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David K. Smith

David K. Smith, Major Professor

We have read this thesis
and recommend its acceptance:

B. Eugene Cofford

Peter S. White

Accepted for the Council:

C. W. Munkel

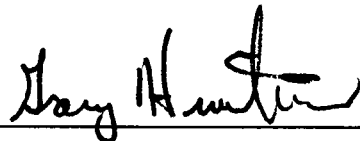
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VERTICAL AND ASPECTUAL DISTRIBUTION OF EPIPHYTIC BRYOPHYTES
ON YELLOW BUCKEYE (AESCULUS OCTANDRA MARSH.)

A Thesis
Presented for the
Master of Science
Degree
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ABSTRACT

Epiphytic bryophytes were intensively sampled on 13 yellow buckeyes (Aesculus octandra Marsh.) located in a cove hardwood forest in the Great Smoky Mountains National Park. Cover and frequency values for the epiphytes were obtained with the use of a 14 x 14 cm quadrat.

The four cardinal compass points (north, east, south, and west) were sampled by four vertical transects centered on these exposures of the phorophyte. The transects extended from the tree base upward to a height of 1.5 m. At each of the four compass points the width of the vertical transect was defined by the distance circumscribed by a 20° arc of the tree's circumference with the center of the arc located at the compass point.

The vertical distribution of the epiphytes on each of the four aspects sampled was examined using ordination (DECORANA) and classification (TWINSpan) techniques. These two complementary approaches revealed the presence of distinct vertical distribution patterns among the epiphytes. Thamnobryum alleghaniense, Anomodon rugelii, Metzgeria conjugata, Eurhynchium hians, and Thuidium delicatulum occurred in the lower region of the transects while Brachythecium oxycladon occurred in the lower and middle regions but was most abundant in the lower region. Anomodon attenuatus and Anomodon rostratus were ubiquitous species on all four aspects. Radula obconica, Anomodon minor, and Lejeunea ulicina were present

in low cover in the middle region of the transects. Cololejeunea biddlecomiae occurred sporadically throughout the transects on each of the four aspects. Forsstoemia trichomitria, Frullania brittoniae, Porella platyphylloidea, Radula complanata, Schwetschkeopsis fabronia, Neckera pennata, Homalotheciella subcapillata, Haplohymenium triste, and Dicranum viride were present in the upper and middle regions of the transects. Ulota crispa, Amblystegium varium, Leucodon julaceus, and Frullania eboracensis were restricted to the upper region of the transects.

The information generated on the vertical distribution patterns of epiphytes by ordination and classification techniques demonstrated that the aspectual effect was most pronounced on the south aspect presumed to be due to the presence of drier microclimatic conditions. Species occurring in the upper and middle regions of the transects on the north, east, and west aspects extended further down the transects on the south aspect, possibly the result of a reduction in competition with other species, primarily the ubiquitous Anomodon attenuatus and Anomodon rostratus. The cover of many of the epiphytes on the south aspect was also considerably reduced as compared to the other three aspects.

A comparison of means (i.e., mean cover/tree/aspect) showed that the north, east, and west aspects were not significantly different from each other yet all had significantly greater cover than the south aspect. Coefficients of community, calculated for all possible two-aspect combinations, also revealed that the north, east, and west aspects were more similar to each other than they were to the south aspect.

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CHAPTER I

INTRODUCTION

Survey of Research on the Vertical and Aspectual Distribution of Epiphytic Bryophytes and Lichens

Numerous studies have been conducted on epiphytic bryophytes and lichens in North America since the late 1930's. These studies have covered a broad spectrum of topics ranging from the use of epiphytes as indicators of levels of atmospheric pollutants to studies attempting to explain observed vertical distribution patterns by examining epiphyte physiology. While some studies have been concerned with either epiphytic bryophytes or epiphytic lichens, the majority of studies have included both groups of organisms. In the present study lichens constituted a very small fraction of the epiphyte species pool and thus were eliminated from consideration.

Some relevant studies that provide background on aspectual and/or vertical distribution of epiphytic bryophytes and lichens are reviewed hereafter. Particular attention will be given to the types of sampling schemes utilized by the various investigators. Included under the heading of sampling schemes are such topics as quadrat design (i.e., size and shape), quadrat placement on the tree (vertically as well as aspectually), the use of non-quadrat techniques, and the type of data collected (cover or frequency).

A detailed discussion of the results of each of the following studies is beyond the scope of this introduction. The results of some of the investigations, as they pertain to the present study, will be discussed at a latter point. Ordination and classification techniques used in analyzing the types of data generated by these studies are considered in a separate section as are studies conducted in the Great Smoky Mountains.

Hale (1952) examined the vertical distribution of cryptogams in a tract of virgin forest in the Flambeau River State Forest in north-central Wisconsin. Ten windthrown trees were chosen for study. Cryptogam sampling involved the use of 1 m high cylindrical quadrats, which encircled the tree trunks, located at seven levels (trunk base, 2 m, 6.5 m, 11 m, 15.5 m, 20 m, and 24.5 m). The quadrats extended 0.5 m on each side of the seven vertical locations with the exception of the base level where the quadrats extended from ground level to 0.5 m.

Lists of the species present within the quadrats were recorded for each of the seven levels. Data were compiled and used in formulating frequency (i.e., number of trees on which a cryptogam occurred regardless of the level divided by total number of trees X 100) and constancy (i.e., number of trees on which a cryptogam occurred at a given level divided by total number of trees X 100) for each cryptogam species.

Although the aspectual distributions of the cryptogams were deemphasized in this study, due to the difficulty in determining

for all the trees which compass direction a given side of the trunk had faced, Hale stated that, in general, species were most abundant on one side of the trunk.

The vertical distribution of the cryptogams was assessed by examining the number of lichen and bryophyte species present at the seven levels sampled. The number of lichen species was found to increase steadily and sharply from 12 species at the base to 45 at the 20 m level (the level where the highest number of lichen species occurred) followed by a rather steep decline to 25 species at the 24.5 m level. There were 15 bryophyte species present at the base level, 9 at 2 m, 15 at 11 m, and only 1 at 24.5 m. It was evident from this analysis that at all levels sampled, with the exception of the base level, lichens formed the dominant epiphyte community.

In addition to examining the number of species present at each of the levels sampled, the constancy of the cryptogams was also investigated. These data added additional support to the observation that bryophytes were dominant at the base of the trees while lichens dominated at higher levels.

Hale (1955) examined the phytosociology of corticolous cryptogams in the upland forests of southern Wisconsin. Cryptogamic vegetation was sampled on 40 trees in each of 72 stands. Cryptogams were sampled at the bases of trees and at a height of 1.3 m above the soil surface. At the base of the trees, cryptogams occurring within a cylindrical quadrat extending from ground level to a height of

30 cm and encircling the trunk were examined and lists of the species present were compiled. A similar procedure was followed with a 40 cm cylindrical quadrat centered at the 1.3 m level.

The aspectual distribution of the cryptogams within the cylindrical quadrats at the two positions was not considered. The species lists compiled for the sampled trees (i.e., the species presence data) were used to calculate the constancy (i.e., number of stands in which a cryptogam was found at least once divided by the total number of stands) and frequency (i.e., number of trees on which a cryptogam was divided by the total number of trees) of each cryptogam.

Of the 88 species of cryptogams encountered in this study (33 bryophytes and 55 lichens), 30 had frequencies of more than 5% at 1.3 m or on tree bases. Of these 30 species 18 were most frequent at 1.3 m (3 bryophytes and 15 lichens) and 12 were most frequent at the tree bases (8 bryophytes and 4 lichens). The results of this study indicated that bryophytes were dominant at the tree bases while lichens dominated at 1.3 m.

Culberson (1955) described the corticolous communities of lichens and bryophytes in the upland forests of northern Wisconsin. Cryptogamic vegetation was sampled using a 35 cm high cylindrical quadrat located at breast height (1.4 m). In 22 of the 70 stands sampled cryptogamic vegetation at the base of the trees was also sampled, again with a cylindrical quadrat, from the soil level to a height of 35 cm. The cylindrical quadrats were not divided into aspectual quadrants, so no consideration could be given to the

influence of aspect on the distribution of the cryptogams. Abundance of cryptogams was measured in terms of quadrat presence only (i.e., no attempt was made to estimate cover).

Sampling at breast height and at the base of the trees allowed a comparison of the vertical distribution of the species encountered. Culberson found that lichens were the dominant cryptogams at breast height while bryophytes dominated the tree bases.

Hale (1965) investigated the vertical distribution of epiphytic lichens and bryophytes in a red maple swamp in Connecticut. Five red maples were selected for study. The trees were cut down and the trunks marked off at intervals of 1.5, 4, 7, and 10 m from the base. Each of these four points served as the midpoint of a 1 m high cylindrical quadrat which encircled the tree. Epiphyte cover was measured with a plastic screen divided into centimeter squares. Cover was measured at the bases of the trees (base level) using a cylindrical quadrat approximately 50 cm in height. Hale did not divide the cylindrical quadrats into compass quadrants since exposure appeared to have little effect on epiphyte distribution.

Although bryophytes constituted only a small portion of the epiphytic flora, vertical distribution patterns were discernible. The base level of the trees was dominated by bryophytes (10 mosses and one liverwort) which formed an intertwining mat that extended to a height of approximately 50 cm. Bryophyte coverage within this level ranged from 50-100%. At the 1.5 m level bryophyte coverage was considerably reduced with only Frullania eboracensis, Platygyrium

repens, and Ulotia crispa being present. Only Platygerium repens and Ulotia crispa remained, both with low coverage, at the 4 m level where the dominant epiphytes were crustose lichens. Bryophytes were absent from the quadrats at the 7 and 10 m levels.

Hoffman and Kazmierski (1969) investigated the ecology of epiphytic bryophytes and lichens on Douglas fir (Pseudotsuga menziesii) on the Olympic Peninsula, Washington. At each of the 20 stands studied, four of the largest trees present were sampled. Northeast and southwest exposures were sampled using 2 X 1 dm plots placed contiguously from the tree bases to a height of 4 m. Epiphyte cover was estimated by using cover classes.

The results of this study clearly indicated that the epiphytic unions of Douglas fir on the Olympic Peninsula exhibited distinct vertical and aspectual distributional patterns. Furthermore, it was evident that these patterns were influenced to a considerable extent by macroclimatic parameters (in this case moisture availability in the form of precipitation) which varied from one area to another.

Hoffman (1971) discussed the epiphytic vegetation on Douglas fir on the Olympic Peninsula, Washington, in terms of diversity. Four diversity indices were used to calculate the diversity of the epiphytic unions previously described by Hoffman and Kazmierski (1969). Cover percentages of the epiphytes were converted to area occupied (square centimeters) and these values were used for calculating diversity. Diversity values were calculated for each 1 m increment of height on both the northeast and southwest exposures of the trees (eight values per tree, four per aspect) at all study sites.

Diversity values (i.e., mean diversity values, $\bar{D}$) followed distinctly different patterns, with respect to height and aspect, in areas with different moisture conditions. A detailed discussion of diversity patterns was provided for mesic, intermediate, and xeric habitats.

Yarranton (1972) examined the distribution and succession of epiphytic lichens on black spruce in the Cochrane district of northern Ontario. Ten trees were sampled in each of five 50 year age groups ranging from 0 to 250 years. Epiphyte abundance (i.e., frequency) was assessed by recording the species present at 1 cm intervals along a tape stretched around the tree bole at 25 cm vertical increments. At each 25 cm level the point samples were grouped into aspectual quadrants (north, east, south, and west) and the relative frequency of occurrence of each epiphyte was calculated.

The mean frequencies of eight epiphytes were examined in relation to aspect and height above the ground. Both aspect and height were found to have a significant influence on the distribution of epiphytic lichens on black spruce.

Stringer and Stringer (1974) studied the corticolous bryophytes in the vicinity of Winnipeg, Manitoba. Epiphytes were sampled in 34 plots of relatively undisturbed forest. In each plot four to ten trees were chosen as being representative of the trees of the stand as a whole. A total of 220 trees were sampled consisting of eight species of deciduous trees. The north, south, east, and west species of the trees were sampled with 25 X 25 cm contiguous

quadrats. Bryophyte cover within each quadrat was estimated with the use of cover classes.

Most epiphytic species were found to exhibit distinct vertical zonation. Ceratodon purpureus, Leptodictyum trichopodium, and Bryum spp. were restricted to humus at the bases of the trees and interpreted as constituents of the forest floor communities. Amblystegium serpens, Mnium cuspidatum, Amblystegium juratzkanum, A. varium, Brachythecium rutabulum, B. salebrosum, B. acuminatum, Leskea obscura/polycarpa, Anomodon minor, and Pylaisiella polyantha, in the order listed, showed a general increasing order in height of their mean vertical range (means being calculated on the basis of data from all four exposures). Orthotrichum speciosum, O. obtusifolium, O. pumilum, and Frullania inflata were restricted to the upper parts (above 22 cm) of the bryophyte colony.

Gough (1975) investigated the distribution and ecology of epiphytic lichens and bryophytes on Douglas fir (Pseudotsuga menziesii) and subalpine fir (Abies lasiocarpa) in the Front Range of Colorado. Six sites ranging from 1,830 m to 3,050 m in altitude were selected for study. Beginning at 1,830 m study sites were located at approximately 305 m intervals, except for Site 3a which was only 60 m above Site 3b, up to and including 3,050 m (Site 1 - 1,830 m, 2 - 2,075 m, 3b - 2,410 m, 3a - 2,470 m, 4 - 2,745 m, 5 - 3,050 m).

Epiphytes were sampled using a corticolous epiphyte tracer (CET) which recorded the linear positions of the epiphytes on a circumferential line-intercept. Tracings were made at six heights

above ground (i.e., 25 cm, 50 cm, 75 cm, 100 cm, 125 cm, and 150 cm) on the 15 trees selected for sampling at each study site. The paper tracings produced by the CET were divided into north, east, south, and west quadrants (with north being the area between NW and NE, east being the area between NE and SE, etc.). The circumference of the line-intercept tracings was measured and the length (i.e., coverage) of each epiphyte on the tracings recorded.

Although most epiphytes were encountered in all quadrants, the majority occurred in the north or west quadrants or both. Aspect had no observable influence on the distributions of Parmelia elegantula, Parmelia sulcata, Parmeliopsis hyperopta, and Phycia aipolia. At Sites 1, 2, 3a, and 3b the south quadrant contained the lowest number of species while at Sites 4 and 5 the west quadrant contained the lowest.

The vertical distributions exhibited by the epiphytes varied with elevation and host tree species. Gough listed the dominant epiphytes of communities characteristic of the tree bases and crowns (despite the absence of quantitative sampling above 150 cm) of Douglas and subalpine fir at various elevations.

Pike et al. (1975) conducted a floristic survey of epiphytic lichens and bryophytes growing on old growth conifers in western Oregon. Six distinct zones, four on the trunk and two associated with the branch systems, were recognized on the overstory Douglas fir.

In the basal zone epiphytic bryophytes covered the bark in an almost continuous layer and were confluent with the forest floor

communities. Dicranum fuscescens and Hypnum circinale were the most abundant species. Stokesiella oregana invaded from the forest floor and was restricted to the basal zone.

On the moist side of the lower trunk zone bryophytes covered most of the bark in the lower part of the zone and occurred as scattered clumps in the middle and upper regions. The dry side of the lower trunk zone, much of which was bare, was dominated by crustose and squamulose lichens. Mosses and large foliose or fruticose lichens occurred mainly at the base of the branch systems where microclimatic conditions resembled those on the moist side.

Foliose and fruticose lichens were the dominant epiphytes of the upper trunk zone. Crustose lichens were also an important element of the epiphytic flora in this region. Dicranum fuscescens and Hypnum circinale were the common mosses occurring mainly at the base of branch systems.

Rasmussen (1975) examined the horizontal and vertical distribution of epiphytic bryophytes in a forest in northern Jutland, Denmark. The study area was located in a Fraxinus excelsior marsh valley with surrounding slopes dominated by Fagus sylvatica. A homogeneous area of 7,000 square meters containing 25 mature trees of both Fraxinus and Fagus was selected for intensive study.

Epiphytic bryophytes were sampled with 20 X 20 cm quadrats located on the north, east, south, and west sides of the trunks at 0.5 m, 1.5 m, and 2.5 m above the ground. Cover of each species was estimated using the Hult-Sernander-DuRietz scale. Although

both cover and frequency values were obtained for the epiphytes, frequency was considered a more objective measure of species abundance and was used in the data analyses whenever possible.

The diversity of the epiphytic vegetation on Fraxinus and Fagus was assessed by examining the number of epiphytic species present on each phorophyte species and by calculating diversity values using the Shannon index. On both Fraxinus and Fagus the number of species present at the four compass points sampled was rather constant although the values for Fraxinus were higher on all four aspects. The number of epiphytic species declined vertically upward on Fraxinus while on Fagus no distinct trend was evident. The vertical variation in diversity values paralleled the trend observed with respect to the number of epiphytic species. Diversity was found to decrease upward on Fraxinus while on Fagus no predictable vertical trends were evident.

Slack (1976) investigated the host specificity of epiphytic bryophytes in the Adirondack Mountains of northern New York State and the southern Blue Ridge Province of North Carolina, part of the southern Appalachian Mountains. Although this study was concerned primarily with host specificity, the vertical distribution patterns of several bryophyte species in the Adirondack Mountains were also examined.

In both the Adirondacks and the southern Blue Ridge the methods of data collection were the same. Four 10 X 20 cm quadrats were located on the north side of trees of all size classes at heights

of 0.5 m, 1.0 m, 1.5 m, and 2.0 m. The decision to sample only the north side of the trees precluded any consideration of the influence of aspect on epiphyte distribution. Cover measurements were made to the nearest 5%.

Mean percent cover of Neckera pennata, Anomodon rugelii, Platygyrium repens, and Pylaisiella intricata on Acer saccharum in the Adirondack Mountain Preserve (one of the four Adirondack study sites) was plotted against distance from the ground in order to evaluate the vertical distribution of these species. Neckera pennata attained its maximum mean percent cover at 1 m, Anomodon rugelii at 0.5 m, Platygyrium repens at 2.0 m, and Pylaisiella intricata also at 2.0 m. Slack felt that these differences in the distribution patterns of the epiphytes were probably the result of differential species responses to vertical microclimatic gradients along the surface of the trunks.

Hoffman and Boe (1977) studied the epiphytic cryptogams on Populus deltoides in northeastern South Dakota and adjacent Minnesota. The north and south exposures of 87 trees were sampled using 1 X 2 dm plots placed contiguously from ground level to a height of 2 m. Cover classes were used to estimate species cover. The average cover of each species was calculated, using class midpoints, for each meter segment of each exposure.

Hoffman and Boe were able to detect quantitative vegetational differences between north and south exposures. The average cryptogam cover on north exposures was 45% while on south exposures it was 19%.

Kenkel and Bradfield (1981) examined the structure of epiphytic bryophyte communities of a wet-temperate coniferous forest in south-coastal British Columbia. The upper surface of 72 trees (25 Thuja plicata, 25 Pseudotsuga menziesii, and 22 Tsuga heterophylla) was sampled at 0.5, 1.0, and 2.0 m from the ground using 15 X 15 cm quadrats. Percent cover estimates were obtained for 14 bryophyte species in a total of 216 quadrats.

Changes in epiphyte composition with height above the ground were examined on all three host species. The majority of the 14 species encountered showed a decline in cover with increasing height on the trunk. Unfortunately, many of the species encountered occurred with such low frequency and cover that the authors found it difficult to explain their distributional patterns.

In examining succession of epiphytic bryophytes in a cove forest near Mountain Lake, Virginia, Studlar (1982b) found that epiphytes on the bases (0-1.8 m) of saplings of six host tree species exhibited vertical zonation by usually occurring in either a lower zone (0-0.3 m) or an upper zone (0.3-1.8 m). Although most species were restricted to the lower zone, Platygyrium repens, Dicranum montanum, Frullania tamarisci, and Frullania eboracensis typically occurred within the upper zone. Many of the species present in the lower zone were members of adjacent humicolous communities that had invaded the bark.

Epiphytes on the bases of mature trees of the same host species were assigned to three zones (i.e., a lower zone: 0-0.4 m, an upper

zone: 0.4-1.8 m, and the entire zone: 0-1.8 m) based on their usual positions within the 1.8 m high cylindrical quadrat.

Trynoski and Glime (1982) examined the horizontal and vertical distribution of epiphytic bryophytes on four deciduous tree species (Acer saccharum, Betula lutea, Populus spp., and Quercus rubra) in central Keweenaw County, Michigan. Bryophyte sampling involved the use of 10 X 10 cm quadrats located on the north, east, south, and west exposures of 124 trees (31 of each taxon). Three quadrats were located on each exposure at the following heights: the base of the trunk, breast height (approximately 1.2 m), and at a point halfway between the base and breast height. The bryophyte species present within each quadrat were recorded and their cover estimated with the aid of a transparent plastic grid.

The vertical distributions of the bryophytes were examined in detail for each of the photophyte species. The subject of aspectual or horizontal bryophyte distribution was addressed by examining the following parameters for each phorophyte species: total bryophyte cover per exposure, mean number of species per exposure, and mean percent cover of bryophytes on each exposure at each height.

The observed distributional patterns were thought to be the result of the differential influence of various macro- and micro-climatic parameters on the bark-inhabiting bryophyte communities.

Epiphytic Bryophyte Studies in the Great Smoky Mountains

Epiphytic bryophyte communities in the Great Smoky Mountains have received relatively little scientific study. Cain and Sharp

(1938) examined terrestrial, epilithic, epixylic (i.e., decorticated log), and corticolous bryophyte communities of six forest associations of the Great Smoky Mountains and classified the assemblages of bryophytes inhabiting those substrates into various unions, alliances, and facies. Although this study did not deal with aspectual distribution, it did describe corticolous bryophyte communities occurring on Aesculus octandra and Tilia neglecta in the Aesculo-Tilietum Association of the cove hardwood forest complex in terms of their vertical position on the trees. Corticolous communities were divided into three community types which corresponded to distinct vertical zones on the trees (i.e., tree butt communities, tree trunk communities, and top limb flora).

The corticolous communities occurring on five trunks of Aesculus octandra and Tilia neglecta were mapped to a height of 1 m above the highest soil line. Large roots protruding above the soil surface were also examined for the presence of corticolous species. Few differences were observed between the bryophyte communities of the two tree species.

Observations were made on tree trunk communities (i.e., those on the main bole above the tree butt communities) in all six forest types studied. Neckera pennata frequently formed a community at middle trunk heights on Aesculus and other phorophyte species. Leptodon trichomitrium often occurred with Neckera pennata and occasionally dominated alone, especially on lower regions of the trunk and at lower elevations within the cove hardwood forest complex.

The top limb flora consisted of relatively few species (Ulotcrispa, Ulotamericana, Frullania asagrayana, Leucodon brachypus, and Leptodon sciuroides) with rather low total cover.

Billings and Drew (1938) investigated the effects of various bark factors on the distribution of corticolous bryophyte communities on several species of trees within the Yellow Poplar-Hemlock Association (Liriodendron-Tsugetum Association) of the cove hardwood forest complex. Ten trees were chosen for intensive study: four Liriodendron tulipifera, two Tsuga canadensis, one Fraxinus americana, one Aesculus octandra, one Fagus grandifolia, and one Castanea dentata. For each tree the moss cover of the tree butt was mapped to a height of 6 ft. above the highest soil line.

Bryophytic unions corresponded well to two groups, one restricted to Tsuga and others of deciduous trees. The communities present on the deciduous trees were distinctly different from those present on Tsuga due primarily to the relatively drier and more acidic bark characteristics of Tsuga.

On nearly all of the trees studied, bryophyte coverage was highest on either the east or south face of the trunks. This distribution pattern was thought to be a consequence of the exposure of these two aspects to moisture-laden downdrafts of cold air from higher elevations. Furthermore, it seemed quite likely that the prevailing winds, which blow in an easterly direction, were responsible for rain being driven against the east face of the trunks.

Norris (1964) examined terrestrial, corticolous, epilithic, and epixylic bryophyte communities in the spruce-fir zone of the

Great Smoky Mountains. Of the 22 unions described in this investigation, only five were found to occur on trees. The Brotherella recurvans union occurred on all tree flares with the exception of those belonging to large, low elevation spruces. The Bazzania trilobata union replaced the Brotherella recurvans union on the flares of these large, low elevation spruces and was found to be restricted to that habitat. The Plagiothecium laetum union occurred on all root bridges where it exhibited very low cover.

The most abundant union on the boles of trees in the spruce-fir zone was the Frullania asagrayana union. This union exhibited considerably higher cover on fir than on spruce (mean cover values were 90% and 20%, respectively).

In ridge forests with relatively open canopies, the Ulotia crispa union was a common occupant of tree trunks occasionally extending down to the tree flares. This union, although present within the vertical range sampled, was observed to be more typical of regions higher up the trunk as well as the forest canopy. This was the only union which showed a distinct preference for one of the two aspects sampled. The Ulotia crispa union was encountered in 274 quadrats with 72% of these occurring on the north side of the trees.

Despite the existence of additional studies conducted in the Southern Appalachians dealing with epiphytic bryophytes (Patterson 1940, Slack 1977, Studlar 1982a,b), the preceding studies have, until now, been the only sources of information on community structure in epiphytic bryophyte communities in the Great Smoky Mountains.

Ordination and Classification Methods and the Analysis of
Epiphytic Bryophyte and Lichen Communities

Ordination and classification methods have not experienced the widespread use among bryophyte ecologists that they have among higher plant ecologists. Although this situation is slowly changing there still exists a wide disparity between the levels of the two related disciplines in terms of the application of multivariate analyses to community data. Bates (1982) stated, "In bryophyte ecology, relatively little use has been made of numerical classification procedures . . ." (see also Jesberger and Sheard 1973; Sheard and Jonescu 1974). Ordination methods have received more extensive use in bryophyte ecology for the analysis of several types of bryophyte communities (e.g., ground, epiphyte, rock, and bog communities). The following discussion outlines studies on epiphytic bryophytes and lichens which have utilized ordination and/or classification methods. These studies are discussed in order to provide the reader with a brief introduction to the types of methodologies which have been used in the analysis of epiphytic cryptogam community data.

Beals (1965) analyzed the corticolous cryptogamic communities of seven forests in south-central Wisconsin using a polar ordination method similar to that developed by Bray and Curtis (1957). Beals located his sample plots at a uniform height on the trees and thus eliminated from consideration the effect of height on epiphyte distribution. Beals stated, "The effect of height on epiphyte distribution is well known and has been studied quantitatively in Wisconsin

(Hale 1952); ordination techniques could be used effectively in further study of this." This investigation is only the second study conducted to date which has made extensive use of ordination methodology in studying the vertical distribution of epiphytic bryophytes (see Kenkel and Bradfield 1981).

Jonescu (1970) examined the distribution of lichens on Populus tremuloides at six sites in west-central Canada. Jonescu used Beals' (1960) ordination method, which was essentially identical to that used by Beals (1965), to ordinate the four stand-quadrants at each of the six sites. A "stand-quadrant" consisted of the pooled data from all trees, according to aspect, within a site. Jonescu also used Beals' (1960) method to produce a single axis ordination of the six study sites for each of the four aspects.

Jesberger and Sheard (1973) utilized both ordination and classification methods in their study of corticolous lichen communities in the southern boreal forest of Saskatchewan. The authors used principal components analysis (PCA), based on an earlier program of Orloci (1966), and an agglomerative polythetic classification procedure also developed by Orloci (1967).

Sheard and Jonescu (1974) used multivariate methods to further analyze Jonescu's (1970) lichen data. The ordination method selected was PCA and the classification was that of Orloci (1967).

Rasmussen (1975) used association analysis, a monothetic divisive classification method, in his study of epiphytic bryophytes in Denmark. The association analysis divided the bryophyte species

into three groups that correlated well with the vertical distribution of the species.

Hoffman and Boe (1977) utilized two different classification methods in their study of epiphytic cryptogams on Populus deltoides--the weighted pair-groups method of Sokal and Sneath (1963) and the agglomerative polythetic method of Orloci (1967).

Kenkel and Bradfield (1981) made extensive use of ordination methods in their study of epiphytic bryophyte communities in south-coastal British Columbia. Three ordination methods were used to investigate the structure of the epiphytic vegetation. They stated:

The distinguishability of three tree species with respect to their epiphytic communities, and compositional changes with height above ground, were examined with principal components analysis and canonical variates analysis. The extent to which patterns of association among epiphytes are similar on different tree species was examined with principal coordinated analysis.

In their study of the epiphytic vegetation of Quercus petraea and Fraxinus excelsior, Bates and Brown (1981) made use of reciprocal averaging (RA), an ordination procedure developed by Hill (1973), and PCA. The results of the RA ordination revealed that the epiphytes of oak and ash varied continuously and were only loosely correlated with phorophyte species. The first RA axis was thought to represent a bark pH gradient with ash at the high pH end of the continuum and oak at the low pH end.

McCune and Antos (1982) used both ordination and classification methods in studying epiphyte communities in Montana. Ordination methods included polar ordination, with endstands (i.e., endpoints)

chosen by subjective and objective methods, RA, and PCA. Stand classification was accomplished using the association analysis method of Williams and Lambert (1959). Discriminant analysis was used to detect misclassified stands, a serious problem with this type of method, which were then reclassified.

Trynoski and Glime (1982) used the unweighted pair-groups method, a polythetic agglomerative classification method, to determine bryophyte associations. This technique was used to search for clusters of species by direction of exposure and for the clustering of samples by height on the tree.

In my study of epiphytic bryophytes on yellow buckeye I have used two relatively new ordination and classification methods. Ordination of both species and samples was performed using DECORANA, a program for detrended correspondence analysis (and RA) written by Hill (1979a). I am aware of only one other study on epiphytic bryophyte communities which has used detrended correspondence analysis (DCA), a method which some ecologists have found to be superior to RA and PCA (Hill and Gauch 1980, Gauch 1982). Slack (1984) has used DCA successfully ". . . to show host specificity of bryophytes (and lichens as well) to the same host trees or phorophytes . . ." in the southern Blue Ridge of North Carolina and the Adirondack Mountains of New York. Slack has also used DCA in the study of oceanic mires in western Sweden (Slack 1982, 1984).

Classification of both species and samples was done using TWINSpan, a program for two-way indicator species analysis written

by Hill (1979b). A review of the literature indicates that this is the first time TWINSpan, a polythetic divisive method of classification, has been employed in the analysis of epiphytic bryophyte communities. An excellent discussion of the use of hierarchical clustering techniques with ecological community data is presented by Gauch and Whittaker (1981). Gauch (1982) also provides an excellent treatment of the use of classification and ordination methods in community ecology.

Purpose of the Study

The primary focus of this investigation was to determine whether or not the epiphytic bryophytes of Aesculus octandra exhibited recognizable vertical and aspectual patterns of distribution. Addressing this question required an initial, detailed description of the bryophyte communities inhabiting the bottom 1.5 m of the trunks of Aesculus octandra. The acquisition of this information allowed the following questions to be answered: (1) do the epiphytes occur within predictable vertical ranges, (2) do the epiphytes show preferences for a particular aspect(s), and (3) if vertical distribution patterns do exist are they influenced by aspect? These questions were answered using ordination and classification methodologies as well as other non-multivariate techniques.

In addition to the above considerations there were two additional (i.e., secondary) objectives of this investigation. The collection of detailed epiphyte community data, in addition to

answering the questions posed by this study, provided baseline data on epiphytic bryophyte community structure which can be used for comparative purposes in future studies. The baseline data acquired in this study may be of particular use in studying the effects of various environmental perturbations (natural or manmade) on biological communities. In addition to obtaining baseline data on epiphyte communities, a secondary objective of this study was to develop a sampling technique, employing the use of quadrats, which would supply accurate, objective estimates of species cover. The development of such a technique would make comparisons between studies more valid if it were to receive widespread use among bryophyte ecologists.

CHAPTER II

MATERIALS AND METHODS

Study Site Description

The study site was located near the source of Jay Bird Branch, a tributary of the Little River, on a northeast facing slope (approximately 62° ENE) at an altitude of 3400 ft on Cove Mountain (35°40'53" North Latitude, 83°36'20" West Longitude) in the Great Smoky Mountains National Park (Gatlinburg Quadrangle, Tennessee-Sevier County, 7.5 Minute Series (Topographic) 157-NE). The Cove Mountain Trail leading from Laurel Falls to the abandoned lookout tower on Cove Mountain passes through the study site at a distance of approximately 2.1 miles from the Cove Mountain trailhead at Fighting Creek Gap on the Little River Road.

Climatological data recorded during the years 1946-1950 at an elevation of 3800 ft. revealed precipitation and temperature means of 78.8 in. and 49.8°F for this five year period (Shanks 1954). More extensive climatological data is available for Gatlinburg, Tennessee (weather station location: Lat. 35°41', Long. 83°32', Elevation 1454 ft.) but due to the large elevational difference between the Gatlinburg station and my study site. The data presented by Shanks (1954) are considered more representative of conditions at my site.

The 13 yellow buckeyes investigated, forming a fairly homogeneous stand, occurred within typical cove hardwood forest. The integrity of the stand was disrupted only by the presence of several eastern hemlocks (Tsuga canadensis (L.) Carr.) and a single sugar maple (Acer saccharum Marsh.). Yellow buckeye reproduction appeared minimal since only two saplings were found within the study site.

Field Methodology

Thirteen yellow buckeyes (Aesculus octandra Marsh.) ranging in diameter, as measured at breast height, from 25.7 cm to 87.6 cm were chosen for intensive study. Several additional yellow buckeyes occurred within the study site but were not sampled due to the presence of large scars on their lower trunks.

Pike et al. (1975) found tree inclination to be "more important than compass direction in determining the horizontal distribution of epiphytes around a trunk." Due to these observations, as well as similar ones made by Barkman (1958) and Rasmussen (1975), special care was taken to sample only vertical trees and thus avoid the complicating factor of tree inclination.

Cover and frequency values for the epiphytes were obtained with the use of a 14 X 14 cm quadrat. Quadrats of similar size have been used successfully by numerous investigators (Hoffman and Kazmierski 1969, Stringer and Stringer 1974, Rasmussen 1975, Slack 1976, Hoffman and Boe 1977, Kenkel and Bradfield 1981, Bates and

Brown 1981, Trynoski and Glime 1982). The quadrat was drawn in ink and photocopied onto an acetate transparency. The acetate transparency was quite flexible and adapted readily to curved surfaces of tree trunks. Brass eyelets, affixed to the four corners of the quadrat, permitted repeated attachment to and removal from the surface of the trunk by means of long T-shaped pins.

The quadrat, a modified version of the design used by Bates and Brown (1981), was constructed such that each of the 100 equally spaced 5 mm diameter circles represented one tenth of 1.0% of the total area of the quadrat. The species occurring within each circle were vocally recorded on magnetic tape. These field recorded data were later transferred to work sheets bearing scaled-down versions of the quadrat. This process was facilitated by a coordinate system of letters and numbers incorporated into the design of the quadrat (see Figure 1).

Species of questionable identity in the field were brought back to the lab for determination. In several of the genera encountered (e.g., the small leafy and thalloid hepatics of the genera Frullania and Metzgeria, respectively) identification to the species level required the use of a compound microscope. Species belonging to these genera were always collected in order to insure correct identification. Nomenclature follows Crum and Anderson (1981) for mosses and Stotler and Crandall-Stotler (1977) for liverworts. Voucher specimens of all bryophytes were deposited in the University of Tennessee Bryophyte Herbarium [TENN].

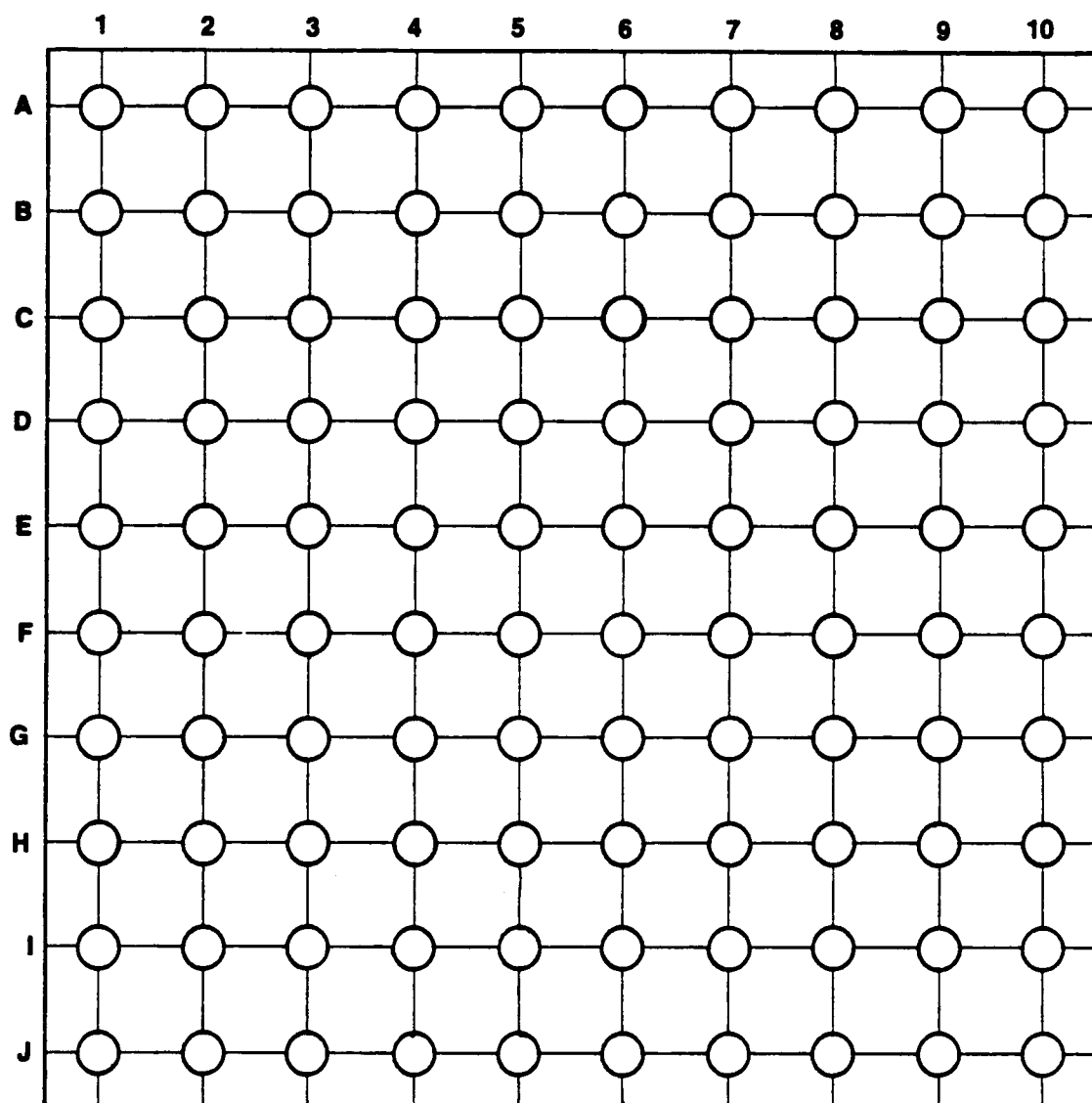


Figure 1. Quadrat used in the sampling of epiphytic bryophytes. Each of the 5 mm diameter circles represents 0.1 of 1.0% of the total area of the quadrat. All bryophyte species encountered were assigned a number thus allowing each circle to be marked with the number of the species occupying it. In instances where two species occupied a single circle a diagonal line was drawn through the circle to separate the two numbers and indicate the presence of two species. Unoccupied circles or half-circles were marked with a checkmark.

The four cardinal compass points (north, east, south, and west) were sampled by four vertical transects centered on these exposures of the phorophyte. The transects extended from the tree base upward to a height of 1.5 m. Since the sampled trees were located on sloping topography 1.5 m was measured at a position intermediate between the upslope and downslope sides of the trunks.

At each of the four compass points the width of the vertical transect was defined by the distance circumscribed by a 20° arc of the tree's circumference with the center of the arc located at the compass point. Determining the width of the transects by this method allowed for the same percentage of circumference of the trunk to be sampled regardless of the diameter of the tree.

The sampling technique employed in this investigation was a hybrid technique which incorporated the methods of point sampling to provide objective cover estimates. Even though true point sampling is a fast and simple technique the information content of the data obtained by this method (i.e., species frequency values) is relatively low. Expanding the points to 5 mm diameter circles allowed for the determination of species cover values which were more informative than simple frequency values.

The 5 mm diameter circles were typically occupied by a single bryophyte species. In this respect the similarity between the circles and point samples becomes apparent. However, it was not uncommon for a species to occupy only part of a circle with the remaining portion being unoccupied (i.e., bare bark) or for two species to

occupy the same circle. In such cases a cover value of one half was assigned to each of the two occupants (i.e., a single species and bare bark or two species) of the circle. In only a few instances did more than two species occur within a single circle. In these cases a cover value of $1/n$, where n was the number of species occupying the circle, was assigned to each occupant of the circle. Of the 36,550 circles examined in this study only 15 contained three species and none contained more than three species.

The sampling technique used in this investigation, due to its objective nature, allowed for greater accuracy in estimating species cover than most of the techniques used previously by other investigators. In the past it has been a common practice to obtain species cover data by estimating the percent of the total area of a quadrat occupied by each species or by assigning species to cover classes. Whereas, gridding the quadrat into square or rectangular units of equal area or the use of cover classes may simplify data gathering, it still does not control error due to the subjectivity inherent in these methods (i.e., the accuracy of the cover estimates is only as good as the investigator's ability to visually estimate cover over unintended bias and time).

The subjectivity problem associated with visual cover estimates is particularly acute when one is attempting to measure cover of pleurocarpous bryophytes which are characteristically freely branched and matted. Epiphytic bryophytes commonly form thick mats that often completely obscure the bark. Large yellow buckeyes typically

support luxuriant mats of several intimately associated pleurocarpous species (see Figure 2). In such instances it can be extremely difficult to make "accurate" cover measurements.

The 13 trees sampled in this study were permanently marked with numbered aluminum tags to facilitate their relocation for future studies. The ability to accurately relocate areas which have been the focus of previous investigations provides future investigators with a data base upon which to make comparative studies (e.g., studies on the effects of various ecological perturbations on epiphyte community structure).

Analytical Methods

Frequency and cover values for all bryophyte species encountered were calculated, according to aspect, for each of the 13 trees sampled. Although both frequency and cover values were available only the latter were used in the data analyses due to their higher information content.

The procedure followed for determining cover values was somewhat involved and is therefore best explained by presenting, in detail, an example showing how the cover values were calculated. Consider, for example, the north aspect of tree number nine. The area of the vertical transect on the north face of this tree was 1990 cm^2 and contained 1073 circles each of which occupied an area of 0.196 cm^2 . Thus the area sampled by the 1073 circles was 210.3 cm^2 . The area sampled divided by the area of the transect X 100 yielded



Figure 2. A bryophyte mat composed primarily of Anomodon rostratus and Anomodon attenuatus on a large yellow buckeye.

a number which represented the percent of the transect sampled by the 1073 circles. In this case 10.57% of the area of the transect was sampled. Since the number of circles per unit area was not constant over all transects, due to the changing dimensions of the transects, the area sampled per transect also fluctuated slightly. The area sampled by the circles, when all 52 transects (13 trees X four transects/tree) are compared, ranged between 9.13% and 12.00%.

Anomodon attenuatus occupied 637 of the 1073 circles located within the transect on the north face of tree number nine and thus had a cover value of 6.27%. Cover values for all species encountered, as well as that for bare bark, were calculated and totaled 10.57%. The species and bare bark cover values obtained in the 10.57% sample served as the basis for extrapolating to a new set of cover values accounting for the total area (100%) of the transect. In this example each species' cover value (and bare bark) was multiplied by 9.46 to put them on a 100% scale. Adjusting the data in this manner resulted in Anomodon attenuatus attaining a cover value of 59.31% for the total area of the transect. The adjusted cover values were used in all data analyses.

Data analysis involved the use of two multivariate approaches: ordination and classification:

ordination and classification techniques organize community data on species abundance exclusively, apart from environmental data, leaving environmental interpretation to a subsequent, independent step (with a few exceptions) (Gauch 1982).

In order to examine the vertical distribution of the epiphytes using ordination and classification techniques a species-by-samples data matrix was constructed for each of the four aspects sampled. The species component of the matrix consisted of those species which occurred on the aspect under consideration for all trees sampled. The only restriction imposed was for species occurring in fewer than 1% of the total number of plots on any given aspect. These were considered rare species and thus were deleted from the data set. Deletion of rare species is often of particular importance in ordinations where an unsatisfactory spread of the points (either species or samples) might otherwise result. The samples component of the matrix consisted of the actual quadrats which comprised the vertical transects of a given aspect over all the trees. The quadrats which made up the vertical transects were each assigned a number with the plot at the top of each transect (i.e., the plot beginning at the 1.5 m mark) always being considered plot number one. Successive plots were numbered sequentially down to the point of soil contact. Since the length of the vertical transect was unique for each tree/aspect combination sampled, due to the sloping topography, the number of quadrats varied both within and among aspects.

The information generated on the vertical distribution patterns of the epiphytes by the application of ordination and classification methods to the species-by-samples data matrices was used in making aspectual comparisons of epiphyte distribution. The similarity (or dissimilarity) of the four aspects was also investigated with

the use of ordination. A species-by-samples data matrix, similar to the ones described previously, was constructed in which the samples were the four aspects instead of quadrats on a single aspect.

Species and samples were ordinated using DECORANA, a FORTRAN program for detrended correspondence analysis and reciprocal averaging (Hill 1979a). DECORANA is program CEP-40 in the Cornell Ecology Program series.

Species and samples were classified using TWINSpan, a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes (Hill 1979b). TWINSpan is program CeP-41 in the Cornell Ecology Program series.

Magnetic tape copies of TWINSpan and DECORANA along with supporting documentation are available at cost from the Section of Ecology and Systematics, Cornell University, Ithaca, New York 14850.

CHAPTER III

RESULTS AND DISCUSSION

Bryophyte Species Richness

In total, 20 genera and 23 species of mosses and six genera and 11 species of hepatics were collected on yellow buckeye. These 34 species are listed in the Appendix (Table 7).

Ordination Results

The results of the application of DCA to the species-by-samples (quadrats) data matrices described in the Materials and Methods are presented according to aspect in two formats. The format for graphic presentation of the positions of species and samples is a two-axis ordination construction, and that of tabulated cover categories by species, in addition to the samples, is arranged in rank order by first-axis ordination scores. Level two classification groupings produced by TWINSpan are also included to integrate the two approaches, and will be discussed with the results of the classifications.

Categories of percent cover (i.e., cover classes) have been used rather than actual cover values to facilitate comparisons between the species. The categories of percent cover were taken from TWINSpan where they represent categories of abundance defined by pseudospecies cut levels. The reader is referred to

the documentation that accompanies TWINSpan for a detailed explanation of pseudospecies and pseudospecies cut levels. The categories of abundance used in TWINSpan (the default parameters) and adopted here, though skewed to the low side of the scale, were deemed appropriate in view of the low cover of many of the epiphytes.

Only the first ordination axis is considered ecologically meaningful (on all four aspects), representing a moisture gradient ranging from moist (the lower end of the transects) to mesic (the upper end of the transects) conditions. This interpretation was supported by the fact that the mean eigenvalue for the first axis (0.527) was 8.9 times larger than the second axis mean eigenvalue (0.059). According to Hill (1979a) "In general, axes for which the eigenvalue is much less than the top eigenvalue are unlikely to be of much significance." It should be noted that the environmental gradient represented by the first axis is really an environmental complex-gradient with moisture availability being the factor considered to have the greatest influence on bryophyte distribution.

Ordination of North Aspect Species and Samples

The north aspect species and samples arranged in rank order by their first-axis ordination scores are shown in Table 1. Ulot
crispa, Metzgeria crassipilis, Eurhynchium hians, and Thuidium
delicatulum exhibited low cover with Ulot and Metzgeria being re-
stricted to the upper end of the transects and Eurhynchium and
Thuidium being restricted to the lower end. Thamnobryum alleghaniense

Table 1. North aspect species and samples (quadrats) arranged in rank order by their first-axis ordination scores using DCA.^a

Species	Samples														
	1	2	4	5	3	6	8	7	9	1	1	1	1	1	
22 ULOT CRI	1	1	1	-	-	-	-	-	-	-	-	-	-	-	
8 FORS TRI	5	4	2	3	3	2	1	1	2	-	-	-	-	-	
15 NECK PEN	4	4	3	2	2	2	1	1	1	-	-	-	-	-	
16 PORE PLA	1	1	-	-	1	1	1	-	1	-	-	-	-	-	
34 METZ CRA	1	-	-	1	1	-	-	-	-	-	-	-	-	-	
9 FRUL BRI	2	2	1	1	1	-	1	-	1	-	-	-	-	-	
10 HAPL TRI	1	-	1	1	1	1	-	1	-	-	-	-	-	-	
21 HOMA SUB	2	2	2	3	2	2	3	2	1	-	1	-	-	-	
32 DICR VIR	1	1	1	1	1	-	2	1	-	-	-	-	-	-	
24 RADU COM	1	1	1	1	1	1	1	1	1	-	1	-	-	-	
37 RADU OBC	-	-	-	1	-	1	1	-	-	-	-	-	-	-	
17 SCHW FAB	1	1	1	2	1	1	2	2	1	-	1	-	-	-	
1 ANOM ATT	4	5	4	5	5	5	5	5	5	5	5	4	4	3	
20 RHOD ROS	-	-	-	-	-	-	1	-	1	1	-	-	-	-	
3 ANOM ROS	3	3	5	4	4	5	5	5	5	5	5	5	5	2	
27 COLO BID	-	1	1	-	1	-	-	-	-	-	1	1	-	-	
4 ANOM RUG	-	-	-	-	1	-	1	-	2	-	1	-	-	-	
13 METZ CON	-	-	-	-	-	1	1	-	1	-	1	1	-	-	
6 BRAC OXY	-	-	-	1	1	1	1	1	3	5	5	5	3	3	
23 EURH HIA	-	-	-	-	-	-	-	-	-	1	-	1	-	-	
25 THAM ALL	-	-	-	-	-	-	-	-	-	3	1	2	4	2	
18 THUI DEL	-	-	-	-	-	-	-	-	-	1	-	-	2	1	

^aNumbers preceding abbreviated species names are code numbers used in the ordination. Values in the body of the table represent categories of percent cover: 1, 0-1%; 2, 2-4%; 3, 5-9%; 4, 10-19%; 5, 20-100%. See text for an explanation of the use of categories of percent cover.

was also restricted to the lower end of the transects but was generally more abundant than either Eurhynchium or Thuidium.

Eurhynchium, Thamnobryum, and Thuidium were considered to be elements of other communities which had invaded the bases of the trunks. Cain and Sharp (1938) and Billings and Drew (1938) interpreted the Thuidium delicatulum and Brachythecium oxycladon unions, which occurred on roots near the soil on both Aesculus and Tilia, as not being strictly corticolous since their frequency of occurrence on bark substrates was dependent upon the accumulation of humus.

Forsstroemia trichomitria and Neckera pennata declined in abundance in a downwardly direction along the upper and middle regions of the transects. Brachythecium oxycladon showed a similar pattern of decline along the transects but in the opposite direction to that exhibited by Forsstroemia and Neckera (i.e., Brachythecium declined in an upwardly direction). Anomodon attenuatus and Anomodon rostratus were ubiquitous species typically displaying moderate to high cover throughout the length of the transects.

Billings and Drew (1938) observed that the Anomodon attenuatus union was the most characteristic and extensive of the bryophyte unions encountered on deciduous trees. This union was commonly found extending throughout the entire vertical range of the region mapped. All deciduous trees examined (including Aesculus), except Castanea, supported a well developed community of Anomodon attenuatus.

Porella platyphylloidea, Frullania brittoniae, Haplohymenium triste, Dicranum viride, Radula complanata, and Schwetschkeopsis fabronia occurred in low abundance in the upper and middle regions of the transects. Homalotheciella subcapillata was also present in the upper and middle regions occasionally attaining moderate cover. These seven species along with Forsstroemia and Neckera comprised a group of species which did not extend into the bottom four samples of the transects (note that sample 12 is placed out of numerical sequence on the first ordination axis). Furthermore, only Homalotheciella, Radula, and Schwetschkeopsis extended into sample 10. The absence of this group of species in samples 11-14 appears to be due to the dominance of Brachythecium and Thamnobryum, coupled with the high cover of Anomodon attenuatus and Anomodon rostratus, in this portion of the transects.

Anomodon rugelii and Metzgeria conjugata occurred sporadically in low cover in both the middle and lower regions of the transects. Cololejeunea biddlecomiae exhibited a similar pattern of distribution but was able to extend into the upper region of the transects. Radula obconica and Rhodobryum roseum were present primarily in the middle region of the transects in low cover.

The positions of the north aspect species on the first and second ordination axes are shown in Figure 3. Eigenvalues for the first and second axes on the north aspect are 0.384 and 0.040, respectively. Species restricted to the upper end of the transects (22 and 34) or with moderate to high cover in this region (8, 15,

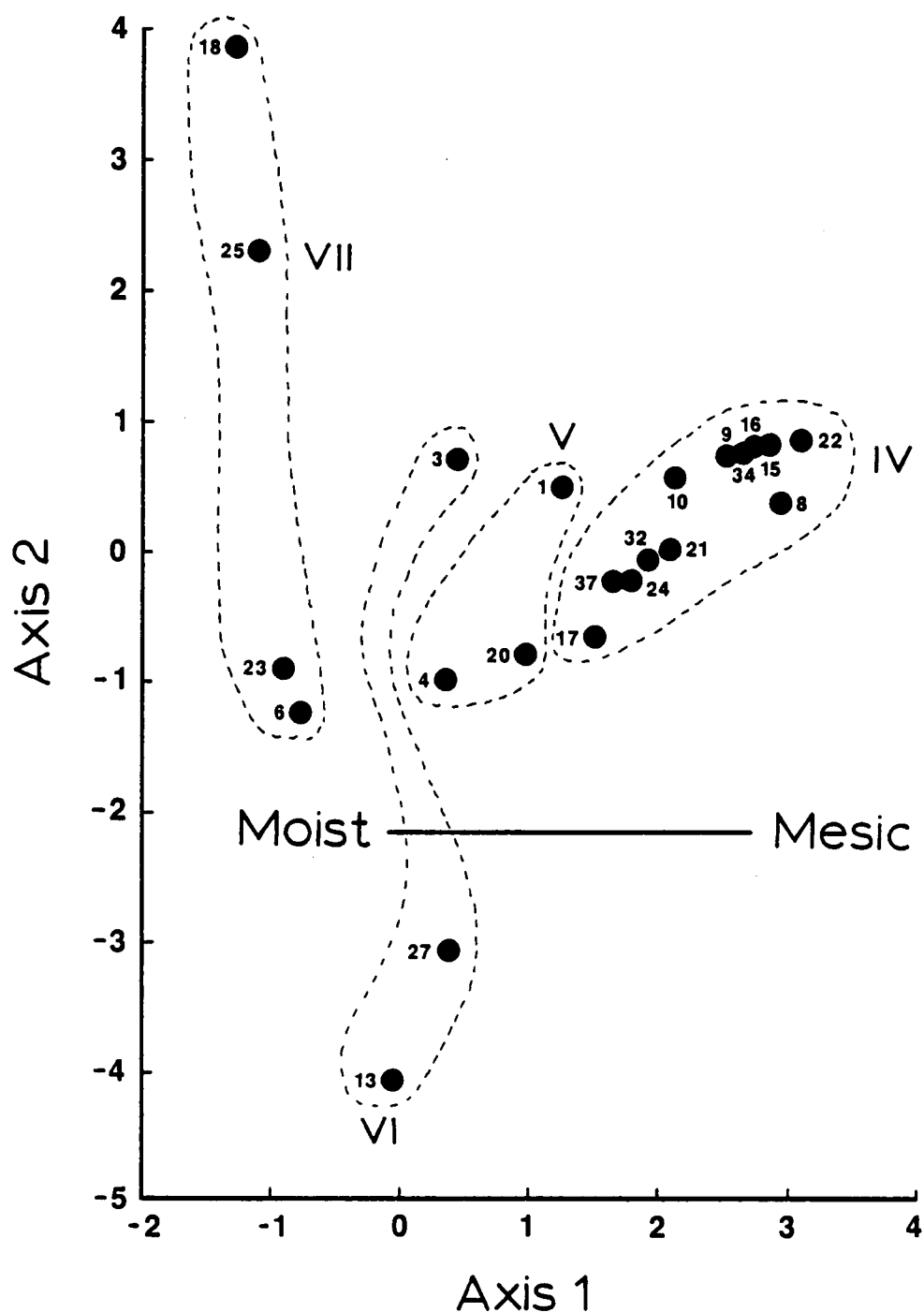


Figure 3. DCA ordination of north aspect species. Eigenvalues for the first and second axes are 0.384 and 0.040, respectively. Species names corresponding to the code numbers shown in this figure are given in Table 1. Level 2 classification groupings are indicated by Roman numerals. Axis scales are in units of average standard deviations of species turnover.

and 9) are clustered together at the mesic end of the first axis. Species occurring within the upper and middle regions of the transects, generally in low cover (10, 21, 32, 24, 37, and 17), occupy a position to the left of the preceding group of species on the first axis. Ubiquitous species 1 and 3 are located in the middle of the first axis as are species 4 and 20, the latter two species being restricted to the middle region of the transects. Species restricted to the lower end of the transects (23, 25, and 18) as well as species 6, which extended into the middle region of the transects but had moderate to high cover at the lower end, are clustered together at the moist end of the first axis.

The positions of north aspect samples on the first and second ordination axes are shown in Figure 4. Sample scores are the mean scores of the species that occur within them. DCA zeroes the sample scores so that the lowest sample score on each axis is zero. The positions of samples along the first axis generally reflect the sequence of quadrats along the transects (gradient) with quadrat one being at the mesic end of the transects and quadrat 14 at the moist end.

Ordination of East Aspect Species and Samples

The east aspect species and samples arranged in rank order by their first-axis ordination scores are shown in Table 2. Radula complanata and Haplohymenium triste occurred in low cover at the upper end of the transects. On the north aspect these species also

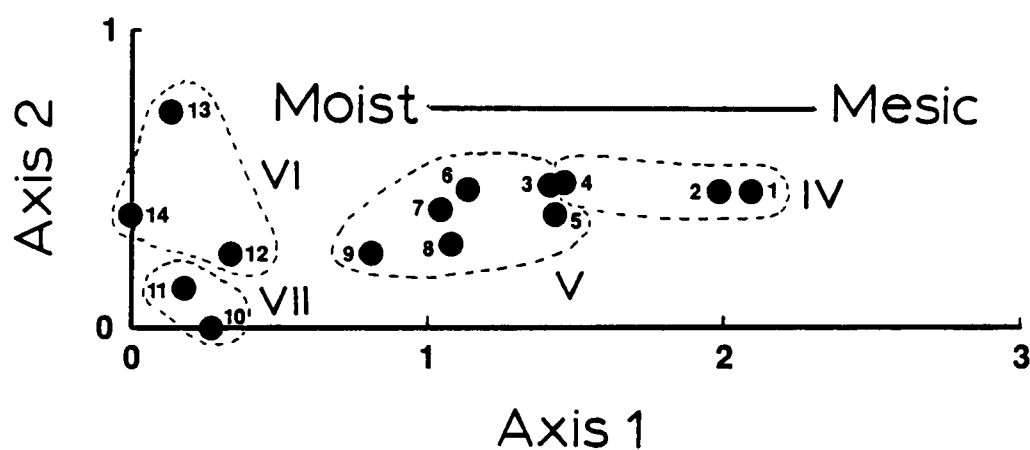


Figure 4. DCA ordination of north aspect samples. Eigenvalues for the first and second axes are 0.384 and 0.040, respectively. Level 2 classification groupings are indicated by Roman numerals. Axis scales are in units of average standard deviations of species turnover.

Table 2. East aspect species and samples (quadrats) arranged in order by their first-axis ordination scores using DCA.^a

Species	Samples												
	3	2	1	4	5	6	7	8	9	0	1	2	3
24 RADU COM	1	1	1	1	1	-	-	-	-	-	-	-	-
10 HAPL TRI	1	1	1	1	1	-	-	-	-	-	-	-	-
15 NECK PEN	3	1	3	2	3	1	1	-	-	-	-	-	-
16 PORE PLA	2	1	1	2	1	1	1	1	-	-	-	-	-
27 COLO BID	1	-	-	1	-	-	1	1	-	-	-	-	-
9 FRUL BRI	2	2	2	3	3	1	1	1	-	-	-	-	-
8 FORS TRI	3	4	4	3	4	3	3	2	1	-	-	-	-
21 HOMA SUB	3	2	2	3	1	2	1	2	2	-	-	-	-
2 ANOM MIN	-	1	1	-	1	2	1	-	-	-	-	-	-
33 LEJE ULI	-	-	-	1	1	1	1	-	-	-	-	-	-
17 SCHW FAB	1	1	-	1	2	2	3	4	2	1	-	-	-
1 ANOM ATT	3	3	4	4	5	5	5	5	5	5	4	4	-
4 ANOM RUG	1	-	-	1	-	-	-	1	1	1	1	-	-
3 ANOM ROS	2	2	2	2	3	2	3	4	4	5	5	2	-
6 BRAC OXY	-	-	-	-	-	1	1	1	2	2	2	-	-
13 METZ CON	1	-	-	-	-	-	-	-	1	1	1	-	-
7 FISS CRI	-	-	-	-	-	-	-	-	-	-	1	1	-
25 THAM ALL	-	-	-	-	-	-	-	-	1	3	5	5	4

^aNumbers preceding abbreviated species names are code numbers used in the ordination. Values in the body of the table represent categories of percent cover: 1, 0-1%; 2, 2-4%; 3, 5-9%; 4, 10-19%; 5, 20-100%.

occurred with low cover but extended well into the middle region of the transects. Neckera pennata exhibited low to moderate cover throughout the upper and middle regions of the transects while Forsstroemia trichomitria occupied the same regions but was more abundant. Neither species exhibited the marked decline in cover beginning at the top of the transects that was evident on the north aspect.

Porella platyphylloidea and Homalotheciella subcapillata were present in the upper and middle regions of the transects in low and low to moderate cover, respectively. The distribution of these two species was similar on both the north and east aspects.

Cololejeunea biddlecomiae occurred sporadically in low cover throughout the upper and middle regions of the transects just as it did on the north aspect. The regions of the transects occupied by Frullania brittoniae and Schwetschkeopsis fabronia were similar on the north and east aspects but both species were more abundant on the east aspect. Anomodon minor and Lejeunea ulicina were present in low cover primarily in the middle portion of the transects. Neither species was present on the north aspect.

Anomodon attenuatus and Anomodon rostratus were ubiquitous species but were less abundant on the east aspect as compared to the north, particularly at the upper end of the transects. The cover of A. rostratus was also considerably less than that of A. attenuatus on the east aspect. Anomodon rugelii was present in low cover primarily at the lower end of the transects although it did occur sporadically higher up the transects.

The range and abundance of Brachythecium oxycladon was considerably reduced on the east aspect as compared to the north. This appears to be due to replacement and increase in cover of Thamnobryum alleghaniense on the east aspect. The vertical range of Thamnobryum on both the north and east aspects was similar but cover values were considerably higher on the latter. Fissidens cristatus and Metzgeria conjugata were present in low cover at the lower end of the transects (except for the occurrence of Metzgeria in sample 3), the former invading the tree bases from adjacent patches of humus.

The positions of the east aspect species on the first and second ordination axes are shown in Figure 5. Eigenvalues for the first and second axes are 0.525 and 0.062, respectively. Species restricted to the lower end of the transects (7 and 25) are located at the mesic end of the first axis. Species occurring primarily at the lower end of the transects (13, 6, 3, and 4), but which were able to extend into the middle region, are clustered together slightly to the left of the preceding group on the first axis. Species 3 is located a considerable distance to the right of species 1 (both were ubiquitous species) which occurs near the middle of the first axis. This is a reflection of species 3 being considerably more abundant at the lower end of the transects than in the middle and upper regions. Species occurring within the upper and middle regions of the transects (17, 33, 2, 21, 8, 9, 27, 16, 15, 10, and 24) form a fairly well defined group located at the mesic end of the first axis.

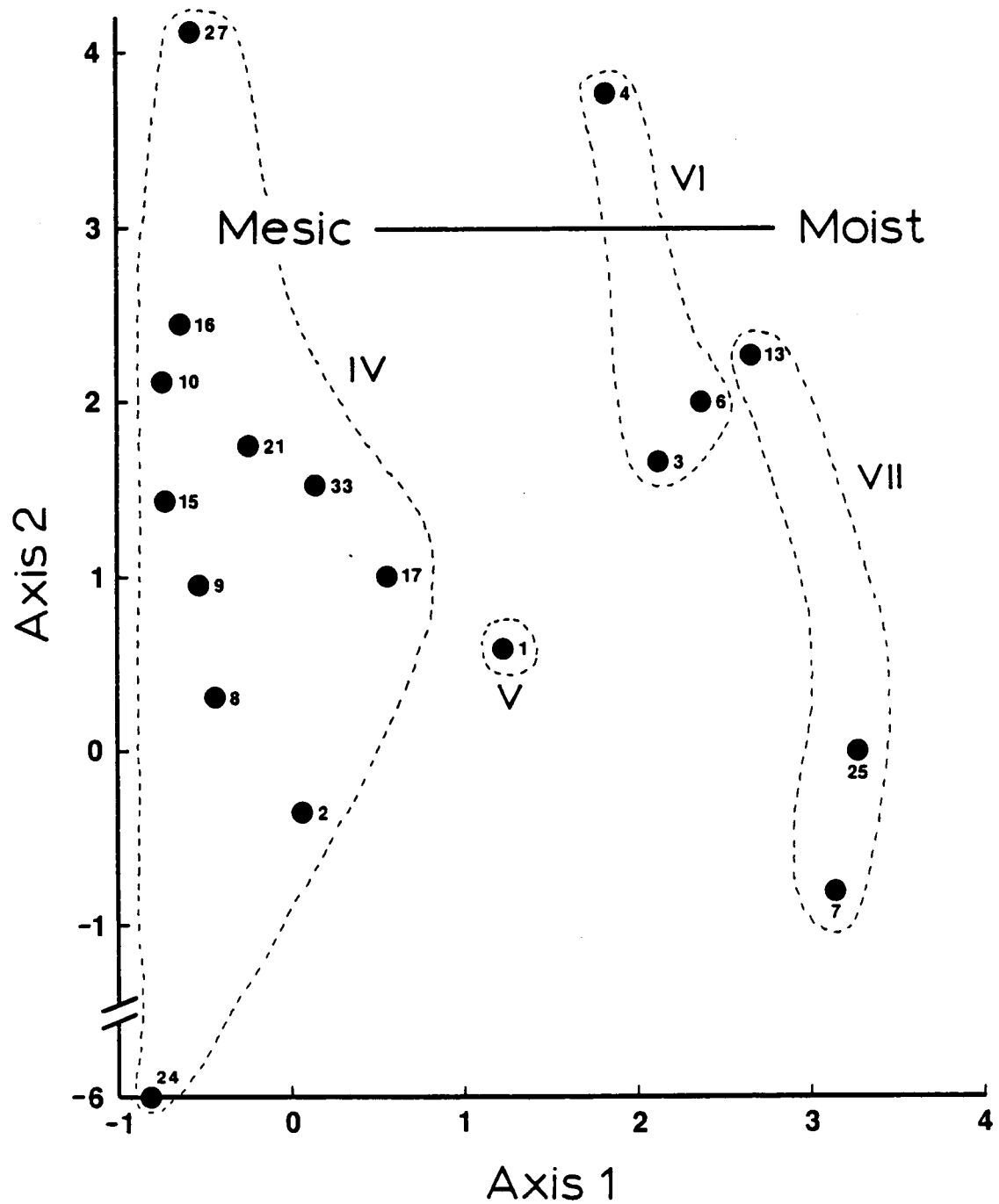


Figure 5. DCA ordination of east aspect species. Eigenvalues for the first and second axes are 0.525 and 0.062, respectively. Species names corresponding to the code numbers shown in this figure are given in Table 2. Level 2 classification groupings are indicated by Roman numerals. Axis scales are in units of average standard deviations of species turnover.

The positions of the east aspect samples on the first and second ordination axes are shown in Figure 6. The sequence of samples on the first ordination axis is identical to the sequence of the quadrats along the transects except for the 180° inversion of samples 1, 2, and 3 by the ordination.

Ordination of West Aspect Species and Samples

The west aspect species and samples arranged in rank order by their first-axis ordination scores are shown in Table 3. Frullania eboracensis occurred in low cover and was restricted to the upper end of the transects. Anomodon minor, Neckera pennata, and Forsstroemia trichomitria were present in moderate cover at the upper end of the transects but declined in cover throughout the middle region of the transects. A similar pattern of distribution was observed for Neckera and Forsstroemia on the north aspect. Anomodon minor was not present on the north aspect.

Dicranum viride and Leucodon julaceus occurred sporadically, in low cover, in the upper and middle regions of the transects. Haplohymenium triste, Frullania brittoniae, and Porella platyphylloidea occurred in low cover throughout the upper and middle regions of the transects. The distribution of these three species on the west aspect was very similar to that observed on the north aspect.

Radula complanata was present in low cover in the upper and middle regions of the transects. Cololejeunea biddlecomiae occurred sporadically, in low cover, in the middle region of the transects.

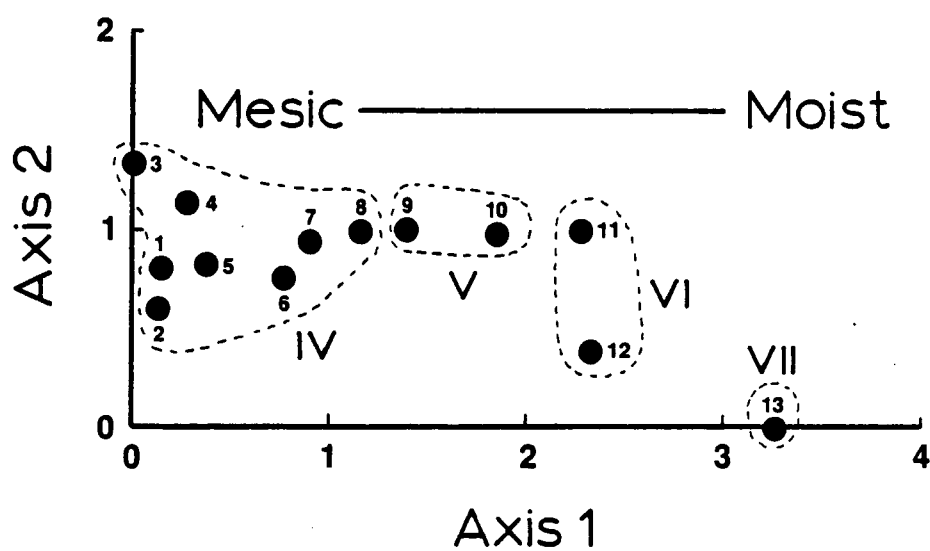


Figure 6. DCA ordination of east aspect samples. Eigenvalues for the first and second axes are 0.525 and 0.062, respectively. Level 2 classification groupings are indicated by Roman numerals. Axis scales are in units of average standard deviations of species turnover.

Table 3. West aspect species and samples (quadrats) arranged in rank order by their first-axis ordination scores using DCA.^a

Species	Samples												
	3	2	1	4	5	6	7	8	9	1	1	1	1
29 FRUL EBO	1	1	1	-	-	-	-	-	-	-	-	-	-
2 ANOM MIN	4	3	3	2	1	-	1	-	1	-	-	-	-
24 RADU COM	1	-	-	1	1	1	-	-	-	-	-	-	-
32 DICR VIR	-	1	1	-	-	1	-	-	-	-	-	-	-
15 NECK PEN	3	2	1	1	2	1	1	-	-	-	-	-	-
12 LEUC JUL	-	1	-	1	1	-	-	-	1	-	-	-	-
8 FORS TRI	3	4	4	4	3	3	2	1	1	-	-	-	-
10 HAPL TRI	1	1	1	2	1	1	-	-	1	-	-	-	-
(FRUL BRI	1	1	2	1	1	1	-	-	1	-	-	-	-
16 PORE PLA	1	1	1	1	1	1	1	1	1	-	-	-	-
21 HOMA SUB	2	2	1	2	2	2	2	2	1	-	1	1	1
27 COLO BID	-	-	-	1	-	-	1	-	-	-	-	-	-
1 ANOM ATT	4	5	5	5	5	5	5	5	5	5	4	4	4
17 SCHW FAB	1	-	1	1	2	2	2	3	2	-	-	-	-
3 ANOM ROS	1	-	2	2	3	4	4	5	5	5	5	5	5
7 FISS CRI	-	-	-	-	-	-	-	1	1	-	1	-	-
4 ANOM RUG	-	-	-	-	-	-	-	1	3	-	2	-	-
6 BRAC OXY	-	-	-	-	1	1	2	3	4	3	4	4	4
13 METZ CON	-	1	-	-	-	-	1	-	1	-	1	1	1
25 THAM ALL	-	-	-	-	-	-	-	-	1	-	2	3	3

^aNumbers preceding abbreviated species names are code numbers used in the ordination. Values in the body of the table represent categories of percent cover: 1, 0-1%; 2, 2-4%; 3, 5-9%; 4, 10-19%; 5, 20-100%.

Homalotheciella subcapillata was a ubiquitous species of low to moderate cover which had a greater range on the west aspect than on any of the other three aspects. Anomodon attenuatus and Anomodon rostratus were also ubiquitous species but were much more abundant than Homalotheciella. A. attenuatus was present in high cover throughout the transects. This pattern was similar to that observed for A. attenuatus on the north aspect. A. rostratus was present in high cover along the lower and middle regions of the transects but declined considerably in cover in the upper region of the transects.

Schwetschkeopsis fabronia occurred in the upper and middle regions of the transects but was most abundant in the latter. Fissidens cristatus, Anomodon rugelii, and Thamnobryum alleghaniense occurred in low to moderate cover in the lower region of the transects. The distribution pattern of Thamnobryum on the west aspect was intermediate between that observed on the south aspect and the north and east aspects.

Brachythecium oxycladon occurred in moderate to high cover at the lower end of the transects and gradually declined in cover into the middle region of the transects. This pattern was similar to that observed for Brachythecium on the north aspect. Metzgeria conjugata was sporadically distributed but occurred primarily in the lower region of the transects.

The positions of the west aspect species on the first and second ordination axes are shown in Figure 7. Eigenvalues for the

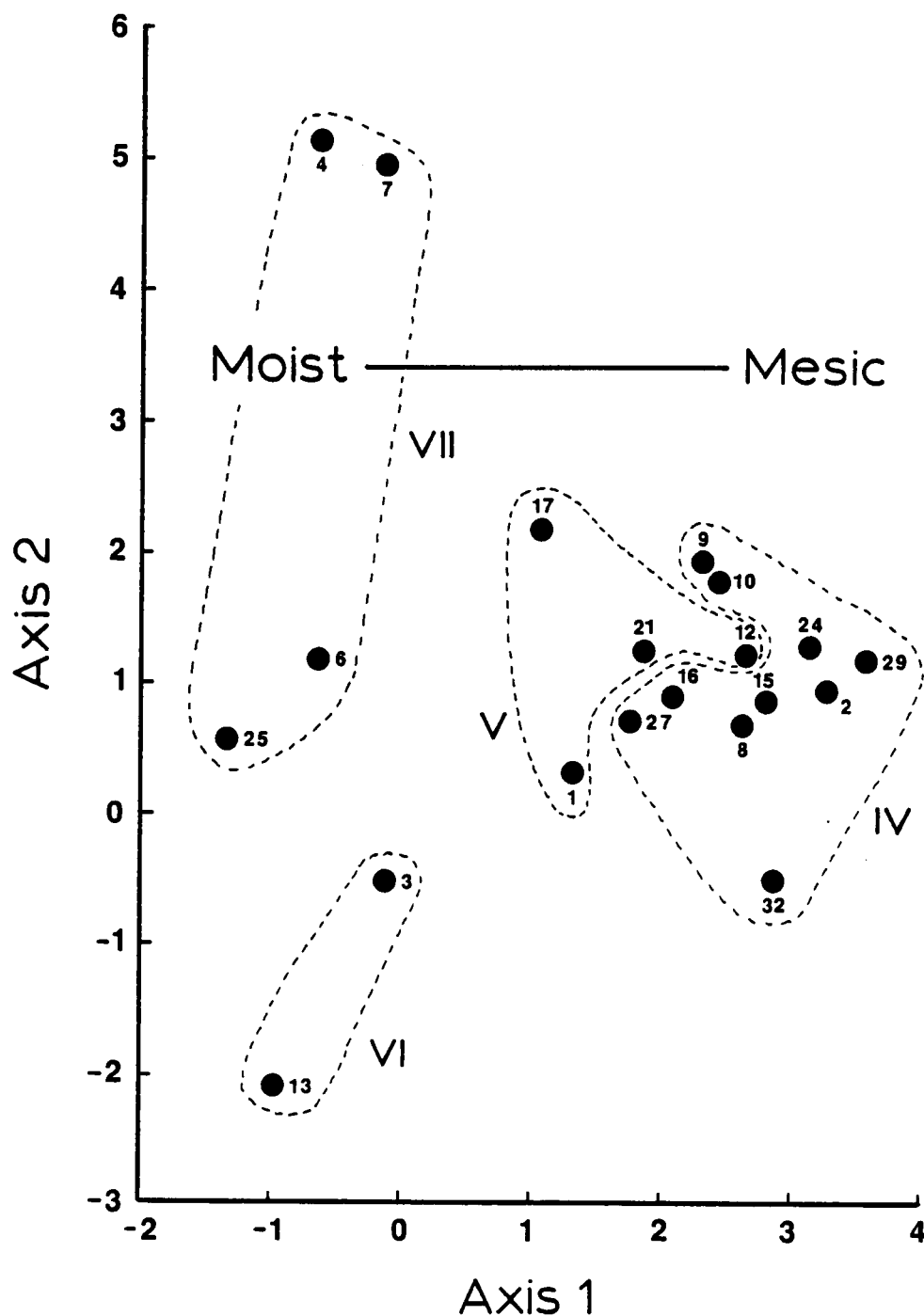


Figure 7. DCA ordination of west aspect species. Eigenvalues for the first and second axes are 0.472 and 0.041, respectively. Species names corresponding to the code numbers shown in this figure are given in Table 3. Level 2 classification groupings are indicated by Roman numerals. Axis scales are in units of average standard deviations of species turnover.

first and second axes are 0.472 and 0.041, respectively. Species occurring in the lower region of the transects (25, 13, 6, 4, 7, and 3) are clustered at the moist end of the first axis. Although species 3 was a ubiquitous species it is included in this group due to its dominance at the lower end of the transects. Species 1 and 17 are located in the middle of the first axis, the former being a ubiquitous species of high cover and the latter showing maximum abundance in the middle region of the transects. The remaining species (27, 21, 16, 9, 10, 8, 12, 15, 32, 24, 2, and 29), which did not occur at the lower end of the transects (except for species 21), are clustered together at the mesic end of the first axis.

The positions of the west aspect samples on the first and second ordination axes are shown in Figure 8. The sequence of samples on the first axis is very similar to the sequence of quadrats along the transects. The order of the first three samples was inverted by the ordination just as it was on the east aspect. Sample 12 was also placed out of numerical sequence by the ordination.

Ordination of South Aspect Species and Samples

The south aspect species and samples arranged in rank order by their first-axis ordination scores are shown in Table 4. The species distribution patterns on the north, east, and west aspects differ considerably from those of many of the same species on the south aspect. The most striking difference between the four aspects is the overall decline in species cover on the south aspect.

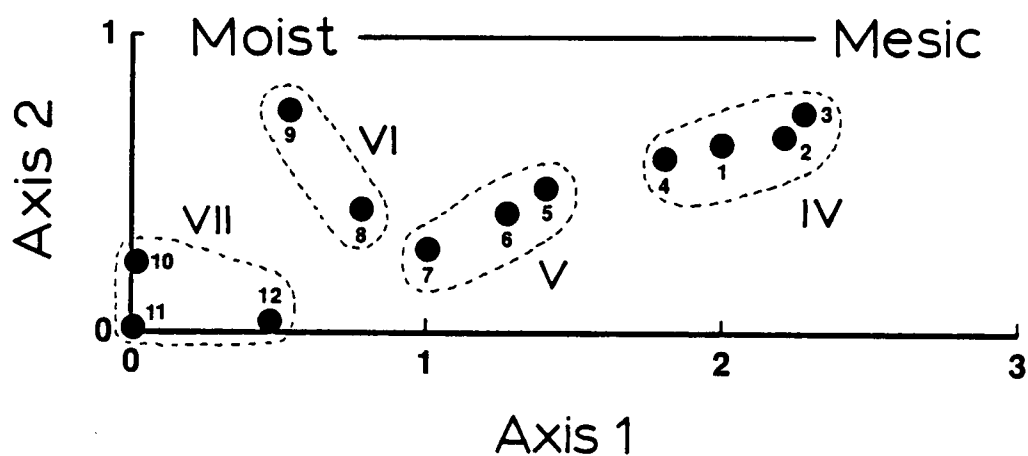


Figure 8. DCA ordination of west aspect samples. Eigenvalues for the first and second axes are 0.472 and 0.041, respectively. Level 2 classification groupings are indicated by Roman numerals. Axis scales are in units of average standard deviations of species turnover.

Table 4. South aspect species and samples (quadrats) arranged in rank order by their first-axis ordination scores using DCA.^a

Species	Samples											
	3	2	1	4	5	6	7	8	9	0	1	1
12 LEUC JUL	1	1	-	1	-	-	-	-	-	-	-	-
31 AMBL VAR	-	1	1	-	-	-	-	-	-	-	-	-
24 RADU COM	1	1	1	1	1	1	-	-	-	-	-	-
15 NECK PEN	-	1	2	1	1	-	1	-	-	-	-	-
9 FRUL BRI	2	3	2	2	1	1	1	1	-	-	-	-
21 HOMA SUB	2	1	1	1	1	1	1	1	1	-	-	-
8 FORS TRI	2	2	3	3	3	2	2	1	1	-	-	-
16 PORE PLA	2	1	1	1	1	1	1	1	1	1	-	-
10 HAPL TRI	1	1	1	1	-	1	1	1	1	-	-	-
26 METZ FUR	-	1	-	-	-	1	-	-	-	-	-	-
27 COLO BID	1	-	-	-	-	1	1	1	-	-	-	-
1 ANOM ATT	1	2	1	1	2	4	4	4	3	3	-	-
17 SCHW FAB	-	-	-	-	1	1	2	3	2	-	-	-
13 METZ CON	-	-	-	-	-	-	1	1	-	1	-	-
6 BRAC OXY	-	-	-	-	-	1	2	2	2	3	-	-
4 ANOM RUG	-	-	-	-	-	-	-	2	2	2	-	-
3 ANOM ROS	-	1	-	1	1	1	3	5	5	5	5	-
25 THAM ALL	-	-	-	-	-	-	-	-	1	1	-	-

^aNumbers preceding abbreviated species names are code numbers used in the ordination. Values in the body of the table represent categories of percent cover: 1, 0-1%; 2, 2-4%; 3, 5-9%; 4, 10-19%; 5, 20-100%.

Leucodon julaceus and Amblystegium varium were restricted to the upper end of the transects where they were present in low cover. Radula complanata and Neckera pennata occurred in low cover in the upper and middle regions of the transects. Homalotheciella subcapillata, Haplohymenium triste, and Porella platyphylloidea were wide ranging nearly ubiquitous species, especially in the case of Porella, which were present in low cover. Frullania brittoniae and Forsstroemia trichomitria were also wide ranging species but exhibited moderate cover in the upper region of the transects.

Homalotheciella subcapillata, Haplohymenium triste, Porella platyphylloidea, Frullania brittoniae, and Forsstroemia trichomitria occurred over a wider range of samples (i.e., they occurred further down the transects) on the south aspect than on the other three aspects (except for Homalotheciella which had its greatest range on the west aspect). This appears to have resulted from a reduction in competition with other species, primarily the ubiquitous Anomodon attenuatus and A. rostratus, which declined in cover along the upper and middle portions of the transects due to the existence of drier conditions (as compared to the other three aspects) in these regions. Forsstroemia trichomitria and Homalotheciella subcapillata showed an overall decline in cover while Porella platyphylloidea, and Haplohymenium triste showed no appreciable change in cover when compared to the north, east, and west aspects. Frullania brittoniae was slightly less abundant on the north and west aspects as compared to the east and south aspects.

Differences in moisture availability between the four aspects did not seem to be as great at the lower end of the transects as they were in the upper and middle regions. The following factors appear to be responsible for reducing aspectual differences, in terms of moisture availability, at the bases of the trees: (1) the accumulation of moisture holding humus, (2) the ability of bryophytes in contact with humus and/or soil to draw moisture from these sources--the "wicking effect," and (3) the presence of a phanerogamic ground cover during most of the year which tends to retard evaporation.

On the north, east, and west aspects Anomodon attenuatus and Anomodon rostratus exhibited the widest range and highest overall cover of any of the species present. On the south aspect A. attenuatus was still a ubiquitous species, occurring in all but one of the samples, but was considerably reduced in abundance particularly in the upper region of the transects. A. rostratus was also wide ranging on the south aspect, occurring in all but two samples, but declined precipitously above sample 8 to less than 1% cover in six of the remaining seven samples. A downward shift in the cover of A. attenuatus and A. rostratus to the lower region of the transects, where environmental conditions are more favorable (i.e., moisture is more abundant), is evidenced on the south aspect.

Stringer and Stringer (1974) found that epiphyte species showed a distinct difference in mean vertical range on different aspects of the trees. In general, the mean vertical ranges of the

14 commonest species were highest on the north aspect followed by the east, west, and south aspects. Although no quantitative data were obtained, the aspectual differences in the mean vertical ranges were thought to be the result of differences in moisture availability.

Billings and Drew (1938) showed that corticolous bryophyte unions occupy distinct vertical zones on the butts of mature trees. Furthermore, their data indicated that vertical distribution patterns were to a certain extent aspect dependent. As an example, consider the west face of the trunks which was found to be the driest face. The west face of the trunks supported a bryophyte mat made up of fewer zones than those which occurred on any of the other faces. The relatively few zones which did occur on the west face were present at lower heights than on the other faces of the trunks. The opposite situation occurred on the moist east face of the trunks. The east face supported a greater number of more mesophytic communities (unions) which were able to extend much higher up the trunks due to the greater abundance of moisture on this face.

Metzgeria furcata and Cololejeunea biddlecomiae were sporadically occurring species of low cover with the latter species confined primarily to the middle region of the transects. Schwetschkeopsis fabronia occurred in low to moderate cover in the middle and lower regions of the transects. On the north, east, and west aspects Schwetschkeopsis occurred in the upper and middle regions of the transects with approximately the same cover. The upper region of the transects on the south aspect appears to be too xeric for

Schwetschkeopsis, hence its downward displacement to the more mesic middle and lower regions.

Metzgeria conjugata was present in low cover in the lower region of the transects. The range and abundance of Brachythecium oxycladon was similar to that on the east aspect. Anomodon rugelii was restricted to the lower region of the transects on this aspect whereas on the north and east aspects it was more widely distributed. The most obvious difference with respect to Thamnobryum alleghaniense between the north, east, and west aspects and the south aspect was its considerable reduction in cover on the latter.

Numerous differences in species distributions between the north, east, and west aspects and the south aspect have been presented in the preceding paragraphs. These differences have been ascribed to differences in available moisture between the four aspects primarily in the upper and middle regions of the transects. The strong influence of available moisture on epiphyte distribution on the south aspect can also be seen by examining the eigenvalues for the first ordination axis on the four aspects. The eigenvalues for the first ordination axis on the north, east, west, and south aspects were 0.384, 0.525, 0.472, and 0.727, respectively. The possession of the highest first axis eigenvalue by the south aspect reflects the fact that this axis, which represents a moisture gradient, accounts for a greater portion of the variance in the data on the south aspect than on the other three aspects.

The positions of the south aspect species on the first and second ordination axes are shown in Figure 9. Eigenvalues for the first and second axes are 0.727 and 0.094, respectively. Species occurring primarily at the lower end of the transects (25, 3, 4, 6, and 13) are clustered together at the moist end of the first axis. Species occurring predominantly in the middle and lower regions of the transects (17, 1, and 27) are located slightly to the right of the preceding group. Wide ranging species of low to moderate cover (26, 10, 16, and 8) occur near the center of the first axis. Species occurring in the upper and middle regions of the transects (21, 9, 24, and 15) are grouped together toward the mesic end of the first axis. Species restricted to the upper end of the transects (31 and 12) are located at the extreme mesic end of the first axis.

The positions of the south aspect samples on the first and second ordination axes are shown in Figure 10. As was the case with the east and west aspects, the sequence of samples on the first axis is identical to the sequence of quadrats along the transects except for the 180° inversion of samples 1, 2, and 3 by the ordination.

The high correspondence between the sequence of quadrats along the transects and the sequence of samples (quadrats) in the ordination, on all four aspects, indicates that the bryophytes are very sensitive to presumably small changes (since sampling occurred over only 1.5 m) in available moisture. This is further supported by the fact that the least correspondence between the sequence of quadrats on the trees and the sequence of samples in the ordinations

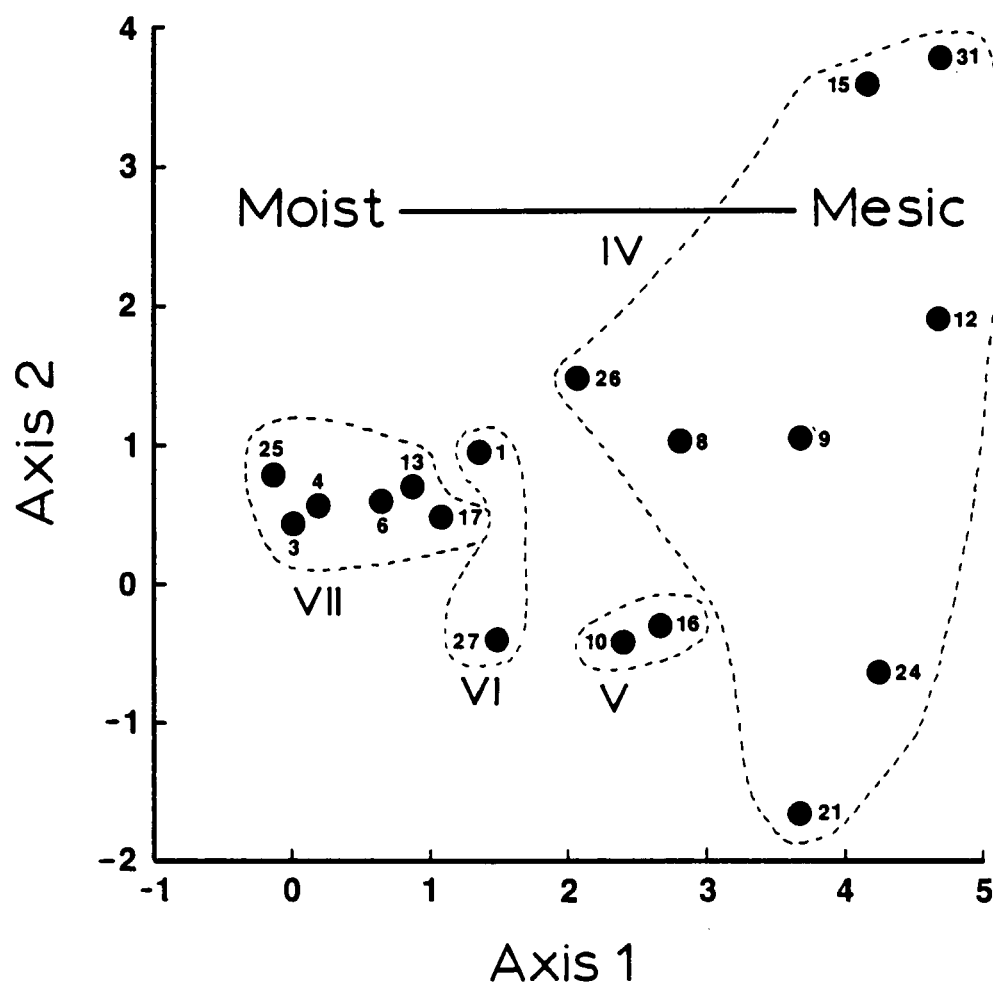


Figure 9. DCA ordination of south aspect species. Eigenvalues for the first and second axes are 0.727 and 0.094, respectively. Species names corresponding to the code numbers shown in this figure are given in Table 4. Level 2 classification groupings are indicated by Roman numerals. Axis scales are in units of average standard deviations of species turnover.

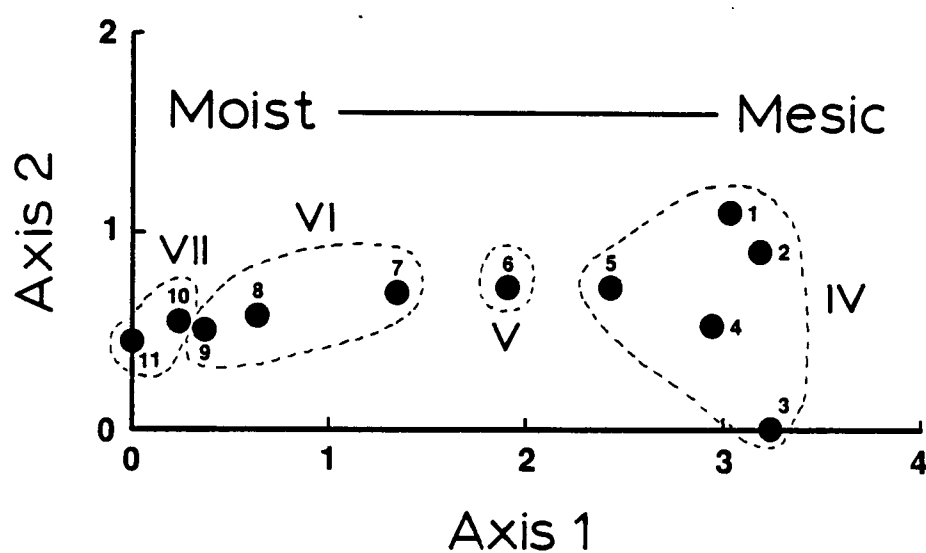


Figure 10. DCA ordination of south aspect samples. Eigenvalues for the first and second axes are 0.727 and 0.094, respectively. Level 2 classification groupings are indicated by Roman numerals. Axis scales are in units of average standard deviations of species turnover.

occurs on the north aspect where moisture is most abundant (i.e., the moisture gradient is less steep on the north aspect than on any of the other three aspects). It appears that moisture is not a limiting factor for many (most?) of the species on the north aspect and that other factors (e.g., competition) are equally or more important in determining species distributions. This is also reflected in the fact that the north aspect has the lowest first axis eigenvalue.

Classification Results

The results of the application of TWINSpan to the species-by-samples (quadrats) data matrices described in the Materials and Methods are presented according to aspect in the form of dendrograms. The dendrograms graphically display the groupings of the species and samples produced by TWINSpan after six levels of division. Level two was chosen as the level at which the groupings produced by TWINSpan (four groups/aspect for both species and samples) were most amenable to environmental interpretation. Level two classification groupings are indicated by IV, V, VI, and VII on the ordination graphs (Figure 3, page 40; Figure 4, page 42; Figure 5, page 38; Figure 6, page 47; Figure 7, page 50; Figure 8, page 52; Figure 9, page 59; Figure 10, page 60) and in the classification dendrograms.

Classification of North Aspect Species and Samples

The groupings of the north aspect species through six levels of division are shown in Figure 11. Group IV consists of those

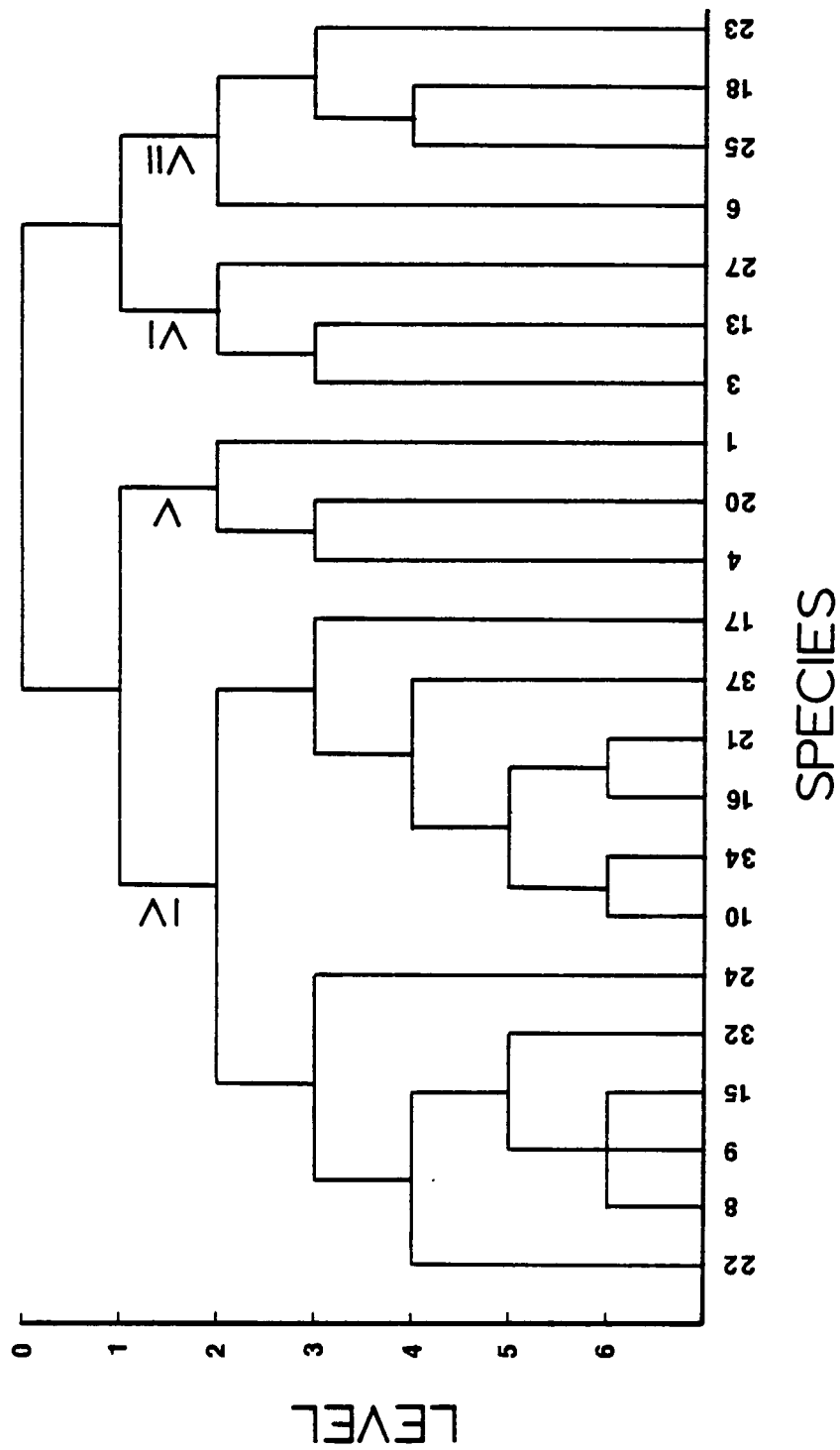


Figure 11. Dendrogram resulting from TWINSpan classification of north aspect species. Vertical scale represents levels of division. Roman numerals indicate level 2 groupings and correspond to those used in Figure 3. Species names corresponding to the code numbers used in this figure are given in Table 1.

species which occurred in the upper and middle regions of the transects in widely varying degrees of cover. Group V consists of species 4 and 20, which occurred primarily in the middle region of the transects, as well as the ubiquitous species 1. Species 3, the other ubiquitous species, was placed in Group VI along with species 13 and 27 which occurred in low cover primarily in the middle and lower regions of the transects. It is difficult to understand why species 1 and 3 with identical ranges and nearly identical cover patterns were placed in different groups by the classification. Group VII consists of those species restricted to (species 25, 18, and 23) or dominant in (species 6) the lower region of the transects. Group VII is a very distinctive group consisting mainly of species which have invaded the bases of the trunks from other habitats.

The groupings of north aspect samples through six levels of division are shown in Figure 12. Group IV consists of those samples located in the upper region of the transects. Group V is comprised of samples located in the middle region of the transects. Group VI consists of only two samples (10 and 11) but is an interesting group because it represents a transition zone between species occurring in Groups IV and V, or Group V only, and those in Group VII. Species 24, 21, 17, and 27 occur in Groups IV, V, and VI reaching their lowest positions on the transects in Group VI. Species 4 and 13 occur in Groups V and VI and also reach their lowest positions on the transects in Group VI. Conversely, species 23 and 25 occur in Groups VII and VI and reach their highest positions on the

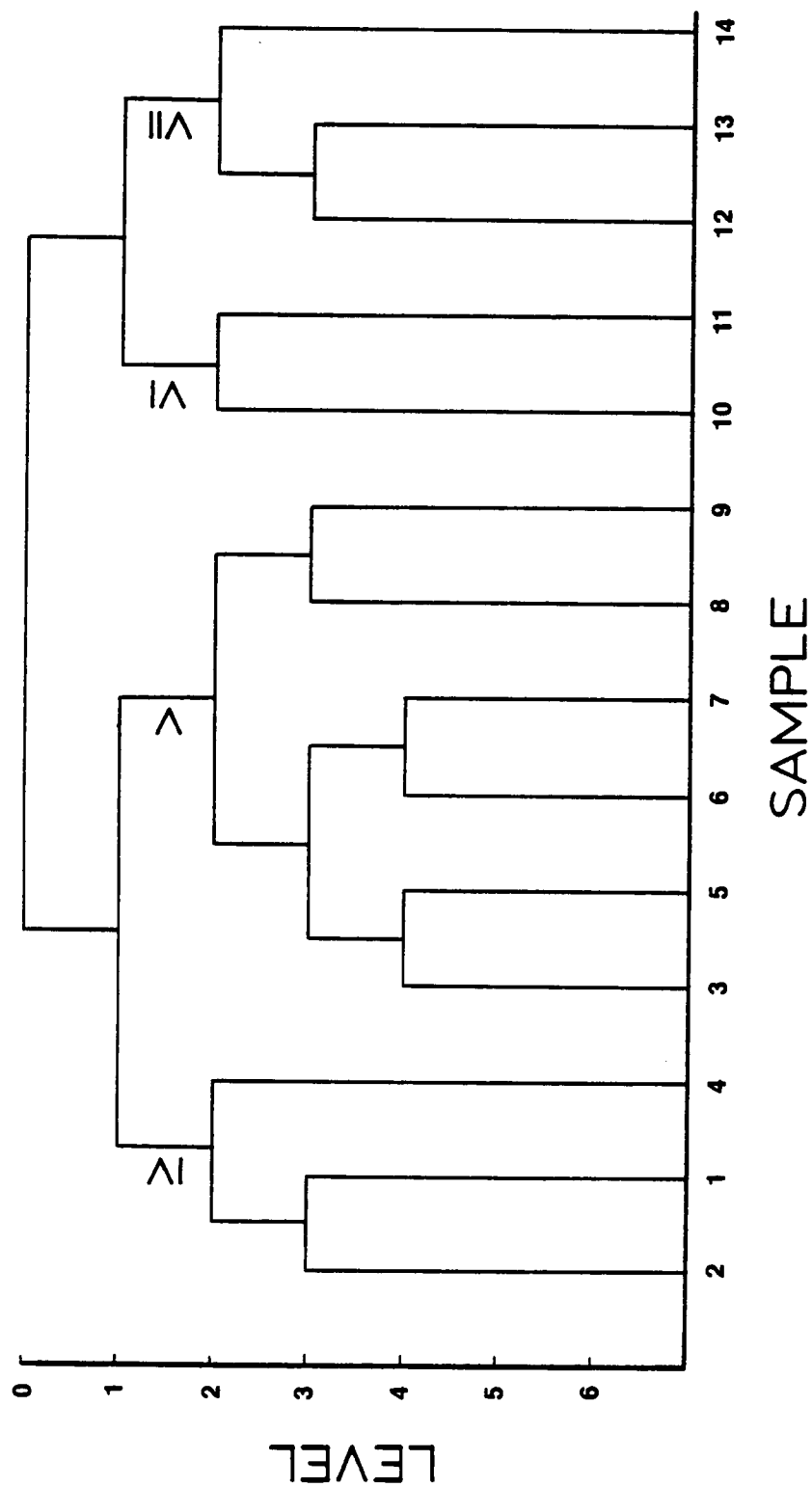


Figure 12. Dendrogram resulting from TWINSpan classification of north aspect samples. Vertical scale represents levels of division. Roman numerals indicate level 2 groupings and correspond to those used in Figure 4.

transects in Group VI. Group VII consists of samples located at the bottom of the transects.

Classification of East Aspect Species and Samples

The groupings of the east aspect species through six levels of division are shown in Figure 13. Group IV consists of those species occurring in the upper and middle regions of the transects. None of the 11 species in Group IV extended into samples 11, 12, and 13 and only one extended into sample 10. Group IV on this aspect was very similar to Group IV on the north aspect. Group V consists solely of the ubiquitous species 1. Group VI consists of species 4 and 6, which occurred primarily in the middle and lower regions of the transects, and the ubiquitous species 3. The two ubiquitous species (1 and 3) are again placed in two different groups as was the case on the north aspect. On the east aspect separation is perhaps based on differences in abundance between the two species particularly in the upper region of the transects. Group VII consists of those species restricted to or dominant in the lower region of the transects. Species 7 and 25 are considered invaders from other communities. Group VII on this aspect is very similar to Group VII on the north aspect.

The groupings of east aspect samples through six levels of division are shown in Figure 14. Group IV consists of samples occurring in the upper and middle regions of the transects. Group V is the transition zone between species occurring in Group IV and those

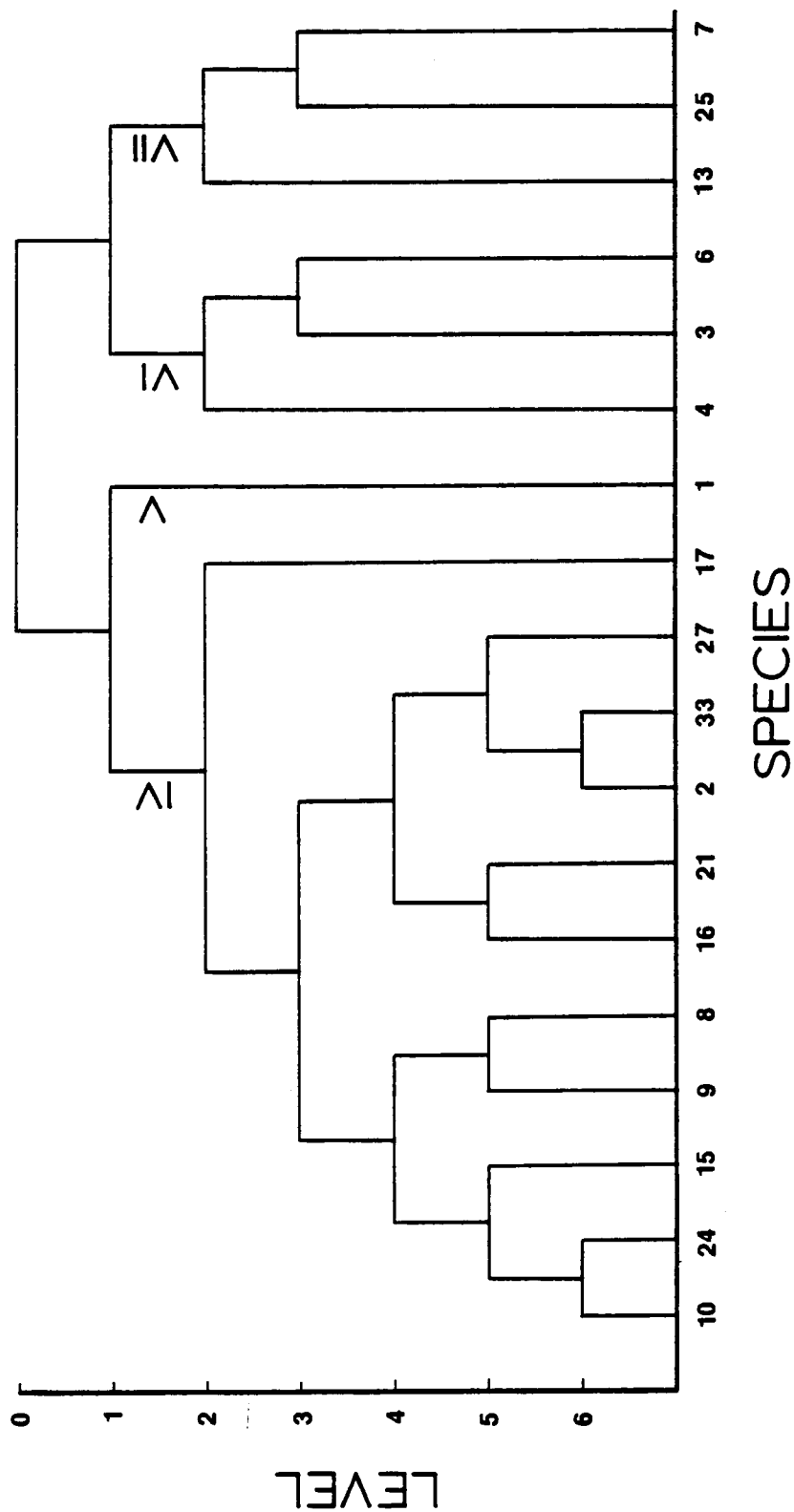


Figure 13. Dendrogram resulting from TWINSpan classification of east aspect species. Vertical scale represents levels of division. Roman numerals indicate level 2 groupings and correspond to those used in Figure 5. Species names corresponding to the code numbers used in this figure are given in Table 2.

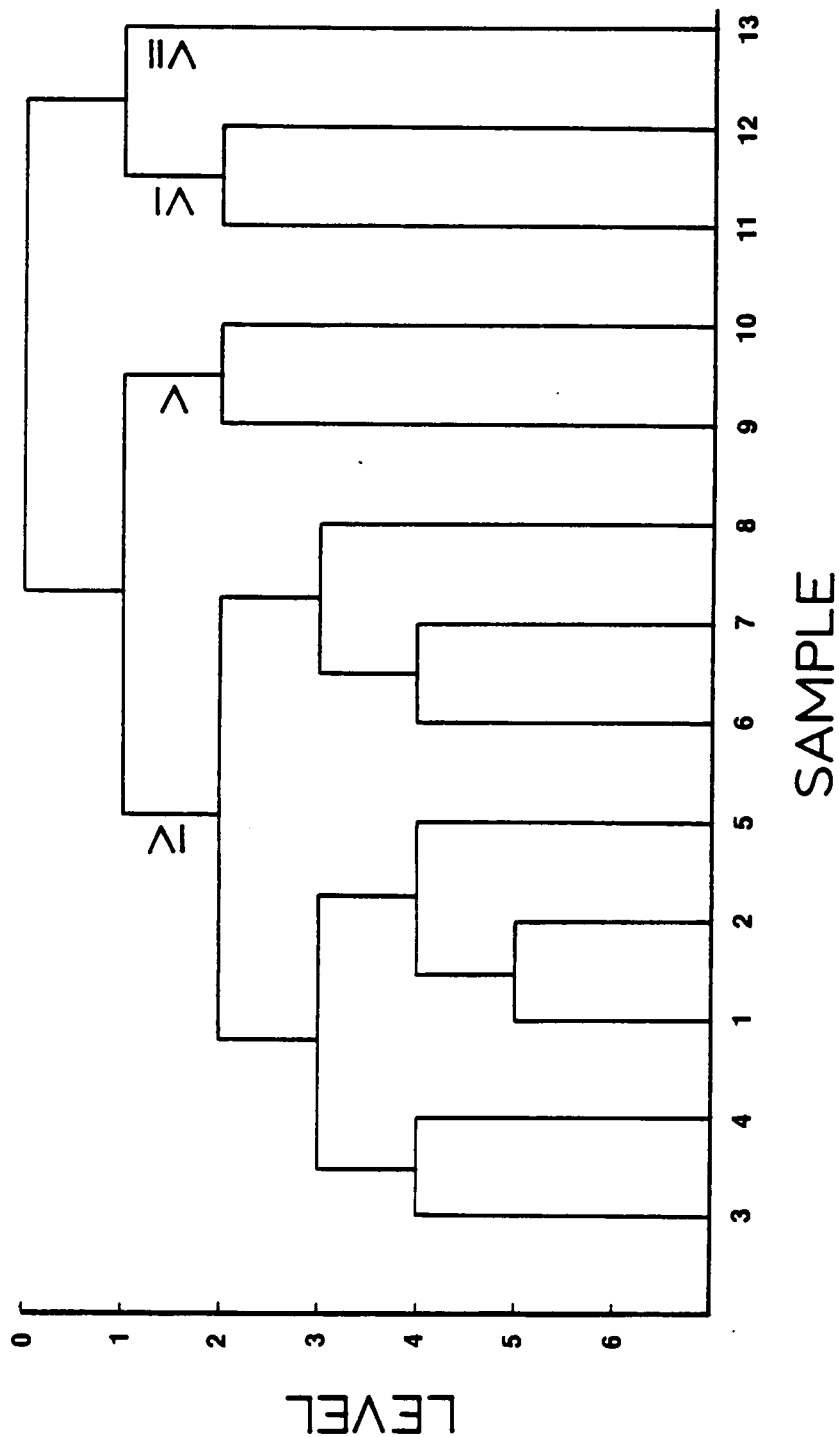


Figure 14. Dendrogram resulting from TWINSpan classification of east aspect samples. Vertical scale represents levels of division. Roman numerals indicate level 2 groupings and correspond to those used in Figure 6.

in Groups VI and VII or Group VI only. Species 8, 21, and 17 reached their lowest positions on the transects in Group V while species 25 reached its highest position in this group. Groups VI and VII consist of samples located at the bottom of the transects. Group VII consists of a single sample which in turn contains a single species. It is the presence of a single species in sample 13 which has resulted in this sample being segregated into its own group rather than being placed in the same group as samples 11 and 12. Note also the disjunct position of sample 13 in the east aspect sample ordination shown in Figure 6, page 47.

Classification of West Aspect Species and Samples

The groupings of west aspect species through six levels of division are shown in Figure 15. Group IV consists of species occurring in the upper and middle regions of the transects. Group V contains the two ubiquitous species 21 and 1, the former being present in low cover and the latter in high cover. Also present in Group IV is species 17, which was most abundant in the middle region of the transects, and the sporadically occurring species 12.

The placement of species 12 in Group V appears somewhat unusual in light of its position on the first ordination axis (see Figure 7, page 50). Species 12 seems to fit better in Group IV, based on its first axis position, than in Group V. A similar situation occurred with respect to species 13. Based on its first axis position species 13 would seem to fit better in Group VII than in Group VI.

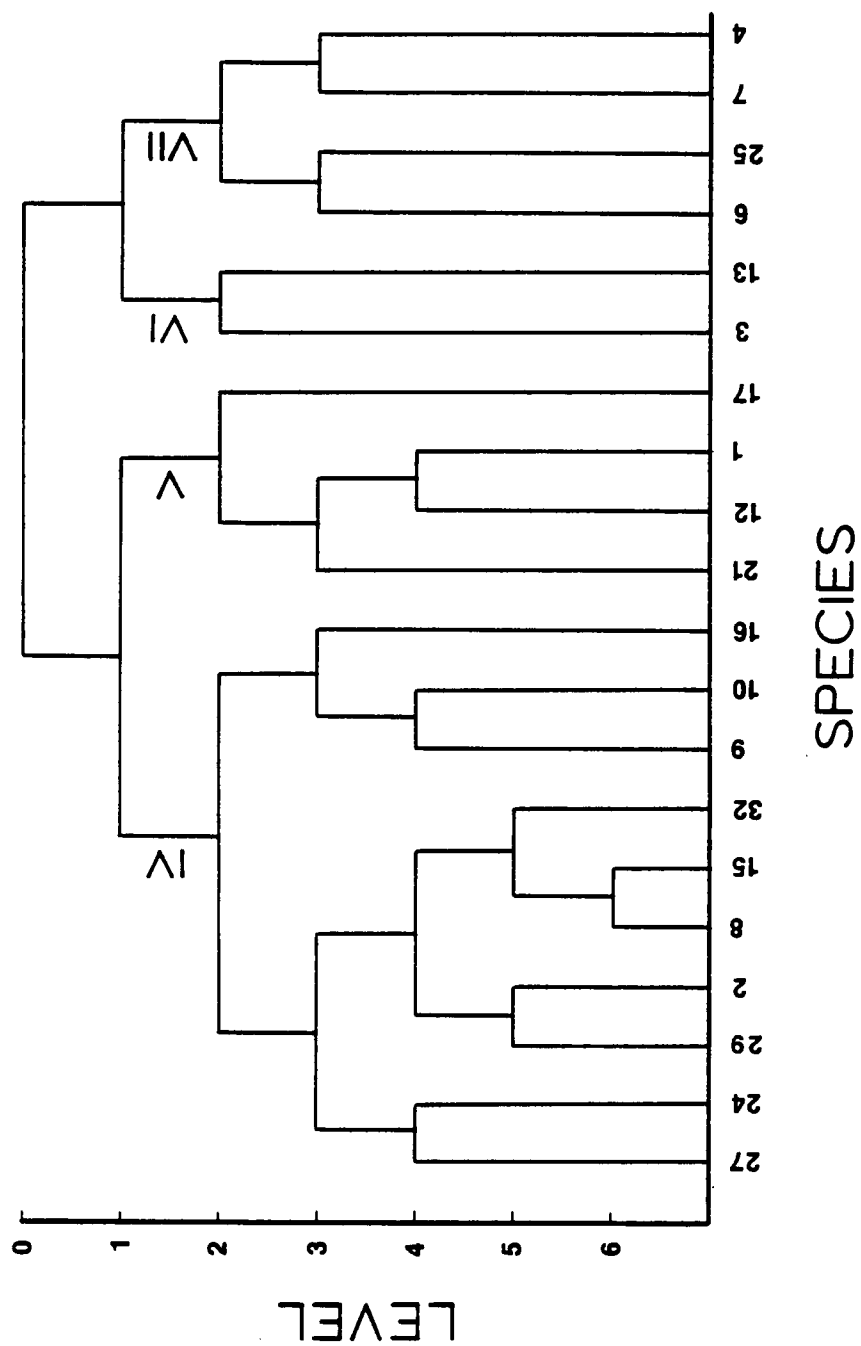


Figure 15. Dendrogram resulting from TWINSpan classification of west aspect species. Vertical scale represents levels of division. Roman numerals indicate level 2 groupings and correspond to those used in Figure 7. Species names corresponding to the code numbers used in this figure are given in Table 3.

The sporadic occurrence of species 12 and 13 throughout the transects, in low cover, may have created problems for the classification algorithm which could explain the unusual placement of these species.

Group VI contains the ubiquitous species 3 and the sporadically occurring species 13. Species 3 was apparently placed in Group VI rather than Group V, which contains the other two ubiquitous species, due to its dominance in the lower region of the transects. Group VII contains species restricted to or dominant in the lower region of the transects.

The groupings of west aspect samples through six levels of division are shown in Figure 16. Group IV consists of samples located at the upper end of the transects while Group V contains samples located in the middle region. Group VI is a transition zone with species 2, 8, 9, 10, 16, 12, and 17 reaching their lower limit and species 25, 7, and 4 reaching their upper limit in this group. Group VII contains samples located at the lower end of the transects.

Classification of South Aspect Species and Samples

The groupings of south aspect species through six levels of division are shown in Figure 17. Group IV consists of those species which occurred in the upper and middle regions of the transects as well as three wide ranging species (9, 8, and 21) which extended into the lower region of the transects. Group V consists of the ubiquitous species 16 along with the wide ranging species 10.

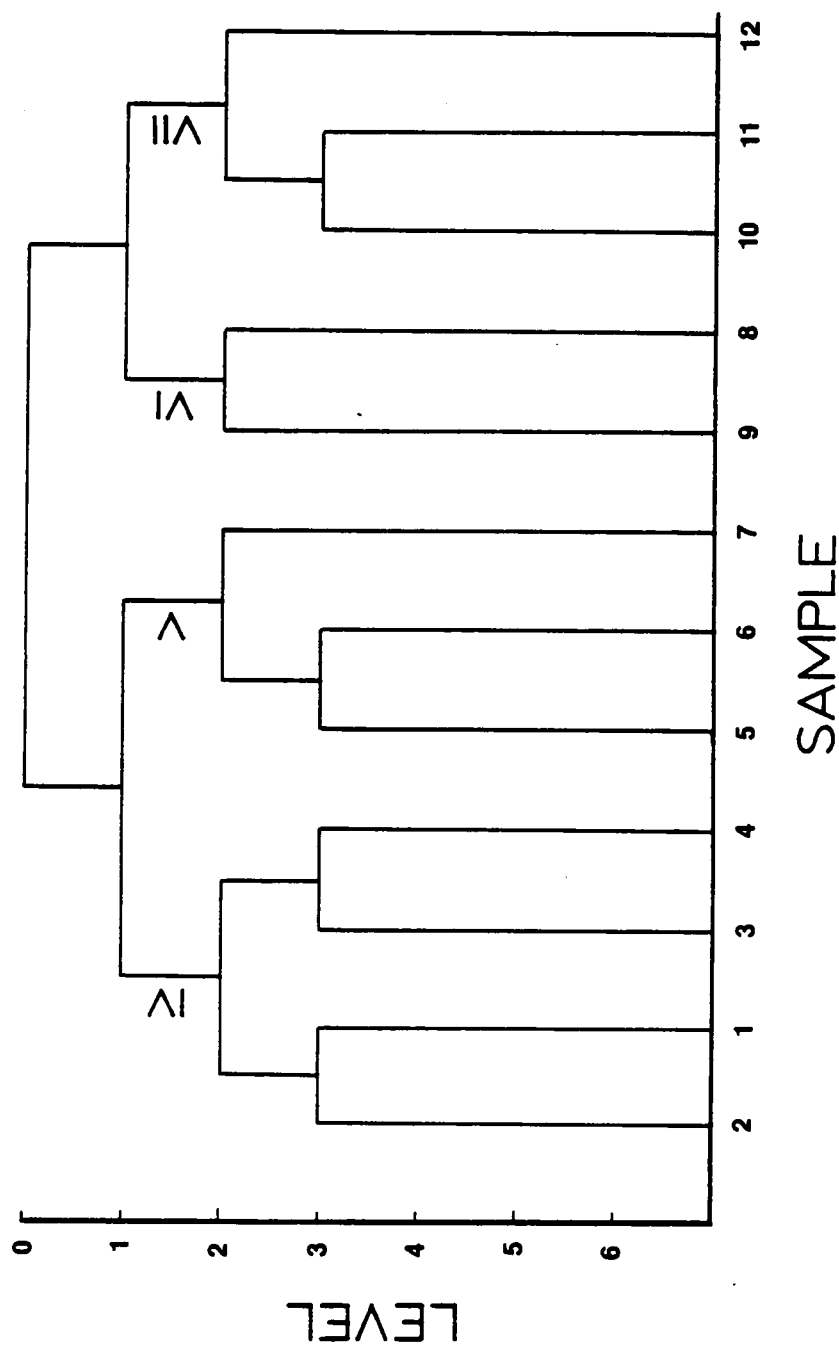


Figure 16. Dendrogram resulting from TWINSpan classification of west aspect samples. Vertical scale represents levels of division. Roman numerals indicate level 2 groupings and correspond to those used in Figure 8.

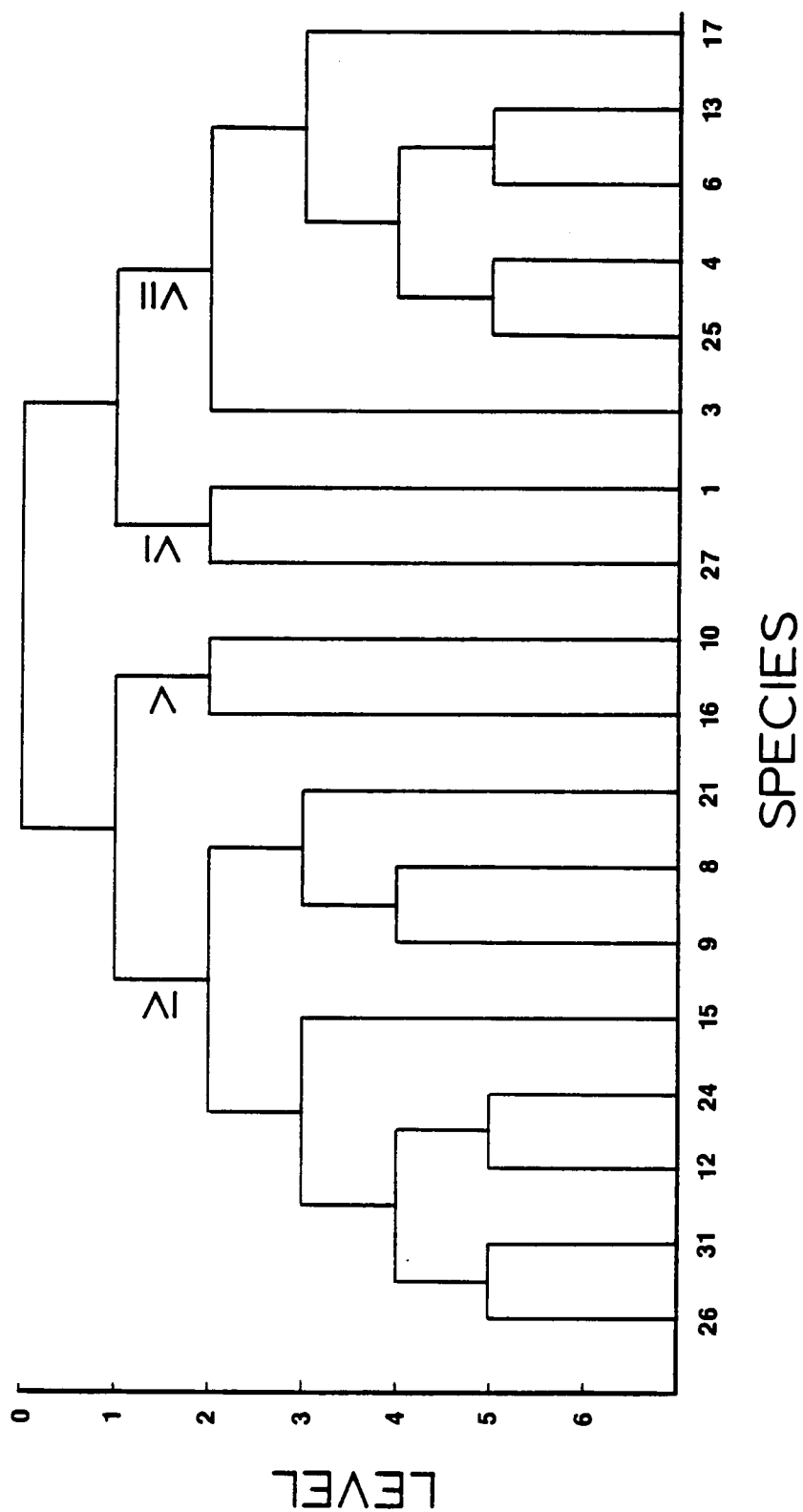


Figure 17. Dendrogram resulting from TWINSpan classification of south aspect species. Vertical scale represents levels of division. Roman numerals indicate level 2 groupings and correspond to those used in Figure 9. Species names corresponding to the code numbers used in this figure are given in Table 4.

Group VI consists of species 27, which occurred primarily in the middle region of the transects, and the ubiquitous species 1 which was most abundant in the middle to lower regions of the transects. Group VII is comprised of species restricted to or most abundant in the lower region of the transects. Group VII contains more species on the south aspect than on any of the other aspects due to the downward displacement of several species caused by drier microclimatic conditions in the upper and middle regions of the transects on this aspect.

The groupings of south aspect samples through six levels of division are shown in Figure 18. Group IV consists of those samples located in the upper and middle regions of the transects. Although Group V contains only sample 6, no ecological significance can be attached to the segregation of this sample into its own group. Group VI is again a transition zone with species 15, 9, 8, 21, 10, and 27 reaching their lowest positions and species 25, 4, and 13 reaching their highest positions on the transects in this group. Group VII consists of samples located at the lower end of the transects.

In examining the vertical distribution of epiphytes using cluster analysis Trynoski and Glime (1982) found that tree base samples were grouped into a distinct cluster while mid- and breast-height samples were generally mixed. The distinctiveness of the basal flora was partially the result of the frequent presence of many humicolous or terricolous species in this area. The unique

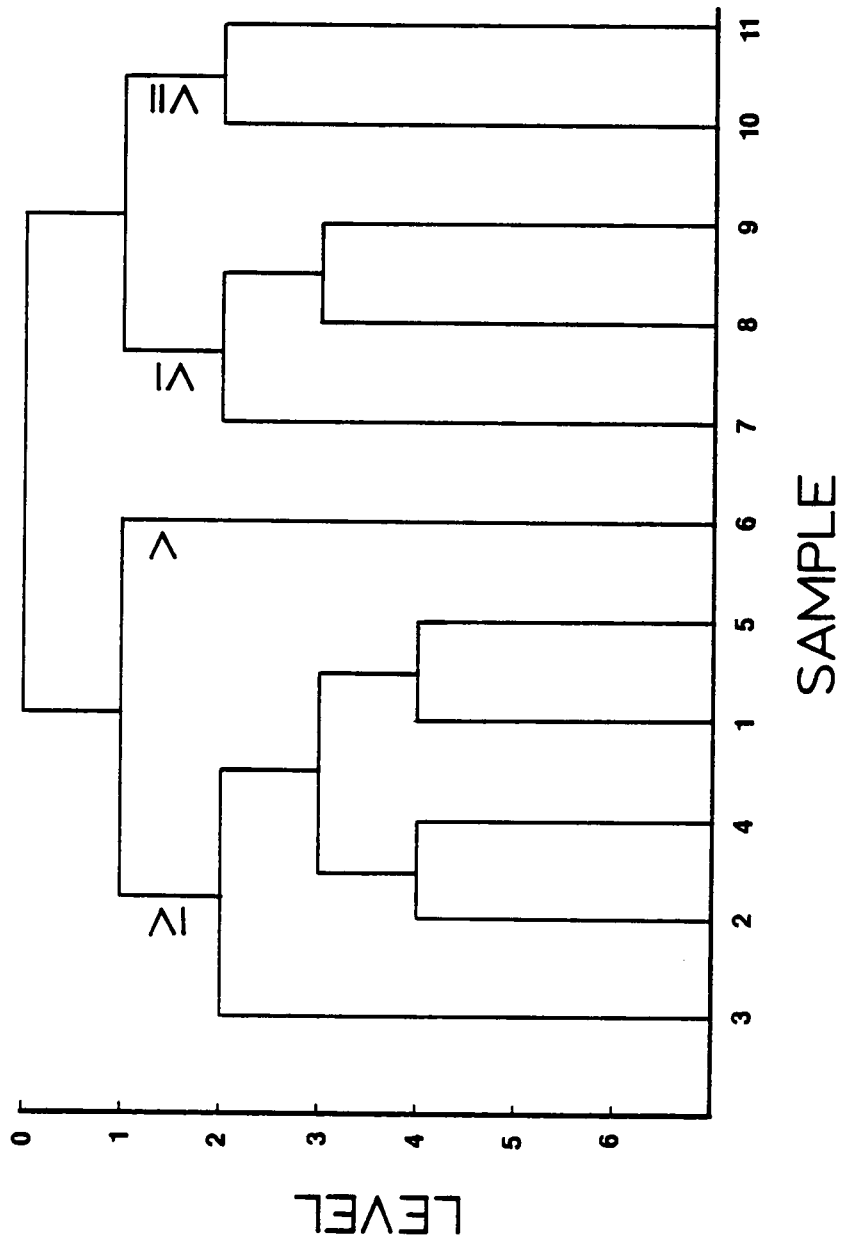


Figure 18. Dendrogram resulting from TWINSpan classification of south aspect samples. Vertical scale represents levels of division. Roman numerals indicate level 2 groupings and correspond to those used in Figure 10.

composition of the basal flora was also evident in the present study. On all four aspects the first division in the species and samples classifications segregated the basal species and samples from the remaining (mid- and breast-height) species and samples. Using association analysis Rasmussen (1975) was also able to divide the epiphytes on Fraxinus excelsior and Fagus sylvatica into three groups that reflected the vertical positions of the species on the trunks.

Aspectual Comparisons Using Ordination and Non-multivariate Methods of Analysis

The differences between the bryophyte communities of the north, east, and west aspects and those of the south aspect, revealed in the preceding sections, provided the impetus to use DECORANA to further investigate the aspectual distributions of the epiphytes. It was felt that the differences between the aspects revealed by comparisons of the ordinations of the vertical distribution data for each aspect would also be revealed by an ordination in which aspects, rather than quadrats, were the samples.

The positions of the samples (aspects) on the first and second ordination axes are shown in Figure 19. On the first ordination axis the north, south, and west aspects are clustered together at the left end of the axis while the east aspect is located to the right of this cluster. Viewing the locations of the aspects in two dimensions reveals a considerable shift in the position of the south aspect while little change is evident in the positions of

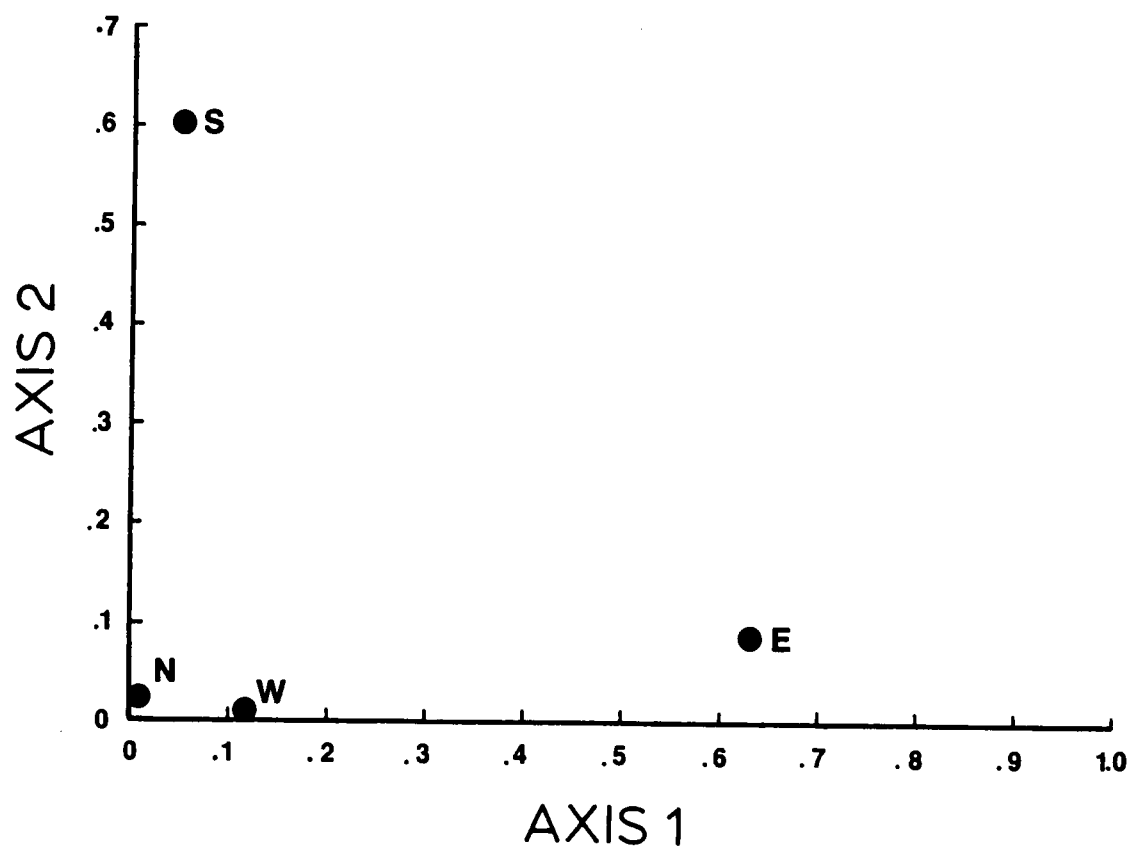


Figure 19. DCA ordination of the four aspects. Eigenvalues for the first and second ordination axes are 0.076 and 0.030, respectively. Axis scales are in units of average standard deviations of species turnover.

north, west, and east aspects. In two dimensions the north and west aspects are similar to one another and both are dissimilar to the south and east aspects which are also dissimilar from each other.

The dissimilarities or differences between the aspects, as reflected by the distance between the points in the ordination space, are relatively small in comparison to the differences seen in previous ordinations. The lengths of both the first and second axes in Figure 19 are less than one standard deviation of species turnover thus indicating that the samples are really quite similar.

It was anticipated that the first ordination axis would represent a horizontal moisture gradient with the north and south aspects located at opposite ends of the gradient and the east and west aspects located at opposite ends of the gradient and the east and west aspects located somewhere in between. Unfortunately, the positions of the aspects on the first ordination axis do not support this theory. The low first axis eigenvalue (0.076) also indicates that aspect position on the first axis explains relatively little of the variation in the data.

Jonescu (1970) used a polar ordination to provide a single axis (linear) ordination of the four stand-quadrants at each of her six study sites. Jonescu found the north and south stand-quadrants to be the most dissimilar at every site. The east and west stand-quadrants were close together in all six ordinations with their positions on the axes, relative to the end stand-quadrants (north and south), varying with the study site.

The inability of the ordination to demonstrate aspectual differences in epiphyte distribution between the north, east, and west aspects and the south aspect led to the use of other methods of analysis. The percent cover of epiphytes arranged according to aspect is shown in Table 5. The total cover on the south aspect was considerably lower (less than 50%) than that on each of the other three aspects. An unplanned comparison of means using the T'-method was used to determine if there were significant differences in cover between the four aspects. Since the total cover/aspect was the sum of the cover of the individual trees, it was possible to determine mean cover/tree/aspect. These were the means used in the unplanned comparisons. The T'-method was used because the east aspect of one tree and the west aspect of another were not included in the data (i.e., slightly unequal sample sizes) due to bark irregularities which considerably reduced epiphyte cover (Sokal and Rohlf 1981). The results of the comparisons, as presented in Figure 20, show that at an alpha level of 0.05 the north, east, and west aspects are not significantly different from each other yet all have significantly higher cover than the south aspect.

Trynoski and Glime (1982) found that on all four host species they studied the north aspect had significantly more cover than either the south or east aspects. The authors further observed that the east aspect supported significantly more cover than the south aspect (on all hosts) except on Quercus where bryophyte cover on the east aspect was significantly greater than that on the west

Table 5. Percent cover of epiphytes according to aspect.^a

Species	Aspects			
	N	E	W	S
22 ULOT CRI	0.02	-----	-----	-----
29 FRUL EBO	-----	-----	0.15	-----
31 AMBL VAR	-----	-----	-----	0.06
8 FORS TRI	5.32	7.45	7.84	4.04
15 NECK PEN	3.14	2.61	1.96	0.43
16 PORE PLA	0.39	1.24	0.75	1.07
34 METZ CRA	0.05	-----	-----	-----
12 LEUC JUL	-----	-----	0.13	0.10
9 FRUL BRI	0.80	2.29	0.97	2.68
10 HAPL TRI	0.37	0.31	0.90	0.73
21 HOMA SUB	2.70	3.63	2.98	1.09
26 METZ FUR	-----	-----	-----	0.04
32 DICR VIR	0.49	-----	0.13	-----
24 RADU COM	0.28	0.23	0.23	0.16
37 RADU OBC	0.03	-----	-----	-----
2 ANOM MIN	-----	0.43	3.07	-----
33 LEJE ULI	-----	0.23	-----	-----
17 SCHW FAB	1.53	3.55	2.35	1.70
1 ANOM ATT	23.27	24.51	28.55	6.05
20 RHOD ROS	0.18	-----	-----	-----
3 ANOM ROS	21.77	10.67	14.94	9.73
27 COLO BID	0.08	0.10	0.02	0.13
4 ANOM RUG	0.25	0.30	0.91	0.54
13 METZ CON	0.20	0.34	0.14	0.03
6 BRAC OXY	6.63	1.11	4.08	1.52
23 EURH HIA	0.15	-----	-----	-----
7 FISS CRI	-----	0.02	0.04	-----
25 THAM ALL	1.14	3.36	0.57	0.12
18 THUI DEL	0.12	-----	-----	-----
Total Cover	68.91	62.38	70.71	30.22
Number of Species	22	18	20	18

^aThe species are arranged to reflect, as closely as possible, their positions on the first ordination axes. Dashed lines indicate species absence on that aspect.

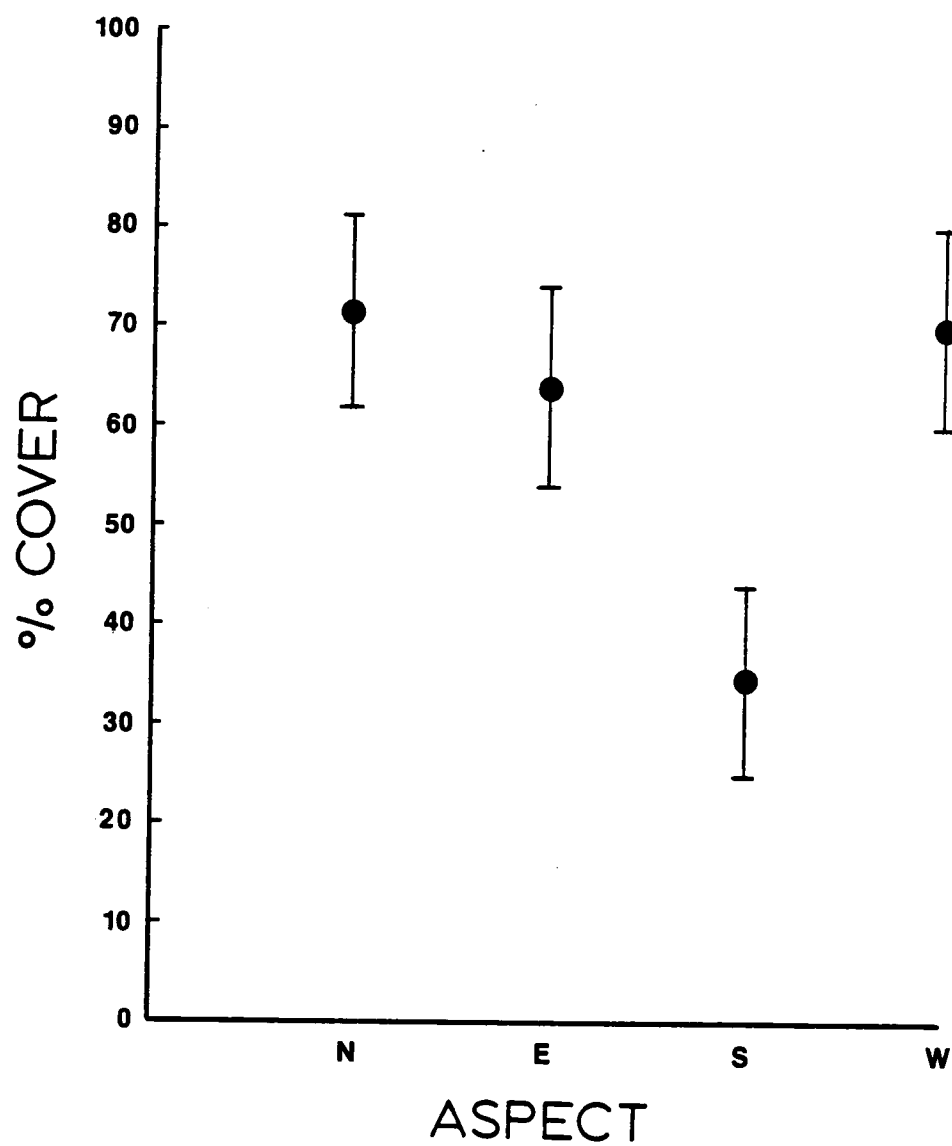


Figure 20. Ninety-five percent comparison intervals for the means of the cover data. Means whose intervals do not overlap are significantly different.

aspect. The difference in bryophyte cover between the west and south aspects was not significant on any of the host species.

Hoffman and Boe (1977) found the overall average cryptogam cover on north exposures of Populus deltoides to be 45% while the overall average cover on south exposures was only 19%.

The north aspect possessed the greatest number of species followed by the west, east, and south aspects. An unplanned comparison of means using the T'-method revealed that the mean number of species/tree on the north aspect was significantly greater ($\alpha = 0.05$) than the mean number of species/tree on the south aspect. No other pairs of aspects were significantly different from each other in terms of the number of species present.

In examining the distribution of epiphytic cryptogams on Pseudotsuga menziesii and Abies lasiocarpa, Gough (1975) found that although most epiphytes were encountered in all quadrants (N, E, S, and W), the majority occurred in the north or west quadrants or both.

Several other points are worthy of mention with respect to the data presented in Table 5. The number of species displaying maximum percent cover on the north, east, west and south aspects are 11, 6, 8, and 4, respectively. These numbers include species restricted to a single aspect. The number of species restricted to the north, east, west, and south aspects are 6, 1, 1, and 2, respectively. A total of 15 species occurred on all four aspects, and of these 15 species, four are least abundant on the north aspect, two on the east, one on the west, and eight on the south aspect.

Yarranton (1972) observed distribution patterns similar to those shown in Table 5 for lichens growing on black spruce. For example, Alectoria nadvornikiana, Parmelia physodes, and Parmeliopsis hyperopta exhibited maximum frequencies in north-facing quadrants, minimum in south-facing quadrants, and intermediate values in east- and west-facing quadrants. Neckera pennata, Radula complanata, and Anomodon rostratus displayed the same distribution pattern in the present study.

Several of the points in the preceding paragraphs correlate well with the two dimensional arrangement of the species produced by the species-by-aspects ordination discussed at the beginning of this section. Figure 21 shows the positions of the species on the first and second ordination axes. Group 1 contains those species which were restricted to the north aspect. These six species (18, 20, 22, 23, 34, and 37) have identical first- and second-axis ordination scores. Group 2 contains species 33, the only species which was restricted to the east aspect. Group 3 contains the two species restricted to the south aspect (both species 26 and 31 have identical first- and second-axis scores) and Group 4 contains the single species (29) restricted to the west aspect. Groups 1A, 2A, 3A, and 4A consist of species showing maximum cover on the north, east, south, and west aspects, respectively, but which are not restricted to those aspects.

Additional evidence to support the division of the four aspects into two groups (i.e., the N, E, and W group and the S group) was

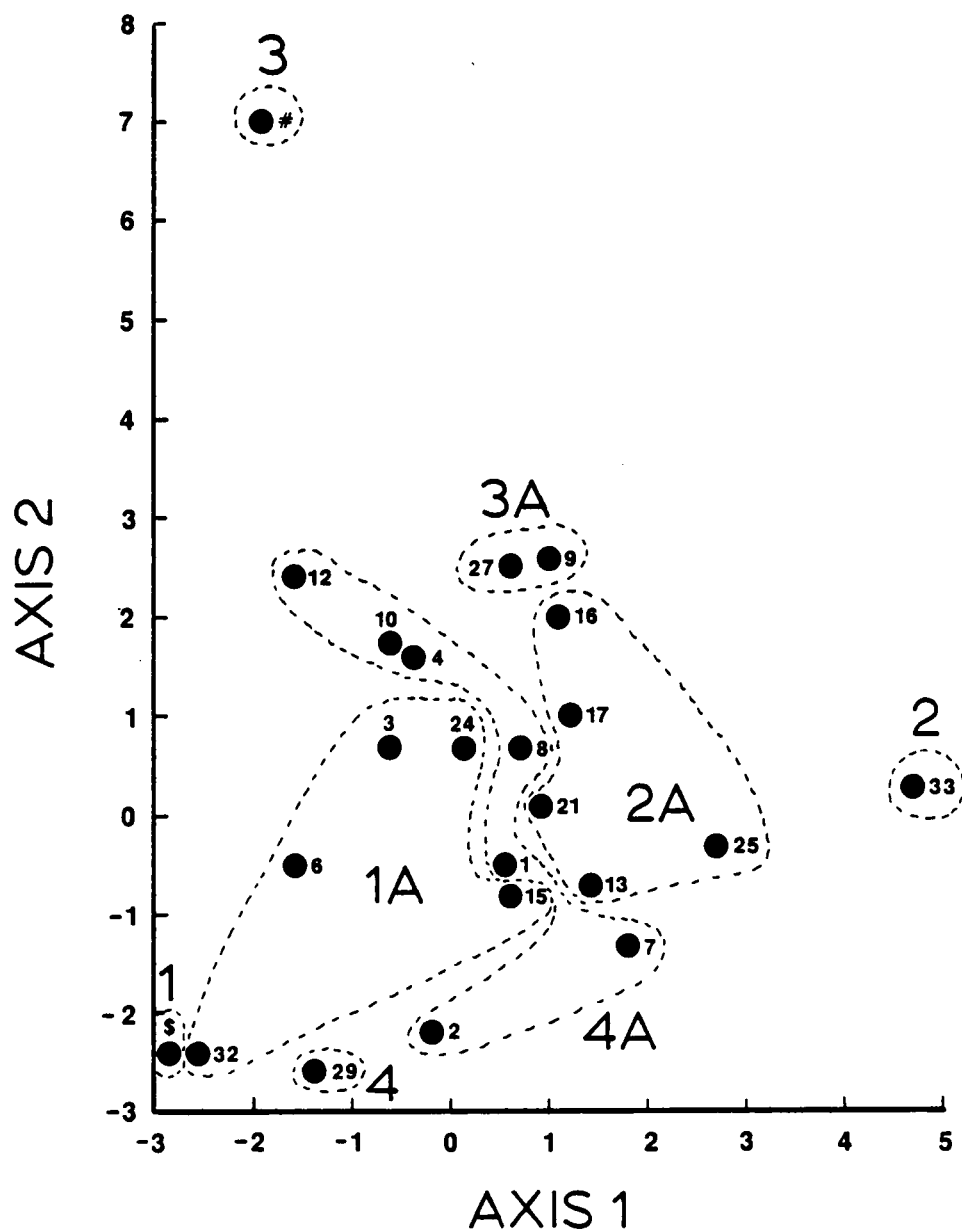


Figure 21. DCA ordination of the species from all four aspects. Group 1 (\$) contains species 18, 20, 22, 23, 34, and 37. Group 3 (#) contains species 26 and 31. See text for an explanation of the groupings. Eigenvalues for the first and second ordination axes are 0.076 and 0.030, respectively. Axis scales are in units of average standard deviations of species turnover.

provided by the calculation of coefficients of community. Coefficients of community, a measure of the similarity between any pair of communities, were calculated for all possible two-aspect combinations. The coefficients of community shown in Table 6 indicate that the north, east, and west aspects are more dissimilar to the south aspect than they are to each other.

Table 6. Coefficients of community calculated for all possible two-aspect combinations.^a

	N	W	E	S
N	-	81.22	77.10	53.65
W	-	-	82.31	55.44
E	-	-	-	61.62
S	-	-	-	-

^aCoefficients were calculated with the formula $(2w/a+b) \times 100$. A value of zero indicates complete dissimilarity while a value of 100 indicates complete similarity (i.e., identical communities).

CHAPTER IV

SUMMARY AND CONCLUSIONS

Ordination and classification techniques applied to epiphyte cover data for each of the four aspects sampled revealed the presence of distinct vertical distribution patterns among the epiphytes. Since the vertical distributions of the epiphytes were aspect dependent (see below), it is difficult to provide overall distributional patterns. Despite this difficulty several generalizations can be made regarding the vertical distribution of many of the epiphytes. Thamnobryum alleghaniense, Anomodon rugelii, Metzgeria conjugata, Eurhynchium hians, and Thuidium delicatulum occurred in the lower region of the transects while Brachythecium oxycladon, most abundant in the lower region, extended upward into the middle regions. Anomodon attenuatus and Anomodon rostratus were ubiquitous species on all four aspects. Radula obconica, Anomodon minor, and Lejeunea ulicina were present at low cover in the middle region of the transects. Cololejeunea biddlecomiae occurred sporadically throughout the transects on all four aspects. Forsstroemia trichomitria, Frullania brittoniae, Porella platyphylloidea, Radula complanata, Schwetschkeopsis fabronia, Neckera pennata, Homalotheciella subcapillata, Haplhymenium triste, and Dicranum viride were present in the upper and middle regions of the transects. Ulotia crispa, Amblystegium varium, Leucodon julaceus, and Frullania eboracensis were restricted to the upper region of the transects.

Only the first ordination axis was considered ecologically meaningful representing a moisture gradient from moist (the bottom of the transects) to mesic (the top of the transects) conditions. This contention was supported by the fact that the first-axis eigenvalues, on all four aspects, were considerably higher than those of the second and subsequent axes. The high correspondence between the sequence of quadrats on the trees and the sequence of samples on the first-axis in the sample ordinations also indicated that the epiphytes were sensitive to small changes in microclimatic conditions that occurred along the length of the transects.

Comparisons of the ordination and classification results from each of the four aspects revealed the influence of aspect on the vertical distribution patterns exhibited by the epiphytes. The effect of aspect on the vertical distribution of the epiphytes varied with aspect but was most pronounced on the south aspect presumably due to the presence of drier microclimatic conditions in the upper and middle regions of the transects on this aspect. Species occurring in the upper and middle regions of the transects on the north, east, and west aspects extended further down the transects (i.e., into the lower region) on the south aspect. This was thought to be the result of a reduction in competition with other species, primarily the ubiquitous Anomodon attenuatus and Anomodon rostratus.

Aspectual differences in species abundance could not be demonstrated by using frequency values (i.e., species presence of absence in the quadrats); rather, cover data is the most important species

and community measurement to discriminate aspectual clines. As an example, Anomodon attenuatus occurred in 14 of 14 quadrats on the north aspect (frequency = 1.0) while on the south aspect it occurred in 10 of 11 quadrats (frequency = 0.91). A comparison of the frequencies of this species on the north and south aspects does not reveal the considerable difference in abundance (biomass) that actually exists between these two aspects. A similar conclusion was reached by Hoffman and Kazmierski (1969) in their study of epiphytic bryophytes and lichens on Pseudotsuga menziesii. They stated, "In our study, presence data alone would not reveal important exposure effects but coverage estimates for each species do."

In addition to influencing the vertical distribution of the epiphytes, aspect also affected epiphyte cover. The most striking example of this was the reduction in epiphyte cover on the south aspect as compared to the north, east, and west aspects. Anomodon attenuatus and Anomodon rostratus exemplify such by a considerable reduction in cover on the south aspect.

A comparison of means (i.e., mean cover/tree/aspect) using the T'-method revealed that at an alpha level of 0.05 the north, east, and west aspects were not significantly different from each other yet all had significantly greater cover than the south aspect. Coefficients of community were also calculated for all possible two-aspect combinations. The coefficients revealed that the north, east, and west aspects were more similar to each other than to the south aspect.

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APPENDIX

Table 7. List of bryophytes encountered on Aesculus octandra Marsh. arranged alphabetically with mosses first and liverworts second.

Taxa
Mosses
<u>Amblystegium varium</u> (Hedw.) Lindb.
<u>Anomodon attenuatus</u> (Hedw.) Hüb.
<u>Anomodon minor</u> (Hedw.) Furnr.
<u>Anomodon rostratus</u> (Hedw.) Schimp.
<u>Anomodon rugelii</u> (C.M.) Keissl.
<u>Brachythecium oxycladon</u> (Brid.) Jaeg. & Sauerb.
<u>Dicranum viride</u> (Sull. & Lesq.) Lindb.
<u>Eurhynchium hians</u> (Hedw.) Sande-Lac.
<u>Fissidens cristatus</u> Wils. ex Mitt.
<u>Forsstroemia trichomitria</u> (Hedw.) Lindb.
<u>Haplohymenium triste</u> (Ces. ex De Not.) Kindb.
<u>Homalotheciella subcapillata</u> (Hedw.) Broth.
* <u>Hypnum fertile</u> Sendtn.
<u>Leucodon julaceus</u> (Hedw.) Sull.
* <u>Mnium affine</u> Bland. ex Funck var. <u>ciliare</u> C.M.
<u>Neckera pennata</u> Hedw.
* <u>Platygyrium repens</u> (Bird.) BSG
<u>Rhodobryum roseum</u> (Hedw.) Limpr.
<u>Schwetschkeopsis fabronia</u> (Schwaegr.) Broth.
<u>Thamnobryum alleghaniense</u> (C.M.) Nieuwl.
<u>Thuidium delicatulum</u> (Hedw.) BSG
<u>Ulota crispa</u> (Hedw.) Brid.
Liverworts
<u>Cololejeunea biddlecomiae</u> (aust.) Evans
<u>Frullania brittoniae</u> Evans
<u>Frullania eboracensis</u> Gott.
* <u>Lejeunea ruthii</u> (Evans) Schust.
<u>Lejeunea ulicina</u> (Tayl.) Gott.
<u>Metzgeria conjugata</u> Lindb.
<u>Metzgeria crassipilis</u> (Lindb.) Evans
<u>Metzgeria furcata</u> (L.) Dum.
<u>Porella platyphylloidea</u> (Schwein.) Lindb.
<u>Radula complanata</u> (L.) Dum.
<u>Radula obconica</u> Sull.

*Species that did not meet the minimum frequency requirement (i.e., 1% of the total number of plots on any given aspect) on any of the four aspects sampled. These "rare" species were not included in the data analyses.

VITA

Gary Steven Huntzinger was born in Somerville, New Jersey on March 12, 1956. He attended elementary schools in Piscataway, New Jersey and graduated from Piscataway High School in June 1974.

In September of 1974 he entered Drew University and in May 1978 received a Bachelor of Arts degree (cum laude) in Botany.

In September of 1979 he began study toward a Master of Science degree in Botany at The University of Tennessee, Knoxville. While engaged in graduate studies at The University of Tennessee, Knoxville, he served as a graduate teaching assistant and taught courses in Biology and Botany.