To the Graduate Council:

I am submitting herewith a thesis written by Benjamin E. West entitled, "Landscape Ecosystem Classification for the Mountain Highlands of the Tellico Ranger District, Cherokee National Forest, Tennessee." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology.

John Rennie, Major Professor

We have read this thesis
and recommend its acceptance:

Accepted for the Council:

Associate Vice Chancellor and
Dean of the Graduate School

LANDSCAPE ECOSYSTEM CLASSIFICATION FOR THE MOUNTAIN HIGHLANDS OF THE CHEROKEE NATIONAL FOREST

A Thesis

Presented for the

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Degree

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Benjamin E. West

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ABSTRACT

A landscape ecosystem classification (LEC) is described for the 26,100 ha Mountain Highlands section (610 m to 1660 m in elevation) of the Tellico Ranger District of the Cherokee National Forest. An LEC is based on the integration of three ecosystem components: landform, soils, and vegetation. The primary objectives of this research were: (1) to understand the spatial patterns and functional relationships of these ecosystem components, and (2) to provide a practical system of classification for use by U.S. Forest Service personnel in the management of forest ecosystems.

Vegetation, soils, and landform data were obtained from ninety 0.04 ha plots located in stands representing late successional stages. Vegetation data were summarized by species and size class in terms of percent cover of the plot area. Two techniques of indirect ordination were used to distinguish site units (plots with similar vegetation): detrended correspondence analysis using DECORANA, and polythetic divisive classification using TWINSPAN. Stepwise discriminant analysis was used to determine those environmental variables that contributed most to the classification of the vegetation. A technique of direct ordination, detrended canonical correspondence analysis, was also used to identify site types from vegetation, soils, and landform variables. Results of the direct and indirect gradient analyses were compared and evaluated in terms of their ability to predict site units.

Five ecological site units were identified and found to be recurring across the landscape. These were: 1) Yellow pine/mixed oak forest, 2) Mixed oak/red maple forest,

3) Cove hardwood/mixed mesophytic forest, 4) Eastern hemlock/yellow birch forest, and 5) Beech forest. Each site unit represents an array of site types which are identifiable combinations of landform and soil features, associated with discrete vegetative communities. A four variable model consisting of elevation, aspect, slope position, and A horizon depth accurately predicted site unit membership over 60% of the time. The primary axial expression of these site units is interpreted as a complex moisture gradient, made up of a combination of all four variables. For the purposes of developing a management strategy, elevation and aspect appear to be sufficient for predicting the distribution of site units across the landscape of the Mountain Highlands.

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INTRODUCTION

The traditional emphasis on timber production as the primary goal of forestry is not compatible with modern resource management, particularly on public lands. Today's forest manager must view the land not only as a source of timber, but as a complex ecosystem supporting a wide variety of plant, decomposer, and animal species. The U.S. Forest Service (USFS), therefore, has adopted a new philosophy of "Ecosystem Management" that emphasizes both sustainable development of forest resources and conservation of unique natural resources. The primary emphasis of this approach is the sustained health and vigor of the entire ecosystem.

Landscape ecosystem classification (LEC) is an attempt to provide an ecological framework to support this new objective. A landscape is made up of ecosystems of various sizes, nested within one another in a hierarchy of spatial sizes (Rowe and Sheard 1981). The primary aim of LEC is to subdivide the landscape into ecosystem units based on this hierarchy of scale and define functionally similar and dissimilar ecological units. The classification of large areas into ecological units provides a useful framework for integrated resource planning and management, biological conservation, and comparing differences in composition, occurrence, interactions, and productivity of plants and animals among ecosystems (Avers et al. 1993). It is important to delineate ecosystems at a level and scale that is appropriate to management objectives and that practitioners and scientists can use and understand.

LEC is based on the integration of three ecosystem components: physiography (landform), soils, and vegetation. Each component has a different role to play at regional and local levels. Interactions among these ecosystem components are what ultimately determine biological productivity differences among ecological units. Exclusive or predominant use of a single component may limit the usefulness and reliability of the classification. Development of an LEC is generally completed in four phases (Jones and Lloyd 1993):

Phase 1: Identification of ecologically equivalent site units (based on the three ecosystem components) in stands relatively free of disturbance. Species possessing narrow ecological amplitudes are identified and used in the delineation of site unit boundaries.

Phase 2: Identification of ecologically equivalent site units in disturbed stands and subsequent comparison of seral vegetation in those units with vegetation in units delineated in Phase 1.

Phase 3: Site unit mapping utilizing ground surveys and geographic information systems (GIS).

Phase 4: Development of management strategies utilizing site unit attributes such as growth and yield, species composition, and successional trends.

The advantage of LEC models is that once a model for a particular landscape has been developed, it is possible to predict vegetation types for a site from the permanent features of its landform and soil characteristics. Because landform exerts a major control over climatic regimes at most scales, and because it is generally the most stable component of terrestrial ecosystems, it provides a fundamental unit upon which to base ecosystem classifications (Rowe and Sheard 1981). Early results of efforts to integrate LEC models into GIS coverages are promising (Jones 1991). It is envisioned that land managers will be able to use GIS to identify ecological site units within a defined landscape and manage these for both sustainable timber production and conservation measures. This is one of the objectives of ecosystem management. Having this information permits foresters to use their knowledge of forest conditions to design and implement forest plans that have broader objectives than those written previously.

The goal of this research is to develop a landscape ecosystem classification system, within an existing framework used by others in the Southern Appalachians, for a portion of the Cherokee National Forest. This study attempts not simply to identify or classify the landform, soil, and vegetation of the area, but also to explain the spatial patterns and functional relationships of the components. A multiple-component approach is "ecological" only to the degree that these relationships are understood and built into the classification. The objectives of this research are to:

1) Identify one or more distributions of species along environmental gradients,

2) Delineate ecologically equivalent site units, and

3) Provide a practical system of classification for use by USFS personnel in the management of forest ecosystems.

LITERATURE REVIEW

Forest Site Classification

Over the years, many methods have been used to identify, classify, and describe forest ecosystems. Numerous systems have been developed with the primary purpose of predicting site productivity from an understanding of site and vegetation relationships. In the United States, site index has been the traditional approach used in classifying sites for timber management. It estimates site quality (productivity) using the height of dominant and codominant trees at a specified age, usually 50 years for eastern hardwoods. Carmean (1975) reviewed some of these techniques and pointed out a number of the restrictions of this approach. He stated, "Direct site index estimates based on tree measurements are only local point observations of site index...Still to be resolved is the problem of abstracting these various point observations into an area site classification of the landscape. Usually these point observations of site index are closely related to recognizable features of soil, topography, and vegetation. Therefore, the basic problem is how to design practical landscape classification systems that use these important features for accurately classifying site quality, and that also include information important for managing other multiple land values and uses." Single-factor methods, employing separate classifications of soils, vegetation, or landform, may not be adequate. Most of the studies summarized below attempted to develop an integrated classification system, such as the one Carmean (1975) advocated.

Several studies on forest productivity in the mid-1900's attempted to relate physiographic features and soil characteristics to site index (productivity). Gaiser (1951) found aspect and distance from the ridge line to be effective in determining the site index of white oak (*Quercus alba*; nomenclature follows that of Radford et al. 1968) in southeastern Ohio. Site index increased with distance downslope from the ridge line and was higher on northern and eastern aspects than on southern and western aspects. The depth of the soil A horizon was also found to be directly correlated with site index.

Trimble and Weitzman (1956) also studied the relationship between several soil variables, topographic data, and site indices for five oak species in West Virginia, western Maryland, and southwestern Pennsylvania. Using regression analysis, they found that four variables have a major influence on site index. These were: 1) aspect, 2) slope position (i.e., distance from the ridge line), 3) slope gradient, and 4) solum depth. Similar to Gaiser (1951), they found that north and east-facing slopes have higher productivity than south and west-facing slopes. Site index increased from ridge line to lower slope and decreased as the slope gradient increased. Also, site index increased with an increase in soil depth. Exposure, or the effect of shading by nearby land masses, and elevation were thought to influence site index; however, these effects were not quantified.

Doolittle (1957) completed a similar study of scarlet oak (*Quercus coccinea*) and black oak (*Quercus velutina*) in the Southern Appalachian Mountains. Using regression analysis, he concluded from several topographic and soil variables that the depth of the A horizon in inches, slope position (measured in percent of distance from bottom to top of the slope), and percent of sand in the A horizon gave the best estimation of site index for these species. Generally, site index increased as the A horizon increased in thickness and percent of sand and slope position decreased.

Ike and Huppuch (1968) studied soil and site factors affecting growth of ten tree species in the Blue Ridge Mountains of Georgia. They concluded that topographic features were more closely related to site quality than were physical or chemical soil properties. The most significant factors determining site quality were those which influenced local climate and moisture supply. These were elevation, slope position, aspect, and slope gradient.

Similar work has also been completed for the Cumberland Plateau in Tennessee. Smalley (1986) developed a forest site classification system for the Highland Rim and Pennyroyal, and for the Cumberland Plateau, based on physiography, geology, soils, and topography. Smalley's classification system is based on identification of landtypes, which are the smallest units of the landscape. Landtypes are areas that have similar soils and productivity as a result of similar climatic and geological processes.

Hammer (1986) conducted a detailed comparison of soil characteristics and tree growth on selected forest landtypes on the mid-Cumberland Plateau. Discriminant analysis was used to determine the minimum number of soil variables required for statistical classification of the landtypes. From thirty-two soil variables measured in the field, nine soil variables, including chemical and physical properties from A and B horizons, were determined to be the most important discriminators for predicting forest landtypes.

Ecological Land Classification

The aforementioned research focused on ways of determining site quality, such as site index, for one or a few species, or used single indicators such as soils or topography to make discrete classifications of forest productivity. Site quality, at its highest, is the sum total of factors affecting the capacity of the land to produce forests. An integration of vegetation along with soils and topography to classify and predict site quality was needed. Intensive methods involving multiple factors have been employed with great success in the last few decades, especially through the use of computers to analyze large, multivariate data sets.

One of the most comprehensive studies of the general vegetation patterns of the Southern Appalachians was performed by Whittaker (1956). His classic study of the vegetation of the Great Smoky Mountains National Park (GSMNP) represents an early attempt to integrate ecosystem components. The focus of his work was to relate gradients of plant assemblages to gradients of environmental characteristics and to identify trends in community composition and structure. He found that vegetation was related to elevation and to a qualitative moisture gradient based on characteristics of landform. He identified 15 vegetation types (13 of which were forest vegetation) by dominant species and plotted these vegetation types as well as relative densities of individual species on axes of elevation and a qualitative representation of the moisture gradient based on aspect. Despite not including any direct soils analysis in his research, Whittaker provided a comprehensive framework upon which subsequent classifications of eastern forests could be based. In most cases, further vegetative classification research in the Southern Appalachians has focused on quantifying species distributions along this moisture gradient.

Using multivariate techniques such as discriminant analysis, ordination, canonical correlation, and cluster analysis procedures, Golden (1974, 1981) reexamined and expanded Whittaker's work in the GSMNP. He analyzed vegetative data from forests found at middle elevations. Six major forest vegetation complexes were identified in relation to elevation, topographic characteristics, slope angle, and aspect. These included: 1) pine complex (pitch pine (*Pinus rigida*) and Table Mountain pine (*Pinus pungens*)), 2) chestnut oak complex (chestnut oak (*Quercus prinus*) in combination with various oaks, and red maple (*Acer rubrum*)), 3) cove hardwoods complex (various combinations of several cove hardwoods including hemlock (*Tsuga canadensis*), buckeye (*Aesculus octandra*), and yellow birch (*Betula lutea*)), 4) hemlock complex (hemlock in combination with silverbell (*Halesia carolina*) and red maple), 5) slope yellow birch complex (yellow birch in combination with hemlock and spruce (*Picea* spp.), and 6) disturbance red maple complex (red maple in combination with sweet birch (*Betula lenta*) and northern red oak (*Quercus rubra*)). Soils data collected by Golden (1981) indicated that soil pH and subsoil clay content were also important in species-site relationships.

Focusing on forest communities within the western GSMNP, Callaway et al. (1987) conducted a study similar to that of Golden (1981). The two goals of this study were: 1) develop a model for topographical quantification of the GSMNP, based on the amount of protection from surrounding landforms, and 2) further analyze the relationship between landform and forest types. Using multivariate techniques, they described twelve forest types and found that elevation, pH of the A horizon, and water-holding capacities of the A and B horizons were the three most discriminating variables in predicting these forest types. However, these two soil variables were highly correlated with landform protection, and it was assumed that the quantification of protection represented a unique measurement of an environmental complex of several related variables. From this perspective, landform protection was shown to be highly significant in predicting forest communities.

Rutledge (1995) attempted to quantify Whittaker's moisture gradient using GIS analysis and creation of another type of topographic index, based on local or microscale topographic conditions. His study area was in the Little Tennessee River watershed in western North Carolina. Using 90 meter resolution raster GIS data for this area and a nearest-neighbor analysis of the aspect of surrounding cells, he calculated a topographic index for individual cells. TWINSPAN analysis was conducted on field data collected from the same area, and eight forest cover types were identified. Discriminant analysis identified the topographic index, elevation, and aspect as the most important variables in discriminating between forest cover types.

The Landscape Ecosystem Approach

Barnes et al. (1982) initiated the landscape ecosystem approach in the United States on the Upper Peninsula of Michigan. After examining the relationships of soil, landform, and vegetation on late-succession, steady state forest stands, they identified 21 ecological types, termed "site units." The Michigan effort developed the terminology of "landscape ecosystem classification," which has been adopted for modeling applications in the southeastern United States.

In South Carolina, Jones et al. (1984) completed a classification of forested ecosystems of the Savannah River Plant site located within the upper Coastal Plain. Eight hardwood and twelve pine-dominated site units were identified. Vegetation was found to vary along an environmental gradient corresponding to topographic position.

McNab (1991a) is currently leading the development of landscape ecosystem classifications for several national forests in the Blue Ridge physiographic province of the Southern Appalachians. Similar to the efforts of Barnes et al. (1982), these classifications are based on landform, soils, and vegetation. The study described in this thesis is similar to cooperative research that has been completed or is ongoing at several Southern Appalachian universities.

McNab (1991b) developed a classification system for the Bent Creek Experimental Forest in North Carolina. The study explored the interaction of these same three ecosystem components in the Asheville Basin of the Southern Appalachians. Five ecological site units were defined based on their vegetative attributes and landform/soil characteristics. Gattis (1992) completed Phase 1 of an LEC for the Highlands Ranger District of the Nantahala National Forest. Her results included the designation of six ecological site units that were correlated with four environmental features: elevation, landform index (McNab 1993), soil solum depth, and epipedon thickness. Elevation was found to be the most highly discriminating variable between site units. Three site units were identified above 1210 m (4000 feet) and three below.

Moffat (1993) also completed Phase 1 of an LEC for the Chattooga Ranger District of the Chattahoochee National Forest. Ten ecological site units were delineated: a riparian unit, four low-level elevation units, four mid-level elevation units, and one high elevation unit. Both Gattis and Moffat used physical landform and soil attributes to determine site unit membership without vegetation information. Moffat developed discriminant function equations using soil and landform variables that predicted membership into site units with 95 percent accuracy.

In Tennessee, similar work has been completed for the Foothills section (areas below 610 m in elevation) of the Tellico Ranger District of the Cherokee National Forest (Yoke 1994). A Phase 1 LEC identified four ecological site units: 1) eastern hemlock—sugar maple—beech, 2) eastern hemlock—rosebay rhododendron, 3) chestnut oak, and 4) chestnut oak—scarlet oak—red maple. Elevation and landform index were determined to be the most discriminant predictors of site unit membership. A follow-up study of this area is currently being developed to identify successional types (Phase 2) on the four site units defined by Yoke.

STUDY AREA

The study area is located in the southern unit of the Cherokee National Forest in the Blue Ridge Province of east Tennessee (Figure 1A). After consultation with USFS personnel, it was determined that sampling should be conducted in the Mountain Highlands of the Tellico Ranger District, located in Monroe County. This district is separated from the GSMNP by the Little Tennessee River to the north, and bounded politically by the Tennessee-North Carolina border to the east, and the Hiwassee Ranger District of the Cherokee National Forest to the south (Figure 1B). The 26,101 ha Mountain Highlands section of the Tellico District consists of areas above 610 m (2000 feet) in elevation (Figure 2). The ecological characteristics of the Mountain Highlands are not currently well-documented, and a Phase 1 LEC for this area, in combination with Yoke's (1994) results, would provide the USFS with a comprehensive classification and evaluation of forest ecosystems for much of the Tellico Ranger District.

Monroe County has a warm, temperate, humid climate, and variations within the county are related to location and topography. Generally, the higher elevations have a cooler and wetter climate than the neighboring valleys have. The lowlands of Monroe County typically receive an average of 127 cm (50 in.) of rainfall annually, whereas the higher elevations of the county receive about 191 cm (75 in.), a difference of approximately 65 cm annually. Mean annual temperature for Monroe County is approximately 13°C (55°F). However, temperatures in the mountains range from two to

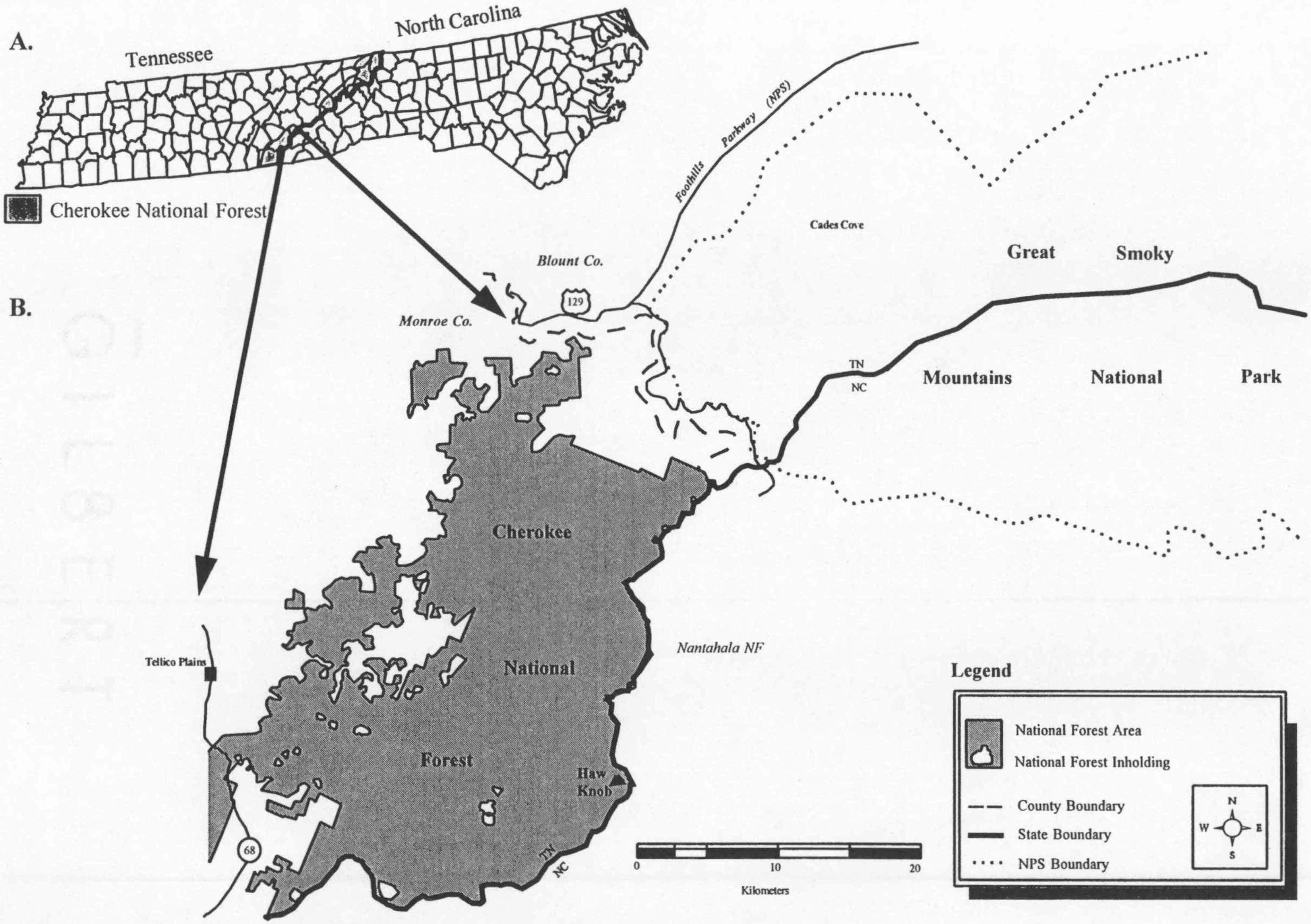

Figure 1. A. Location of the southern unit of the Cherokee National Forest, Tennessee.
B. Location of the Tellico Ranger District, Monroe County, Tennessee.

Tellico Ranger District, Cherokee National Forest

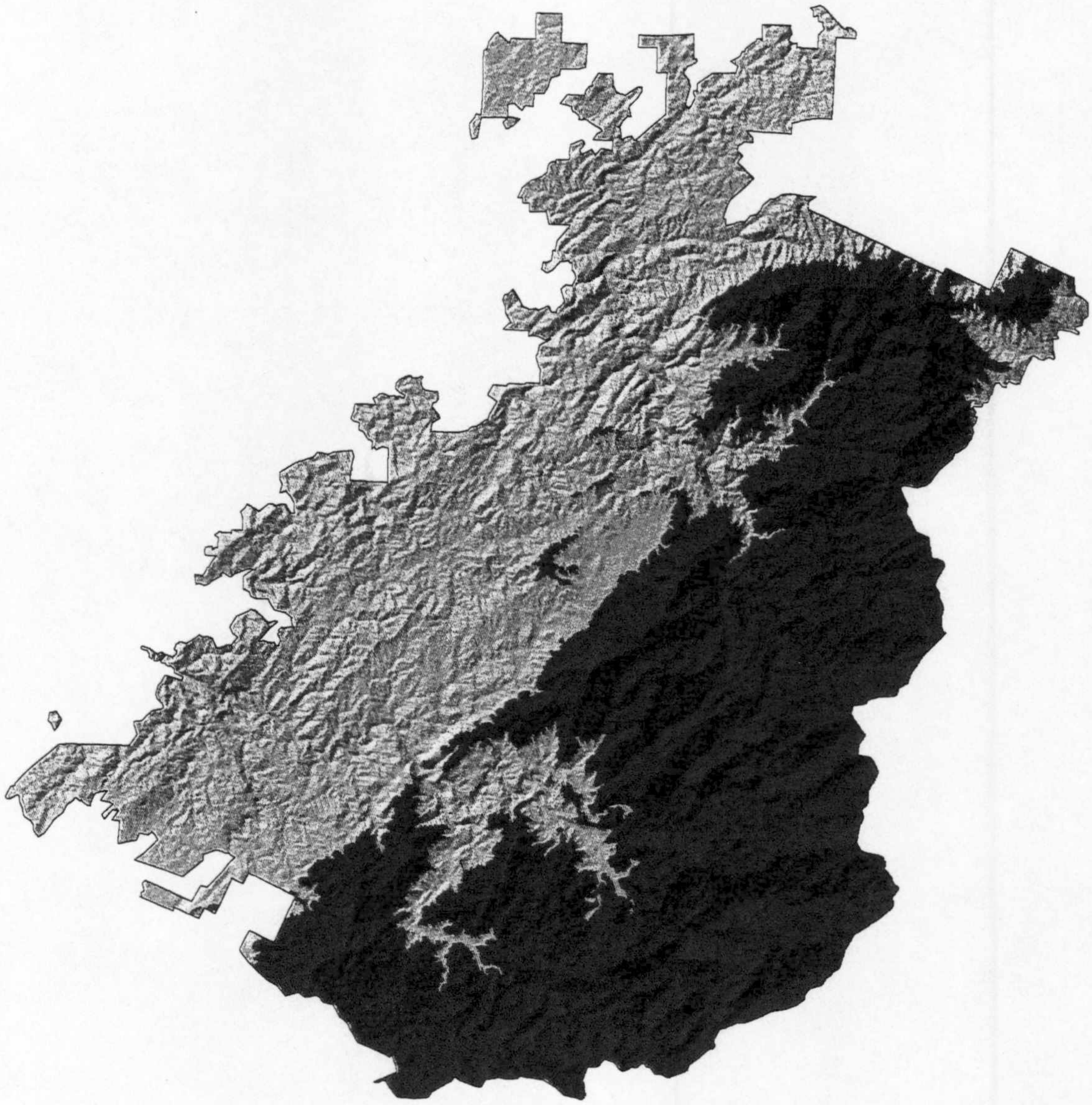

Figure 2. Tellico Ranger District, Cherokee National Forest, Tennessee. Green (dark) areas represent the Mountain Highlands (areas greater than 610 m in elevation). (Source: Defense Mapping Agency 30 meter digital elevation model)

eight degrees cooler than those in the lowlands (USDA 1981).

Typically, soils of the mountains reflect the cooler and wetter climate of the mountains. Such differences in soils are associated with altitude, exposure, and parent material. Parent material in this area is predominantly phyllite, slate, sandstone, and quartzite. All of the soils in the Mountain Highlands are classified as Inceptisols. The main subgroups include Typic and Umbric Dystrochrepts, and Typic Haplumbrepts (Scott ND). Most of the soils found in this area belong to two soil associations, the Ditney-Brookshire-Jeffrey association and the Sylco-Citico-Brookshire association. Several of the same soil mapping units occur in both associations. Typically both associations tend to be loamy and stony, with depths varying from shallow to very deep depending on slope position. Both associations can be found on narrow ridgetops along steep mountainsides or in deep coves. Generally, however, the Sylco-Citico-Brookshire association occupy areas with steeper slopes. The Ranger-Citico-Fletcher soil association is also found in this area (Scott ND).

The known history of human occupation of the Southern Appalachians is long and filled with many different peoples. Archeological evidence suggests it was perhaps 10,000 years ago when the first Native Americans hunted in these forested mountains. Bass (1977) concludes that prehistoric settlement patterns included use of the Unaka Mountains primarily for hunting, while permanent settlements were located in the lower drainages of the Little Tennessee River. During this period, due to the limited occupation of the higher elevations by Native Americans, the incidence of fire was probably low. In later periods, as agriculture was introduced, settlement patterns became more permanent and stable.

Habitations were fairly evenly distributed across the landscape between the uplands and lowlands, with an emphasis on settlement along valley bottomlands and floodplains. Fire became much more extensively used for clearing of land for agriculture (Chapman 1985; Delcourt et al. 1986).

In addition to agricultural clearing, Native Americans might have used fire for many other reasons. Hudson (1976) states that when hunting, they used fire to surround and drive game. They would also burn the forest to clear the thick underbrush to reduce the threat of dangerous forest fires and to keep the forest open, to improve habitat for deer and buffalo, and to make gathering of acorns and chestnuts easier. Delcourt and Delcourt (1996, unpublished data) studied the pollen and charcoal-particle record of a bog in western North Carolina to attempt to characterize the relationship between the use of fire by Native Americans and vegetation composition in the Southern Appalachians. Interpreted within the context of the existing archeological record, they have found that through the use of selective burning, Native Americans probably played an important role in determining the composition of the vegetation of the Southern Appalachians.

In 1905, the U.S. Geological Survey considered three agents to be the most injurious to the existence of the native forest in this area: fire, logging, and clearing of lands for farming (Ayres and Ashe 1905). Ayres and Ashe considered clearing of the land for agricultural purposes as the most damaging to the forested landscape. Natural or anthropogenic forest fires were also an important part of the ecosystem dynamics. These fires were widely regarded as destructive to forest composition and reproduction. As a result, there was an increased emphasis on fire suppression throughout most of the twentieth century.

Logging operations were not widespread before the turn of the twentieth century, due to the difficulty of access to many of the forested areas at higher elevations. As technology improved, large timber companies moved in with massive logging operations. Part of the study area was acquired by the Smoky Mountain Timber and Improvement Company in the early 1900s. Railroad lines were constructed along the two main drainages of this area, Citico Creek and Tellico River, and eventually connected with the Little River Railroad, which came out of the now Great Smoky Mountains National Park. The railroad line was completed around 1910. Logs were removed on narrow-gauge tramways that were built up the stream valleys and on the mountain slopes (Weals 1991). Names and ownership of the land changed throughout these times, but by the late 1920s, virtually all of this area had been cut over and harvested.

Around this same time, Congress authorized the federal government to acquire lands for protecting the headwaters of navigable streams, and the federal government began purchasing such areas in southeast Tennessee and northeast Georgia. In 1920, President Woodrow Wilson officially designated these lands as the "Cherokee National Forest." In 1936, President Franklin D. Roosevelt issued another proclamation that enlarged the area of the national forest and redrew the boundaries so that it was exclusively within Tennessee, dividing it into southern and northern sections (Harvey Broome Group 1992).

METHODS AND DATA ANALYSIS

Sampling Procedures

Forest stands for use in the study were selected to represent the range of site conditions in the study area, including in particular, stands with mature vegetation of each possible vegetation type for the area. Natural stands more than 75 years old were initially identified using stand age data supplied by USFS personnel. Ground reconnaissance verified stand suitability. Stand suitability was based on finding stands that included homogenous mixtures of overstory and understory species, and showed no recent evidence of fire, disease, or logging (Jones et al. 1984). In addition, sample sites were selected to represent an inclusive range of environmental conditions within the study area. A matrix was constructed based on slope type and aspect. Aspect was broadly classified as either north-facing (315° to 135°) or south-facing (136° to 314°); and five classes of slope position were identified from USGS topographic maps: 1) ridges, 2) upper side slopes, 3) middle side slopes, 4) lower side slopes, and 5) coves. These were combined to form nine combinations of landform and aspect in which sampling would take place. At this stage of plot location, ridges were considered to have no aspect. A total of ninety plots was established in mature stands meeting the above topographic criteria.

Methodology for sampling vegetation was based on Jones' (1988) study of old-growth forests in South Carolina. A series of nested plots was established in each sample stand (Figure 3). In the 0.04 ha circular plot (400 m^2), species and canopy coverage were

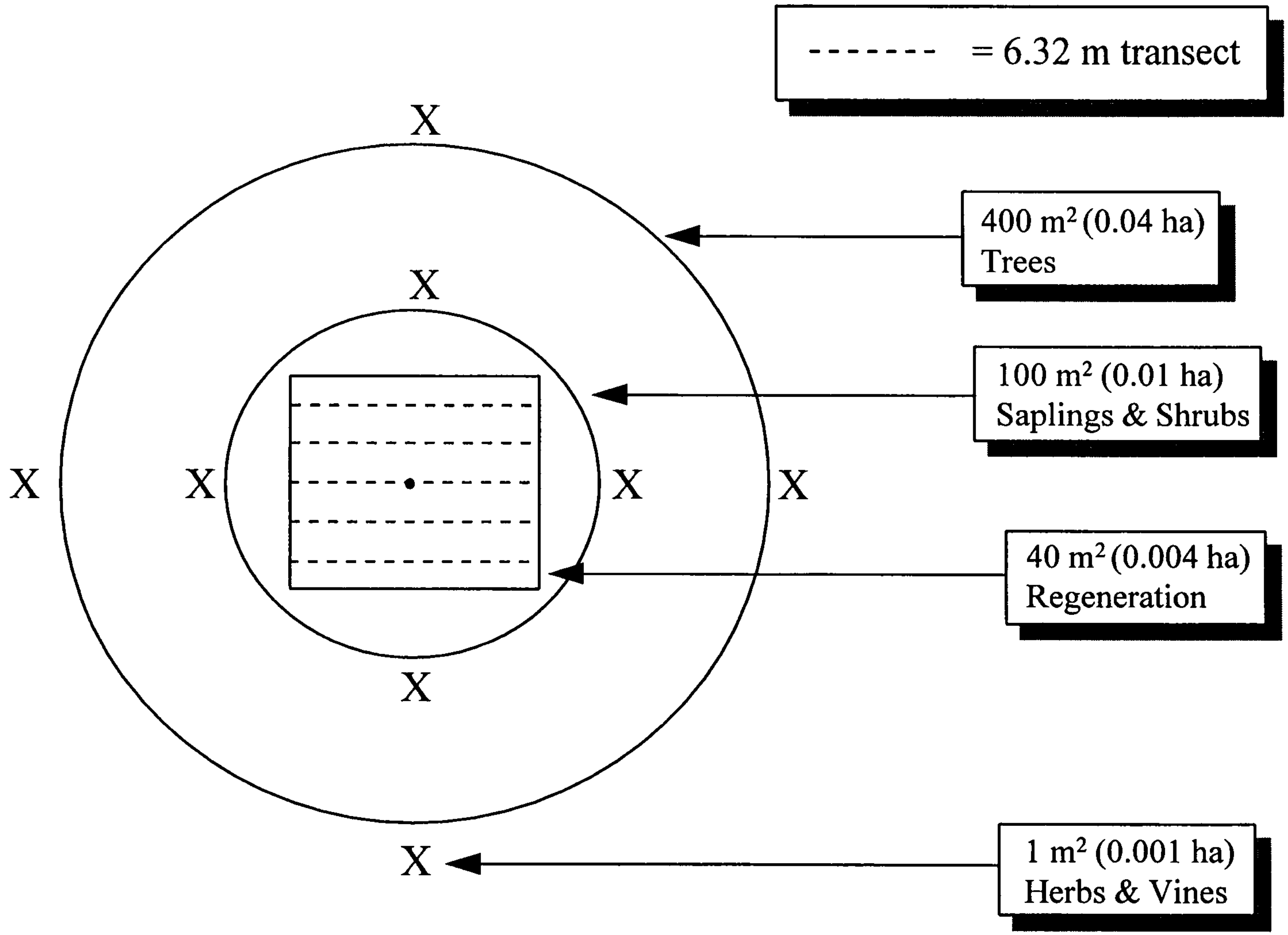

Figure 3. Arrangement and sizes of plots used to sample vegetation.

recorded for each tree greater than 12.5 cm in diameter at 1.3 m from the ground (dbh). In the 0.01 ha circular plot (100 m^2), species and canopy coverage were recorded for each sapling and shrub less than 12.5 cm dbh and at least 1.3 m in height. Within a 0.004 ha square plot (40 m^2), species and length of crown interception along five, 6.32 m transects were recorded for regeneration and shrubs less than 1.3 m tall. A modification of Daubenmire's (1959) coverage class was used to estimate herbaceous cover by species within eight, 1 m^2 square plots along the perimeters of the 0.04 ha and the 0.01 ha circular plots. Coverage refers to the proportion of the plot covered by the vertical projection of plant crowns to the ground surface. Basal area of canopy dominants was determined for each plot. A canopy closure index was derived for each plot by measuring canopy closure with a concave densiometer at plot center and at four places along the edge of the 400 m^2 circular plot and taking the average of the five measurements. Higher values represent a more open canopy. Sources used for species identification included Radford et al. (1968) and Wofford (1989). Species nomenclature throughout this document follows that of Radford et al. (1968).

The following landform variables were recorded for each plot: 1) aspect, 2) slope angle, 3) elevation, 4) slope position, 5) landform index (McNab 1993), and 6) terrain shape index (McNab 1989). Aspect was recorded as azimuth in degrees from plot center with a hand compass, and then transformed into a linear scale ranging from 0 for southwest aspects, to 2 representing northeast aspects (Beers et al. 1966). To have a complete data set, aspect was determined for all plots, even ridges. Aspect for ridgetops was defined by the prevailing direction of the ridgetop landform. By means of a Suunto clinometer, slope angle in percentage was measured from plot center to the plot edge above and below plot center and an average of the absolute value of these measurements was taken. Elevation was measured in meters using a barometric altimeter. Slope position was determined by the estimated location of the plot between the ridgeline, which was given a score of 100, and the bottom of the slope, usually a streambed, which was given a score of 0.

The degree of exposure for each plot was quantified using landform index (LFI) and the geometric shape of the plot was quantified using terrain shape index (TSI). The LFI value is the average of eight slope gradient measurements in percent scale, taken from plot center to the surrounding horizon at 45 degree intervals. Higher LFI values are indicative of more protected landforms, such as lower side slopes or coves, while lower, even negative, values are associated with more exposed landforms, such as ridges and upper side slopes. The TSI value is the average of eight slope gradient measurements in percent scale, taken from plot center to the perimeter of the plot at 45 degree intervals. Positive TSI values indicates a plot with a concave shape, while a negative value represents a convex plot shape.

Soil variables were limited to those that could be measured in the field. A soil pit was dug in each plot and the following were recorded: humus thickness, A horizon thickness, and solum thickness (in centimeters). The soil solum is defined as the upper portion of the soil profile (A and B horizons) in which the processes of soil formation are active. The percentage of coarse fragments was noted.

Data Analysis

Vegetation data were summarized by species and size class in terms of percent cover of the plot area. Relative coverage was calculated for all strata. Relative density was calculated only for the three largest size classes: tree, sapling and shrub, and regeneration. Importance Value (IV) 200 (relative coverage + relative density) was determined for all strata except the herbaceous stratum, where IV 100 (relative coverage) was used. A data matrix based on these importance values was composed of 294 species and 90 plots. Vegetation occurring in each stratum was considered to be an individual species. Therefore, each stratum class of a species was considered a "pseudospecies."

The indirect ordination technique of detrended correspondence analysis (DCA) was performed on the matrix of species and pseudospecies importance values using the computer program DECORANA (Hill 1979). The goal of ordination is to determine the dominant patterns of variation within the vegetation data across the range of sites sampled. DCA is a method of ordination whereby species and plots are arranged along hypothetical environmental gradients (ordination axes). The output from DCA is a diagram in which species and plots are represented by points in two-dimensional space along these ordination axes. Interpretation of an ordination of sample plots is such that points that are close together correspond to plots that are similar in species composition, and points that are far apart correspond to plots that are dissimilar in species composition. Similarly, for a species ordination, each point on the diagram corresponds to a species, and the distances between points are an approximation of their similarity in terms of distribution within the sample plots. Because of this output, it is often called a "cluster analysis."

The vegetation data were also analyzed using TWINSPAN (Hill 1979), a computer program that classifies floristic data by using a polythetic divisive technique. This technique uses all the species recorded and starts with all the plots as a group and progressively divides them into groups with fewer members based on their similar vegetational attributes (Gauch 1982). This approach is computationally efficient and can be used to analyze large data sets. Because of its many desirable features, TWINSPAN is commonly used for classifying floristic data (Jongman et al. 1995). TWINSPAN was used in conjunction with DECORANA to avoid subjectivity in the delineation of site units. The program provides for several options in conducting the analysis, and several analysis strategies were attempted. However, the final TWINSPAN classification utilized all the default settings, with the exception of the species cut levels. Since importance values ranged from 0 to 200, four cut levels (0, 5, 20, and 40) were used to more accurately reflect the range of importance values.

DCA ordination and TWINSPAN classification are both methods of indirect gradient analysis because the patterns of the floristic data are identified independently of any previous ideas about controlling environmental factors or successional sequences (Kent and Coker 1992). The site units are then related to environmental variables in a second stage of analysis using stepwise discriminant analysis (SWDA) to detect possible environmental gradients (SAS Institute 1988). SWDA selects from a set of variables those that contribute the most to differentiation among class types. In this case, simple discriminant functions are constructed in which those environmental variables are selected that optimally predict the classification. The landform variables used in this analysis included aspect, slope gradient, elevation, slope position, landform index, and terrain shape index. Soil variables used in this analysis included humus depth, A horizon depth, and solum depth.

As a comparison with the indirect techniques, detrended canonical correspondence analysis (DCCA) was also applied to the data using the computer program CANOCO (ter Braak 1987). DCCA is considered a direct ordination or gradient analysis technique and is used to identify ecological units from vegetation, soils, and landform data. This technique differs from the indirect method because it incorporates the correlation and regression between floristic data and environmental variables within the ordination analysis itself. Using multiple regression, together with the techniques of DCA, an integrated ordination of species together with associated environmental data is obtained. The ordination diagram of DCCA displays site, species, and environmental variables.

Results of the direct and indirect gradient analyses were compared and evaluated in terms of correlation coefficients, significance levels, and prior knowledge of the ecosystem.

RESULTS

Indirect Ordination and Classification

The initial vegetation data matrix was composed of 90 plots and 294 species and pseudospecies. Species and pseudospecies that occurred in only one plot were removed from the analysis. The final data matrix was composed of 90 plots and 241 species and pseudospecies. DCA ordination using DECORANA and TWINSPAN classification of this matrix resulted in the identification of five plot clusters or "site units" (Figure 4). As a first step, DCA ordination results were used to place the individual plots in ordination space, followed by a subjective designation of site units. Next, TWINSPAN was used to reduce some of the subjectivity in assigning plots to site units from DCA. TWINSPAN divided the data set into progressively smaller site units based on similar vegetative composition among plots. Classification and final assignment of site unit membership of the plots using TWINSPAN analysis agreed with the delineation of the site units by DCA, with the exception of the classification of two plots.

The only disagreement between DECORANA and TWINSPAN occurred in Site Units 2 and 4. Two plots that DECORANA clustered with Site Unit 4 were classified into Site Unit 2 by TWINSPAN. From the TWINSPAN output, one of the plots was a borderline classification with the rest of Site Unit 2 after the first division. After three divisions, TWINSPAN classified these two plots into their own unit, segregating them from the rest of the plots comprising Site Unit 2. Upon further review of species

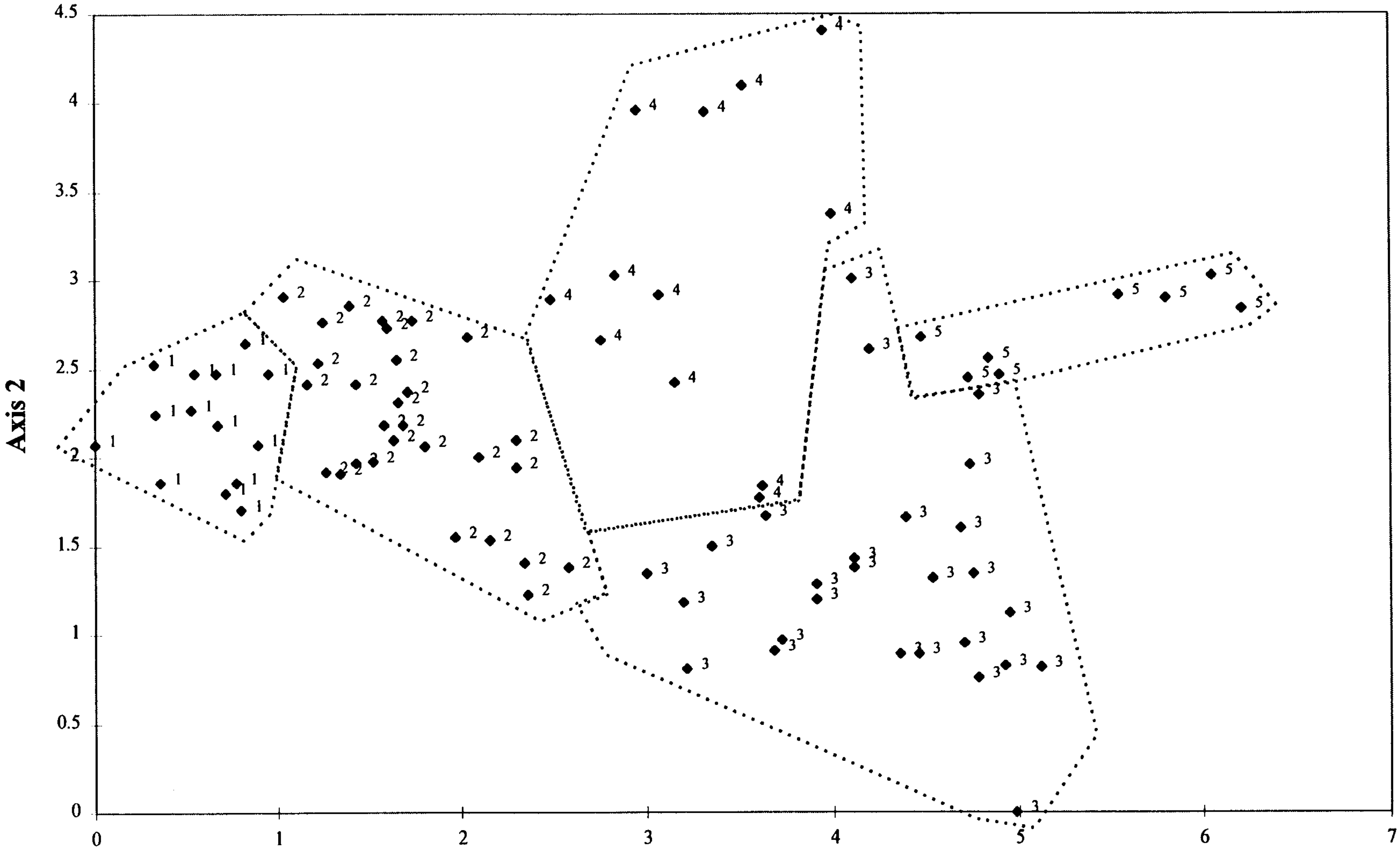

Figure 4. DCA ordination of ninety plots using DECORANA. Numbers represent TWINSPAN derived site units. Lines are subjectively drawn to show site unit membership.

composition and importance values in these two plots, it was determined that they were floristically different from other Site Unit 2 plots, and DECORANA provided the most ecologically significant delineation of these plots. Therefore, they were assigned to Site Unit 4.

Each point in Figure 4 represents an individual plot. The location of each plot is determined by the weighted average of the importance values of the species that occur in it, the weighting of each site being proportional to the relative importance of each species (Hill and Gauch 1980). The greater the distance between any two points, the greater the difference in floristic composition of the plots which they represent. Axis 1 and Axis 2 represent hypothetical environmental gradients. Because indirect ordination of the plots and species is not constrained by environmental variables, Axis 1 and Axis 2 in Figure 4 remain unlabeled. Assignment of a particular environmental variable(s) to those axes occurs after discriminant analysis.

DCA summarizes the main variation in the vegetation data by employing a method of Gaussian ordination for each axis. Each hypothetical environmental axis is constructed such that the species data optimally fit Gaussian response curves along this axis. The units of the ordination diagram are in standard deviations. As an approximation, a species along a hypothetical environmental gradient should appear, rise to its mode, and disappear within four standard deviations (Gauch 1982). Similarly, a complete turnover in the species composition of samples is expected to occur in about four standard deviations. Therefore, plots that are separated by at least four standard deviations can be expected to have no species in common. This is considered "beta diversity"—the diversity of species from one habitat to the next rather than the diversity within a single habitat, often referred to as alpha diversity (Whittaker 1975). DCA Axis 1 and Axis 2 have beta diversities of 6.21 and 4.41 standard deviations, respectively. The long length of both axes represents a significant amount of species diversity in all plots. Specifically, because there are more than four standard deviations separating Site Unit 1 and Site Unit 5 along Axis 1, plots comprising these units have virtually no species in common. Separation of site units is distinct, although overlap clearly occurs between Site Units 3 and 4.

Figures 5 through 8 depict the DCA ordination of individual species by stratum. Similar to the plot ordination, each point represents a species and its location is determined by the weighted average of its importance values across all plots in which it occurs. This weighted average indicates the relative position of the center of the species' distributions along the hypothetical environmental axis as described above (Hill and Gauch 1980). Therefore, the abundance or probability of occurrence of a species decreases with distance from its location in the diagram. The distances between the points are expressions of how similar the species are in their distribution across all plots. Of particular significance, is the long length of both axes in these figures. Similar to the plot ordination, this shows the great amount of species diversity that exists in all plots.

DCA produces its results in terms of eigenvalues and eigenvectors. Eigenvalues are values that represent the relative contribution of each variable to the explanation of the total variation in the data. The eigenvalue in DCA is always a number between 0 and 1; the higher the value, the more important the ordination axis. Typically, the eigenvalues decrease in size and importance with successive axes. Axis 1 accounted for more

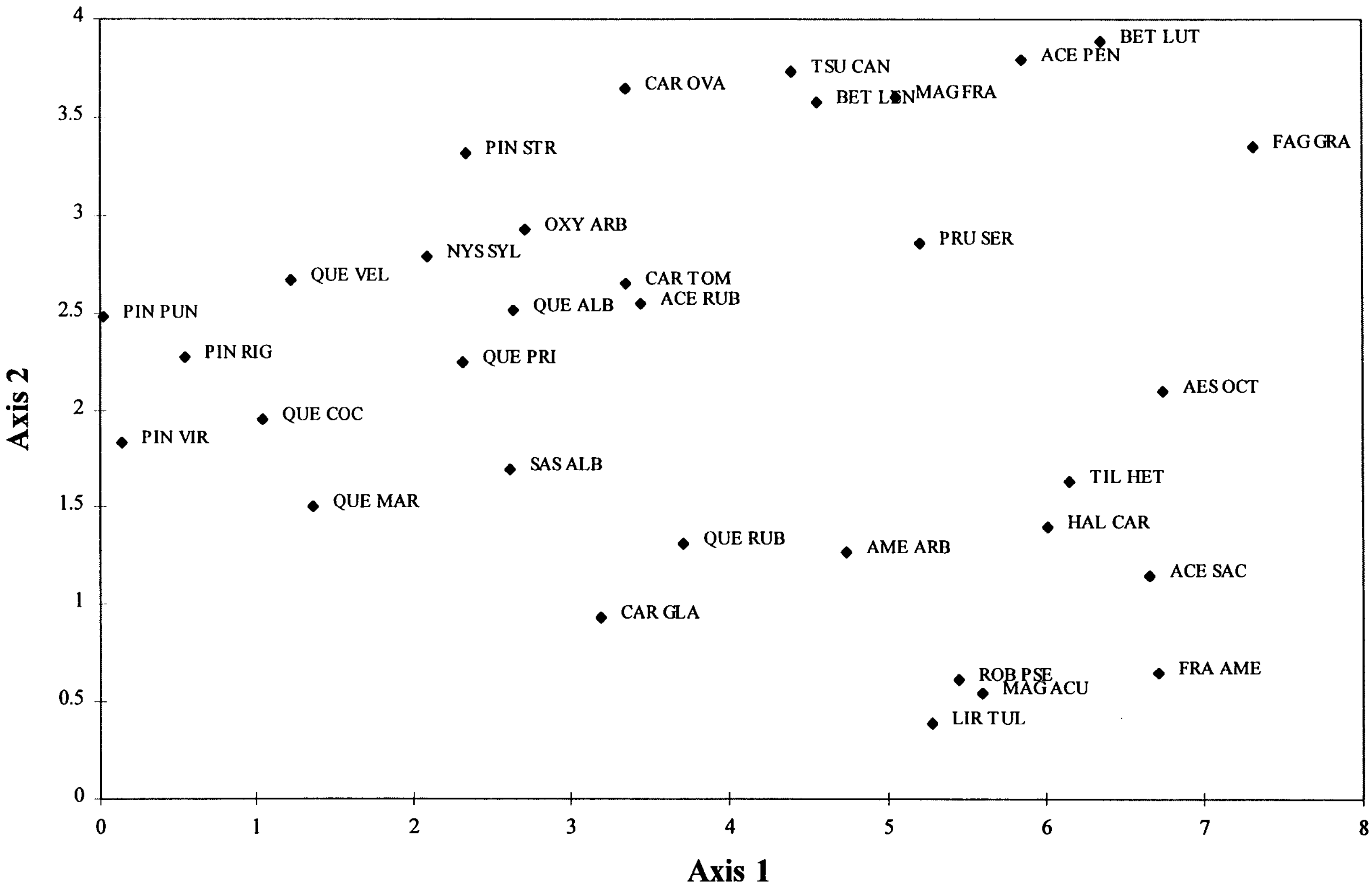

Figure 5. DCA ordination of the tree stratum using DECORANA. Species abbreviations consist of the first three letters of the genus followed by the first three letters of the species epithet.

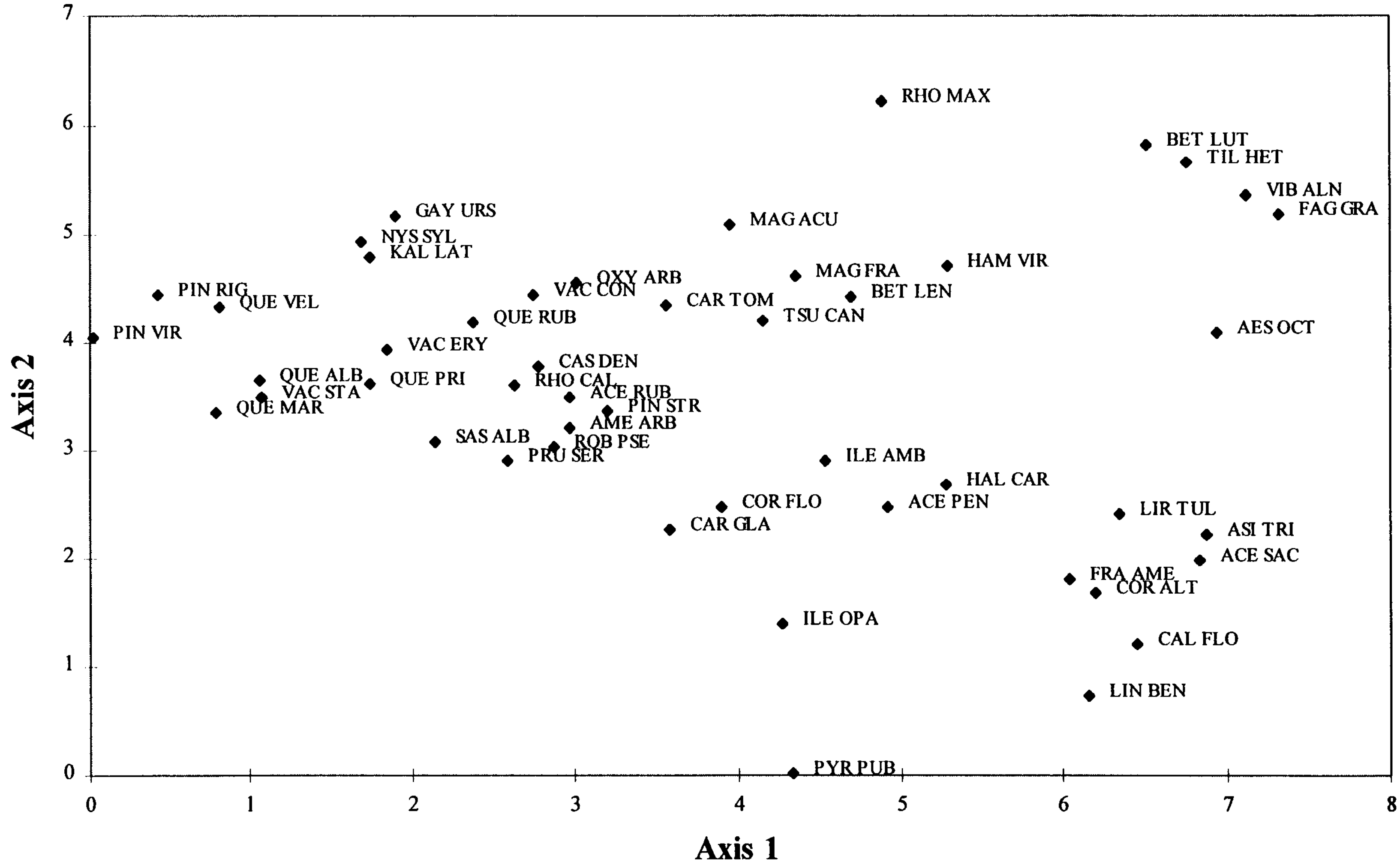

Figure 6. DCA ordination of the sapling and shrub stratum using DECORANA. Species abbreviations consist of the first three letters of the genus followed by the first three letters of the species epithet.

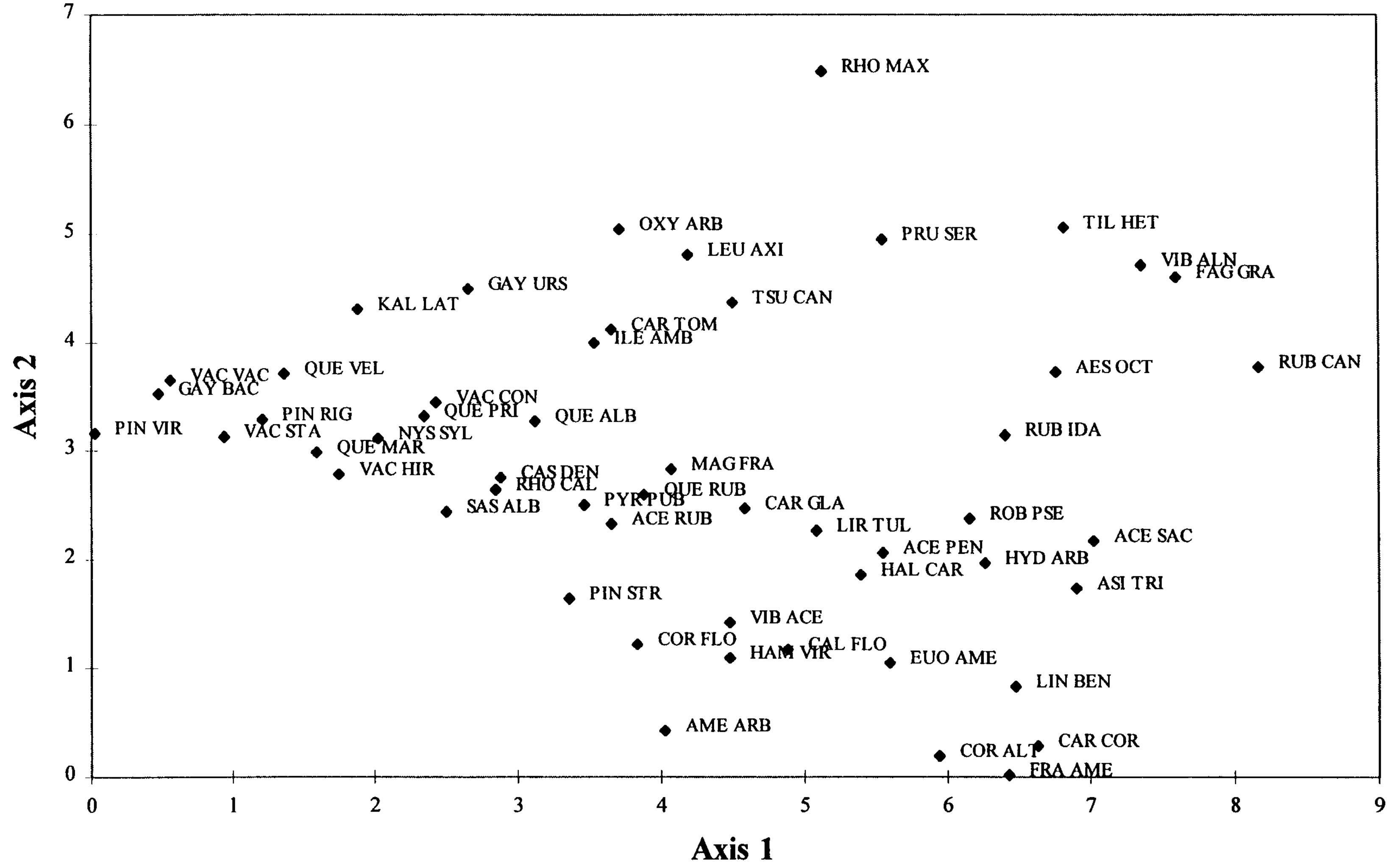

Figure 7. DCA ordination of the regeneration stratum using DECORANA. Species abbreviations consist of the first three letters of the genus followed by the first three letters of the species epithet.

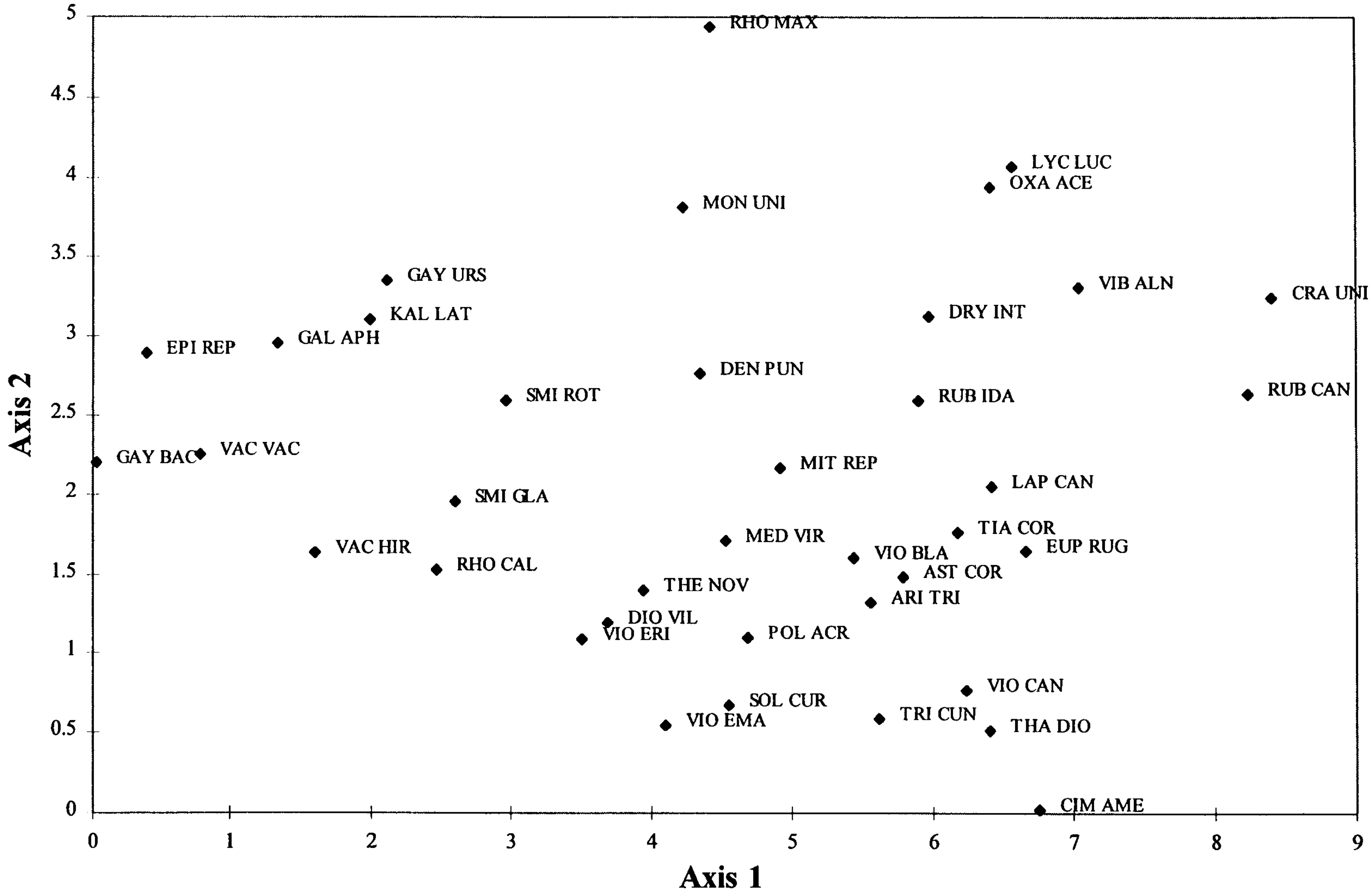

Figure 8. DCA ordination of the herbaceous stratum using DECORANA. Species abbreviations consist of the first three letters of the genus followed by the first three letters of the species epithet.

variation in the species distributions than Axis 2, as evidenced by an eigenvalue of 0.753 for Axis 1 and an eigenvalue of 0.387 for Axis 2.

Stepwise Discriminant Analysis

To determine the relationship between vegetation, soils, and landform, nine environmental variables were used as data for a stepwise discriminant analysis (SWDA) on the site units designated by DECORANA and TWINSPAN. These variables included elevation, aspect (transformed), percent slope, slope position, landform index, terrain shape index, humus depth, A horizon depth, and solum depth. Site units were considered as the class variables in the analysis. Stepwise selection begins with no variables in the model, and at each step the variable is entered that contributes most to the discriminatory power of the model. When all variables in the model meet the criterion to stay and none of the other variables meets the criterion to enter, the stepwise selection stops (SAS 1988). Results of this analysis identified six out of the nine landform and soil variables as significant at the 0.15 level (Table 1). Elevation appears to be the most important discriminating variable, accounting for over 54% of species variation, followed by slope position and aspect. Both slope position and aspect discriminated among site units about equally, contributing approximately the same amount of explanation of variation.

Cross-validation of the environmental variables selected by SWDA (Table 1) was performed to determine how successfully the variables could be used in combination to predict membership into the five site units produced through DCA ordination and TWINSPAN classification. Using a two variable model comprised of elevation and slope

Table 1. Significant variables identified through SWDA from 9 environmental variables, 90 plots, and 5 site units. Significance level for entry and retention = 0.15.

Environmental Variable	R^2	**F Statistic**	**Probability > F**
Elevation	0.5470	24.151	4.0×10^{-13}
Slope Position	0.3594	11.223	3.0×10^{-7}
Aspect	0.3404	10.324	9.0×10^{-7}
A Horizon Depth	0.2796	7.764	2.0×10^{-5}
Solum Depth	0.1929	4.779	1.65×10^{-3}
Humus Depth	0.1668	4.004	5.18×10^{-3}

position, site unit membership was accurately predicted 56% of the time (Table 2). Overall classification ability of a similar two variable model using elevation and aspect was only slightly less at 55% (Table 3). It is interesting to note the relative differences in predictive ability for each site unit based on these two variable models.

Comparing Tables 2 and 3, elevation and slope position classify all five site units slightly more evenly, the lowest classification occurring in Site Units 2 and 4. When aspect is substituted for slope position, prediction of Site Unit 4 decreases considerably with about an equal increase in Site Unit 1 prediction. It can be inferred from these results that slope position is much more important in delineating Site Unit 4, than is aspect, and that aspect is a major factor in the classification of Site Unit 1 plots. Site Unit 5 is the same in both models, which allows the interpretation that elevation is the most important variable in determining Site Unit 5 composition. Another important aspect of these tables

Table 2. Classification results of cross-validation discriminant analysis using two environmental variables (elevation and slope position) and five site units. Numbers expressed as percentages.

	Predicted Site Unit				
Actual Site Unit	1	2	3	4	5
1	**62**	8	23	7	--
2	23	**23**	27	27	--
3	18	--	**63**	19	--
4	--	16	17	**42**	25
5	--	--	--	12	**88**
Classification accuracy rate: 56%					

Table 3. Classification results of cross-validation discriminant analysis using two environmental variables (elevation and aspect) and five site units. Numbers expressed as percentages.

	Predicted Site Unit				
Actual Site Unit	1	2	3	4	5
1	**92**	8	--	--	--
2	43	**17**	23	17	--
3	19	7	**70**	4	--
4	17	33	8	**9**	33
5	--	--	--	12	**88**
Classification accuracy rate: 55%					

is the location of the misclassified observations. The majority of misclassified plots were placed in Site Units 2 and 4.

Surprisingly, when elevation, slope position, and aspect were used as a three variable model, overall classification ability remained at 55% (Table 4). All three variables in the model increase the prediction of Site Unit 2, but decrease the prediction of Site Unit 1. Again, prediction of Site Unit 4 is lowest and that of Site Unit 5 is highest. When A horizon depth was added into the model, the predictive ability of the classification improved to 60% (Table 5). The addition of A horizon depth strengthened the overall classification, especially in Site Units 2 and 4. However, similar to the other models, the majority of misclassified plots were located in these two site units. Accuracy of the classification was reduced to 55% when a five variable model was used (addition of solum depth). Final analysis of all six environmental variables that were identified as significant through SWDA further reduced the predictive ability of the model to only 41%, with Site Unit 5 being the least accurately predicted followed by Site Units 4 and 1 (Table 6). Most interesting from this table is the overall reduction in classification accuracy of Site Unit 5. Compared to the other models, the strength of elevation as the main discriminator in Site Unit 5 membership is weakened by the addition of solum depth and humus depth into the model. Therefore, it appears that the four variable model consisting of elevation, slope position, aspect, and A horizon depth is the most accurate predictor of site unit classification.

Table 4. Classification results of cross-validation discriminant analysis using three environmental variables (elevation, slope position, and aspect) and five site units. Numbers expressed as percentages.

	Predicted Site Unit				
Actual Site Unit	1	2	3	4	5
1	**77**	15	--	8	--
2	24	**30**	23	23	--
3	--	19	**70**	11	--
4	--	42	17	**8**	33
5	--	--	--	12	**88**
Classification accuracy rate: 55%					

Table 5. Classification results of cross-validation discriminant analysis using four environmental variables (elevation, slope position, aspect, and A horizon depth) and five site units. Numbers expressed as percentages.

	Predicted Site Unit				
Actual Site Unit	1	2	3	4	5
1	**77**	23	--	--	--
2	17	**47**	6	30	--
3	--	19	**70**	11	--
4	8	17	17	**33**	25
5	--	--	--	25	**75**
Classification accuracy rate: 60%					

Table 6. Classification results of cross-validation discriminant analysis using six environmental variables (elevation, slope position, aspect, A horizon depth, solum depth, and humus depth) and five site units. Numbers expressed as percentages.

	Predicted Site Unit				
Actual Site Unit	1	2	3	4	5
1	**38**	54	--	8	--
2	13	**53**	10	23	--
3	--	11	**74**	15	--
4	--	42	25	**25**	8
5	--	--	--	87	**13**
Classification accuracy rate: 41%					

Direct Ordination

DCCA is a combination of indirect ordination (DCA) and multiple regression. The resulting ordination is a product of the variability of the environmental data as well as the variability of the species data. Figure 9 shows the DCCA ordination of all ninety plots, using the same TWINSPAN derived site units as in Figure 4. Interpretation of this figure is similar to Figure 4; each point represents an individual plot. However, DCCA ordination represents the variation in species composition over the plots as can be explained by the environmental variables. Figure 9 expresses a similar pattern of variation

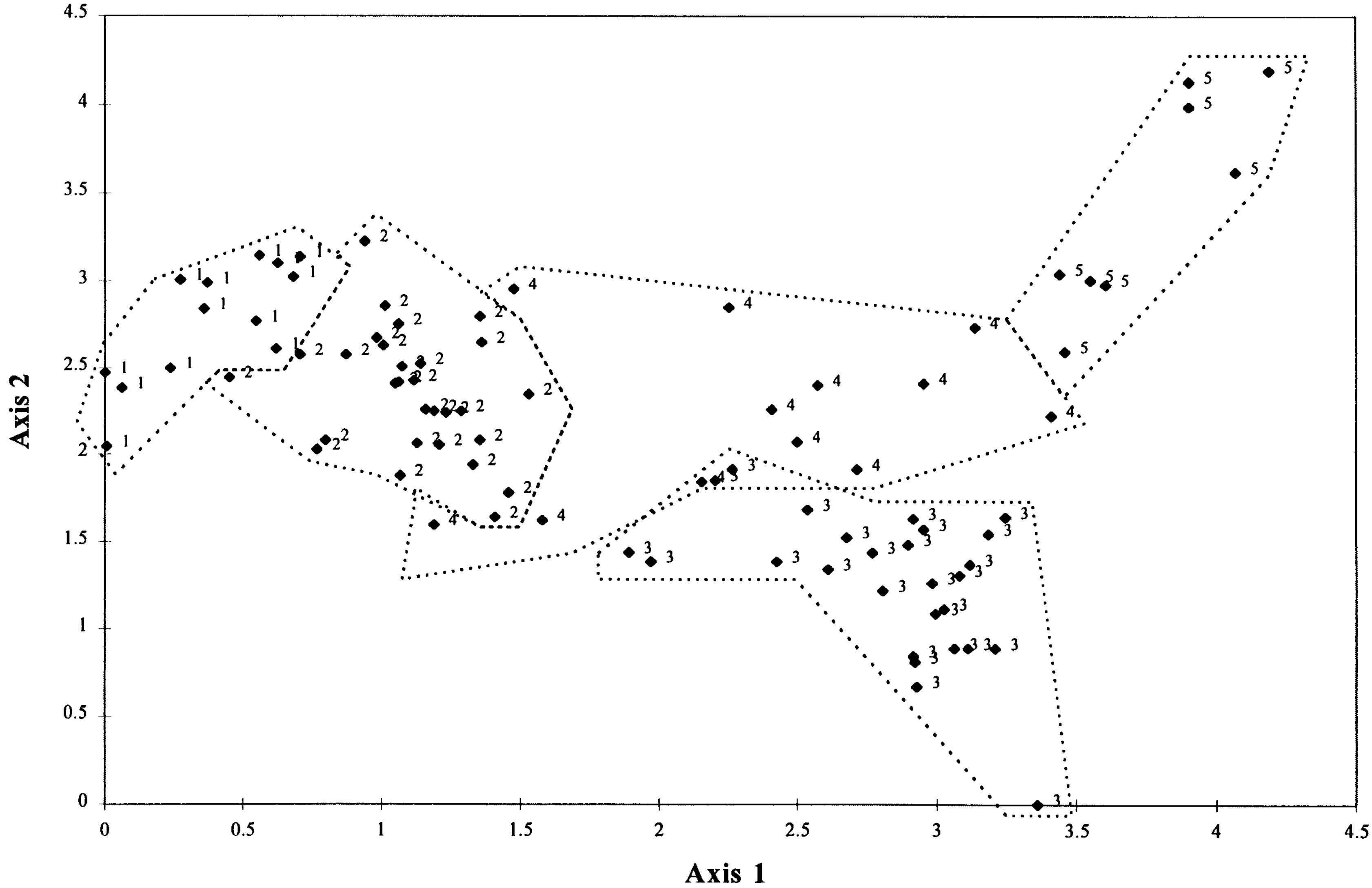

Figure 9. DCCA ordination of ninety plots using CANOCO. Numbers represent TWINSPAN derived site units. Lines are subjectively drawn to show site unit membership.

in plot (and species) distribution as in DCA (Figure 4). However, unlike DCA, there is a much greater degree of overlap of site units, especially in Site Unit 4. This spread of Site Unit 4 agrees with the classification results from the discriminant analysis, which showed the low predictive ability for Site Unit 4.

DCCA uses multiple regression to select the linear combination of environmental variables that explains the greatest portion of the variation in the species scores on each axis (ter Braak 1986). Table 7 lists the correlation coefficients of environmental variables with axes. All nine environmental variables were used in the analysis. By interpreting the signs and relative magnitudes of the correlation coefficients, one may infer the strength of correlation between an environmental variable and a particular axis, as well as the relative importance of each environmental variable for predicting site unit membership. Aspect and elevation appear to be the most important predictors of site unit membership, with aspect being more highly correlated with Axis 1 and elevation more highly correlated with Axis 2. In addition, slope position and landform index are relatively highly correlated with Axis 2. Not surprisingly, slope position and landform index are highly negatively correlated with each other—increasing slope position leads to lower landform index.

DCCA, like DCA, produces its results in terms of eigenvalues, which are values that represent the relative contribution of each variable to the explanation of the total variation in the data. The eigenvalues in DCCA are usually smaller than those in DCA; however, similar to DCA, they are always a number between 0 and 1, and the higher the value, the more important the ordination axis. Table 7 shows that the first eigenvalue of DCCA (0.52) is somewhat lower than the first eigenvalue of DCA (0.75). Typically, the

Table 7. DCCA correlation coefficients of environmental variables with species ordination axes, axes eigenvalues, and species-environment correlation.

Environmental Variable	Axis 1	Axis 2
Aspect	0.48	-0.54
Elevation	0.39	0.59
A Horizon Depth	0.32	-0.15
Landform Index	0.22	-0.37
Slope Position	-0.18	0.40
Solum Depth	0.17	0.13
Humus Depth	0.14	0.18
Slope	-0.09	0.17
Terrain Shape Index	0.08	-0.04
Eigenvalue	0.52	0.33
Species-environment correlation	0.86	0.87

eigenvalues decrease in size and importance with successive axes. Similar to DCA, Axis 1 accounted for more variation in the species distributions than Axis 2, as evidenced by an eigenvalue of 0.52 for Axis 1 and an eigenvalue of 0.33 for Axis 2. Multiple regression of the species scores of the first canonical axis on the environmental variables resulted in a species-environment multiple correlation of 0.86. The species-environment correlation is a measure of how well the extracted variation in community composition can be explained by the environmental variables. A similarly high correlation is also shown between species variation and environmental variation for the second canonical axis.

The most important part of the output from DCCA is the creation of biplots of either the plot ordination or the species ordination, together with the environmental factors. Figures 10 and 11 display the DCCA direct ordination of plots and environmental variables (site/environment biplot), and species (tree stratum only) and environmental variables (species/environment biplot), respectively. Similar biplots can be constructed with other strata; however, the tree stratum was selected since these are used as indicator species in the description of each site unit in later sections. The plots and species points have the same interpretation as in DCA. The environmental variables are represented by arrows or vectors. Only the directions and relative lengths convey meaningful information. The length of an arrow is proportional to its importance and the angles between the arrows reflect the intercorrelations between the variables. An example of this is shown by the relationship between slope position and landform index (LFI). Because they are highly negatively correlated, the arrows for these two environmental variables point in opposite directions. The angle between an arrow and each axis is a representation of its degree of correlation with the axis, and the vector length indicates the strength of the correlation (ter Braak 1987). Therefore, from Figures 10 and 11, it is obvious that aspect and elevation are the two most important environmental variables. These figures display graphically the results described in Table 7—Axis 1 is more correlated with aspect because of the length of the arrow and the small angle between the axis and the environmental vector. Similarly, elevation is more correlated with Axis 2.

Such diagrams show the main pattern of variation in site unit composition as accounted for by the environmental variables, and also show, in an approximate way, the

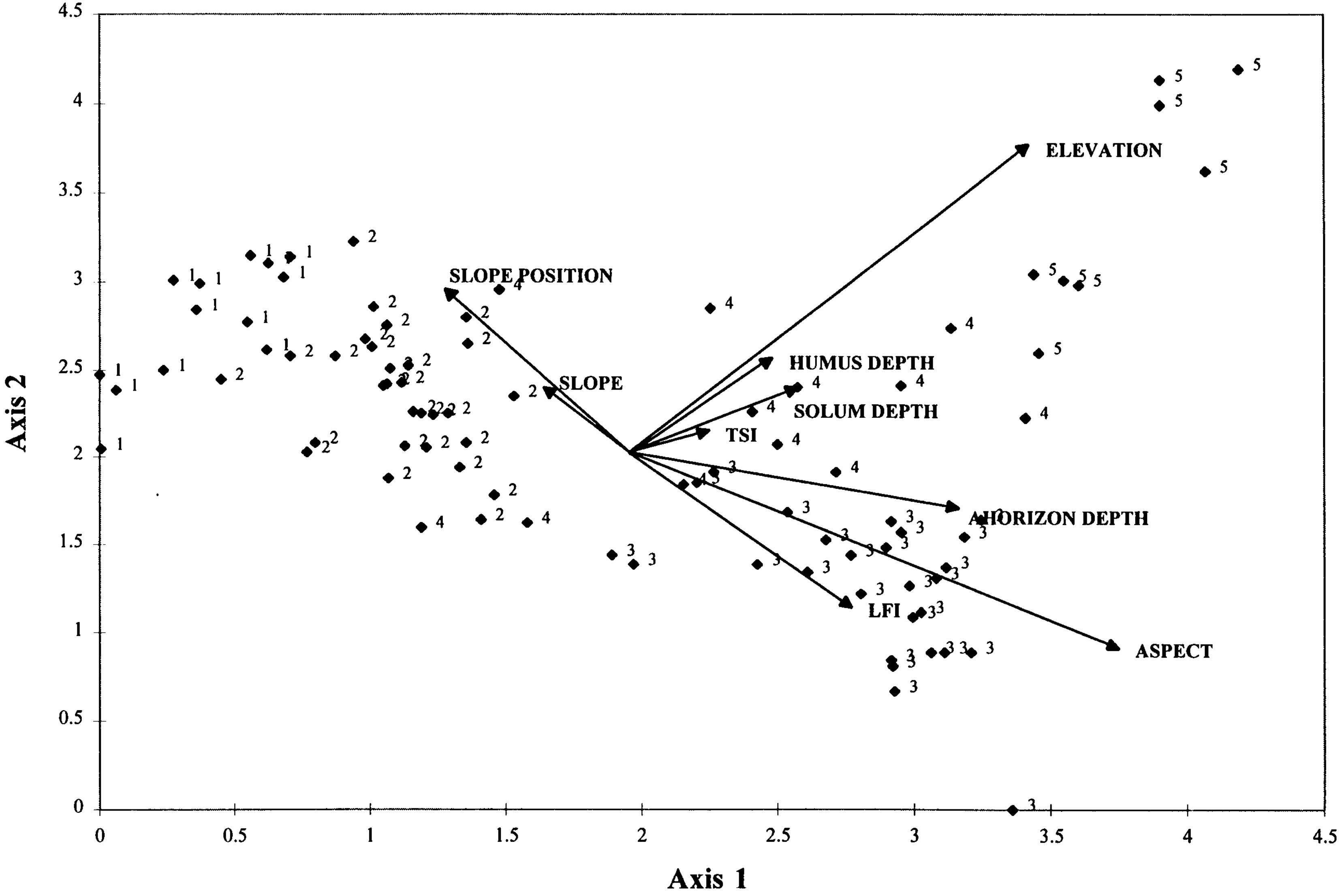

Figure 10. DCCA ordination of plots and environmental variables (arrows) using CANOCO.

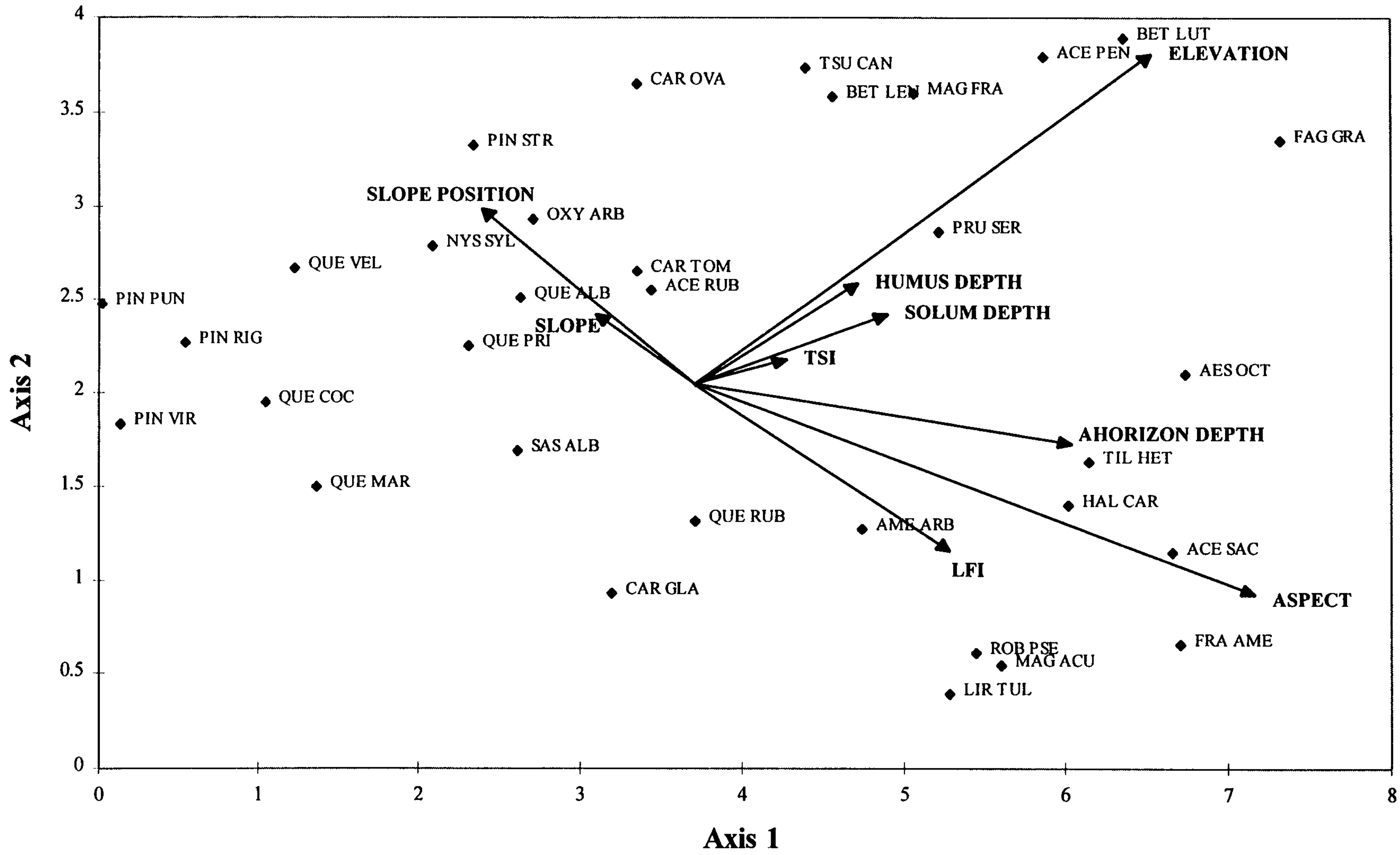

Figure 11. DCCA ordination of tree species and environmental variables (arrows) using CANOCO.

distributions of the species along each environmental variable. The easiest way to interpret the biplot is: each arrow representing an environmental variable determines a direction or "axis" in the diagram, and the species points are projected onto this axis. As an example, the points of a few species are projected onto the axis for elevation in Figure 12 and onto the axis for aspect in Figure 13. The arrows for elevation and aspect have been extended in both directions and perpendiculars have been constructed to these axes from twelve species points. The location of these endpoints indicates the relative position of the centers of a species distribution along the elevational and aspect axes. These projection points indicate the relative value of the weighted average of each species with respect to elevation and aspect. This weighted average is defined as the average of the values of each environmental variable at those sites at which that species occurs. The weighting of each site is proportional to species importance values. Thus, the order of the projection points corresponds approximately to the ranking of the weighted averages of all species with respect to that environmental variable (ter Braak 1988). The length of the perpendicular projection from a site/species point onto an environmental axis has no ecological meaning.

Therefore, Figure 12 can be interpreted to show trends in the distribution of canopy dominants across an elevational gradient. Beech (*Fagus grandifolia*) and yellow birch (*Betula lutea*) are found at the highest elevations, and the yellow pines and scarlet oak (*Quercus coccinea*) are at the lowest elevations. Figure 13 shows trends for aspect. Buckeye (*Aesculus octandra*), silverbell (*Halesia carolina*), and tulip poplar

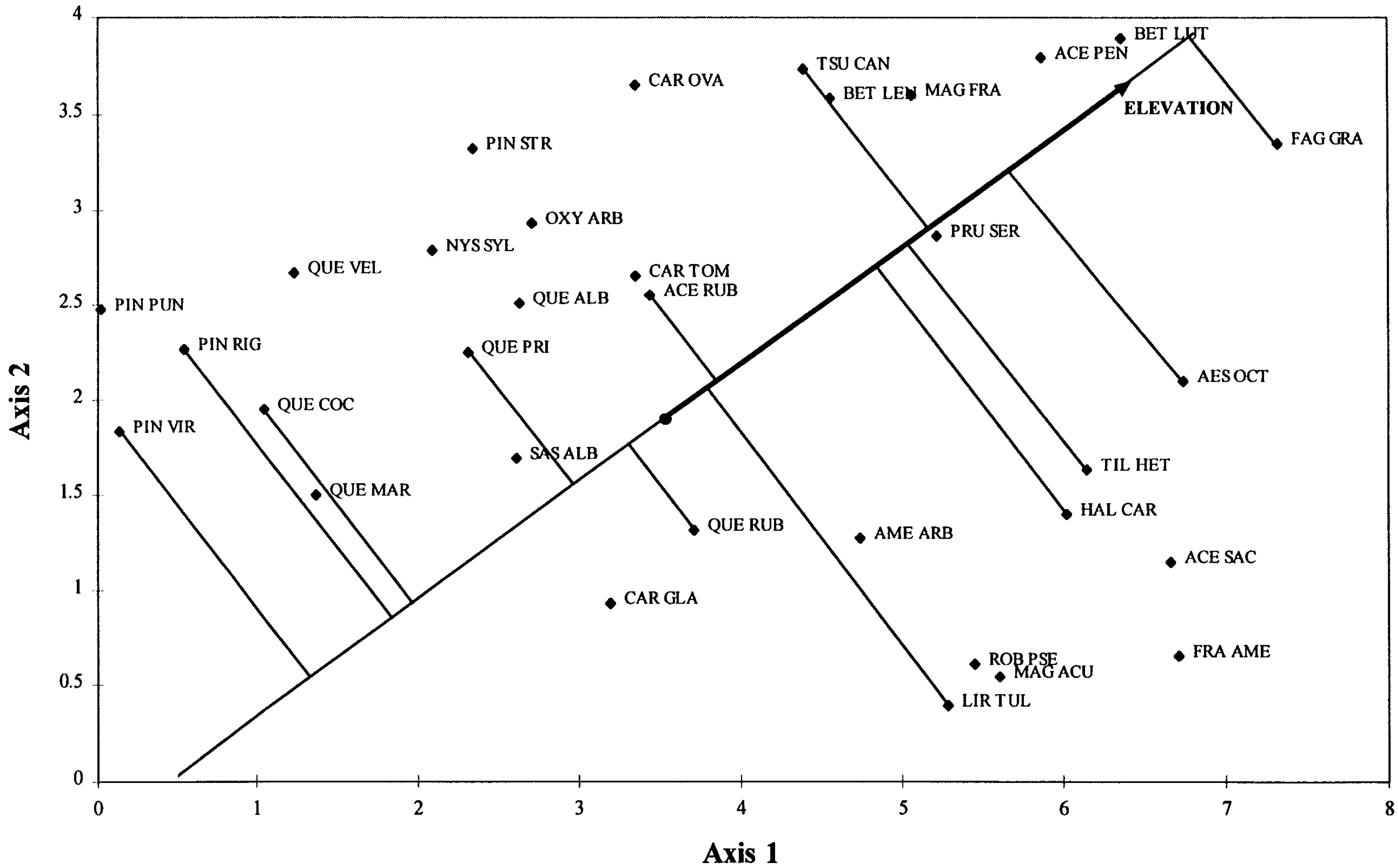

Figure 12. Inferred ranking of twelve tree species along a gradient of increasing elevation, based on the biplot interpretation of Figure 11. Similar interpretations can be made for all species.

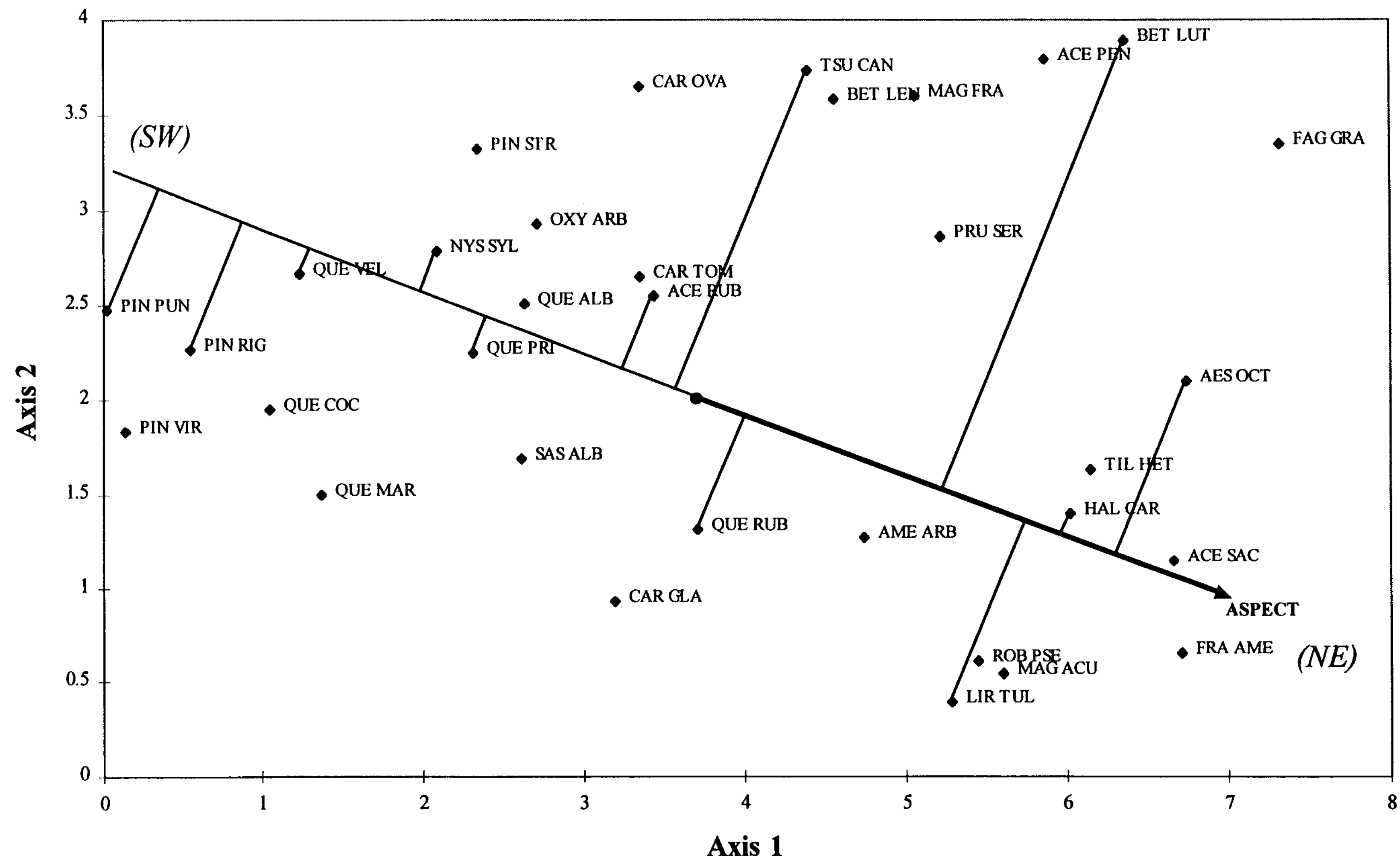

Figure 13. Inferred ranking of twelve tree species along a gradient of increasing transformed aspect (0 to 2), based on the biplot interpretation of Figure 11. Similar interpretations can be made for all species.

(*Liriodendron tulipifera*) are located in areas with the highest transformed aspect (north-east facing slopes ~ 2.0); whereas the yellow pines and black oak (*Quercus velutina*) are found in areas with the lowest transformed aspect (south-west facing slopes ~ 0.0). All vegetation data are not displayed to keep the diagram from being too crowded; however, these kinds of trends can be shown for all species. Similar interpretations can be made for the distribution of sites or site units in relation to an environmental gradient (Figure 10). It can be inferred that Site Unit 5 is located in the highest elevations and Site Unit 3 is located in areas with the highest transformed aspect. Conversely, Site Unit 1 is located in areas with the lowest transformed aspect. Also, similar trends can be interpreted for the other arrows. Site Units 3, 4, and 5 are found in areas with the lowest slope position, highest landform index, and deepest A horizons; whereas Site Units 1 and 2 have the opposite.

Using the results provided by SWDA and DCCA, it was possible to assign an environmental interpretation for Axis 1 of the DCA ordination diagram (Figure 4). Since no environmental variable is perfectly correlated with Axis 1, it is best represented as a complex moisture gradient, comprised of a combination of elevation, aspect, A horizon depths, and slope position. Generally, arrangement of species and plots progress from xeric to mesic areas, from left to right in the diagram. However, Axis 1 is best interpreted as a gradient of increasing transformed aspect (0 to 2), from left to right; Axis 2 as increasing elevation. In addition, because of the relatively high correlation between A horizon depth and Axis 1 in DCCA, Axis 1 can also be explained as a gradient of increasing A horizon depth. A similar interpretation of Axis 2 could be made for slope position and landform index—Axis 2 is a gradient of increasing slope position or decreasing landform index. These interpretations are not exact, because of the confounding influence of all environmental variables in explaining site unit variation. Theoretically, a third, or even fourth, axis could be extracted that explains more of the variation in the species data and shows greater separation of site units. However, additional axes generally contribute less and less to the explanation of variation. Five site units representing gradual change along a moisture gradient, primarily related to aspect and elevation, are described in the following section.

Ecological Site Unit Description

Figures 5 through 8, along with the designation of indicator species by the TWINSPAN analysis, were used to establish site unit membership for various species. Because each plot in Figure 4 lies at the centroid of the species points that occur at that plot, it can be inferred from Figures 5 through 8 which species are likely to be present at a particular plot, or in this case group of plots or site unit (Jongman et al. 1995). Table 8 includes representative species for each site unit. These species were designated by TWINSPAN as indicator species, or, based on relative importance values, they were determined to be major components of a site unit. Appendix A lists all species and pseudospecies by stratum and their mean importance values for each site unit. Table 9 includes the mean of each environmental variable, summarized for each site unit.

Table 8. Mean importance values for selected species by site unit. Maximum score for any stratum (T=Trees, S=Saplings and Tall Shrubs, R=Regeneration and Low Shrubs) is 200. Species were selected by TWINSPAN as indicator species or based on relative importance values. Parentheses indicate the five highest importance values for each site unit.

	Ecological Site Unit				
Species	**1**	**2**	**3**	**4**	**5**
Acer rubrum (T)	23.76	(48.81)	30.45	41.36	34.00
Acer saccharum (T)			28.98	12.32	34.90
Aesculus octandra (T)			25.60		(38.17)
Betula lenta (T)		14.30	30.61	45.49	8.57
Betula lutea (T)		10.83	33.61	(46.66)	33.44
Fagus grandifolia (T)			17.85	44.55	(80.24)
Halesia carolina (T)		11.76	42.77	37.54	(46.83)
Liriodendron tulipifera (T)		20.45	(61.77)	22.65	
Pinus pungens (T)	13.45				
Pinus rigida (T)	30.96	14.64	5.35		
Pinus virginiana (T)	(63.92)	9.38			
Prunus serotina (T)		7.87	31.91		10.71
Quercus alba (T)	(51.85)	45.88		16.62	
Quercus coccinea (T)	23.85	23.50			
Quercus marilandica (T)	39.30	10.56			
Quercus prinus (T)	47.66	(56.70)	14.29	26.29	
Quercus rubra (T)	16.37	31.00	37.32	18.53	5.86
Quercus velutina (T)	(49.52)	37.90		4.96	
Tilia heterophylla (T)			36.21		
Tsuga canadensis (T)		26.46	16.86	(48.76)	31.84
Acer rubrum (S)	33.02	38.92	30.60	15.97	
Fagus grandifolia (S)		5.41		23.34	(114.23)
Kalmia latifolia (S)	(98.17)	(54.44)	2.06	5.16	
Liriodendron tulipifera (S)		7.24	(57.71)		
Pinus rigida (S)	8.87				
Pinus virginiana (S)	47.76				
Quercus prinus (S)	29.14	15.82			
Rhododendron calendulaceum (S)	9.28	24.89			
Rhododendron maximum (S)		18.01	(78.14)	(125.37)	
Tilia heterophylla (S)			45.19		23.90
Tsuga canadensis (S)	4.96	(49.13)	(49.65)	(74.19)	30.79
Acer pensylvanicum (R)		9.18	(47.28)	31.75	29.16
Gaylussacia ursina (R)	(59.20)	(136.93)	40.80	(111.68)	1.00
Vaccinium hirsutum (R)	33.46	21.01			
Vaccinium vacillans (R)	24.97	4.92	4.25		
Viburnum alnifolium (R)					(56.63)

Table 9. Mean of all environmental variables by site unit.

	Ecological Site Unit					
Environmental Variable	**1** (n=13)	**2** (n=30)	**3** (n=27)	**4** (n=12)	**5** (n=8)	**Grand Average**
Elevation (ft)	2945.38	2885.67	2789.44	3291.67	4537.50	3066.39
Elevation (m)	897.75	879.55	850.22	1003.30	1383.03	934.64
Aspect (transformed)	0.30	0.83	1.49	0.85	1.06	0.98
Slope (%)	46.54	47.80	39.26	37.92	46.88	43.66
Slope Position	72.31	47.17	28.33	42.08	61.88	45.78
Landform Index	21.59	28.42	36.78	29.34	23.00	29.58
Terrain Shape Index	-2.57	0.12	-0.31	1.29	-0.03	-0.26
Canopy Closure Index	12.83	8.42	6.60	4.88	8.55	8.05
Basal Area (m^2/ha)	28.61	33.21	40.98	42.47	38.45	36.58
Humus Depth (cm)	4.77	4.13	4.00	5.67	5.50	4.51
A Horizon Depth (cm)	17.77	16.20	20.81	21.33	19.25	18.77
Solum Depth (cm)	90.92	90.37	91.41	99.33	107.25	93.46

Site Unit 1 - Yellow Pine/Mixed Oak Forest

The stands comprising Site Unit 1 (n=13) consist of a mixture of yellow pines and oaks. In more than one third of the stands, Virginia pine (*Pinus virginiana*) and pitch pine (*Pinus rigida*) share dominance, while various oaks have less importance in the canopy. In the remaining stands, several species of oaks share dominance: white oak (*Quercus alba*), black oak (*Quercus velutina*), and chestnut oak (*Quercus prinus*). Table Mountain pine (*Pinus pungens*) was found in only a few stands and is not very well represented throughout this site unit. Common understory and mid-canopy constituents, particularly in the stands that were not pine dominated, include sourwood (*Oxydendrum arboreum*), black gum (*Nyssa sylvatica*), scarlet oak (*Quercus coccinea*), blackjack oak (*Quercus marilandica*), and sassafras (*Sassafras albidum*). A characteristic feature is the dense continuous ground cover of ericaceous shrubs (*Kalmia latifolia, Vaccinium hirsutum, V. vacillans, Gaylussacia ursina*, and *G. baccata*). For the most part, the only herbaceous plants able to grow underneath such a thick shrub layer are trailing arbutus (*Epigaea repens*), galax (*Galax aphylla*), and greenbrier (*Smilax rotundifolia, S. glauca*).

Site Unit 1 is associated with low Axis 1 scores (Figure 4). These sites are the most xeric of the five site units, as indicated by a number of the environmental variables. All sites are either southwest or south-facing (0.30 transformed aspect). Also, these areas have the lowest landform index values as well as the highest average slope position. Basal area is the lowest for this site unit, and canopy closure index values are the highest, indicative of a more open canopy. Elevations range from 700 m to 1075 m, but stands are typically found below 900 m. Three soil series were encountered in this site unit: Ditney Series, Sylco Series, and Spivey Series, with the predominant soil mapping unit being the Ditney loam (Scott ND). This is a moderately deep, well-drained soil found on mountainsides and upper side slopes. There are no unique soil characteristics associated with this site unit, with mean humus (5 cm) and solum (91 cm) depths similar to Site Units 2 and 3.

Site Unit 2 - Mixed Oak/Red Maple Forest

As site conditions become slightly less xeric, the yellow pine constituent from Site Unit 1 disappears and stands become dominated by a mix of oaks and red maple (*Acer rubrum*). Stands in Site Unit 2 (n=30) are the most common of all ecological site units. Chestnut oak is the most prevalent oak species, occurring as a dominant or codominant in over two-thirds of the stands. Other canopy and sub-canopy species include white oak, black oak, red oak (*Quercus rubra*), hemlock (*Tsuga canadensis*), and flowering dogwood (*Cornus florida*). Red maple occurs in all five site units and certainly appears to be the most adaptable of all tree species encountered. However, mean importance values are the highest in Site Unit 2, and over half of the stands have red maple as a dominant or codominant canopy species.

Kalmia latifolia is still prominent in the understory, but does not form as continuous a shrub layer as in Site Unit 1. Huckleberry (*Gaylussacia ursina*) is another species that appears to tolerate a wide range of site conditions, being found in all site units. However, it assumes more influence in Site Unit 2, often forming continuous undergrowth covering the entire stand floor. Flame azalea (*Rhododendron calendulaceum*) and buffalo nut (*Pyrularia pubera*) are also very common shrub species. Leucothoe (*Leucothoe axillaris*) is a common shrub in stands found along streams or with lower slope position. The herbaceous stratum is slightly more rich than Site Unit 1, especially when there is not a continuous layer of blueberry (*Vaccinium* spp.) or huckleberry. Tangles of greenbrier are common throughout most stands. In the less xeric conditions, there is the appearance of some ferns (*Athyrium thelypterioides*, *Polypodium virginianum*, and *Polystichum acrostichoides*) and violets (*Viola* spp.).

Site Unit 2 is found at similar elevations as Site Unit 1, around 900 m. However, it appears that the differences between these two areas are related to aspect and slope position. Stands in Site Unit 2 occupy areas with intermediate exposure, southeast and northwest-facing aspects (0.83 transformed aspect), and have mean slope positions around mid-slope (47). Landform index is also higher for this site unit, indicating lower slope position. These stands have higher basal area and a canopy that is more closed than Site Unit 1. Seven soil series were encountered in this site unit: Ditney Series, Brookshire Series, Sylco Series, Spivey Series, Citico Series, Shelocta Series, and Jeffrey Series, with the predominant soil mapping unit being the Ditney loam (Scott ND). Soil profile characteristics were similar to Site Unit 1, with slightly shallower humus depth (4 cm) and solum (90 cm) depth.

Site Unit 3 - Cove Hardwood/Mixed Mesophytic Forest

Whether one uses the terminology of Whittaker (1956) or that of Braun (1950), stands comprising Site Unit 3 (n=27) are the most diverse of the five site units. A total of twelve species are either dominants or codominants throughout this unit. These include tulip poplar (*Liriodendron tulipifera*), silverbell (*Halesia carolina*), basswood (*Tilia heterophylla*), red oak, red maple, sweet birch (*Betula lenta*), buckeye (*Aesculus octandra*), black cherry (*Prunus serotina*), sugar maple (*Acer saccharum*), yellow birch (*Betula lutea*), white ash (*Fraxinus americana*), and bitternut hickory (*Carya *cordiformis*), in order of their importance. At first, an attempt was made to subdivide this site unit into several smaller, more distinct site units. However, upon analysis of the TWINSPAN and DECORANA output, no subtypes could be reasonably determined with a sufficient sample size to merit further subdivisions. Because the species composition and combination of dominants and codominants varied greatly from place to place, all plots were assigned to one site unit.

Tulip poplar has the highest mean importance value for this site unit and occurs as a dominant in half of the stands. Silverbell is the second most important component of the overstory. Generally, species composition in the sub-canopy is very similar to that of the canopy. A few species, such as striped maple (*Acer pensylvanicum*), witch hazel (*Hamamelis virginiana*), and alternate-leaf dogwood (*Cornus alternifolia*), are common in the understory and were not found to reach canopy height. Pawpaw (*Asimina triloba*) is not widespread throughout this site unit; however, when encountered, it is locally abundant. Similarly, rosebay rhododendron (*Rhododendron maximum*) is a common shrub in stands found along streams or in lower slope positions, and often forms dense thickets. Other common shrubs included sweetshrub (*Calycanthus floridus*), spicebush (*Lindera benzoin*), and strawberry bush (*Euonymus americanus*).

The herbaceous stratum has the highest species richness of all site units. Of 135 total herbaceous species identified in all stands, 93 are found in Site Unit 3. The next highest amount (71) is found in Site Unit 2. In stands where rosebay rhododendron is common, herbaceous diversity is low, likely due to the limited amount of light reaching the forest floor. However, in most stands, the forest floor is covered with a large variety of ferns, wildflowers, and other herbs. Many low shrubs or tall herbs such as bugbane (*Cimicifuga americana, C. racemosa*), blue cohosh (*Caulophyllum thalictroides*), and maple-leaf viburnum (*Viburnum acerifolium*) often completely cover the ground. Other common herbs include foamflower (*Tiarella cordifolia*), white-topped aster (*Aster cordifolius*), mayapple (*Podophyllum peltatum*), wood nettle (*Laportea canadensis*), jewelweed (*Impatiens pallida*), and several members of the Liliaceae.

Site Unit 3 has the lowest mean elevation representation of all site units, although only slightly less than Site Units 1 and 2. The main difference between the first two site units and this site unit is again related to aspect and slope position. Stands in Site Unit 3 occupy the most mesic sites—those facing either north or east. In addition, these stands are found either along streams, in coves, or low in position along the slope. Consequently, this site unit has the highest average landform index values. Because these areas are well protected, they have the second highest basal area of any site unit, and the canopy at full seasonal development is almost completely closed. Six soil series were encountered in this site unit: Spivey Series, Ditney Series, Brookshire Series, Sylco Series, Citico Series, and Shelocta Series, with the predominant soil mapping unit being the Spivey cobbly loam (Scott ND). This soil mapping unit consists of deep, well-drained soils found in coves, hollows, and lower side slopes. There are no unique soil characteristics associated with this site unit, with mean humus (4 cm) and solum (91 cm) depths similar to Site Units 1 and 2.

Site Unit 4 - Hemlock/Birch Forest

Stands comprising Site Unit 4 (n=12) have similar tree species composition as Site Unit 3; however the distribution of species and number of combinations of dominants is not nearly as even as in Site Unit 3. These areas are most influenced by three canopy species: hemlock, yellow birch, and sweet birch. Other canopy and subcanopy constituents include silverbell, beech, sourwood, red maple, and serviceberry (*Amelanchier arborea*). Tulip poplar is found with much less regularity in this site unit than in Site Unit 3.

In those stands in which hemlock is a dominant species, rosebay rhododendron frequently forms dense thickets which are three to four meters tall. In cases such as this, very few herbaceous plants can grow and the majority of regeneration is hemlock and rosebay rhododendron. Most regeneration occurs as part of small gap dynamics when older, larger birch (particularly yellow birch) fall. Herbaceous plants that are found here must exist under low light conditions. These include several ferns (*Dennstaedtia punctilobula*, *Dryopteris intermedia*, and *Athyrium asplenioides*), partridge berry (*Mitchella repens*), and downy rattlesnake plantain (*Goodyera pubescens*). Some species, such as the common wood sorrel (*Oxalis acetosella*) and shining clubmoss (*Lycopodium lucidulum*), are typically found only in association with hemlock.

The Hemlock/Birch site unit shows the widest range in elevation, 786 m (610 m to 1396 m), as well as the widest range of site tolerance. These stands have an average slope position (42) and landform index value (29) that is very similar to Site Unit 2; however, rather than being aggregated mostly at mid-slope, they are found anywhere from coves to upper slopes and ridges. Also, similar to Site Unit 2, stands in Site Unit 4 occupy areas with intermediate exposure, southeast and northwest-facing aspects (0.84 transformed aspect). It appears that the primary difference between this site unit and Site Unit 2 is elevation. Mean elevation for this site unit is over 1000 m. Three soil series were encountered in this site unit: Jeffrey Series, Brookshire Series, and Citico Series, with the predominant soil mapping unit being the Jeffrey loam (Scott ND). This is a moderately deep, well-drained soil found on ridgetops and upper side slopes. Jeffrey soils are strongly acid or very strongly acid throughout the profile. Forest soils forming underneath hemlock tend to be more acidic than that of hardwood stands (Rogers 1980). These areas also have deeper soils, especially in the humus layer and A horizon. A thick mor humus layer normally develops under canopies of hemlock and under thick shrub coverage of rosebay rhododendron. This site unit has the most continuously closed canopy, which is directly a function of the dense hemlock canopy and rosebay rhododendron sapling/shrub layer.

Site Unit 5 - Beech Forest

Certainly the most distinct of all site units, stands in Site Unit 5 (n=8) are dominated by American beech (*Fagus grandifolia*) in all strata. Whittaker (1956) described "two" types of beech forests in the Great Smoky Mountains, based on differences in aspect. Even with a limited number of samples, there appears to be a similar distinction between north and south-facing beech stands in this area. North-facing stands appear to resemble a northern hardwood forest, with beech as the primary component and a combination of several species from Site Units 3 and 4. Other important canopy species include silverbell, buckeye, sugar maple, yellow birch, and hemlock, all common in other site units. Striped maple, hemlock, silverbell, and Fraser magnolia (*Magnolia fraseri*) are found in the understory, nearly equal to beech. Hobblebush (*Viburnum alnifolium*) and two blackberries (*Rubus idaeus, R. canadensis*) are the most common shrubs. The herbaceous layer is lush, often covered in ferns (*Dryopteris intermedia, Dennstaedtia punctilobula*, and *Thelypteris noveboracensis*). Species diversity in the canopy and sub-canopy is much lower as one crosses the ridgeline into south-facing stands. These stands are almost completely dominated by beech in all strata. The understory is cluttered with small beech stems. Whittaker (1956) called it a "beech orchard." The herbaceous layer has a similar variety of ferns, hobblebush, and blackberry.

Site Unit 5 is characterized by high Axis 1 and Axis 2 scores (Figure 4), as elevations are the highest for any unit, ranging from 1240 m to 1550 m. Stands are located across north and south-facing aspects. Landform index is low as slope position is high for these areas. These areas had a similar basal area to Site Units 3 and 4, with canopy closure similar to Site Unit 2. Three soil series were encountered in this site unit: Jeffrey Series, Brookshire Series, and Spivey Series, with the predominant soil mapping unit being the Jeffrey loam (Scott ND). Soils are deepest in this site unit, with an average solum depth of over 100 cm. Mean humus depth (5.5 cm) is very similar to Site Unit 4.

DISCUSSION

Forest Type Comparisons

Similar studies in the Southern Appalachians have found vegetation distribution to be related to different combinations of elevation, landform, and soil features. Whittaker's (1956) monograph on the vegetation of the Great Smoky Mountains concluded that moisture, as defined by the interaction of elevation, topographic shape, and slope aspect, was the primary environmental variable that determined the vegetation present at a given site. Whittaker developed mosaic charts of the 16 vegetation communities which he classified based on increasing elevation on the Y-axis and a topographically-defined moisture gradient on the X-axis (going from mesic to xeric). This research shows similar trends, only the X-axis is reversed in this study (going from xeric to mesic). Whittaker's elevational range (450 m to 1900 m) was much broader than this study (610 m to 1550 m), and included higher elevation red spruce (*Picea rubens*) and Fraser fir (*Abies fraseri*) forests not encountered in this study area.

Other similarities to Whittaker's results include an increase in canopy coverage, in general, along the moisture gradient from Site Unit 1 to Site Units 3, 4, and 5. The amount of light intercepted by the developed canopy consequently increases along this gradient. Average site productivity (as basal area) and species diversity increase with increasing soil moisture along this same gradient. Figure 14 shows the general trend in overall species richness—increasing along this gradient, with a drop-off in higher elevations. Herbaceous richness shows a similar trend through Site Units 1, 2, and 3;

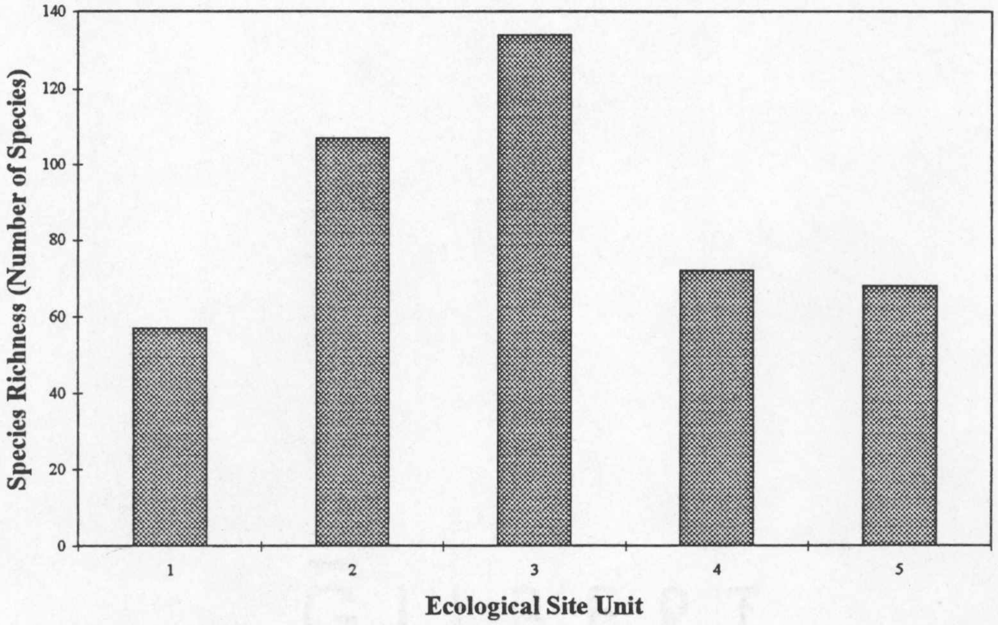

Figure 14. Overall species richness of individual site units.

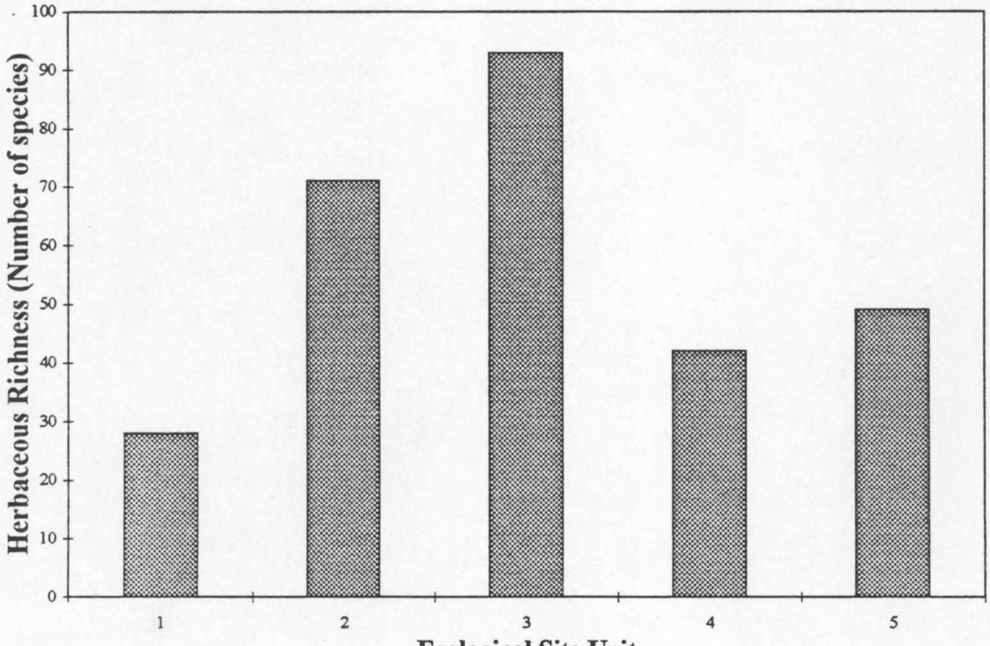

Figure 15. Herbaceous species richness of individual site units.

however, a decrease occurs in Site Units 4 and 5 (Figure 15). Site Unit 4 is dominated by eastern hemlock and rosebay rhododendron. Because of the low light conditions and higher acidity in the soil, the herb layer may be almost absent. Similarly, herb richness is low in Site Unit 5, the upper elevation beech forests, likely due to the orchard-like nature of the forest and domination by a few clonal species (Whittaker 1956).

The five site units in this study are closely related to three of Whittaker's forest types and a combination of several others. Site Unit 1 corresponds to a combination of Whittaker's Virginia pine forest and pitch pine heath. These are open forests located on south and south-west facing slopes. Canopy dominants are a mixture of yellow pines and several oak species. The shrub and herb layer is strongly dominated by plants in the Ericaceae family. Whittaker did not consider these pine forests to be a seral stage in hardwood succession. He classified these pine stands as "topographic or edaphic climaxes of their dry and exposed sites," and fire was described as critical to their maintenance. However, unlike Whittaker's pine forest types, which were determined to be reproducing well and "in balance, " the yellow pine constituents in this site unit are not in balance by this same criteria.

Eight of the thirteen plots comprising Site Unit 1 have either Virginia pine or pitch pine as a canopy dominant or codominant, but only two of these thirteen plots have either of these species in large numbers in the sapling stratum, and there is virtually no yellow pine representation in the regeneration stratum in any of the plots. From these results, it can be inferred that the pine forests, as once interpreted by Whittaker, are disappearing. No evidence of recent fires (charred stumps or logs) was observed in any of the thirteen plots. Fire may have been responsible for the original establishment of the stands, but no evidence of this was obtained. It is likely that fire suppression has created an environment where the more shade tolerant hardwood species can outcompete the pine, eventually leading to a forest composed mainly of mixed oak species.

Golden (1974) recognized the existence of an oak-pine forest type that was essentially ecotonal between chestnut oak forest and pure stands of Table Mountain pine and pitch pine forest types. Typically they were found on ridges and south-southwest facing upper side slopes. Callaway et al. (1987) recognized a scarlet oak-yellow pine type with similar characteristics to Golden's oak-pine forest. It is likely that Site Unit 1 corresponds best with this ecotonal yellow pine-mixed oak type. Three of the plots in Site Unit 1 were clearly dominated by Virginia and pitch pine; however, none of the other ones formed pure stands of yellow pine.

Site Unit 2 is the most extensive of all site units in this study. Chestnut oak is dominant, followed by red maple and several other oaks. This site unit corresponds to a combination of several of Whittaker's oak dominated forest types: red oak-pignut hickory, chestnut oak-chestnut, chestnut oak-chestnut heath, red oak-chestnut, and white oak-chestnut. These forest types were once widespread throughout the Great Smoky Mountains and found mainly on south and west facing slopes. Chestnut oak was considered the most important oak species in the overstory with various combinations of other oaks and hickories. Northern red oak was shown to replace chestnut oak as a canopy dominant at higher elevations. Whittaker's work recognized the historical importance of American chestnut (*Castanea dentata*) in these forest types; however, by the time of his field work most of the chestnut canopy dominants were dead. Death of the chestnuts significantly altered the structure and composition of the affected forest stands by opening canopies and permitting increased reproduction of other species. These included red maple, chestnut oak, sourwood, and black gum.

Further site units or forest types could have been segregated out from Site Unit 2; however, unlike other studies (Golden 1981, Callaway et al. 1987, Gattis 1992, Moffat 1992), this was not attempted. Instead, general species trends were noted across the range of environmental conditions that occurred in Site Unit 2. Most interesting is the overall importance of red maple. Although the wide ecological amplitude of red maple is well documented (Burns and Honkala 1990), it is rarely cited as a major overstory component. Whittaker did not recognize red maple as an important overstory component; however, it was prolific as seedlings and small saplings. Golden (1981) recognized a "disturbance red maple complex" that developed after death of American chestnut or some other form of disturbance. Yoke (1994) suggests the increasing influence of red maple is caused by a combination of openings created by the chestnut, fire suppression, logging or other anthropogenic disturbances, and the wide ecological amplitude of red maple. These explanations seem valid for this study area as well, especially because of the overall dominance of red maple, not only in the overstory, but also in the sapling and regeneration strata.

Referring back to Figures 11, 12, and 13, distributions of individual species along various environmental gradients can be shown using the species-environment biplot. Of all the oak species, it is evident that northern red oak and white oak are found in the more mesic sites at higher elevations with higher transformed aspect. This is similar to results found by Whittaker (1956), Golden (1974), Callaway et al. (1987), and Gattis (1992). Similarly, scarlet oak was an important canopy dominant in Yoke's (1994) lower elevation mixed oak forest, and Figure 12 shows scarlet oak occurring primarily in the lower elevations. The location of northern red oak and red maple in relation to the moisture gradient is interesting. Both species occur in a large number of plots, and therefore tolerate a wide range of environmental conditions. This trend is shown by both species being located approximately in the center of the elevational and aspect gradients, indicative of the broad ecological amplitudes that they exhibit throughout the study area. Of local importance, American chestnut saplings are equally distributed among Site Units 1 and 2, with slightly better regeneration in Site Unit 2.

Site Unit 3 corresponds closely to Whittaker's cove hardwoods forest or Braun's (1950) mixed mesophytic forest. Both plant ecologists described six to eight species that make up 80 to 90% of the canopy of cove forests, dominating stands in different combinations. Overall species richness is highest in this site unit, related primarily to the increased soil moisture levels and the subsequent abundance and variability of herbaceous plants.

As with Site Unit 2, it is possible that further subtypes of Site Unit 3 could have been designated. Callaway et al. (1987) designated several mesic forest types including tulip poplar, hemlock-tulip poplar, basswood-buckeye, hemlock-silverbell-beech, northern red oak, and buckeye-yellow birch. However, on average, their success of classification of these forest types from discriminant analysis using environmental variables was lowest when compared to other forest types. Similarly, Yoke's (1994) mesic site unit, comprised of eastern hemlock, sugar maple, American beech, and white ash, was classified with the lowest success of all four site units.

As a result, Site Unit 3 was not segregated into various subtypes of Whittaker's cove hardwoods or Braun's mixed mesophytic forest. Instead, trends in vegetation distribution were noted from Figures 11, 12, and 13. A specific high elevation basswood-buckeye forest type was not delineated, as in Callaway et al. (1987); however, these species are well represented in higher elevation stands. Black cherry was noted as locally important at higher elevations in the Smokies (Whittaker 1956), and the same is true in the higher elevations of this study area. Tulip poplar is located at mid-elevations but in areas with north-east facing slopes (highest transformed aspect), the highest landform index, and the lowest slope position. These characteristics are typical for most species in Site Unit 3.

Site Unit 4, consisting primarily of eastern hemlock and yellow birch, was the most difficult to classify consistently. It is found over the widest range of elevations, and its average aspect and slope position are similar to that of Site Unit 2. In fact, the misclassifications of Site Unit 4 membership using the four variable model of elevation, aspect, slope position, and A horizon depth occurred relatively evenly across Site Units 2, 3, and 5. Braun (1950) and Gattis (1992) did not consider stands of hemlock in the Southern Appalachians as a distinct community from the more typical mixed mesophytic communities having a lower percentage of hemlock. However, many other researchers have. Whittaker (1956), Golden (1981), Yoke (1994), and Rutledge (1995) all classified separate hemlock-dominated forest types. Golden and Rutledge further classified distinct birch-hemlock forest types, because of the common occurrence of eastern hemlock with both yellow and sweet birch, particularly at higher elevations.

Whittaker (1956) said, "The hemlock forest type is most distinctive, with heaviest hemlock dominance, densest heath growth, and most impoverished herb stratum on steep slopes at higher elevations. Below 2,500 feet the hemlock forest gradually merges with the cove forests; and hemlock becomes only one of the dominants, though the most important one, of lower-elevation cove forests." The findings of this study are similar to Whittaker's. He identified silverbell, yellow birch, sweet birch, Fraser magnolia, and sometimes beech as important canopy associates. Figure 12 shows a cluster of the same species, with the exception of silverbell, at the some of the highest elevations. Even though silverbell does not cluster with the rest of the site unit, it was a common associate in this site unit and was often found in the higher elevations.

Classification of this site unit was certainly confounded by the wide, regional, ecological amplitude of hemlock. Four of the twelve plots classified into Site Unit 4 were located in coves between 610 m and 650 m; whereas the remaining plots were found at a variety of slope positions between 950 m and 1400 m. Golden (1981) found hemlock to occur in a wide range of sites, achieving its greatest prominence in the middle elevations (900 - 1250 m). The lower elevation, hemlock-dominated cove forests could have been lumped with the rest of Site Unit 3. Similarly, the higher elevation stands could have been placed into Site Unit 5. However, eastern hemlock stands are so different from the other deciduous cove and northern hardwood forests in overall characteristics that these stands were placed in a separate site unit. Essentially, these sites are all ecological equivalents.

The common denominator between forested stands of Site Unit 4 is the extreme interception of light created by the dense canopies of rosebay rhododendron and hemlock.

Site Unit 5 was the most distinct site unit, occurring only at the highest elevations, with beech as the overwhelming canopy dominant. Whittaker (1956) identified two distinctly different American beech forests, depending on aspect, and as described in the results, both these types were recognized in this study area. Golden (1974) also recognized two beech forest subtypes—beech orchards, similar to Whittaker, and beech flats, higher elevation cove forests found at lower slope positions. Six of the eight beech-dominated stands in this site unit were more like the beech orchards. The other two stands were more like the beech flats, found at lower slope positions with less slope gradient. Mercer (1969) has shown that reproduction of beech trees is almost exclusively by suckering in areas called "beech gaps," most often found in areas where environments are severe. This description would certainly apply to stands in this site unit at the highest elevations of the Tellico Ranger District.

Significance of Environmental Variables

Besides Whittaker (1956), several other researchers have concluded that a complex moisture gradient, as defined by different topographic variables, is responsible for vegetation distribution in the Southern Appalachians. Golden (1974) concluded that vegetation pattern in the Great Smoky Mountains appears to be most directly related to elevation and topography (including aspect). Callaway et al. (1987), Gattis (1992), Yoke (1994), and Rutledge (1995) all reach similar conclusions. Each study identified slightly different combinations of topographic variables that were the best predictors of vegetation occurrence and productivity differences across the Southern Appalachian landscape. Overall, however, elevation was consistently the most important environmental variable. This research is no different.

The general use of soil variables in landscape ecosystem classification has proven to be inconsistent in predicting vegetation distribution in the Southern Appalachians. Generally, soil chemical variables have been found to be weak discriminators between site quality in this area. Soil physical properties tend to perform much better. Gattis (1992) and Moffat (1993) both determined that soil solum thickness, epipedon thickness, or humus form could be used to discriminate between site units.

In most studies, however, soil variables have been shown to be less reliable than topographic variables in predicting site quality and vegetation relationships. Ike and Huppuch (1968) found that topographic site variables were more discriminating in determining vegetation patterns than soil properties in the mountains of northeast Georgia. Golden (1974) found that differences in soil characteristics across vegetation types were too great to be an accurate predictor of vegetation patterns. McNab (1991b), in classifying local ecological units in the Asheville basin and surrounding Pisgah Mountains in North Carolina, included variables from digitized soils maps and found that they did not contribute significantly to forest prediction. This failure was attributed to the highly complex soils of the Southern Appalachians. Most soil mapping units consist of several combinations of soil types which makes it difficult, if not impossible, to assign specific edaphic conditions to a given location. For this study, with the exception of thickness of the A horizon, measured soil characteristics performed poorly overall to the discrimination of site units.

One of the most important applications of any classification system is the development of a model which can be used for land management decisions. By combining the results of indirect and direct ordination, an interpretive model has been produced (Figure 16). This model is applicable to the Mountain Highlands of the Tellico Ranger District in the Cherokee National Forest and attempts to simplify the complex interrelationships of soil, landform, and vegetation. Using this model as a template, a conceptual landscape ecosystem classification map has been developed for the Mountain Highlands (Figure 17). This map was created in a raster environment using the GRID module of ARC/INFO (ESRI 1994) by developing an "aspect" grid from the digital elevation model grid for the district and overlaying both grids. Site units were assigned grid values based on the model shown in Figure 16 and mapped accordingly.

Site Unit 2 is the most extensive site unit and is found on 8,685 ha of the total 26,101 ha. Site Unit 3 (7,522 ha) is the next most common site unit, followed by Site Unit 1 (5,509 ha), Site Unit 4 (3,760 ha), and Site Unit 5 (625 ha). Similar to other GIS derived maps of forest cover distribution, Figure 17 should be interpreted somewhat loosely because it is a relatively simplified depiction of a very complex situation. As with any predictive model, those who use these results should exercise caution in extending these vegetation/landform/soil relationships beyond the environmental resource limits of the study area.

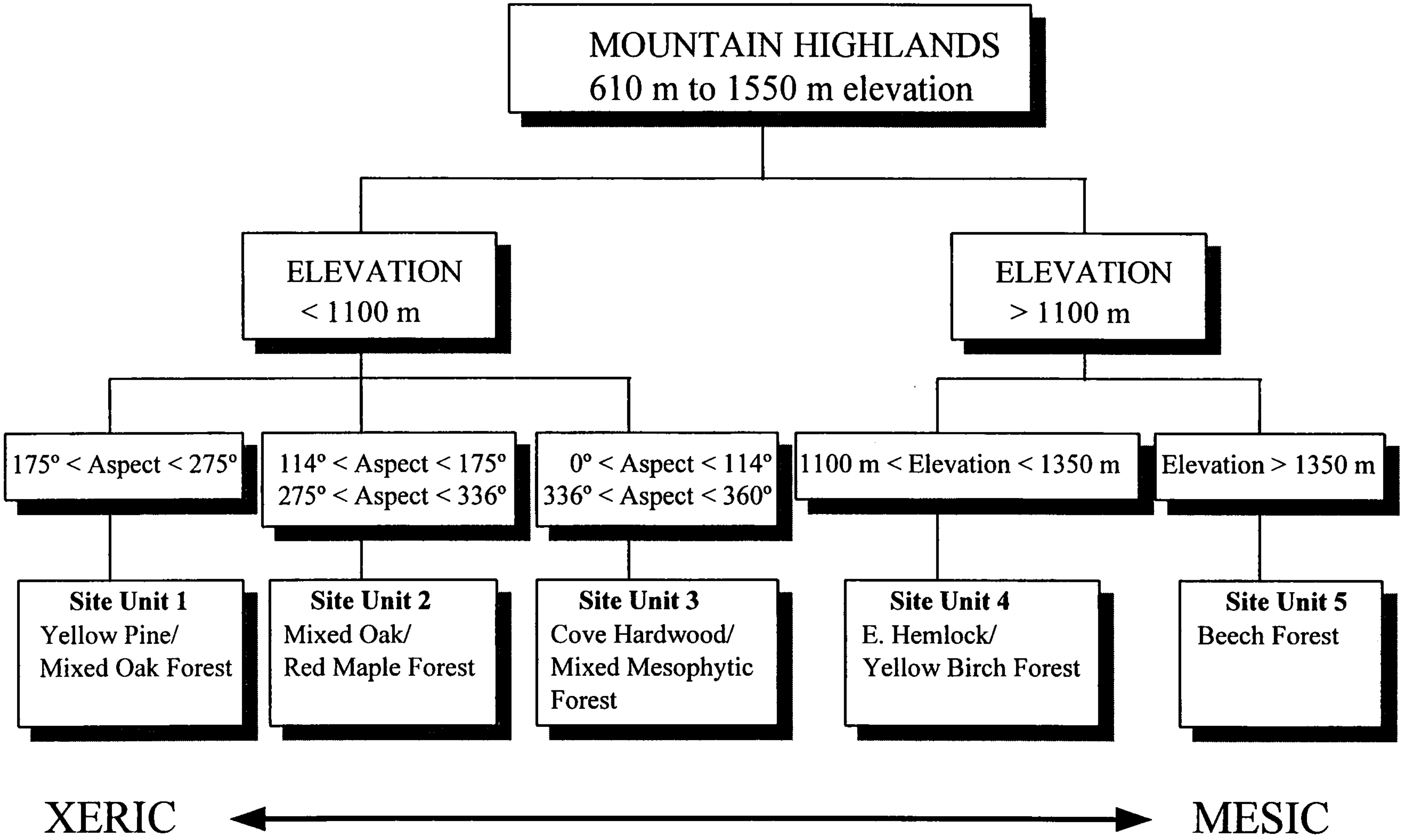

Figure 16. Landscape ecosystem classification model for the Mountain Highlands of the Tellico Ranger District, Cherokee National Forest, Tennessee.

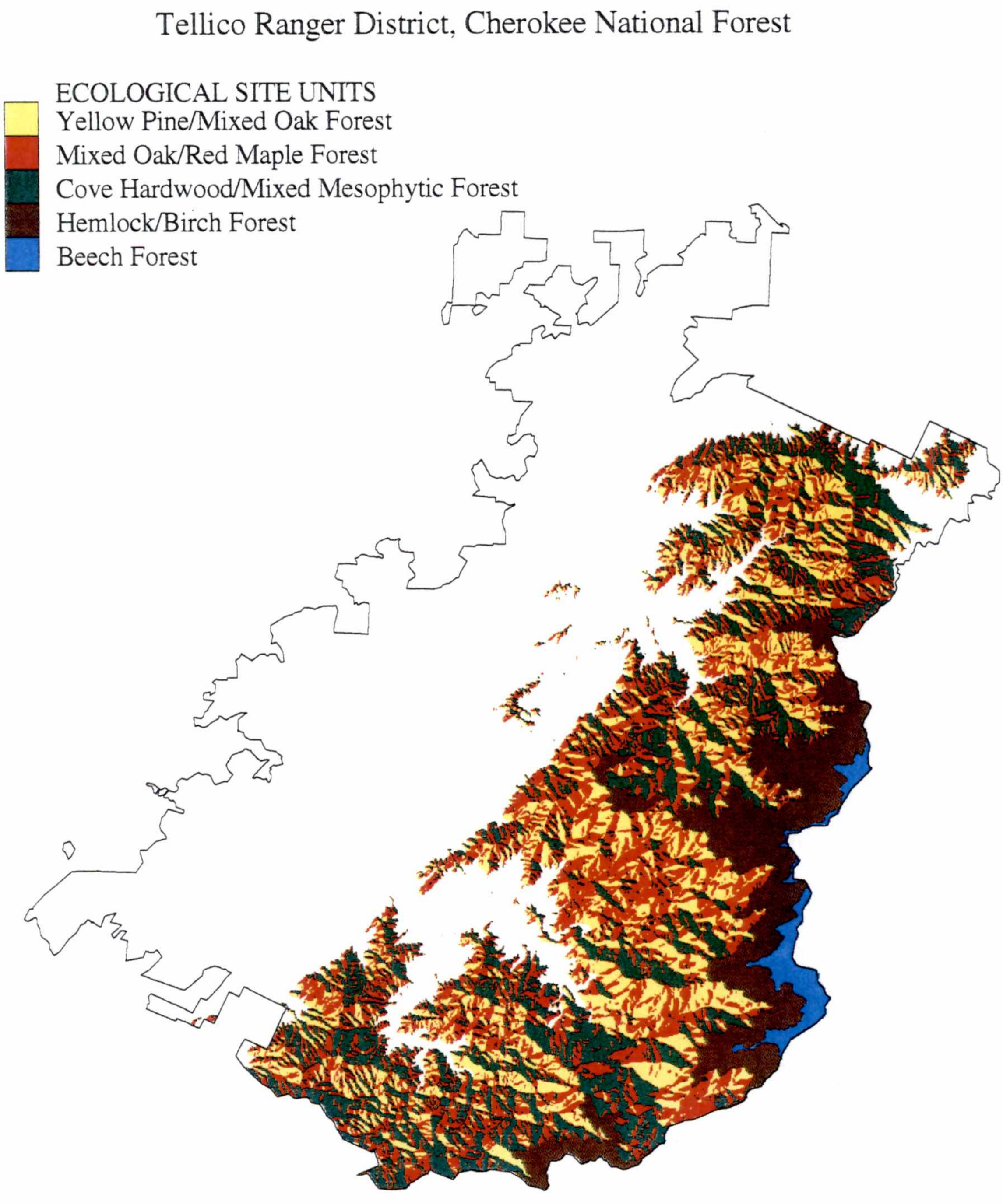

Figure 17. Landscape ecosystem classification map for the Mountain Highlands of the Tellico Ranger District, Cherokee National Forest, Tennessee.

Forest Productivity

Forest managers are interested in productivity—being able to distinguish between a site that is more productive and will produce bigger trees than another area. The ability to predict net primary productivity (NPP) in various forest ecosystems is of immense practical and theoretical value. NPP is the energy base for all secondary production and represents a large amount of potentially harvestable material or organic matter for long-term storage in soils and the forest floor (Waring and Schlesinger 1985). Although this study did not attempt to measure net primary productivity in the field, a system of land classification is developed that reflects the potential productivity of the land to support natural biotic communities. Using basal area to compare site unit differences in productivity, Table 10 shows that productivity increases across the DCA Axis 1 moisture gradient (from Site Unit 1 to Site Unit 4), and in the most severe environments of the highest elevations, basal area decreases slightly in Site Unit 5.

Table 10. Mean basal area and canopy closure index by site unit.

	Ecological Site Unit				
Environmental Variable	**1**	**2**	**3**	**4**	**5**
Basal Area (m^2/ha)	28.61	33.21	40.98	42.47	38.45
Canopy Closure Index (CCI)	12.83	8.42	6.60	4.88	8.55

There are clear restrictions upon potential forest production related to climate, as indicated by topographic relationships (Leith 1975). In a particular area, such as the Great Smoky Mountains, local differences in soil depth, slope, and aspect may cause restrictions in available water and differences in NPP. For example, production rates by drought-adapted pine are substantially lower than for other forest types growing at comparable elevations (Whittaker 1975).

Studies by Gaiser (1951), Trimble and Weitzman (1956), Doolittle (1957), and Ike and Huppuch (1968) demonstrate the strong influence of topographic variables on site productivity. Higher productivity for hardwoods is generally found on north facing slopes, lower productivity on south-facing slopes. This is generally attributed to increased available soil moisture and deeper soils on the north-facing aspects. In his review of predicting forest site quality in the United States, Carmean (1975) considered aspect as a very important site feature in hilly and mountainous areas. Since DCA Axis 1 is most strongly correlated with aspect and elevation, similar results are clearly shown in Table 10.

Landform position and landform shape have also been strongly correlated with productivity (McNab 1993). Aspect and landform position affect solar radiation interception which indirectly affects soil moisture losses resulting from evaporation and transpiration. In addition, soil moisture levels are affected by position on a slope due to soil moisture movement and drainage. Ridges and upper side slopes lose moisture downhill to lower slope positions. Gattis (1992) and Yoke (1994) found landform index (LFI), a quantification of protection, to be an important variable in discriminating between site units (and productivity). In this study, LFI performed poorly as a discriminator of site unit membership, particularly in the stepwise discriminant analysis. However, slope position, which is highly negatively correlated with LFI, was determined to be a critical variable in discriminating between site units. Therefore, it is inferred that slope position is explaining the same environmental effects on vegetation as LFI, that is, protection created by surrounding landforms.

Another interesting result from this research, one not analyzed further statistically, is the use of a canopy closure index to predict productivity differences between site units. As described in the Methods section, a canopy closure index (CCI) was derived for each plot by measuring canopy closure with a concave densiometer at five places in the plot and taking the average of these measurements. Higher values represent a more open canopy. In several studies, the amount of leaf area has been shown to be an important structural index of productivity. Webb et al. (1983) found that NPP was well correlated with the maximum foliage present in a broad survey of coniferous and deciduous forests. Foliage area is often expressed as a leaf area index (LAI) representing all of the upper surfaces of leaves projected downward to a unit area of ground beneath the canopy. LAI increases as the canopy becomes more dense, with less light reaching the forest floor. Gholz (1982) estimated LAI for several vegetation types in Oregon and found that NPP appeared to correlate better with maximum leaf area than with any other single environmental variable.

LAI was not measured in the field in this study; however, the CCI index derived for each plot is an approximation of LAI, because it is based on the amount of light that reaches the ground. The use of this index as an indicator of productivity differences appears to agree with the results of others. Referring back to Table 10, basal area (productivity) increases across the DCA Axis 1 moisture gradient, and the CCI decreases in a similar fashion. At the highest elevations, basal area decreases, and CCI increases in Site Unit 5. This index was not used in the discriminant analysis to predict site unit membership, because it does not represent the more permanent features of the landscape, such as landform or soils data. However, it does provide additional useful information on stand characteristics of individual site units, and presumably productivity differences as well.

Lloyd (1991) has developed a conceptual framework for integrating results from ecological land classifications that can be used to predict growth and yield. In the designation of ecological site units, site quality differences are identified from landform and soils data. In the Mountain Highlands, such units occur along a moisture gradient that translates into site quality differences. Separate growth curves, similar to the ones developed for site index, are then developed for each site unit. In similar work, Rennie (1991) attempted to develop growth and yield models based on landtypes identified by Smalley (1984) on the Cumberland Plateau in Tennessee. On a more basic level, one of the most commonly used applications of landscape ecosystem classifications is in guiding the selection of the best species to plant on a given site. Beyond applied silvicultural or productivity related actions, nearly every type of land management decision requires the type of information an ecologically based land classification system can provide.

CONCLUSIONS

A prerequisite to sustaining ecosystems is the inventory and classification of landscape structure and composition. Landscape ecosystem classification involves the delineation of landscapes into easily recognizable units. Landform, soils, and vegetation are the delineation criteria in this study.

On forested land within the Mountain Highlands of the Tellico Ranger District, five site units were identified and found to be recurring across the landscape. These were: 1) Yellow pine/mixed oak forest, 2) Mixed oak/red maple forest, 3) Cove hardwood/mixed mesophytic forest, 4) Eastern hemlock/yellow birch forest, and 5) Beech forest. Each site unit represents an array of site types which are identifiable combinations of landform and soil features, associated with discrete vegetative communities. A four variable model consisting of elevation, aspect, slope position, and A horizon depth accurately predicted site unit membership over 60% of the time. The primary axial expression of these site units is interpreted as a complex moisture gradient, made up of a combination of all four variables.

For the purposes of developing a management strategy, elevation and aspect appear to be sufficient for predicting the distribution of site units across the landscape (Figure 16). At elevations below 1100 m, aspect appears to be the most important environmental factor that influences vegetation composition. The lower elevations of the Mountain Highlands receive less annual rainfall than the higher elevations. Therefore, the importance of topography and its close relationship with microclimate in the lower elevations must be stressed. Site Unit 1 is located exclusively in areas with south-west facing aspect, and generally has the lowest productivity. Site Unit 3 is the opposite, located on north and east facing slopes, with the highest productivity. Site Unit 2 occupies a wide range of aspects, but falls basically between Site Units 1 and 3. At higher elevations, the effect of increasing elevation in determining vegetation distribution is much more pronounced, primarily due to the increased amount of precipitation that is received and other climatic factors (lower temperatures, increased wind). For this reason, aspect is less important, and elevation is the variable that best discriminates between Site Units 4 and 5.

An essential component of implementing ecosystem management is the development of ecosystem classification maps. McNab (1996) attempted to define a regional classification based on smaller ecological site units using multivariate techniques, instead of GIS applications. Five locally-defined ecological sites were aggregated into two broader, more extensive landscape types. He concluded that each landscape type can be described by a unique set of environmental features, most of which can be mapped using GIS. This should be the focus of future research efforts—integrating results from studies like this and others, i.e., Yoke (1994), Moffat (1993), and Gattis (1992), into the silvicultural and planning efforts of the U.S. Forest Service. Identification of successional pathways (Phase 2) provides the last link to a complete classification of forest ecosystems. Emphasis currently must be focused upon the development of applied ecological tools that integrate this ecological information into forest management practices. Arbitrarily defined compartments and stands should be replaced by ecologically-defined site units as the appropriate forest management unit. Combining a landscape ecosystem classification with GIS coverages allows the planning and organization of complex silvicultural and other forest management objectives to become possible and practical.

Ecosystem management is both a description and a prescription. It is not a new idea. It reminds us to view the forest holistically, rather than focus on individual natural resources such as timber or wildlife or aesthetics. It reminds us that we cannot do just one thing to an ecosystem—every action produces a complex chain of reactions. Landscape ecosystem classification attempts to deal with the definition, recognition, and representation of complex ecosystems across gradients of both space and time. The results of this LEC should provide a forest manager with both a comprehensive description of forested ecosystems of the Mountain Highlands of the Tellico Ranger District in the Cherokee National Forest, as well as the basis for sound, ecologically-based land-use prescriptions for this area.

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APPENDIX

Table A.1. Average importance values (200) for tree stratum.

	Site Unit				
Species	**1**	**2**	**3**	**4**	**5**
Acer pensylvanicum		10.50	7.88	12.31	21.06
Acer rubrum	18.34	49.41	30.45	41.36	34.00
Acer saccharum			28.98	12.32	34.90
Aesculus octandra			25.60		38.17
Amelanchier arborea		11.07	13.19	23.54	19.16
Betula lenta		14.30	30.61	45.49	8.57
Betula lutea		10.83	33.61	46.66	33.44
Carya cordiformis			21.42	5.53	
Carya glabra	32.54	18.20	11.92	10.45	
Carya ovata		6.75		5.23	
Carya tomentosa		12.69			
Cladastris lutea			10.31		
Fagus grandifolia			17.85	44.55	80.24
Fraxinus americana			22.98		
Halesia carolina		11.76	42.77	37.54	46.83
Ilex opaca				4.55	
Liquidambar styraciflua				21.33	
Liriodendron tulipifera		20.45	61.77	22.65	
Magnolia acuminata			12.12		13.15
Magnolia fraseri		8.99	11.09	24.50	36.49
Nyssa sylvatica	19.58	8.85	8.44	5.81	
Oxydendrum arboreum	23.47	18.69	10.20	56.94	
Pinus echinata	4.43				
Pinus pungens	14.89	7.69			
Pinus rigida	32.10	15.55	5.35		
Pinus strobus	8.34	19.76		5.08	
Pinus virginiana	77.56	9.36			
Platanus occidentalis			8.22		
Prunus serotina		7.87	31.91		10.71
Prunus virginiana		9.16			
Quercus alba	51.85	45.88		16.62	
Quercus coccinea	23.85	23.50			
Quercus marilandica	39.30	10.56			
Quercus prinus	45.76	57.18	14.29	26.29	
Quercus rubra	16.37	31.00	37.32	18.53	5.86
Quercus velutina	51.82	36.84		4.96	

Table A.1. Continued.

	Site Unit				
Species	**1**	**2**	**3**	**4**	**5**
Rhododendron maximum				4.90	
Robinia pseudo-acacia		4.48	8.35		
Sassafras albidum	11.42		7.90		
Tilia heterophylla			36.21		
Tsuga canadensis		26.46	16.86	48.76	31.84

Table A.2. Average importance values (200) for sapling and shrub stratum.

	Site Unit				
Species	**1**	**2**	**3**	**4**	**5**
Acer pensylvanicum		23.52	45.72	17.74	58.00
Acer rubrum	29.64	40.13	30.60	15.97	
Acer saccharum			85.38	5.96	6.01
Aesculus octandra			33.52		7.05
Amelanchier arborea	6.80	8.58			
Asimina triloba			52.89		
Betula lenta		8.74	26.58	4.34	
Betula lutea			80.56	23.60	12.30
Calycanthus floridus			21.86		
Carya glabra	27.74	14.96	22.71		
Carya tomentosa		6.07			
Castanea dentata	19.61	18.16	6.08		
Cladrastis lutea			15.74		
Clethra acuminata		13.37			
Cornus alternifolia			25.75		
Cornus florida		57.45	20.22		
Crataegus uniflora					4.76
Fagus grandifolia		5.41		23.34	114.23
Fraxinus americana		3.87	19.94		
Gaylussacia ursina	14.08	23.01			
Halesia carolina	5.47	34.82	56.50	14.10	47.27
Hamamelis virginiana	15.17	11.43	40.55	18.93	10.91
Ilex ambigua	9.31		11.94	68.31	19.29
Ilex opaca			15.51	8.92	
Kalmia latifolia	98.17	54.44	2.06	5.16	
Lindera benzoin			14.16		
Liriodendron tulipifera		7.24	57.71		
Magnolia acuminata		5.23		29.51	
Magnolia fraseri		13.92	28.78	9.02	20.31
Nyssa sylvatica	20.71	16.05	16.35		
Oxydendrum arboreum	23.96	25.59	14.81	55.42	
Pinus echinata	4.26				
Pinus pungens	5.16				
Pinus rigida	8.87				
Pinus strobus	28.96	21.99	15.95		
Pinus virginiana	60.94	8.23			

Table A.2. Continued.

	Site Unit				
Species	**1**	**2**	**3**	**4**	**5**
Prunus serotina	5.88	5.41			
Prunus virginiana	5.84				
Pyrularia pubera		4.62	53.18	9.91	
Quercus alba	19.51	8.04			
Quercus marilandica	5.51				
Quercus prinus	29.14	15.82			
Quercus rubra	11.31	9.85	3.60		
Quercus velutina	9.16	5.19			
Rhododendron calendulaceum	6.22	23.71			
Rhododendron maximum		18.01	78.14	125.37	
Robinia pseudo-acacia	7.27	4.24			
Rubus canadensis					27.74
Sassafras albidum	24.41	19.19	25.48		
Tilia heterophylla			45.19		23.90
Tsuga canadensis	4.96	49.13	49.65	74.19	30.79
Vaccinium constablaei	5.79	7.47		4.76	2.57
Vaccinium erythrocarpum		8.84			
Vaccinium stamineum	18.06	11.93			
Viburnum alnifolium					16.60

Table A.3. Average importance values (200) for regeneration and low shrubs.

	Site Unit				
Species	**1**	**2**	**3**	**4**	**5**
Acer pensylvanicum		9.18	47.28	31.75	29.16
Acer rubrum	12.37	18.21	19.43	26.30	4.08
Acer saccharum			38.92	2.17	13.24
Aesculus octandra			60.53	6.43	6.06
Amelanchier arborea	3.62	2.64	9.42		
Asimina triloba			81.05		
Betula lenta		3.89			
Calycanthus floridus		19.73	33.94	63.77	
Carya cordiformis	1.32		15.45		
Carya glabra	1.90	7.94	11.22		
Carya tomentosa		3.88			
Castanea dentata	6.05	8.15	6.32		
Cornus alternifolia			4.81		
Cornus florida		9.86	4.62		
Crataegus uniflora					4.18
Euonymus americanus			26.87	5.36	
Fagus grandifolia				10.43	52.86
Fraxinus americana		2.34	40.56		
Gaylussacia baccata	26.73				
Gaylussacia ursina	72.78	129.53	40.80	111.68	
Halesia carolina	0.85	15.14	30.65	15.51	8.92
Hamamelis virginiana	6.91	2.59	13.31	25.80	4.39
Hydrangea arborescens			24.02		
Ilex ambigua	4.98	1.60			3.69
Ilex opaca			6.13		
Kalmia latifolia	58.66	34.11	46.13	22.12	
Leucothoe axillaris		43.01	8.46	167.32	
Lindera benzoin			10.49		
Liriodendron tulipifera		3.86	11.00		
Lyonia ligustrina	18.06				
Magnolia acuminata	2.13				
Magnolia fraseri	4.62	4.94	3.77	6.29	2.43
Menziesia pilosa					9.30
Nyssa sylvatica	5.28	4.29	3.93		
Oxydendrum arboreum	3.79	5.54	6.69	61.50	
Pinus rigida	10.29	2.65			

Table A.3. Continued.

	Site Unit				
Species	**1**	**2**	**3**	**4**	**5**
Pinus strobus	1.82	2.16	5.05		
Pinus virginiana	0.89				
Prunus pensylvanica		2.54			
Prunus serotina	1.54	11.73	10.33	43.89	25.50
Prunus virginiana		4.92			
Pyrularia pubera	20.06	77.59	58.34	66.83	
Quercus alba	7.21	11.71	1.32		
Quercus marilandica	6.80	4.82			
Quercus prinus	17.46	11.85	5.06	10.38	
Quercus rubra		17.64	13.22	13.32	
Quercus velutina	15.18	9.24			1.58
Rhododendron calendulaceum	8.51	14.01	1.21		
Rhododendron maximum		2.60	39.47	144.31	
Robinia pseudo-acacia	1.89	1.22	16.70		
Rubus canadensis					126.74
Rubus idaeus		0.91	21.36		23.01
Sambucus pubens			9.78		
Sassafras albidum	51.43	26.70	23.94		
Tilia heterophylla			29.69		87.32
Tsuga canadensis		10.66	9.14	57.99	8.01
Vaccinium constablaei	14.38	11.46		24.06	
Vaccinium erythrocarpum		7.35	3.09		
Vaccinium hirsutum	21.27	33.23			
Vaccinium stamineum	14.61	11.37			
Vaccinium vacillans	26.48	6.53	4.25		
Viburnum acerifolium		8.94	6.22		
Viburnum alnifolium					56.63

Table A.4. Average importance values (100) for herbaceous stratum.

	Site Unit				
Species	**1**	**2**	**3**	**4**	**5**
Adiantum pedatum			0.27		
Angelica triquinata					3.13
Arisaema triphyllum		0.82	2.61	2.33	0.58
Aristolochia macrophylla			2.52		
Asplenium platyneuron			0.25		
Aster cordifolius		1.35	9.36	5.71	8.57
Astilbe biternata			4.14		
Athyrium asplenioides		7.04	4.75	8.54	8.94
Athyrium thelypterioides		8.29	3.90		1.44
Botrychium virginianum			0.75		
Cacalia atriplicifolia		2.32	3.66		
Calycanthus floridus	4.32	5.04	4.91		
Campanula americana		1.35			
Cardamine diphylla		1.59	2.40		1.86
Caulophyllum thalictroides			7.50		
Chimaphila maculata	0.93	2.08	1.58	4.76	
Cimicifuga americana			9.36		
Cimicifuga racemosa			6.74		1.44
Clintonia umbellulata			0.65		
Collinsonia canadensis		2.32	0.55		
Conopholis americana	0.47	1.00	0.59		
Crataegus uniflora					8.41
Cryptotaenia canadensis			0.74		
Cypripedium acaule			3.43		
Cystopteris protrusa			4.65		
Dennstaedtia punctilobula		11.79	8.21	22.17	14.98
Desmodium nudiflorum		2.28	7.44		
Dioscorea villosa		2.07	1.96	2.13	0.72
Disporum languinosum			3.29		3.11
Dryopteris campyloptera			2.11		
Dryopteris intermedia		3.09	13.38	14.74	22.01
Dryopteris marginalis		0.39	2.26		
Epigaea repens	8.46	1.92			
Euonymus americanus		0.95	3.88	6.93	
Eupatorium rugosum			3.72		4.62
Galax aphylla	17.13	7.32		1.75	

Table A.4. Continued.

	Site Unit				
Species	**1**	**2**	**3**	**4**	**5**
Galium circaezans		1.36	1.40		
Galium triflorum		1.56	1.28	2.33	
Gaultheria procumbens		3.95		5.45	
Gaylussacia baccata	13.44				
Gaylussacia frondosa	3.72				
Gaylussacia ursina	30.15	47.15		6.91	
Geranium maculatum		2.70	1.82		
Geum canadense			1.59		
Goodyera pubescens		0.41	0.51	9.76	
Hepatica acutiloba			1.44		
Heuchera villosa			2.81		
Hexastylis arifolia		2.39			
Hexastylis heterophylla		1.69			
Houstonia longifolia				1.22	
Houstonia purpurea		2.45	0.94		
Hydrangea arborescens			1.75		
Hypoxis hirsuta		2.60			0.48
Ilex ambigua	1.52	1.06			
Impatiens pallida			4.28		
Jeffersonia diphylla			0.95		
Kalmia latifolia	15.15	11.55	6.86	33.33	
Krigia virginica		0.88			19.64
Laportea canadensis		0.39	5.76		1.79
Leucothoe axillaris		17.55	11.02	32.96	
Ligusticum canadense	0.68	3.00	0.41		
Lindera benzoin			0.99		
Lycopodium lucidulum				12.04	9.07
Lysimachia quadrifolia	3.26	2.91			
Maianthemum canadense					1.96
Medeola virginiana		0.86	2.38	5.27	4.11
Melampyrum lineare	0.37	2.66	0.25	5.88	
Menziesia pilosa					2.68
Mitchella repens			3.35	10.46	6.39
Monarda clinopodia			3.26		
Monarda didyma			0.30		
Monotropa uniflora		0.66		6.25	1.12

Table A.4. Continued.

	Site Unit				
Species	**1**	**2**	**3**	**4**	**5**
Osmorhiza claytonii			1.60		
Osmunda cinnamomea				1.22	
Oxalis acetosella			4.25	17.59	15.31
Panicum sp.		2.09			
Parthenocissus quinquefolia		1.32	1.83		
Philadelphus inodorus				5.56	
Pilea pumila			6.43		
Podophyllum peltatum			5.13		2.80
Polygonatum biflorum		1.52	2.05	1.77	
Polygonatum pubescens			1.26		0.55
Polypodium virginianum		13.64			
Polystichum acrostichoides		15.43	7.76	9.53	2.87
Potentilla canadensis		3.12			
Pteridium aquilinum	2.38				
Pyrularia pubera		7.14	5.52	2.35	
Ranunculus recurvatus			3.43		0.54
Rhododendron calendulaceum	3.74	6.96			
Rhododendron maximum		4.48	5.62	40.90	
Rhus radicans	0.47				
Ribes rotundifolium					3.27
Rubus allegheniensis		0.39	3.02	0.98	
Rubus canadensis					16.56
Rubus hispidus	0.47				
Rubus idaeus		1.74	4.85		10.14
Sanguinaria canadensis			0.40		
Sanicula canadensis			1.69		
Scutellaria serrata			4.88		
Smilacina racemosa		0.79	5.05	1.18	1.23
Smilax glauca	4.41	3.70	1.68	5.57	0.47
Smilax rotundifolia	13.77	10.54	5.08	11.34	0.77
Solidago curtisii	0.59	4.42	5.33	6.56	2.29
Stachys clingmanii					2.87
Stachys latidens			2.14		
Streptopus roseus		0.66			
Thalictrum dioicum			4.53		
Thalictrum thalictroides			0.32		

Table A.4. Continued.

	Site Unit				
Species	**1**	**2**	**3**	**4**	**5**
Thelypteris noveboracensis		15.97	13.93	17.19	13.07
Thelypteris phegopteris			0.58		
Tiarella cordifolia			7.47	1.22	2.98
Tovara virginiana			1.48		
Trautvetteria carolinensis			1.90		
Trillium cuneatum			0.42		
Trillium grandiflorum			2.58		1.24
Uvularia perfoliata			2.88		
Vaccinium constablaei	6.09	3.84			2.68
Vaccinium erythrocarpum	3.73	3.48			
Vaccinium hirsutum	32.01	19.98			
Vaccinium stamineum	5.87	2.63			
Vaccinium vacillans	20.85	10.41		4.76	0.45
Veratrum parviflorum		0.69	3.53		6.38
Veratrum viride					2.87
Viburnum acerifolium		1.40	5.24		
Viburnum alnifolium				5.88	10.56
Viola blanda	0.47	4.11	7.09	5.40	6.00
Viola canadensis		0.91	5.45		
Viola emarginata		2.12	1.34	2.20	2.01
Viola eriocarpa	0.76	2.27	2.39	7.32	0.31
Viola hastata	0.47	2.22	1.49	5.40	
Viola rotundifolia			2.27		1.92
Viola septentrionalis		6.35			
Vitis aestivalis		1.09			
Vitis rotundifolia			1.12		2.40

VITA

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