Journal of the Torrey Botanical Society 128(2), 2001, pp. 150–164

Sampling to assess species diversity of herbaceous layer vegetation in Allegheny hardwood forests[1]

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RISTAU, T. E. AND S. B. HORSLEY (USDA Forest Service, Forestry Sciences Laboratory, PO Box 267, Irvine, PA 16329) and L. H. MC CORMICK (School of Forest Resources, The Pennsylvania State University, University Park, PA 16802). Sampling to assess species diversity of herbaceous layer vegetation in Allegheny hardwood forests. J. Torrey Bot. Soc. 128:000–000. 2001.—The optimum frequency and time of sampling required to generate comprehensive diversity indices of herbaceous species in Allegheny hardwood forests was studied. Four 8-ha sites on the Allegheny National Forest were sampled monthly from May to August in 1992 and 1993 for herbaceous layer species composition and percent cover. Each site included 60 circular 4-m^2 plots. Fifteen tally combinations created by combining sample times (1, 2, 3 and 4 at a time) were used to generate diversity indices. Herbaceous species in Allegheny hardwood forests were categorized as common or infrequent. Common plants were present throughout the growing season and their abundance remained stable. Infrequent plants differed in abundance and presence throughout the study. Coverage of several plants increased from May to July as they became fully developed. Species richness increased with number of sample times. The Shannon Diversity index and the Shannon Evenness index did not show differences attributable to time of sampling. Sampling for herbaceous species diversity in Allegheny hardwood forests should include two inventories, one early and one late in the growing season.

Key words: vegetation sampling, species diversity, diversity indices, herbaceous plants.

Establishment of standards for sampling herbaceous layer vegetation has been a concern of researchers and land managers for some time particularly with respect to plot size (Wilson et al. 1972; Mueller-Dombois and Ellenberg 1974), sampling standards (Peet et al. 1998; Shmida 1984; Stohlgren et al. 1995), use of quadrats or random searches (Palmer 1995; Palmer et al. 1995; Goff et al. 1982), number of plots required (Mueller-Dombois and Ellenberg 1972; Magurran 1988), and the measure of abundance. Because the aboveground abundance of many herbaceous species varies seasonally, it is difficult to accurately describe the diversity of vegetation in these communities. When and how often to sample often depend on the availability of personnel and budget appropriations. Understanding the tradeoff between sampling schemes and the effect they have on reported diversity is important when making decisions related to sampling design.

The spatial distribution and relative abundance of herbaceous plants in the understory has been studied at least since the beginning of the 20th century (Young 1934; Jennings 1939). Early plant ecologists recognized the importance of soils, water, and light in determining the suitability of sites for establishing certain plant species. The number of species a site can support is directly related to the variety of conditions present (Whittaker 1972). Habitat classification systems that provide data on the effects of site factors on herbaceous communities have been developed for the western United States more often than for the East (Daubenmire and Daubenmire 1968; Pfister and Arno 1980; Kotar 1988; Cook 1996). The composition of canopy tree species has been associated with the composition of herbaceous species beneath them (Whitney and Foster 1988; Crozier and Boerner 1984). Soil nutrient availability, landscape position, and water availability also are related to species composition and abundance in the forest understory (Spies and Barnes 1985; Davis et al. 1998; Crozier and Boerner 1984; Whitney 1991).

Silvicultural treatments also can affect understory plants. Studies to determine the effects of

Received for publication January 28, 2000, and in revised form March 23, 2001.

[1] We acknowledge Todd Bowersox and Margaret Brittingham of the Pennsylvania State University for assistance in overseeing this work. Earlier drafts of this manuscript were reviewed for content by: David deCalesta, James Finley, Coeli Hoover, Christopher Nowak, Susan Stout, and 2 anonymous reviewers. David Randall, USDA Forest Service Mathematical Statistician, provided a statistical review. We acknowledge technical assistance by the staff of the USDA Forest Service, Forestry Sciences Laboratory in Irvine, PA.

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silvicultural practices on diversity have been conducted in many areas of the United States (Mc Minn 1992; Gove et al. 1992; Wang and Nyland 1993; Niese and Strong 1992; Stout 1994). Most studies are concerned almost exclusively with woody species and show a general trend toward increasing species richness following silvicultural treatment. Thomas et al. (1999) reported an increase in herbaceous species cover and richness with thinning and fertilization, but a negative effect on richness with fertilization alone. A combination of environmental factors that are natural or created through silviculture creates conditions that favor particular vegetation patterns. Effective sampling schemes should adequately sample these conditions. Natural or manmade changes in any of these factors can affect species abundance or composition.

In recent years, both land managers and the public have become alarmed by reports that the world's flora and fauna are decreasing in diversity (Salwasser 1990, Soc. of Am. For. 1991) at the genetic, species, community and regional levels (Ledig et al. 1990). These losses have been associated with increased levels of anthropogenic activity (Ehrlich 1990).

Monitoring changes in diversity requires an understanding of appropriate sampling methods. The sampling scheme used plays a significant role in the interpretation of results (Magurran 1988). Specifically, frequency, the time of sampling, and sampling intensity all can influence results. Few studies have compared the effect of specific sampling time, though many have included more than one sampling during the growing season. Goebel et al. (1999) compared seasonal differences in herbaceous flora of mature second-growth forests with those of old-growth forests in southeastern Ohio. Samples taken in early spring, late spring, and during the summer revealed that the old-growth forest sites had higher species richness, species diversity, and forb cover than the second-growth forests in every sample period. Rogers (1982) noted a lack of quantitative and geographically extensive sampling of spring herbaceous communities in the literature. He sampled stands across the Great Lakes region and found that vernal herbs were less abundant in nutrient-poor mineral soil, and that summer green and semi-evergreen taxa were more likely on nutrient-poor soils. Nixon and Brooks (1991) sampled herbaceous vegetation monthly during the growing season in two Texas clearcut forests, but did not discuss differences due to season of sampling.

The Allegheny hardwood forest occupies about 12 million acres in western Pennsylvania, and adjacent areas of New York, West Virginia, Maryland and Ohio (Marquis 1973). In the Pennsylvania portion, which includes the Allegheny National Forest, a large proportion of stands has dense ground cover of rhizomatous ferns (*Dennstaedtia punctilobula, Thelypteris noveboracensis*) (Allegheny Nat. For. 1986; Horsley 1994). These plants are present in spring, but are not fully expressed until the summer. By that point, many other herbaceous species are overtopped by a dense mesh of intertwined fern fronds that require manipulation to observe plants growing beneath them. Most research on understory flora in this region has focused on species that may affect commercial tree seedling establishment (e.g., the ferns) under the area's overabundant deer herd (Marquis and Brenneman 1981). In this paper we discuss seasonal variation in composition and abundance of herbaceous plants in the Allegheny plateau-top forest in northwestern Pennsylvania. We describe patterns of seasonal variation in herbaceous species abundance and diversity on unglaciated plateau-top sites, as well as the effect of frequency and time of sampling on calculated diversity indices.

Methods. STUDY SITE LOCATIONS AND DESCRIPTIONS. Four 8-ha study sites in the Allegheny National Forest were chosen for study (Table 1). Forest stands were representative of the Allegheny hardwood forest type ($\geq$ 25% overstory basal area in black cherry (*Prunus serotina* Ehrh.) (Marquis and Ernst 1992). Black cherry and red maple (*Acer rubrum* L.) accounted for the largest proportion of basal area at each site (Table 1). Each stand recently had received a partial overstory removal to promote the establishment of woody seedlings. The seedling layer of these stands was dominated by abundant, small (< 15 cm) black cherry and red maple, and larger American beech (*Fagus grandifolia* Ehrh.), striped maple (*Acer pensylvanicum* L.), and birch (*Betula* sp. L.) up to 4.5 m tall.

DATA COLLECTION. We collected data during the 1992 and 1993 growing seasons. Each of the four study sites was visited as closely as possible to the middle of four months (May, June, July, August). In 1992, site selection was not completed until May 28, so 1992 data collection was later than in 1993: May (May 28–June 6), June (July 6), July (July 27–July 30), and August

Table 1. Locations and conditions at the study sites. Years since cutting reflects the condition when the study was initiated in 1992. All stands were 75 to 80 years old and of similar site quality. Percent of total basal area was determined using a 10-factor prism.

Site	Location	Species composition (% basal area)[1]	Deer density (animals/ km^2)	Mean overstory diameter (cm)	Years since cutting
Seldom Seen Corners	Forest County near the town of Marienville, PA	60-BC, 20-RM, 12-AB, 3-WA, 1-CUC, 1-BIR, 1-YP	9.6	43.9	4–5
Route 66	Elk County between the towns of Russell City, PA and Pigeon, PA	47-RM, 31-BC, 11-SM, 5-EH, 4-AB, 3-BIR	11.6	35.8	4–5
Kane Experimental Forest	Elk County half way between Highland, PA and Wilcox, PA	67-BC, 12-RM, 11-SM, 9-EH, 1-AB, 1-BIR	10.8	37.1	8–10
Forest Road 185F	Elk County half way between Highland, PA and Wilcox, PA	66-BC, 19-RM, 9-AB, 4-EH, 2-SM, 1-BIR	11.6	35.6	4–5

[1] AB = American beech (*Fagus grandifolia* Ehrh); BC = black cherry (*Prunus serotina* Ehrh.): BIR = Black and yellow birch (*Betula* sp. L.); CUC = cucumber magnolia (*Magnolia acuminata* (L.) L.); EH = eastern hemlock (*Tsuga canadensis* (L.) Carr); RM = red maple (*Acer rubrum* L.); SM = sugar maple (*Acer saccharum* L.); WA = white ash (*Fraxinus americana* L.); YP = yellow-poplar (*Liriodendron tulipifera* L.).

(August 18). In 1993, sites were visited on schedule. A 4-m^2 plot size was chosen because Wilson et al. (1981) demonstrated that 1- to 4-m^2 plots were adequate for sampling herbaceous species in several cover types, including hardwoods in Pennsylvania. Analysis of diversity-area curves from unpublished data sets on the Allegheny hardwood forest type before sampling using the Brillouin index of diversity showed that 60 sample plots were more than adequate. The Brillouin index is correlated with richness and appropriate for random and non-random data (Magurran 1988). Thus, on each visit we sampled 60 temporary 4-m^2 plots.

The 60 plots were sampled on a systematic grid with lines 30 m apart and plots spaced at intervals of 18 m. A hand compass and calibrated pacing were used to measure directions and distances on the grid. The grid was established along the four cardinal directions unless landscape features prevented their use. Plot centers were established where grid lines intersected. The exact plot locations were different at each visit by design to avoid damage to plants caused by repetitive sampling; it often was necessary to manipulate dense fern cover typical of these stands (Horsley 1994) to observe the plants growing beneath it. This method represented a tradeoff between strict spatial plot location and potential plot damage due to sampling. Temporary plots have the benefit that it may be easier to observe infrequent or rare plants over time due to the spatial increase in sampling effort; richness often is correlated with sample effort (Magurran 1988).

Sample plots were circular with a radius of 1.13 m. The plot radius was marked on the ground with four 1.13-m-long fiberglass rods placed on the forest floor in the cardinal directions radiating from the plot center. Plants within or with parts leaning into the plot were identified and the percentage of the plot covered by each species was recorded. Percent cover was chosen as a measure of abundance because many herbaceous plants are clonal, making it difficult to distinguish between discrete individuals (Cook 1983; Magurran 1988; Whitford 1949). We estimated percent cover visually in 1% intervals up to 5%, then by 5% intervals up to 100%. Because plants occurred in overlapping layers, the total cover on a plot could exceed 100%. Observers carried a cloth square representing 5% of 4-m^2 in the field to aid in estimation; a hole in the middle of the cloth represented 1% of 4-m^2. Species present on the plot, but not covering 1% of plot area, were recorded as 1% cover to indicate presence. Species abundance is the mean of 60 plots for each location.

DATA PREPARATION. Field data were analyzed by calculating several diversity indices (see below) for each location and month of sampling using the SP-INDEX computer program (Ristau et al. 1995). In addition to each month of sam-

Table 2. Mean abundance for the 1992 growing season by month. The means in this table comprise all locations and months in which the species occurred. Abundances (mean percent cover) are shown with standard errors in parentheses where there was more than one observation in the data set.

Common name	Species	May	Jun	Jul	Aug
Jack-in-the-pulpit	*Arisaema atrorubens* (Ait.) Blume	0.05 (0.03)	0.004	0.03 (0.02)	0.02
Aster sp.	*Aster* sp.	0.01	0.004	0	0
White wood aster	*Aster divaricatus* L.	0.01	0.02	0	0
Flat topped white aster	*Aster umbellatus* Mill.	0.004	0.01	0.02	0.02
Short husk grass	*Brachelytrum erectum* (Schreb.) Beauv.	1.42 (0.52)	1.66 (0.77)	2.08 (0.83)	1.46 (0.18)
Sedge sp.	*Carex* sp. Lam	2.69 (0.68)	4.28 (1.29)	3.89 (0.50)	2.91 (0.61)
Goldthread	*Coptis trifolia* L.	0	0	0	0.004
Wild oat grass	*Danthonia compressa* Aust.	0	0.19	1.62 (0.81)	1.61 (0.50)
Hayscented fern	*Dennstaedtia punctilobula* (Michx.) Moore	8.70 (1.52)	14.83 (4.28)	16.20 (4.57)	13.37 (2.34)
Spinulose wood fern	*Dryopteris spinulosa* (Muhl.) Underw.	1.49 (0.52)	3.00 (1.15)	4.01 (0.66)	3.89 (0.42)
Beechdrops	*Epifagus virginiana* (L.) Bart.	0.01	0	0.01	0
Trout lily	*Erythronium amerianum* Ker.	0.64 (0.24)	0	0	0
Teaberry	*Gaultheria procumbens* L.	0	0.02	0	0
Grass sp.	Poaceae family	0.32 (0.11)	0.55 (0.18)	1.07 (0.45)	0.39 (0.11)
Rush sp.	*Juncus* sp. L.	0.004	0	0	0.01
Lycopodium annotinum	*Lycopodium annotinum* L.	0	0	0.02	0.02
Lycopodium clavatum	*L. clavatum* L.	0.01	0.08	0	0.24 (0.22)
Lycopodium complanatum	*L. complanatum* L.	0.04	0.07 (0.06)	0.43 (0.36)	0.20
Lycopodium lucidulum	*L. lucidulum* Michx.	1.61 (1.54)	2.27 (2.09)	2.35 (2.11)	1.29 (1.17)
Lycopodium obscurum	*L. obscurum* L.	2.10 (1.88)	1.60 (1.38)	1.70 (1.63)	1.54 (1.24)
Wild lily of the valley	*Maianthemum canadense* Desf.	0.13 (0.07)	0.35 (0.22)	0.35 (0.25)	0.21 (0.11)
Indian cucumber root	*Medeola virginiana* L.	0.62 (0.34)	0.53 (0.15)	0.38 (0.12)	0.38 (0.13)
Partridgeberry	*Mitchella repens* L.	0.16 (0.06)	0.22 (0.08)	0.17 (0.07)	0.25 (0.12)
Indian pipes	*Monotropa uniflora* L.	0	0	0	0.004
Interrupted fern	*Osmunda claytonia* L.	0	0.01	0	0.004
Common wood sorrel	*Oxalis montana* Raf.	0.54 (0.29)	0.79 (0.44)	0.58 (0.30)	0.75 (0.41)
Dwarf ginseng	*Panax trifolius* L.	0.07 (0.05)	0.01	0	0
Deer tongue grass	*Panicum clandistinum* L.	0.01	0.02 (0.01)	0.06 (0.04)	0.01 (0.01)
Solomonseal	*Polygonatum biflorum* (Walt.) Ell.	0.08 (0.03)	0.06 (0.06)	0.11 (0.06)	0.08 (0.04)
Common cinquefoil	*Potentilla simplex* Michx.	0.004	0.008	0	0
Allegheny blackberry	*Rubus allegheniensis* L.	2.15 (0.57)	3.31 (1.09)	4.46 (1.77)	4.01 (1.26)
Dewberry	*R. hispidus* L.	0.05 (0.04)	0.05 (0.03)	0.01 (0.01)	0.15 (0.15)
Ribes sp.	*Ribes* sp. L.	0	0	0.01	0
Sheep sorrel	*Rumex acetosella* L.	0	0.02	0	0.01
Rough stemmed goldenrod	*Solidago rugosa* Ait.	0.05 (0.03)	0.05 (0.04)	0.03 (0.02)	0.01
False solomonseal	*Smilacina racemosa* (L.) Desf.	0	0.01	0	0
New York fern	*Thelypteris nove-boracensis* Nieuwl.	1.94 (0.88)	4.01 (1.14)	4.16 (1.78)	3.68 (1.56)
Star flower	*Trientalis borealis* Raf.	0.09 (0.04)	0.14 (0.04)	0.08 (0.03)	0.05 (0.04)
Trillium sp.	*Trillium* sp. L.	0.05 (0.02)	0.04 (0.03)	0.02 (0.01)	0.04
Maple-leafed viburnum	*Viburnum acerifolium* L.	0	0.01	0	0
Violets	*Viola* sp. L.	0.96 (0.14)	0.80 (0.18)	1.10 (0.17)	1.04 (0.14)
Grape sp.	*Vitis* sp. L.	0.004	0.01	0.08	0.004

Table 3. Mean abundance for the 1993 growing season by month. The means in this table comprise all locations and months in which the species occurred. Abundances (mean percent cover) are shown with standard errors in parentheses where there was more than one observation in the data set.

Common name	Species	May	Jun	Jul	Aug
Jack-in-the-pulpit	*Arisaema atrorubens* (Ait.) Blume	0.02	0.03 (0.02)	0.02	0.004
Aster sp.	*Aster* sp.	0	0.004	0	0
White wood aster	*Aster divaricatus* L.	0.004	0	0	0.004
Flat topped white aster	*Aster umbellatus* Mill.	0.01	0.04 (0.03)	0.01	0.02
Rattlesnake fern	*Botrychium virginiana* (L.) Swartz	0	0.004	0	0
Short husk grass	*Brachelytrum erectum* (Schreb.) Beauv.	1.60 (0.55)	2.20 (0.54)	2.80 (0.67)	2.36 (0.63)
Sedge sp.	*Carex* sp. Lam	3.43 (0.72)	6.03 (0.72)	3.57 (0.78)	3.20 (0.64)
Spring beauty	*Claytonia virginica* L.	0.004	0	0	0
Goldthread	*Coptis trifolia* (L.) Salisb.	0	0.10 (0.10)	0	0
Wild oat grass	*Danthonia compressa* Aust.	1.29 (0.42)	0.05 (0.03)	1.78 (0.42)	2.84 (1.06)
Hayscented fern	*Dennstaedtia punctilobula* (Michx.) Moore	3.32 (0.92)	16.91 (2.74)	19.15 (4.22)	16.67 (1.04)
Spinulose wood fern	*Dryopteris spinulosa* (Muhl.) Underw.	0.39 (0.10)	2.83 (0.65)	3.40 (0.44)	4.81 (1.44)
Beechdrops	*Epifagus virginiana* (L.) Bart.	0	0	0	0.004
Trout lily	*Erythronium americanum* Ker.	4.87 (2.57)	0	0	0
Grass sp.	Poaceae family	0.27	0.05	0.04	0
Round leafed orchid	*Habenaria orbiculata* (Pursh.) Torr.	0.004	0	0	0
Touch-me-not	*Impatiens pallida* Nutt.	0	0.01	0	0
Lycopodium annotinum	*Lycopodium annotinum* L.	0.12 (0.08)	0.08	0.05	0.10 (0.08)
Lycopodium clavatum	*L. clavatum* L.	0.004	0	0.004	0
Lycopodium complanatum	*L. complanatum* L.	0.38	0.27 (0.19)	0.43	0.72 (0.72)
Lycopodium lucidulum	*L. lucidulum* Michx.	2.01 (1.88)	2.15 (1.93)	2.08 (1.96)	2.30 (2.13)
Lycopodium obscurum	*L. obscurum* L.	2.69 (2.26)	2.20 (1.80)	3.38 (3.05)	3.18 (2.87)
Wild lily of the valley	*Maianthemum canadense* Desf.	0.47 (0.25)	0.32 (0.16)	0.21 (0.14)	0.24 (0.16)
Indian cucumber root	*Medeola virginiana* L.	0.43 (0.19)	0.28 (0.13)	0.20 (0.04)	0.30 (0.14)
Partridgeberry	*Mitchella repens* L.	0.06 (0.02)	0.12 (0.03)	0.10 (0.05)	0.25 (0.06)
Interrupted fern	*Osmunda claytonia* L.	0.02	0	0	0.08
Common wood sorrel	*Oxalis montana* Raf.	0.71 (0.33)	1.45 (0.31)	1.83 (0.98)	0.96 (0.46)
Dwarf ginseng	*Panax trifolius* L.	0.12 (0.07)	0.004	0	0
Deer tongue grass	*Panicum clandistinum* L.	0	0.100 (0.05)	0.01	0.49 (0.35)
Woolly panic grass	*P. lanuginosum* Ell.	0.07 (0.06)	0.60 (0.23)	0.08	0.05 (0.04)
Solomonseal	*Polygonatum biflorum* (Walt.) Ell.	0.08 (0.04)	0.09 (0.05)	0.07 (0.05)	0.07 (0.04)
False buckwheat	*Polygonum scandens* L.	0.06 (0.06)	0	0	0
Christmas fern	*Polystichum acrostichoides* (Michx.) Shott.	0	0	0.01	0
Common cinquefoil	*Potentilla simplex* Michx.	0	0	0	0.08 (0.08)
Allegheny blackberry	*Rubus allegheniensis* L.	2.68 (0.79)	5.20 (1.47)	4.65 (1.64)	4.35 (1.32)
Dewberry	*R. hispidus* L.	0.01	0.08 (0.05)	0.03	0.07 (0.04)

Table 3. Continued.

Common name	Species	May	Jun	Jul	Aug
Sheep sorrel	*Rumex acetosella* L.	0	0.02 (0.02)	0	0
Goldenrod sp.	*Solidago* sp.	0.02	0	0.004	0
Rough stemmed goldenrod	*S. rugosa* Ait.	0.004	0.02 (0.01)	0.004	0.09 (0.09)
False solomonseal	*Smilacina racemosa* (L.) Desf.	0	0.004	0	0
Greenbrier	*Smilax rotundifolia* L.	0	0.004	0	0
New York fern	*Thelypteris nove-boracensis* Nieuwl.	0.66 (0.15)	3.51 (1.70)	4.21 (2.02)	3.19 (1.36)
Star flower	*Trientalis borealis* Raf.	0.17 (0.08)	0.16 (0.08)	0.07 (0.03)	0.004
Trillium sp.	*Trillium* sp. L.	0.13 (0.07)	0.04 (0.02)	0.04 (0.01)	0.02 (0.01)
Hobble bush	*Viburnum alnifolium* Marsh.	0.004	0	0	0
Violets	*Viola* sp. L.	1.79 (0.53)	1.40 (0.14)	1.60 (0.50)	1.17 (0.29)
Grape sp.	*Vitis* sp. L.	0.004	0	0.02	0.004
Barren strawberry	*Waldsteinia fragaroides* (Michx.) Tratt.	0.02	0	0	0

pling, data sets for each month were combined using all possible combinations of the four sample times taken one, two, three, or four at a time. There were 15 "tally combinations." When a tally combination was for more than a single month, the maximum value of abundance recorded in any of the months for that species was used. This avoided penalizing species that were not present throughout the entire growing season.

EXPERIMENTAL DESIGN AND STATISTICAL ANALYSIS. The study data were analyzed using the SAS procedures GLM and MIXED (SAS 1988). Mixed-model analysis of variance was conducted, with locations (4) and years (2) as random variables, and tally combinations (15) as a fixed variable. Thus, inference could be extended beyond the 2 years sampled, and to other partially cut unglaciated plateau-top Allegheny hardwood sites. Residual analyses detected no significant correlations of errors among the different tally formulations; thus, we considered it appropriate to model tally formulation. The model also included all two-way interactions. Data for each diversity index were analyzed separately. Main effects were tested using Satterthwaite approximate F-tests. Pair-wise comparisons of least squares means for tally formulations were made using contrasts with the Tukey-Kramer adjustment to estimate the best time or combination of times to sample for diversity. A p-value of ≤ 0.05 was considered significant in all tests in the ANOVA, and Tukey-adjusted contrasts.

GROUPING OF PLANTS. Plants often have been grouped into three categories of similar phenology. For example, Beatty (1984) grouped species into ephemeral (plants found only in the spring), aestival (plants whose abundance increases during the growing season), and evergreen (plants present throughout the growing season). Moore and Vankat (1986) described the seasonal groups as spring, spring/summer, and summer based on time of species presence. We used an indicator species approach to create objective groups of species with similar abundance trends. The TWINSPAN program (Hill 1979) identified groups of plants with affinity for a given sample time. Data from each year were analyzed separately. TWINSPAN normally is used to link indicator plants to particular locations where conditions are favorable. We linked species to sample times rather than sample location, thus producing a list of "indicators" of sampling time.

HERBACEOUS SPECIES DIVERSITY. We chose a set of five diversity indices to test for differences in diversity among months or combinations of months of sampling: richness (number of species), the Berger-Parker index, the Margalaf index, the Shannon Diversity index, and the Shannon Evenness index. The Berger-Parker index is a measure of the degree to which a single species is dominant. The Margalef index uses richness and the number of individuals (percent cover in this study) to express diversity and was chosen for its ability to detect differences among communities. The Shannon Diversity index evaluates the sum of the proportional abundances of the species and was included due to its wide use. The Shannon Evenness index is a proportion of the calculated Shannon Diversity index to a "virtual maximum value" for the index if all of the individuals were distributed evenly among the species (Magurran 1988). We assumed that diversity was best represented when values of calculated indices were at a maximum.

Results. SEASONAL PATTERNS OF HERBACEOUS SPECIES. A total of 42 and 48 species were found across all locations and dates of sampling in 1992 and 1993, respectively (Tables 2–3). All species were perennial with the exception of Indian pipes (*Monotropa uniflora* L.) and sheep sorrel (*Rumex acetosella* L.) which can be either annual or perennial. In both years, hayscented fern (*Dennstaedtia punctilobula* (Michx.) Moore), New York fern (*Thelypteris nove-boracensis* Nieuwl.), and spinulose wood fern (*Dryopteris spinulosa* (Muhl.) Underw.) were most abundant, followed by *Rubus* sp., grasses, and sedges. Species such as violets (*Viola* sp.), the Lycopodiums (*Lycopodium* sp.), wild lily-of-the-valley (*Maianthemum canadense* Desf.), Jack-in-the-pulpit (*Arisaema atrorubens* (Ait.) Blume), trout lily (*Erythronium americanum* Ker.), spring beauty (*Claytonia virginica* L.), dwarf ginseng (*Panax trifolius* L.), Indian cucumber root (*Medeola virginiana* L.), common wood sorrel (*Oxalis montana* Raf.), Solomon's seal (*Polygonatum biflorum* (Walt.) Ell.), partridge berry (*Mitchella repens* L.), and rough-stemmed goldenrod (*Solidago rugosa* Ait.) were common but of low abundance. Species that were infrequent or rare included rush (*Juncus* L. sp.), false Solomon's seal (*Smilacina racemosa* (L.) Desf.), greenbrier (*Smilax rotundifolia* L.), common cinquefoil (*Potentilla simplex* Michx.), false buckwheat (*Polygonum scandens* L.), white wood aster (*Aster divaricatus* L.), flat-topped white aster (*Aster umbellatus* Mill.), hobblebush (*Viburnum alnifolium* Marsh.), star flower (*Trientalis borealis* Raf.), Christmas fern (*Polystichum acrostichoides* (Michx.) Shott.), sheep sorrel (*Rumex acetosella* L.), Indian pipes (*Monotropa uniflora* L.), beech drops (*Epifagus virginiana* (L.) Bart.), *Ribes* L. sp., *Trillium* L. sp., and *Vitis* L. sp. Abundance data for all species are highly variable for a variety of reasons e.g., different microhabitat and growth requirements.

Data in Tables 2 and 3 show that species can be grouped into three or four categories. A spring group included species present only early in the growing season. A spring/summer group contained species that emerge in the spring and expand throughout the summer. A summer group consisted of species that emerge and are present in the summer. An evergreen group included plants that are present all year. Hay-scented and New York fern are examples of spring/summer plants that increased in abundance during the growing season, while other species in that group, e.g., common wood sorrel, wild lily-of-the-valley, and the club mosses were constant in abundance across sample times. Due to the temporary nature of the sample plots, species such as trout lily, dwarf ginseng, Jack-in-the-pulpit, and several others were present in only 1 or 2 months with no apparent abundance trend among months. Some species "come and go" throughout the growing season; this is an artifact of the sampling method. Characteristics obtained from the literature combined with our data show that some of these species, e.g., trout lily, spring beauty, and dwarf ginseng are spring species (Bierzychudeck 1982; Gleason and Cronquist 1991). Abundance trends for the average condition held across all locations and for individual locations and years (data not shown). Species composition differed from month to month for infrequent or rare species, again due to the sampling method. Ferns, grasses, and *Rubus allegheniensis* L. dominated all locations.

Results of the TWINSPAN analysis were similar for both years with a few exceptions. Spring species were not found in 1992, presumably because of the lateness of sample initiation. Only the 1993 TWINSPAN analysis is presented (Fig. 1). TWINSPAN grouped the data in five 5 (>0, >5, >26, >51, and >76) relative abundance classes (percent cover of individual species divided by the sum all species coverage) for each species and sample time. A set of binary digits (zeroes and ones) was displayed as TWINSPAN

TWINSPAN OUTPUT 1993

SPECIES	ABUNDANCE BY MONTH JUN	JUL	MAY	AUG	BINARY GROUP	
Arisaema atrorubens	3	3	-	1	0000	
Panicum clandistinum	5	2	-	-	000100	
Botrychium virginianum	1	-	-	-	000101	
Smilacina racemosa	1	-	-	-	000101	
Impatiens pallida	2	-	-	-	000101	INFREQUENT SPECIES GROUP 1
Coptis trifolia	5	-	-	-	000101	
Rumex acetosella	2	-	-	-	000101	
Smilax rotundifolia	1	-	-	-	000101	
Aster sp.	1	-	-	-	000101	
Polystichum acrostichoides	-	2	-	-	00011	
Solidago sp.	-	1	-	-	00011	
Erythronium americanum	-	-	5	-	00100	
Claytonia virginica	-	-	1	-	00100	
Panax trifolia	-	-	5	-	00100	
Waldsteinia fragaroides	-	-	1	-	00100	INFREQUENT SPECIES GROUP 2
Polygonum scandens	-	-	4	-	00100	
Habenaria orbiculata	-	-	1	-	00100	
Viburnum alnifolium	-	-	1	-	00100	
Lycopodium clavatum	-	1	1	-	00101	
Viola sp.	5	5	5	-	00110	
Mitchella repens	5	5	4	-	00110	
Grass sp.	4	4	5	-	00111	
Trientalis borealis	5	4	5	1	010	
Trillium sp.	3	3	5	2	011000	
Aster umbellatus	3	3	2	3	011001	
Dennstaedtia punctilobula	5	5	5	5	01101	
Dryopteris spinulosa	5	5	5	5	01101	
Thelypteris nove-boracensis	5	5	5	5	01101	
Sedge sp.	5	5	5	5	01101	SPECIES WITH CONSTANT PRESENCE
Brachelytrim erectum	5	5	5	5	01101	
Panicum lanuginosum	5	4	4	4	01101	
Lycopodium obscurum	5	5	5	5	01101	
Lycopodium complanatum	5	5	5	5	01101	
Lycopodium lucidulum	5	5	5	5	01101	
Lycopodium annotinum	5	4	5	5	01101	
Maianthemum canadense	5	5	5	5	01101	
Medeola virginiana	5	5	5	5	01101	
Polygonatum biflorum	5	4	5	4	01101	
Vitis sp.	-	2	1	1	0111	
Rubus allegheniensis	5	-	5	5	10	
Oxalis montana	5	-	5	5	10	
Aster divaricatus	-	-	1	1	1100	INFREQUENT SPECIES GROUP 3
Osmunda claytonia	-	-	3	5	1101	
Rubus hispidus	-	3	-	4	1110	
Danthonia compressa	-	-	-	5	1111	
Potentilla simplex	-	-	-	5	1111	
Solidago rugosa	-	-	1	5	1111	
Epifagus virginiana	-	-	-	1	1111	
	0	0	0	1		
	0	0	1			
	0	1				

Fig. 1. TWINSPAN results from the 1993 vegetation sampling. Months and species are ordered and grouped to show which species are indicators of particular abundance trends by month. TWINSPAN used five relative abundance classes (>0, >5, >26, >51, and >76) for each species and sample time. Binary digits define the group separations.

output indicating where the ordered species list can be split into groups. Moving from left to right in Figure 1, binary groups are more specific; the first column of zeroes and ones defines the first split and each subsequent column is more specific. Sample times were ordered in the same manner, grouped in like categories based on species. Some groupings generated by TWINSPAN made biological sense while some others were not useful.

Four biologically interpretable TWINSPAN groups were generated. Three groups consisted of species that were rare or infrequent in Allegheny hardwood forests. These plants were found only in 1 or 2 months and may be present, apparently disappear, then be present again due to a sampling artifact. The fourth group represented the more frequent and evenly distributed species in the forest.

SPECIES COMMON IN ALL MONTHS. Species common in all months included some that have relatively constant abundance: *Aster umbellatus* Mill., *Dryopteris spinulosa* (Muhl.) Underw., Grass sp., *Lycopodium annotinum* L., *L. complanatum* L., *L. lucidulum* Michx., *L. obscurum* L., *Maianthemum canadense* Desf., *Medeola virginiana* L., *Mitchella repens* L., *Oxalis montana* Raf., *Polygonatum biflorum* (Walt.) Ell., *Rubus allegheniensis* L., *Trillium* sp., and *Viola* sp. (Table 3, Fig. 1). Grass sp., *Mitchella repens* L., *Oxalis montana* Raf., *Rubus allegheniensis* L., and *Viola* sp. were misclassified into infrequent groups due to low abundance in one month, but were split from their respective infrequent groups at a lower level; we chose to include them where they fit biologically. Plants in the common group grow most in the early part of the season and then partition resources to reproduction and storage during the remainder of the growing season. The Lycopodiums are evergreen plants with fairly constant abundance throughout the growing season. Many plants in the common group reproduce vegetatively from stolons or rhizomes, or sexually with spores. Some of the plants in this group have changing abundances (Table 3): *Brachelytrum erectum* (Schreb.) Beauv., *Carex* Lam. sp., *Dennstaedtia punctilobula* (Michx.) Moore, *Panicum lanuginosum* L., *Thelypteris nove-boracensis* Nieuwl., *Vitis* L. sp., and unidentified grass species. Aboveground parts of these plants senesce at the end of the growing season and then emerge from perennial belowground structures in the spring. The ferns arise from rhizomes early in the growing season and often are the dominant species even in the early part of the growing season. Ferns increase in percent cover until July when the fronds are fully expanded. Grasses and sedges form new shoots early in the spring and continue growing throughout the summer. Blackberries showed a similar pattern.

INFREQUENT OR RARE SPECIES. This group is the sum of infrequent/rare groups (1, 2, 3) generated by TWINSPAN (Fig. 1). Since rarity or infrequency is common to all three categories, we present them as one large group but discuss them separately based on when they were encountered. Group 1 includes species found primarily in June or July: *Arisaema atrorubens* (Ait.) Blume, *Aster* sp., *Botrychium virginianum* (L.) Swartz, *Coptis trifolia* ((L.) Salisb., *Impatiens pallida* Nutt., *Panicum clandistinum* L., *Polystichum acrostichoides* (Michx.) Shott., *Rumex acetosella* L., *Smilacina racemosa* (L.) Desf., *Smilax rotundifolia* L., and *Solidago* sp. These species are examples of those in the spring/summer group that germinate in late spring and are present throughout the summer. Because of their rarity, they were only found in June or July.

Group 2 includes species found primarily in May: *Claytonia virginica* L., *Erythronium americanum* Ker., *Habenaria orbiculata* (Pursh.) Torr., *Lycopodium clavatum* L., *Panax trifolius* L., *Polygonum scandens* L., *Viburnum alnifolium* Marsh., and *Waldsteinia fragaroides* (Michx.) Tratt. Three May species, (*Claytonia virginica* L., *Erythronium americanum* Ker., and *Panax trifolius* L.) are spring ephemerals whose aboveground life cycle is completed before overstory tree leafout. Spring ephemerals were not found in large numbers during the 1992 growing season because sampling was delayed. Other species in this group were rare or infrequent plants picked up only in May due to spatial variation of sample plots.

Group 3 included plants found primarily in August: *Aster divaricatus* L., *Danthonia compressa* Aust., *Epifagus virginiana* (L.) Bart., *Osmunda claytonia* L., *Potentilla simplex* Michx., *Rubus hispidus* L., and *Solidago rugosa* Ait.

SAMPLING TIMES AND COMBINATIONS. Mean values of diversity indices for each month and tally combination (combination of months) are shown in Table 4. Species richness ranged from an average of 19.6 species in July to 29.6 when all sample times were combined. The highest value for richness in a single month was 22.5

Table 4. Species diversity indices by tally combination averaged across all sites, and both years with standard error of the mean for each index in each combination.

Tally combination	Diversity Index				
	Richness	Margalef	Berger-Parker	Shannon Diversity	Shannon Evenness
May	22.5 ± 0.6	2.9 ± 0.1	0.31 ± 0.03	2.1 ± 0.1	0.86 ± 0.02
June	21.6 ± 0.8	2.6 ± 0.1	0.37 ± 0.05	2.0 ± 0.1	0.81 ± 0.03
July	19.6 ± 0.6	2.4 ± 0.1	0.37 ± 0.05	2.0 ± 0.1	0.82 ± 0.03
August	20.0 ± 0.7	2.4 ± 0.1	0.37 ± 0.04	2.0 ± 0.1	0.83 ± 0.03
May/June	26.9 ± 0.8	3.3 ± 0.1	0.35 ± 0.05	2.1 ± 0.1	0.83 ± 0.03
May/July	24.8 ± 0.4	3.0 ± 0.1	0.35 ± 0.05	2.1 ± 0.1	0.84 ± 0.03
May/August	25.8 ± 0.7	3.1 ± 0.1	0.34 ± 0.04	2.2 ± 0.1	0.85 ± 0.02
June/July	25.0 ± 0.9	3.0 ± 0.1	0.35 ± 0.04	2.1 ± 0.1	0.84 ± 0.03
June/August	25.0 ± 0.8	3.0 ± 0.1	0.34 ± 0.04	2.1 ± 0.1	0.84 ± 0.03
July/August	22.9 ± 0.5	2.7 ± 0.1	0.36 ± 0.05	2.1 ± 0.1	0.84 ± 0.03
May/June/July	28.1 ± 0.8	3.3 ± 0.1	0.32 ± 0.05	2.2 ± 0.1	0.85 ± 0.03
May/June/August	28.9 ± 0.8	3.5 ± 0.1	0.33 ± 0.05	2.2 ± 0.1	0.85 ± 0.03
May/July/August	27.0 ± 0.6	3.2 ± 0.1	0.34 ± 0.05	2.2 ± 0.1	0.85 ± 0.03
June/July/August	26.5 ± 1.0	3.1 ± 0.3	0.33 ± 0.04	2.1 ± 0.1	0.85 ± 0.03
May/June/July/August	29.6 ± 0.9	3.5 ± 0.1	0.32 ± 0.04	2.2 ± 0.1	0.85 ± 0.03

(May). The highest richness for a 2-month combination was 26.9 (May–June). May, June, and August constituted the best 3-time combination at 28.9. The Margalef index ranged in value from 2.4 in July or August alone to 3.5 for all sample times. Values for this index were highest in May (single time combination), May–June (2-time combination), and May–June–August (3-time combination) with values of 2.9, 3.3, and 3.5 respectively. There was little variation in the Berger-Parker index; values ranged from 0.31 to 0.37. There also was little variation in the Shannon Diversity index; values ranged from 2.0 to 2.2. There was little variation with time of sampling in the Shannon Evenness index; values ranged from 0.81 to 0.86. The observed mean differences in Table 4 are large compared with standard errors for richness and the Margalef index. Standard errors varied less for the Berger-Parker, Shannon Diversity and Shannon Evenness indices. Thus, richness and the Margalef index are more statistically capable of detecting differences due to time of sampling.

P-values from analysis of variance tests of differences among tally combinations are shown in Table 5. Neither year nor location were significant factors for species richness. However, a significant year by location interaction ($p<0.001$) indicated a richness effect in some years at some locations. This probably was the result of the difference in sampling times between the two years or of heavy defoliation by the elm spanworm at the Kane Experimental Forest and Forest Road 185F locations in 1992; all four areas were defoliated in 1993. Elm spanworm removed nearly all of the foliage from American beech trees in both the overstory and understory; other species also were defoliated at each location. Defoliation occurred from May through July and limited refoliation was noted for some American beech trees. The defoliation primarily affected tree species, though minimal defoliation was noted on the herbaceous plants. This may have affected richness by allowing germination of species that require high light levels. The heavily defoliated canopy also increased the amount of light reaching the understory, causing species such as the ferns to ex-

Table 5. Significance levels from analysis of variance.

Source of variation	DF	Species richness	Margalef	Berger-Parker	Shannon	Shannon Evenness
Year	1	0.917	0.715	0.424	0.378	0.135
Location	3	0.823	0.751	<0.001	0.004	<0.001
Year × Location	3	<0.001	<0.001	0.022	<0.001	0.203
Tally combination	14	<0.001	<0.001	0.530	0.096	0.398
Year × Tally combination	14	0.571	0.318	0.001	<0.001	0.002
Tally combination × Location	42	0.424	0.429	0.359	0.644	0.116
Error	42					

pand their coverage. The year, location, year by tally combination and tally combination by location terms were not significant ($p \geq 0.424$).

The specific tally combination used did affect the species richness value ($p < 0.001$). The 4-month combination sampled the most area because each sample consisted of new plot locations and therefore was the best estimate of true richness available (Table 6). Comparison of other tally combinations with the 4-month combination provided the most meaningful information. All single-month samples had lower richness values than those obtained sampling 4 times (i.e., $p \leq 0.05$). Sampling twice, once in May and again in June or August, was similar to sampling all 4 months ($p \geq 0.05$). The May–July combination had lower richness than that obtained sampling all 4 months. All 3-month combinations were statistically equivalent to sampling 4 times.

Results for the Margalef index were similar to those for richness. Tally combinations ($p < 0.001$) and year by location ($p < 0.001$) were significant (Table 5). Significant interaction terms for the Margalef index can be explained in the same way as richness because it emphasizes richness in its calculation. The May sample had the highest Margalef index of all single months; values were similar to those for the 2-, 3-, or 4-month combinations (Tables 4, and 7). Tally combinations for the Margalef index that included May were not statistically different from sampling in all months.

The Berger-Parker index was not sensitive to time of sampling overall (Table 5). A significant year by tally combination interaction indicates differences in one of the years. Locations also were different using this index ($p < 0.001$). Significant year by location and year by tally combination interactions ($p \geq 0.022$) likely were due to the differences in sample time between years and the elm spanworm defoliations.

The Shannon Diversity index also was not sensitive to time of sampling; tally combination did not produce a significant main effect ($p = 0.096$). There was a significant location effect ($p = 0.004$), a year by location interaction ($p < 0.001$), and a year by tally combination interaction ($p < 0.001$) (Table 5). Tally combination did affect this index in 1992, hence the significant interaction.

The Shannon evenness index was not affected by time of sampling ($p = 0.398$), but differed among locations ($p < 0.001$), and there was a significant year by tally combination interaction

Table 6. Tukey adjusted (overall α of 0.05) p-values for LSMeans comparison of species richness for tally combinations.

	(M)ay	(J)une	(Ju)ly	(A)ug	M-J	M-Ju	M-A	J-Ju	J-A	Ju-A	M-J-Ju	M-J-A	M-Ju-A	J-Ju-A	All 4
(M)ay	•														
(J)une	0.998	•													
(Ju)ly	0.136	0.555	•												
(A)ug	0.266	0.802	1.000	•											
M-J	0.007	0.001	<0.001	<0.001	•										
M-Ju	0.396	0.084	0.002	0.003	0.473	•									
M-A	0.066	0.011	<0.001	<0.001	0.981	0.993	•								
J-Ju	0.724	0.214	0.004	0.009	0.214	1.000	0.868	•							
J-A	0.266	0.051	<0.001	0.002	0.640	1.000	1.000	1.000	•						
Ju-A	1.000	0.958	0.066	0.136	0.014	0.640	0.136	0.921	0.472	•					
M-J-Ju	<0.001	<0.001	<0.001	<0.001	0.958	0.051	0.326	0.018	0.084	0.001	•				
M-J-A	<0.001	<0.001	<0.001	<0.001	0.555	0.011	0.084	0.004	0.018	<0.001	1.000	•			
M-Ju-A	0.005	<0.001	<0.001	<0.001	1.000	0.396	0.958	0.171	0.555	0.011	0.981	0.640	•		
J-Ju-A	0.014	<0.001	<0.001	<0.001	1.000	0.724	1.000	0.396	0.868	0.031	0.802	0.326	1.000	•	
All 4	<0.001	<0.001	<0.001	<0.001	0.958	0.051	0.326	0.018	0.084	0.001	1.000	1.000	0.981	0.802	•

Table 7. Tukey adjusted (overall α of 0.05) p-values for LSMeans comparison of Margalef index for tally combinations.

	(M)ay	(J)une	(Ju)ly	(A)ug	M-J	M-Ju	M-A	J-Ju	J-A	Ju-A	M-J-Ju	M-J-A	M-Ju-A	J-Ju-A	All 4
(M)ay	•														
(J)une	0.303	•													
(Ju)ly	0.003	0.314	•												
(A)ug	0.010	0.730	1.000	•											
M-J	0.808	0.013	<0.001	<0.001	•										
M-Ju	1.000	0.763	0.012	0.046	0.341	•									
M-A	1.000	0.127	0.001	0.004	0.981	0.964	•								
J-Ju	0.716	1.000	0.096	0.314	0.051	0.991	0.395	•							
J-A	0.998	0.837	0.016	0.059	0.278	1.000	0.930	0.997	•						
Ju-A	0.084	1.000	0.757	0.990	0.003	0.319	0.032	0.926	0.388	•					
M-J-Ju	0.957	0.028	<0.001	<0.001	1.000	0.565	1.000	0.104	0.480	0.007	•				
M-J-A	0.473	0.005	<0.001	<0.001	1.000	0.141	0.796	0.018	0.110	0.001	0.998	•			
M-Ju-A	1.000	0.219	0.002	0.007	0.902	0.996	1.000	0.586	0.989	0.058	0.988	0.601	•		
J-Ju-A	1.000	0.688	0.009	0.036	0.407	1.000	0.984	0.978	1.000	0.263	0.644	0.174	0.999	•	
All 4	1.000	0.185	0.002	0.006	0.937	0.992	1.000	0.522	0.978	0.048	0.995	0.666	1.000	0.997	•

(p=0.002) (Table 5). The significant year by tally combination interaction probably was due to the difference in sample times over the 2 years and the elm spanworm infestation.

Discussion. SEASONAL PATTERNS OF HERBACEOUS SPECIES. Despite the artifact in the methods used that resulted in rare or infrequent species appearing, disappearing, and then reappearing, we have shown that time of sampling influences estimates of abundance for plants that increase in coverage during the growing season. For example, hayscented fern fronds expand over a period of about 45 days at the beginning of the growing season. Therefore, sampling should occur in July or August to better capture its abundance. However, the spring ephemerals and plants that flower during the spring are often difficult to identify when flowers are not present, and cannot reliably be identified late in the growing season. Thus, based on phenology alone, at least two sampling times are required for adequate representation of species richness and abundance in herbaceous communities of the unglaciated Allegheny high plateau. Although ecologists have known this for many years, many investigators sample in only one season.

TWINSPAN was useful for grouping species with apparently similar phenologies. The design of this study actually prevented the program from grouping species on a purely seasonal basis. Some groups contained particular plants because the temporary plots we used were in different locations each month. Using the TWINSPAN procedure as a starting point and then inspecting abundance results allowed meaningful groupings of the species on the unglaciated Allegheny high plateau. The constant-presence group contained plants present throughout the growing season, though some species were low in abundance early in the season and increased to a maximum later (spring/summer species). Other species maintained similar high or low abundance levels throughout the growing season (semi-evergreen). Richness of species in this group is not affected by sampling time. The infrequent groups, including spring ephemerals, may be absent from species lists because the plants are present for a short time in the spring or because sampling systems fail to find them. This is an important finding in that rare or infrequent plants were missed in certain months despite the relatively large number of 4-m^2 plots. Choosing one sample time and using plots alone underestimate the richness of infrequent species. One might expect differences in abundance and species presence to affect the diversity measures; yet, we found this was true only for richness (Table 4). These results probably were due partly to use of temporary plots and partly to the ephemeral nature of some species. Although TWINSPAN generated three different infrequent groups based on months sampled, evenness and the Shannon Diversity index did not differ through time.

SAMPLING TIMES AND COMBINATIONS. Methods used to standardize sampling to assess diversity such as the Whittaker method (Peet et al. 1998; Shmida 1984; Stohlgren et al. 1995) or to vary the number of quadrats based on the richness of the area (Magurran 1988; Mueller-Dumbois and Ellenberg 1972) may make it more difficult to describe herbaceous species. In a forest stand, Whittaker plots sample a small portion of the community and use small 1-m^2 subplots for abundance estimates. Palmer (1995) pointed out that while it is fairly simple to sample at a small scale, such as the study plot, preservation of species often is desired on much larger spatial scales. Quadrats sample over a larger area but do not include measurements between plots. The species-accumulation graphs we used to determine the required number of quadrats suggest that 20 to 35 plots are needed for a stable diversity line in this community type. If this were true, one would expect that any sample of 20 to 35 plots would provide a similar diversity estimate. What actually occurred was that quadrat sampling each month, even at a high intensity of sixty 4-m^2 quadrats per 8-ha location, missed several species that were present throughout the growing season. This occurred because infrequent species, that occupy small microhabitats, were picked up by chance when the plots were moved each month. TWINSPAN showed this by placing plants known to be evergreen or at least known to be persistent throughout the growing season in infrequent groups rather than the group of species common in all months. The fact that plot-based sampling, even at high intensity, fails to detect infrequent species supports the suggestion of Palmer et al. (1995) that generating a flora list for an area might be the best way to determine species presence. An intuitive solution to the problem of sample error would be the use of permanent plot locations, though this would not have been acceptable for two reasons: 1) some species that appeared on the temporary plots each month would not have been encountered, and 2) repeated measurement of plots with dense fern cover would be destructive to plot integrity. A better solution is an intense random search like that described by Goff et al. (1982) for identification of threatened and endangered species. Their method entails a timed search in which the investigator wanders to unique microhabitats within the study area.

EFFECT ON DIVERSITY INDICES. In a single month-by-month comparison, only species richness is affected greatly by time of sampling. The trend in species richness throughout the two growing seasons sampled in this study was a decline in numbers of species from May through July as spring ephemerals senesced. When spring ephemerals are present, most spring/summer and summer species also are present, making richness highest during this period. When months are combined, differences in sample size became more important. As the number of visits to a site increased, so did values of richness, and the Margalef and Shannon indices. Magurran (1988) suggested that richness often is positively correlated with sampling effort. Each visit provided a new sample of the vegetation with plots physically located in different places. Infrequent or rare plants that inhabit the location may not be recorded in all sample periods. Again, this supports the suggestion of Palmer et al. (1995) that developing a flora or more extensive search is preferable when richness is of interest.

Evenness measures (Berger-Parker and Shannon Evenness) were not affected by combining sample times; even though plants like hayscented and New York fern have lower abundance early in the growing season than later, they are sufficiently widespread to dominate the understory even before their foliage is fully expanded. Sampling in May and June or May and August were the best 2-time tally combinations for collecting data to be used in calculating diversity indices that incorporate species richness as a component.

CONCLUSIONS. Diversity indices are not influenced as much by time of sampling in Allegheny hardwood forests as one might expect. Richness and indices where richness is emphasized generally are maximized in the late spring when ephemerals and spring/summer groups coexist. However, for accurate abundance information to be presented, sampling for spring ephemerals in forested communities should be conducted before overstory tree leafout. For northwestern

Pennsylvania, this generally means sampling should occur before the end of May. Many other species flower during this period, and the presence of a flower is required for positive identification of many species. For example, violets are present all year but they flower only from early May through mid-June. The same is true for *Trillium* species, *Polygonatum biflorum* (Walt.) Ell., *Maianthemum canadense* Desf., *Trientalis borealis* Raf., and *Oxalis montana* Raf.. Some of these plants can be identified without flowers, though with greater difficulty.

Representative characterization of herbaceous diversity incorporating measures of species richness requires sampling during the spring ephemeral/flowering period, and during the mid- to late summer period. Representative sampling for other diversity measures can be conducted any time during the spring or summer unless accurate abundance data also are desired. If both abundance and diversity data are desired, at least two samples are required, preferably in May and July or in May and August. Including a random search like that described in Goff et al. (1982) is recommended if accurate richness data are required. Ristau (1998) showed that when quadrats are combined with random searches, significantly greater species richness is detected under several conditions. Stohlgren et al. 1998 compared four techniques in a grassland community with similar results. In their work a modified Whittaker style plot with an exhaustive search in a 20- by 50-m area found higher richness than with the other three methods that excluded exhaustive searches.

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