are utilized by deer (Marquis, 1974; Bramble and Goddard, 1953), and may have been more heavily browsed if herbaceous forage was less available. The potential for interactions between deer browsing and other environmental stresses to impact forest understory community dynamics is poorly understood and deserves further invesigation.

Classification and ordination revealed no clear geographical separation of herb layer communities in either year. Although these analyses indicated that Tiadaghton communities were less like those in other core areas, this was only evident in 1988. The relatively different vegetation at Tiadaghton was also detected by similar analyses of the overstory community (and site factors) during site selection (Long et al., 1991). This tends to validate our original approach that focused on the dominant vegetative stratum along with disturbance history, physiography and soil physical properties as a sufficient and practical basis for choosing ecological analogs.

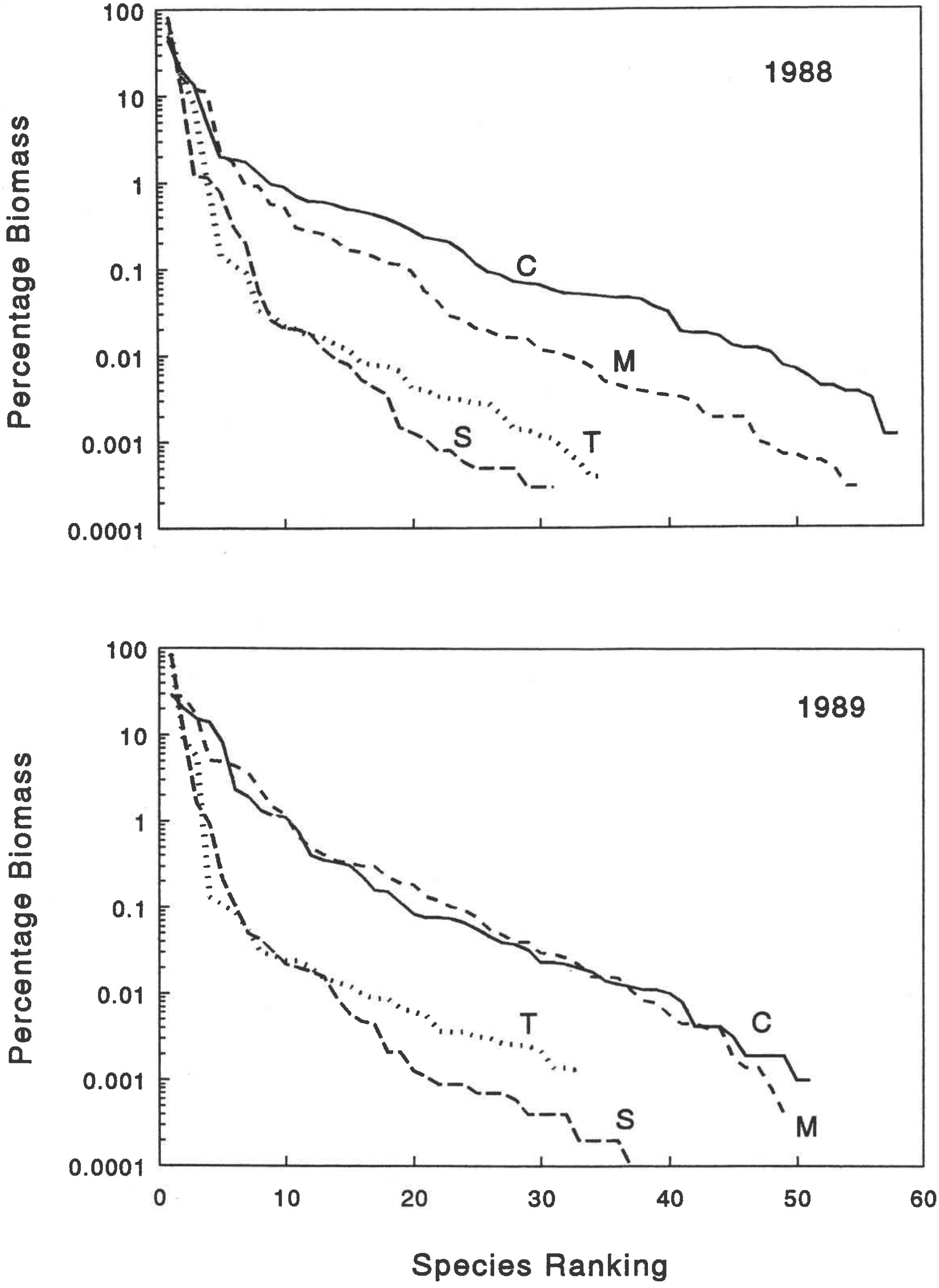


Figure 5. Dominance-diversity curves for core areas in 1988 and 1989.

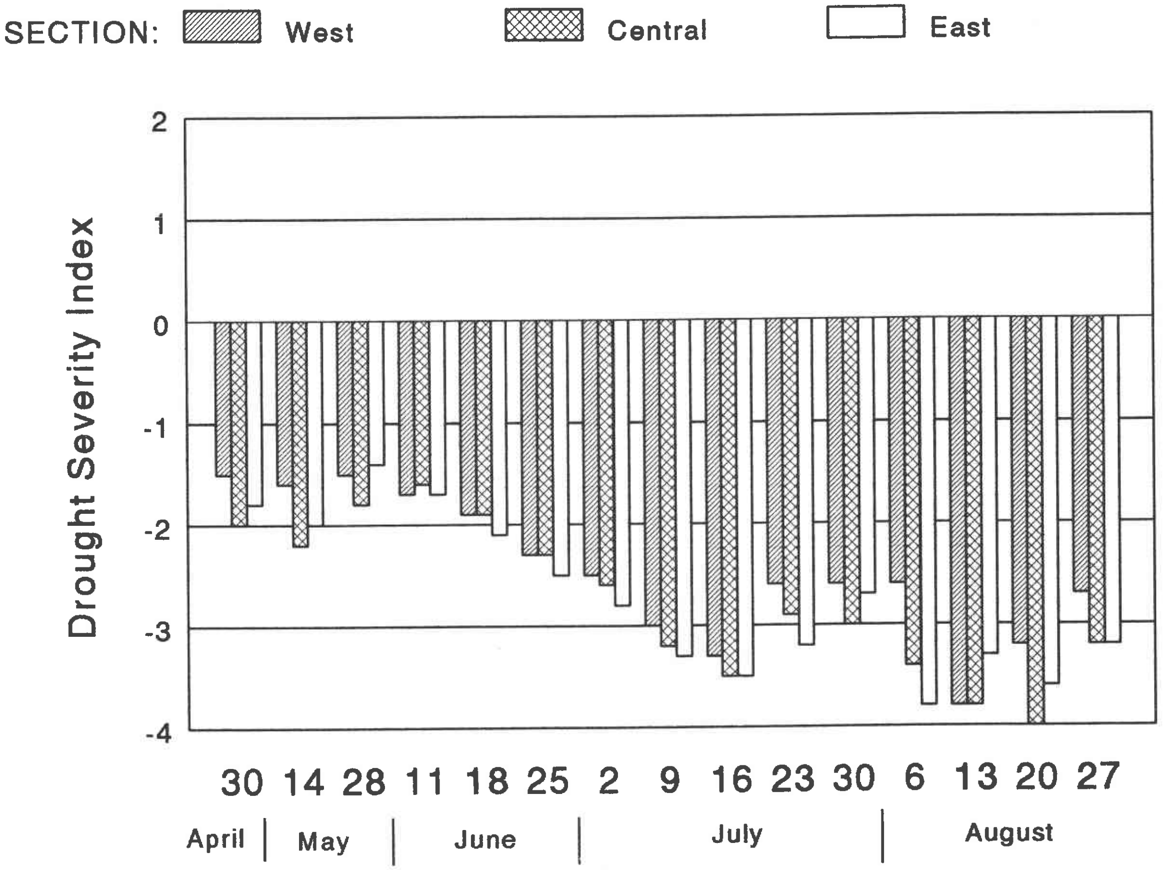


Figure 6. Palmer Drought Severity Indices during the 1988 growing season for climatic divisions corresponding to western, central and eastern sections of the study area (National Weather Service, 1988).

Two important temporal differences detected by classification and ordination were a reduction in mesic site indicator species and an increase in apparent vegetative similarity, particularly regarding Tiadaghton. Several investigators found inherent resistance to changes in spatial distribution among certain of the same species within herb-layer communities similar to ours (Hughes and Fahey, 1991; Collins and Pickett, 1988). Distributions of these species, especially the "stress-tolerators" (Grime, 1979), are hypothesized to develop under favorable conditions, and are maintained by a capacity to tolerate subsequent environmental stresses (Hughes and Fahey, 1991). Our results suggest that, despite any such resistance to broad-scale (successional) changes, this forest herb community can exhibit large annual-scale biomass variation, presumably in response to environmental fluctuation such as the 1988 drought.

Whatever the cause(s) of the annual biomass variation, mesic species were reduced in biomass to the extent that they were less useful for classifying (and ordinating) plots in 1989. The 1989 analyses were therefore less revealing of subtle variations in herb-layer community structure among these relatively analogous sites. This underscores the importance of considering the impact of recent climatic or other environmental perturbations when using the herb stratum to detect experimental effects or to compare sites at a single point in time. Also revealed is the capacity for large annual variability of this herb layer community.

Monitoring herb layer biomass in this oak forest ecosystem offers a sensitive means for detecting short-term environmental fluctuations such as annual climate variation. This short-term variability could have a large effect on interpretations of experiments that are based on single or infrequent measurements. Conversely, annual monitoring will eventually yield estimates of the short-term variability that can potentially be used to identify vegetation trends with statistical confidence.

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