MULTIFACTOR CLASSIFICATION OF ECOLOGICAL LAND UNITS IN NORTHEASTERN LOWER MICHIGAN

By

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A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Forestry

1997

ABSTRACT

MULTIFACTOR CLASSIFICATION OF ECOLOGICAL LAND UNITS
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An integrated classification of ecological land units was developed in northeastern lower Michigan based on associations of understory and ground-flora species, and key soil morphological and physical characteristics. A series of complementary multivariate, graphical, and tabular analyses of floristic and soils data were utilized in the classification process. The utility of eliminating understory and ground-flora species in the classification of multifactor ecological land units using a geometric interpretation of a correspondence analysis was assessed. Species whose squared cosines summed to less than 45% in the first five dimension of a correspondence analysis were eliminated from the floristic data set, and a reduced data set was re-analyzed and compared to earlier results.

Correspondence analysis and detrended correspondence analysis were robust to the inclusion of low display quality species, and both procedures were effective in distinguishing ecological land units in commonly occurring and high quality species space. The use of high quality species improved the consistency in the number of groups derived from three agglomerative and one divisive clustering procedure, and the assignment of samples to groups when compared to results based on commonly occurring species. The utility of eliminating low display quality species in cluster analyses was

corroborated in the reanalysis of data used to formulate a second independently derived classification by Host (1987).

Principal component analysis of soils data identified important variables used in differentiating ecological land units, and produced ordination diagrams that grouped samples into meaningful classes of soil, understory, and ground-flora conditions. Agglomerative clustering of samples based on soil variables failed to identify the same groups as ordination space partitioning of samples in soil variable space, or as the ordination and clustering of samples based on ground-flora.

The continuous distribution of samples ordinated in species or soil variable space required use of clustering and tabular analyses, and comparisons of floristic and soil analyses to effectively partition regions containing different ecological land units. The iterative application of a series of complementary ordination, clustering, graphical, and tabular analyses was effective in defining multifactor ecological land units for northeastern lower Michigan.

This is dedicated to my parents, John and Agda Cleland,
and to my wife and daughters Cathy, Alyssa, and Heather.

ACKNOWLEDGMENTS

I would like to express my gratitude to a number of faculty at Michigan State University. My advisor Dr. James B. Hart encouraged me to enter into a Ph.D. program, and ensured that my program met the rigor and caliber of research necessary to fulfill the requirements of the university and the degree. I would like to acknowledge my committee members, Drs. Don Dickman, Doug Lantagne, and Rique Campa for their encouragement, patience, and careful review of my dissertation. I would especially like to thank Dr. Carl Ramm for his assistance and guidance in the appropriate use and interpretation of multivariate methods. I would also like to thank Drs. Larry Leefers and Michael Vasievich, who provided emotional support throughout my program.

I would like to acknowledge Dr. Burton Barnes of the University of Michigan for his research leadership in multifactor ecological land classification. James Jordan of the Ottawa National Forest translated research concepts into practical classification and mapping systems that have been applied throughout the Lake States.

I would like to thank a number of Forest Service employees for their assistance and support in my research program. Drs. Thomas Crow and Forest Stearns provided constant support and inspiration while demonstrating that qualities of greatness are measured first by a person's compassion and humility, then their innate ability, discipline, and accomplishment. Dr. Eunice Padley, Jeff Bruggink, and Pete Greaney assisted in field sampling and in interpreting ecological relationships within the study area, and were great allies in applying ecological land classification in natural resource and ecosystem management. Richard Watson taught me to question accepted approaches to soil survey and ecological land classification, and shared his considerable insights into the nature of forest ecosystems in Michigan.

Finally, I would like to thank my family for their support and sacrifice while I was taking classes and writing the dissertation. My wife Cathy and daughters Alyssa and Heather all shared the strain of my program. My father John (Bill) Cleland, who passed away shortly after my comprehensive written and oral examinations, expressed his fatherly pride by silently allowing me to concentrate on academic needs instead of family responsibilities.

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INTRODUCTION

RESEARCH GOALS

There were three problems related to ecological land classification addressed in this research. First, multifactor classification of ecological land units had not been undertaken within the study area of northeastern Lower Michigan. Second, the sequential application and interpretation of multivariate, graphical, and tabular methods on floristic and environmental data for fully integrated ecological land classification had not been previously documented. Third, the utility of using understory and ground-flora species highly correlated with low-dimensional ordination space (Greenacre 1993, 1984) to classify multifactor ecological land units and component ecological species groups had not been investigated.

The primary goal of this research was to develop an integrated classification of ecological land units in northeastern Lower Michigan based on associations of ground-flora and understory species and key soil morphological and physical features. Two secondary goals met while achieving the primary goal were: (i) to utilize and document a series of complementary multivariate, graphical, and tabular analyses of ground-flora and soils data in the classification process, and (ii) to determine if the classification of multifactor ecological land units could be improved by eliminating understory and ground-flora species that were poorly correlated ($r^2 < .45$) with the first five dimensions of a correspondence analysis, and species that occurred interior to the arch of the first two dimensions of a correspondence analysis, prior to application of several ordination and clustering methods.

To meet the first goal, I used ordination, clustering, graphical, and tabular analyses of understory and ground-flora and soils data in a series of iterations. Commonly occurring understory and ground-flora species were analyzed initially, followed by the analysis of soils data, and then an analysis of ground-flora with high fidelity to the first five dimensions of a correspondence analysis was conducted. After these data sets were interrogated, data on overstory composition was analyzed using ordination and tabular methods and related to earlier results. A final set of synthesis tables was used to derive an integrated multifactor ecological classification.

To meet the second goal, I displayed results at each step of the classification process and in subsequent discussions. Figures and tables were presented in a sequence of analyses of floristic and soil data sets. Objective numerical analyses were used in conjunction with subjective tabular methods. Clustering results were used in initial ordination space partitioning of samples in both species and soil variable space to ensure objectivity and enable replication. Subsequent analyses were compared to initial results using graphs and tables. Steps used in arriving at results could thus be repeated by other investigators with a minimum of subjective decisions made that affect the final classification.

To meet the third goal, I explored the use of a geometric interpretation of correspondence analysis to identify species most strongly correlated with the first five principal coordinates or dimensions. Following initial eigenanalyses and clustering of commonly occurring ground-flora, a criteria was set for retention of species for subsequent ordination and clustering procedures. An arbitrary limit was set as other research indicating appropriate limits was not available for guidance. If forty-five per cent of the overall variability of species in the forty-five dimensional sample space of the full data set was not accounted for in the first five dimensions, species were eliminated from further analyses (personal comm. Dr. Carl Ramm). A reduced data set was reanalyzed using the same ordination and clustering procedures, and results of the two sets of analyses were compared using tabular and graphical methods.

These research goals involved both the application and refinement of multivariate procedures routinely used in ecological classification. In order to assess the utility of eliminating low fidelity species in the classification process, a classification had to first be developed. However, assessing the effects of constructing a more parsimonious data set for ecosystem classification based on the same data set used to develop the initial classification may be questionable. This is analogous to developing a predictive equation for a sample and only testing the model on the same sample. For this reason, I not only compared clustering and ordination results between a larger and reduced data set to meet the third goal, I also reanalyzed a data set for which results have been published and tested in field applications (Host 1987).

PROBLEM STATEMENT

Two problems related to ecological land classification were addressed by the goals stated for this research. The first problem was one of classification methodology. The second problem was the quantification of species' fidelity to environmental gradients. These problems, which are interrelated and mutually inclusive, are discussed briefly.

Problem one: Classification Methodology

Limitations of single factor approaches to the classification of forest land potentials led to the development of multifactor systems in the latter part of the twentieth century (Avers and Schlatterer 1991, Padley 1989, Hix 1988, Host et al. 1987, Albert et al. 1986, Spies and Barnes 1985, Pregitzer and Barnes 1984, Barnes et al. 1982, Jordan 1982). Multifactor land classification uses groups of plants as indicators of important environmental conditions in conjunction with direct measures of environment to formulate classification units.

In the development of multifactor ecological land classification systems, the decision to use a particular ordination method in the analysis of ground-flora data, in particular correspondence analysis versus detrended correspondence analysis, reportedly may affect results and interpretations of eigenanalyses (Greenacre 1993, 1984, Palmer 1993, Minchin 1987, Peet et al.1987, and Hill and Gauch 1982). Furthermore, clustering methods used to identify "natural groupings" are inherently more subjective than ordination methods (Jongman et al. 1987, Gauch 1982). Clustering results are influenced by the choice of variables (Fowlkes et al. 1988), by the transformation or weighting of these variables (Milligan and Cooper 1988, Jongman et al. 1987, Stoddard 1979), by the choice of polysynthetic divisive or agglomerative procedures (Spies 1985a), and by the linkage method chosen in the case of agglomerative clustering. Inclusion of superfluous, or "noisy" variables also confounds clustering results (Fowlkes et al. 1988). These limitations to any single approach to ordination and classification led to recommendations to use a series of complementary methods in the ecological classification process (Digby and Kempton 1987, Pielou 1984, Gauch 1982), yet most ecological classification research involves the use of a single set of methods, without corroboration with other methods, followed by reporting of results. In this research, a series of complementary methods were used and compared to one another to derive the classification of multifactor ecological land units and their components.

Another methodological problem relates to the definition of indicator plant communities. In classic plant phytosociology, indicator species are used as indirect expressions of environmental gradients presumed to be the cause of latent structure in patterns in composition and relative abundance of ground-flora communities, hence the reference to ordination of vegetation as indirect gradient analyses (Barton 1994, Backus 1993, Allen et al. 1991, Allen and Peet 1990). Terms used to describe such species include species with narrow ecological amplitudes (Pregitzer 1981), species with high fidelity (Host 1987), and species with an affinity to a given environmental setting. Thus most community classifications rely upon indirect gradient analyses of species-species relationships to infer important environmental conditions, and use species-species relationships to define plant associations (Barton 1994, Parker 1994, Kent and Coker 1992, Pfister et al. 1977, Daubenmire and Daubenmire 1968).

A different approach to classifying vegetation relies upon the evaluation of species-environment relationships (John and Dale 1990), instead of species-species relationships, to define communities. In ecological land classification, resulting groups are called "ecological species groups" (Host and Pregitzer 1991, Archambault et al. 1989, Spies and Barnes 1985b, Pregitzer and Barnes 1982). Yet in multifactor applications, a range of ecological species groups have been reported as occurring within a given ecological classification unit (Hix 1988, Host 1987). In essence, this amounts to retrofitting independently defined component systems by simply conceptually overlaying classifications. Since "ecological species groups" in a strict sense connote associations of species based on their relationships to environment (Mueller-Dombois and Ellenberg 1974), this research compared results of analyses of floristic and environmental variables in a series of iterations to identify congruent changes in ecological species groups and environmental conditions.

Problem Two: Quantification of Species Fidelity to Environmental Gradients

In the ordination of vegetation, the first few axes generally account for the majority of the overall variability of species in full-dimensional sample space (Digby and Kempton 1987, Gauch 1982). Nearly all research on plant-soil relationships report that the first few axes of an ordination of vegetation are related to environmental gradients, primarily soil or topographically controlled moisture and to a lesser extent nutrient availability (Host 1987, Spies and Barnes 1985a, Pregitzer 1981). Thus species with the greatest linear relationship, or correlation, with the first few principal coordinates would have the highest fidelity, or indicator value, to environmental gradients expressed low dimensional subspaces provided that other sources of variability such as disturbance were filtered by a well defined sample frame (van Groenewoud 1992).

The geometric interpretation of the quality of individual points in a given subspace of a correspondence analysis provides a means of quantifying species' fidelity to principal coordinates (Greenacre 1984). In a correspondence analysis, the squared cosines of the angles between a point and each axis of a set of axes can be added across any number of dimensions; the sum of squared cosines across all dimension sums to one. This sum of squared cosines, or display quality, is a measure of how well points are represented in a particular set of axes, and is mathematically analogous to the correlation of a species to a given multidimensional subspace (Greenacre 1993). In this research, groups of species with high correlations or fidelity to low-dimensional subspaces were used to define ecological species groups associated with underlying environmental gradients, and to define multifactor ecological land classification units.

The determination of species with high fidelity to low-dimensional subspaces also facilitated an improved interpretation of ordination diagrams. All species are represented in ordination diagrams, yet not all species are "indicators" of the environmental or other gradients expressed in diagrams of 2 or 3 visually observable dimensions (personal comm. Dr. Carl Ramm). Some species' profiles will not be accurately represented in low dimensional subspaces because they lie more along higher planes or within higher multidimensional subspaces (Greenacre 1993, 1984). In these instances, species that are actually poorly related to a low-dimensional ordination space are arrayed along side species that are closely related to the two or three dimensional ordination space being observed. This results in an obscured interpretation of species and groups of species with high indicator value, or fidelity, to underlying gradients expressed by a particular subspace. In this research, superfluous species were filtered prior to interpreting ordination diagrams.

ALTERNATIVE FOREST LAND CLASSIFICATION SYSTEMS

Two basic types of forest land classification and mapping systems are used in natural resource research, planning and management. The first classifies and maps current conditions of land areas, whereas the second classifies and maps potential of land areas (Jones 1994, Rowe 1980). Inventories of current conditions measure attributes such as age, stocking, and composition of forest stands, or locations of endangered species. Inventories of potentials include soil surveys, habitat typing, site index estimates, and multifactor ecological land classification (Pregitzer and Barnes 1984, Moon 1984). Each of the latter types of systems have a primary purpose of identifying land areas that have similar capabilities for management (Jensen et al. 1991). Although the objectives of soil surveys, habitat typing, site index, and ecological classification strongly overlap, the assumptions underlying each system are markedly different.

Soil Survey

Information about soil properties is critical to managers. Soil directly influences plant community composition and productivity, and strongly influences the capacity of the land to produce vegetation (Zak et al. 1989, Bruggink 1988). Maintaining long-term soil productivity is imperative to sustainable forest management, and knowledge of soil properties is needed in planning the construction and maintenance of physical structures such as roads, facilities, and so forth.

In 1893, a new concept of soil was published by V.V. Dokuchaev in Russia (Glinka 1927, Vilenskii 1957). Soils were conceived to be independent natural bodies resulting from interactions of climate, vegetation, parent materials, relief, and time. In 1892, E.W. Hilgard extended this concept to soil science in the United States, emphasizing relationships between soils and climate. Coffey (1912) later articulated that "the soil is an independent, natural body, a biogeological formation, differing essentially from the rock that undelies it, although closely related to it . . . . " As stated in Soil Taxonomy (1975), "this was a revolutionary concept. The soil scientist did not need to depend wholly on inferences from the underlying rocks, the climate, or other environmental factors, considered singly or collectively; rather, he could go directly to the soil itself and see the integrated expression of all these in its morphology." This concept of soils assumes that soil morphology fully integrates other important physical and biological factors.

Soil surveys are conducted to provide land managers information for many uses such as agricultural crop production, building and road construction, septic system installation, forest management, and so on. Traditional soil surveys have been found inadequate for predicting timber production and forest land management potentials, (Carmean 1979), and the need to tailor soil surveys for forest management purposes has been well documented (Grigal 1984, Moon 1984, Zanner and Hannah 1972, Gysel and Arend 1956). Moreover, the criteria used in soil classification, and many of the laboratory analyses used to characterize soils, are based on agricultural needs and calibrations. Alternate criteria and laboratory methods based on forest rather than agricultural crop response are needed (Stone 1975).

Vegetation Classifications

Information about vegetation and vegetative potentials is essential to forest and wildlife managers (Arno et al. 1986, Coffman et al. 1983, Pregitzer and Barnes 1982). The earliest scientific classification of vegetation is generally credited to Alexander von Humbolt (1807) who systematically classified areas dominated by plants into vegetation types based on plant physiognomy (McIntosh 1978, Whittaker 1973). Other early influential plant ecologists (Show 1822, Kerner 1895, Giesbach 1872, Drude 1890, Warming 1895 and 1909, and Schimper 1903) also largely described vegetation based on similarities in physiognomy. In Finland, Cajander (1926) identified forest types based on combinations of tree species and ground-flora communities, and demonstrated that the growth rate of a given tree species varied depending on forest type.

This early work led to the development of "habitat types" in the United States. Daubenmire (1952) defined a habitat type as all the land capable of supporting a particular plant association at climax. Climax plant associations are described by Kotar and Coffman (1984) as late stages in succession "whereby the plant species are apparently self-regenerating in predictable patterns and have long been free of disturbance by fire, grazing, logging, etc."

Habitat type classification systems typically rely solely on climax vegetation, even though many landscapes support plant communities in a variety of successional stages due to anthropogenic and natural disturbance (Dzwonko 1993, Franklin et al.1993, Foster 1992, Delcourt et al. 1983, Pfister et al. 1977). Climax vegetation is classified in relatively undisturbed conditions to describe habitat types, then habitat types are identified in disturbed lands based on remnants of typical climax plant associations (Kotar et al. 1988, Kotar and Coffman 1984).

Classifications based on vegetation made similar presumptions as soil surveys with respect to the integrative power of plant indicators. Plant phytosociology has assumed that "the climax community reflects the most meaningful integration of environmental factors affecting vegetation" and that "each habitat type represents a relatively narrow segment of environmental variation" . . . "that uses the plant community as an integrated indicator of environmental factors (Kotar et al. 1988)."

In their classic work of 1968, Daubenmire and Daubenmire state "it is clear . . . that no useful correlation exists between vegetation types as described herein and (soil) profile types distinguished on the basis of color, texture, structure, depth, sequence or horizon, etc." Many studies, however, have shown that plants, particularly ground-flora species, can be used to indicate specific soil properties (McIntyre 1994, Boeye and Verheyen 1994, Franklin and Merlin 1992, Whitney 1991, Haase 1990, Pregitzer and Barnes 1982, Grigal and Arneman 1970, Waring and Major 1964). Ground-flora species groups have also been associated with overstory species composition, glacial physiography, and nutrient cycling rates (Host and Pregitzer 1992, Padley 1989, Zak et al.1986, Spies and Barnes 1985b, Barnes 1984, Moon 1984, Pregitzer and Barnes 1984, Peet and Loucks 1977, Curtis 1959). In Canada, Rowe (1971), and Rowe and Sheard (1981) have described similar associations.

There are several advantages to the use of vegetation in determining land capability. Vegetation is easily observed, whereas observing soil conditions requires labor-intensive methods (Bekele 1994, Pregitzer and Barnes 1984). In many instances there are predictable relationships between ecologically important soil factors (e.g., pH, organic matter content, soil texture, and nutrient availability) and the distribution of ground-flora (Haase 1990, Odland 1990, Prentice and Cramer 1990, Padley 1989, Zak et al. 1986, Spies and Barnes 1985a, Barnes 1984, Jones 1984, Moon 1984, Pregitzer and Barnes 1982). Habitat type systems provide significant information about plant community composition, and provide a basis for grouping observations to study processes such as forest growth or succession and extrapolate results to similar sites (Arno 1986).

The major drawback of habitat typing is that it is based on one component of the ecosystem, namely vegetation, and is not linked to the more stable abiotic factors (Pregitzer and Barnes 1984). Because the habitat typing system uses only vegetation to determine the classification of a land area, it cannot differentiate among ecosystems where disturbance has eliminated or changed the composition and relative abundance of plant indicators (Cook 1996, Meier et al. 1995, Gilliam et al. 1995,. Roberts and Christensen 1987, Marquis and Brenneman 1981), where deep-lying soil characteristics affect overstory growth (Host 1987, Hannah and Zahner 1970), or where compensating factors have produced similar plant communities. Rowe (1984) discussed the limitations of the use of vegetation as the prime indicator of forest land potential, contending the chief deficiency of vegetation is that it is just one part of the ecosystem.

The single factor approach of habitat typing for land classification is analogous to soil classification, using climax vegetation types instead of soil morphology as the basis for identifying environmental conditions influencing ecological systems. Yet plant ecologists do not agree on the assumption that there is a fixed and predictable endpoint in the successional pathways in plant community composition through time (Cook 1996, Abrams 1985).

"Ecological species groups" is another approach to Vegetation classification. This approach relies upon species-environment relationships instead of species-species relationships to distinguish communities (Host and Pregitzer 1994, Archambault et al. 1989, Spies and Barnes 1985b, Pregitzer and Barnes 1982). The method is based on the premise that communities are combinations of species whose composition is dependent upon local environment (Rydgren 1994, Archambault et al 1989, Mueller-Dombois and Ellenberg 1974).

Mueller-Dombois and Ellenberg (1974) recommend establishing species groups using any of three methods. The first is to conduct field investigations and subjectively identify groups of species with similar ecological relationships. The second is to study the ecological behavior of individual species in relation to single site factors until relationships can be expressed in figures. The third is to use tabular methods or correlative studies for species groups by identifying which of the differential or highly correlated species form ecological groups.

The major drawback of ecological species groups is that it is based on one factor, vegetation, although communities are linked to the more stable abiotic factors, as opposed to habitat typing. The omission of environmental factors in this single factor approach precludes development of several research and management applications including studies of whole systems for research on processes such as carbon and nutrient cycling, and management information needs such as limitations for road construction, equipment operability, and other physically constrained management options.

Site Index

Site index is the most common and widely applied method of predicting the growth potential of forests in the Lake States. Site index is a direct measure of height growth at a base age (Grigal 1984, Carmean 1979), and its use depends upon finding trees whose height growth has not been suppressed, or damaged by ice or wind. Height growth is usually well related to timber volume production and site index is widely used in yield tables and computer simulations.

Site index alone yields no information about plant community composition, succession, or soil (Carmean 1975, Jones 1969). It is primarily a tool for estimating the potential for timber production in normally stocked, even-aged stands, and cannot by itself provide the information needed for integrated resource management (Pregitzer 1981).

Multifactor Ecological Land Classification

Studies comparing classification systems have shown that combinations of physiography, soil, and vegetation data provided better classifications than any single component used separately (Palmer 1990, Spies and Barnes 1985a, Pregitzer and Barnes 1984). The basic goal of multi-factor ecological land classification is to identify land areas with different management potentials by discerning congruent changes in community and environment and defining class limits for each component based on mutual relationships (Jensen et al. 1991, Hart 1988). This goal is accomplished by the simultaneous sampling, analysis, and mapping of biotic and abiotic variables (Host 1987). In this approach, both species-species relationships and species-environmental relationships are identified. Changes in species composition are related to underlying environmental gradients to produce an integrated classification of land units.

The concepts underlying multifactor ecosystem classification began to emerge as early as 1789, when Alexander von Humboldt wrote that, "All natural bodies are interrelated. Find a certain type of soil and a certain type of plant and you will find a certain type of rock." In the century following Alexander von Humboldt's observations, Gutrovich (1894) developed a system in Russia that classified different kinds of forests based on species composition and landscape topography. During the 1920's, a study of site relationships was conducted in West Germany, eventually leading to the classification and inventory of the state of Baden-Wurttemburg (Barnes 1984). The German system employed a regional hierarchy based upon climatic and physiographic influences, and a local hierarchy based upon topography, soil and ground-flora.

In the 1940's, G.A. Hills developed a site classification system in Ontario that included vegetation and physiography after finding that soil surveys or habitat types alone did not adequately classify land for both agricultural and forestry uses. Stan Rowe continued this work throughout the 1960's and 1970's, describing "landscape units" based on geomorphology, incorporating principles of both community ecology and habitat typing, and emphasizing practical aspects of classification and inventory.

In the 1980's and 1990's, a number of researchers applied multifactor concepts in the evaluation and classification of forests and forested landscapes in Michigan and Wisconsin. This includes work by Barnes et al. (1982), Jordan (1982), Pregitzer and Barnes (1984), Spies and Barnes (1985a), Albert et al. (1986), Host et al. (1987), Hix (1988), Archambault (1989), and Padley (1989).

Multifactor land classification uses groups of indicator plants as indirect expressions of important environmental conditions in conjunction with direct measures of environment (e.g., climate, landforms, and soils) to define taxa. Ecological units are then mapped using both vegetative and environmental criteria identified in the classification process, with interpretations made possible given spatially explicit information (Johnson 1992, Brenner and Jordan 1991). The modern approach to multifactor ecological classification builds upon systems developed by numerous researchers throughout the twentieth century (Cajander 1926, Koppen 1931, Fenneman 1938, 1950, Hills 1952, Whitaker 1960, Kuchler 1964, Daubenmire and Daubenmire 1968, Wertz and Arnold 1972, Corliss 1974, Rowe 1980, Eyre 1980, Jordan 1982, Barnes et al. 1982, Bailey 1983, Jones et al. 1983, Driscoll et al. 1984, Smalley 1986, McNab 1987, Omernik 1987, Jensen et al. 1991, Cleland et al. 1992, 1996).

LITERATURE REVIEW of ECOLOGICAL CLASSIFICATION METHODS

Ecological classifications in various forms have been developed using relevees (species lists ordered by sampling quadrants), tabular analyses, and more recently by various multivariate numerical methods (Host and Pregitzer 1991, Retuerto and Carballeira 1991, Spies and Barnes 1985a, Gauch 1984, Mueller-Dombois and Ellenberg 1974). Braun-Blanquet's procedure of 1921 used tabular methods in successive approximations to identify groups of species occurring in similar samples, and to identify samples with similar species composition. These early tabular classification techniques were informal and inherently subjective (Whittaker 1960, Mueller-Dombois and Ellenberg 1974), and thus the recognition of differential species groups and groups of similar samples depended on the individual investigator's understanding of species-species and species-environmental relationships within a study area.

In the past few decades, more objective multivariate procedures have been applied in ecological classification research (Digby and Kempton 1987). Research problems are often approached in an overall program using ordination for indirect and direct gradient analyses, clustering to group samples and variables, and tabular synthesis of results to corroborate patterns detected through ordination and clustering (Gauch 1982).

In these procedures, explorative data analyses are used to detect intercorrelations among variables, to check assumptions of data structure underlying particular analyses and suggest appropriate transformations, and to identify sample outliers using descriptive statistics and graphical displays of raw data. Ordination is also used in an exploratory data analysis sense to detect outliers, and in a multivariate sense to screen variables, reduce dimensionality, and summarize community and environmental patterns (Gauch 1982).

Ordination is often followed by clustering to identify natural groupings of samples and species. Results of ordination and clustering may be compared, and subsets of data may be interrogated to further elucidate relationships. Several complementary analysis techniques may be applied to the same data set, with the analysis progressing by successive refinement. Community patterns may be compared with environmental patterns to produce an integrated interpretation of ordination and classification results. The communication of results is promoted, however, by employing a moderate number of commonly used, relatively standardized methods (Pielou 1984, Romesburg 1979). Finally, hypothesis testing methods may be used a posteriori to assess ecosystem-level differences in processes such as productivity (Host et al. 1988), successional pathways (Host et al. 1987) and nutrient cycling (Zak et al. 1986, 1990).

Ordination

Ordination, a primary tool for examining continuous change in ground-flora distributions, is a matrix approximation technique used to identify important variables, summarize data in a scatter diagram (Bray 1957), and reduce the dimensionality of a multivariate data set (Causton 1988, Gauch 1982). Important variables are those with the highest weights and loadings, or correlations, with the first few eigenvectors. The reduction of dimensionality aims to provide low-dimensional summaries of high-dimensional data sets that ideally account for a large part of the total variability lying in higher dimensional space (Morzuch and Ruark 1991, Krzanowski 1988). In ecological studies, ordination is also used to discover latent structure of vegetation data due to species' responses to underlying environmental gradients (Prentice 1977).

Principal component analysis (PCA; Morrison 1976), correspondence analysis (CA; Hill 1974, Greenacre 1984, 1993), and detrended correspondence analysis (DCA; Hill and Gauch 1980) are among the most commonly used ordination techniques in modern ecological studies. These are variance-maximization methods that involve rotating the axes of a multidimensional cloud of points in multivariate space. This maximization of variance is equivalent to minimizing the variance of the projection distances from the axis. The first axis, or eigenvector, is in the direction that accounts for as much variance as possible along the ordination axis. A second axis is then found that is orthogonal to the first axis that accounts for the maximal remaining variance, and so on, for as many axes as desired.

Geometrically, the general intentions of PCA, CA, and DCA are identical; a multidimensional cloud of points is projected efficiently in fewer dimensions which maximally account for the structure of a cloud of points in multidimensional space (Oksanen and Huttunen 1989, Gauch 1982). The methods of projection differ, however, due to the selection of particular distance measures, selection of the weights attributed to the points, and the positioning of the origin (Greenacre 1984). Centered PCA uses Euclidean distances, equal weights for points, and location of the origin at the centroid;

non-centered options are also available. CA and DCA use chi-squared distances, weights for sample or species points proportional to the total for the species or sample, respectively, and an origin at the centroid (Liebart et al. 1984).

The eigenstructure decomposition used in these methods is based on an assumed underlying linear model (Morrison 1976). Thus a data set must meet several assumptions, primarily that the variables have normal distributions and have uncorrelated errors (Dale 1976, Hotelling 1933). For descriptive purposes not involving formal tests of hypotheses, departures from multivariate normalcy are acceptable in the use of PCA (Gauch 1982).

Principal Component Analysis

PCA is used to reduce a data set with a relatively large number of correlated variables by transforming linear combinations of the original data to a data set with fewer uncorrelated variables (Newcomer 1984) that retain most of the information content of the original data in a reduced subspace (Morzuch and Ruark 1991, Jongman et al. 1987). The first component accounts for a certain portion of the generalized variance present in the original data set; successive components account for decreasing proportions of the variance while remaining uncorrelated with previous components.

The relative amount of the total variation explained by each principal component is calculated by examining its variance (i.e., the eigen roots) relative to the overall variability (Morrison 1976). If a large proportion of the overall variability in a data set is accounted for in the first few principal components, these components can be used to summarize the whole of the variability and covariability of the original variates (Morzuch and Ruark 1991). In the end, however, PCA results must be assessed in terms of ecological utility; mere percentage of variance accounted for has not been found a reliable indicator of the quality of results (Gauch 1982).

PCA requires continuous data as it operates on a variance-covariance matrix or correlation matrix. The correlation matrix is commonly used when variables have dissimilar scales and ranges, unequal variances, or violate other assumptions underlying the model (Padley 1989). Data with dissimilar scales and unequal variances will inevitably emphasize variables with large means and variances, and such emphasis may be unwarranted. The use of the correlation matrix avoids rather than solving this problem, but is considered satisfactory if all the variables used are of similar importance (Chatfield and Collins 1980, Morrison 1976).

Examining the coefficients, also termed weights, for each variable permits identification of the variables that are most important, or, which account for a large portion of the variation and would therefore be best for use in predictive models (Padley 1989, Pregitzer and Barnes 1984). Important variables may also be identified by examining the correlations, also called factor loadings or factor patterns, of the raw variables with the PC's; factor loadings should correspond with factor weights. A correlation indicates the importance of a variable, so that those with high correlations are those which express a large amount of variation in the dimension being considered.

Correspondence Analysis

Correspondence analysis (CA) was developed to analyze counts or measures of species abundance (Causton 1988, Host 1987). CA produces an ordination of species and samples. Species scores, when graphed, reflect the relative positions of individual species across all samples in response to one or more environmental or temporal gradients (Hauser and Mucina 1981). Sample scores can be used to produce another ordination, with similar samples plotting close together and dissimilar samples plotting far apart. CA also provides information on the importance of individual species and sample points, and the relationship of species and samples to principal axes, termed coordinates, in a reduced subspace using a geometric interpretation (Greenacre 1984).

A cross-tabulation is converted into a contingency table in CA by dividing profiles of variable and sample frequencies by variable and sample totals. These sets of relative frequencies add up to a constant of one or 100, depending on whether the data are proportions or percentages, respectively. The geometry of such data has special properties that allow a geometric interpretation of the data structure. Rather than simply representing species in sample space, or samples in species space, a vector going from the origin to the sample points could represent samples or species (Greenacre 1993, 1984). It is then possible to describe much of the information about sample or species relationships in terms of the angles between pairs of vectors because the angles can be expressed by their cosines which has statistical meaning because the cosine is identical to the correlation coefficient between the two samples or species. Cosines of angles between vectors for sample pairs are analogous to a samples-by-samples dissimilarity matrix for which the dissimilarity measure used is the correlation coefficient after subtraction from one (Greenacre 1993).

CA uses the chi-squared statistic as a measure of the discrepancy between the observed frequencies in a contingency table and the expected frequencies. The chi-squared statistic measures how far row or column profiles are from their average profiles. The chi-squared distance function is similar to the Euclidean distance in physical space, except that each squared difference between coordinates is divided by the corresponding element of the average profile (Liebart et al. 1984).

In a CA, each row or column profile of relative frequencies has a unique weight associated with it, called a mass, which is proportional to the column or row sum, respectively, in the original cross-tabulation. The average profile is the sum of each profile weighted by that profile's mass.

The total variability, or inertia of a contingency table is the chi-squared statistic divided by the total of the table. Total inertia can be decomposed into principal inertias associated with each principal axis, into inertia associated with each element in a contingency table, and into the partial contributions of each element to each respective principal inertia (Greenacre 1993).

That component of inertia along a principal axis, called principal inertia, is the inertia of the row points (or column points) projected onto the axis (Greenacre 1993, 1984). Hence the first principal inertia is the total inertia of a set of projected points lying on the straight line along the first principal coordinate. Second and higher axis principal inertias are determined using the same process.

Principal inertia can be further broken down into row and column components along individual principal axes, termed partial contributions (Greenacre 1993, 1984). These partial contributions to inertia for either sample or species sum to one in each dimension, and are a measure of the contribution of each entity to the inertia of that principal axis.

The relative contributions of each principal axis to a point's inertia are also determined in CA. In the geometric interpretation of these relative contributions, the cosine of an angle between a point in multidimensional space is determined by projecting that point perpendicularly onto the principal axis. A vector is then extended to a point intersecting a circle in standard position with a circle of radius one. This point has a pair of coordinates that can be described by cosine and sine functions; the cosine of the angle is equal to the ratio of the derived vectors. The square of this ratio is the contribution of the respective principal axis to the sample or variable inertia. Relative contributions can be thought can be being equivalent to squared correlations between the profile points and the principal axes (Greenacre 1993, 1984).

The decomposition of each principal inertia over the samples or rows is a measure of the contributions of each principal coordinate to the inertia of these profiles. This decomposition indicates which points are best explained by the combination of axes forming subspaces by examining the squared cosines for each axis (Greenacre 1993, 1984).

A particularly useful feature of CA is the geometric interpretation of the quality of individual points in a given subspace (Greenacre 1984). The squared cosines of the angles between a point and each axis of a set of axes can be added across any number of dimensions; the sum of squared cosines across all dimension sums to one. This sum of squared cosines, or quality, is a measure of how well points are represented in a particular set of axes. An examination of the quality of display of each point helps to diagnose which points are far off the plane and whose positions are thus inaccurate in the map. The accuracy of display, or display quality is the percentage of inertia accounted for in a specific subspace (Greenacre 1993, 1984).

Points are often distributed along an arch in CA. Some points, however, may be interior, or even central to the arch, and other points may be on the periphery of the arch. Interior points indicate species with especially broad or undiscriminating (weedy) distributions, and similarly, samples with a broad or mixed collection of species. Peripheral points indicate species with especially narrow distributions, having strong indicator value, and suggest samples with a simple collection of similar species (Gauch 1982).

Detrended Correspondence Analysis

In vegetation analyses, PCA and CA assume that species abundances change linearly along environmental gradients. When nonlinearities occur, CA produces an arch effect due to the compression of first axis ends (Peet et al. 1987, Hill and Gauch 1980). Moreover, a vegetation data matrix generally consists of some measure of species presence or abundance arranged by species and samples. Since species are often absent from many sample plots, data matrixes often contain a high proportion of zeros. For reasons inherent to the mathematics of the technique, these high proportions of zeros also tend to distort the second and subsequent principle axes (Host and Pregitzer 1991).

Hill (1979) argues that the arch effect is a high-order dependence of the second and higher eigenvectors on the first eigenvector, so that a given distance of separation in the ordination does not carry a consistent meaning in terms of implied differences between the samples or species. If these derived orthogonal and linearly independent eigenvectors are related by a quadratic or higher-order relation, information on important secondary gradients in the data may be deferred to higher axes. The interpretation of results is thus made more difficult because spurious axes must be distinguished from valid axes, and higher axes in higher dimensions may have to be explored to detect meaningful gradients (Hill and Gauch 1980).

This limitation of traditional ordination methods led to the development of DCA (Hill 1979). The detrending procedure aims to remove the quadratic dependence of the second axis on the first axis while extracting a second axis. In detrending, the first axis is divided into segments, and within each segment, the sample scores are readjusted to have a zero average. The readjustment of scores results in a set of detrended scores that are used to derive a new axis based on residual variation.

Wartenberg et al. (1987) are skeptical of the value of detrending. They assert that the archlike curvature is an inherent property of successive-replacement data that results from the partial overlap in the distribution of species along a one-dimensional environmental gradient. They suggest DCA can hide the real data structure, and even introduce new distortions. Similarly, Greenacre (1984) criticized detrending because the control over geometry is lost. Okasen (1988) found that when the two first eigenvalues of CA are close to each other, their order can be reversed due to random variation in the data. In DCA, the second axis is detrended with respect to the first and therefore very variable configurations result when the orientation of the first axis in the plane is changed. This can lead to situations where the detrended solutions are very unstable under random variation and therefore can only be casually interpreted. These findings suggest additional limitations in the use of DCA.

Van Groenewoud (1992) recommended that the only way to get reasonable results using CA or DCA is to restrict the sampling mainly to one gradient, or pre-stratify the samples before analysis to represent mainly one gradient at a time. Concluding that all ordination methods are influenced by data curvature and scaling, Greenacre (1993) recommends reporting the arch unscaled in two dimensions.

Clustering

The objective of clustering procedures, commonly called classification, is to identify naturally occurring groups based on all variables in a multivariate data set (Host et al. 1993). Both the process of classification and the choice among classification techniques are more complex and more subjective than those of ordination (Gauch 1982). The utility of a given technique is therefore judged in relation to others, and often several classification techniques are applied to the same data sets with results compared afterwards.

The most commonly used classification methods in ecological land classification include polythetic hierarchical agglomerative clustering and polythetic hierarchical divisive clustering. The term polythetic means that information on all variables is used to assign observations to a cluster, as opposed to earlier monothetic methods that used single variables in a non-multivariate analysis (Gauch 1982).

Polythetic agglomerative clustering has two steps. In ecological studies, the species-by-species data matrix is first used to compute a samples-by-samples dissimilarity matrix using any of several distance measures such as Euclidean distance or percent dissimilarity (Jongman et al. 1987). Second, an agglomeration procedure is applied successively to build up a hierarchy of increasingly large clusters, starting with clusters consisting of a single member, and agglomerating these hierarchically until finally a single cluster contains all the species (Gauch 1982).

In agglomerative clustering methods, the groups that closest resemble each other are always fused. The definition of closest, or dissimilarity, between groups differs among methods; the linkage method selected determines the dissimilarity, or distance between two clusters (Jongman et al. 1987). The most common linkage methods used in ecological studies include complete-linkage (or furthest-neighbor), single-linkage (or nearest neighbor), average-linkage, and Ward's method (or minimum-variance) clustering (Digby and Kempton 1987). Flexible-beta linkage has also been found to recover underlying cluster structures efficiently (personal comm. Dr. Carl Ramm).

The simplest polythetic divisive classification is subjective ordination space partitioning (Hill 1977). Sample points are positioned in low-dimensional ordination space and partitions are placed subjectively by drawing lines through sparse regions of the cloud of sample points.

Two-way indicator species analysis (TWINSPAN; Hills 1979) is another polythetic divisive clustering technique. TWINSPAN begins with all species or samples (depending on the objectives) in a single cluster, and divides these into smaller clusters by first ordinating data by CA. Species characterizing the CA axis extremes are emphasized to polarize the samples, and the samples are then divided into two clusters by breaking the ordination axis near its middle. This procedure is repeated until each cluster has no more than a chosen minimum number of members. A corresponding species classification is produced, and the samples and species hierarchical classifications are used together to produce an arranged data matrix similar to a Braun-Blauquet table.

Van Groenewoud (1992) asserts that TWINSPAN does not perform a cluster analysis, and thus does not discern spatial vegetative patterns. He concludes that the usefulness and reliability of TWINSPAN depends on how well CA extracts axes that have ecological meaning, how well the CA axes are divided into meaningful segments, and how closely species are associated with certain segments of the multivariate coenoplane.

A methodological problem in applied clustering involves the decision of whether or not to standardize the input variables prior to the computation of a Euclidean distance or other dissimilarity measure (Milligan and Cooper, 1988, Stoddard 1979). A number of transformations are commonly used, including logarithmic transformations, square-root transformations, exponential transformations, range transformations, standardization to mean of zero and unit variance, and transformation to an ordinal scale (Jongman et al.

1987). Cooper (1988) found that transformation by the range of a variable gave consistently superior recovery of the underlying cluster structure.

Standard clustering algorithms can fail to identify clear cluster structure if that structure is confined to a subset of variables (Fowlkes et al. 1988). The inclusion of unnecessary variables in cluster analysis can therefore mask cluster structure, resulting in mixed assignments of observations. Consequently, superfluous and redundant variables are often screened prior to clustering through exploratory data analyses including descriptive statistics and ordination, regression analysis, or other methods.

Chapter II.

ECOLOGICAL LAND UNITS FOR UPLAND FOREST ECOSYSTEMS OF NORTHEASTERN LOWER MICHIGAN

INTRODUCTION

Multifactor ecological classification systems have been developed in areas of Michigan and neighboring Wisconsin at regional down to local scales. At local scales, these efforts identified soil-plant relationships (Hix 1988, Host 1987, Spies and Barnes 1985a, Pregitzer and Barnes 1984), and studied stand-level processes such as forest growth (Host et al. 1988, Greaney 1987), succession (Host et al. 1987, 1988), and regeneration (Bruggink 1988), and soil nutrient cycling (Padley 1989, Zak et al. 1989). At landscape- and regional levels, patterns in biomass (Host et al. 1988), ground-flora and overstory composition (Host and Pregitzer 1992), nutrient cycling (Zak and Pregitzer 1990, Zak et al. 1989), surficial geology-plant-soil relationships (Albert et al. 1986), and climatic gradients and classification (Denton and Barnes 1988) have also been documented.

These research efforts applied concepts of regionalization and spatial hierarchies (Bailey 1991, Gallant et al. 1989, Albert et al. 1986, O'Neil et al. 1986, Barnes et al. 1982, Rowe 1980) in which ecosystems are conceived as occurring in a nested geographic arrangement, with smaller ecosystems embedded in larger ones (Allen and Starr 1982). Regionalization is based on an understanding that the structure and function of ecosystems are largely regulated along energy, moisture, nutrient, and disturbance gradients (Cleland et al. 1985). These gradients are affected by numerous environmental and biological factors including climate, geology, soils, flora, fire, and wind, and these factors vary at different spatial and temporal scales (Cleland et al. 1996, Spies and Barnes 1985a, Barnes at al. 1982, Jordan 1982).

At global, continental, and regional scales, ecosystem patterns correspond with climatic regions, which change mainly due to latitudinal, orographic, and maritime influences (Denton and Barnes 1988, Bailey 1987). Within climatic regions, landforms modify macroclimate (Bailey 1987, Smalley 1986, Rowe 1984), and affect the movement of organisms, the flow and orientation of watersheds, and the frequency and spatial pattern of disturbance by fire and wind (Swanson et al. 1988). Within climatic - geomorphic regions, water, plants, animals, soils, and topography interact to form ecosystems at local scales (Pregitzer and Barnes 1984, Major 1969). Thus ecological systems exist at many spatial scales, from the global ecosphere down to regions of microbial activity.

While the association of multiple factors is all important for understanding ecological systems, not all factors are equally important at all spatial scales (Cleland et al. 1992). The integration of important factors at relevant spatial scales provides the basis for ecological land classification. At local scales, ground-flora, understory, topographic, and soils are commonly used as a basis for classification and mapping ecological land units. The challenge of ecosystem classification is to distinguish natural associations of ecological factors at different spatial scales, and to define and map ecological land units that reflect these different levels of organization (Cleland et al. 1996).

Regionalization is also important in understanding the emergent properties of ecosystems. The concept of emergent properties in ecological systems was formally introduced by Salt (1979), who first expressed that "An emergent property of an ecological unit is one which is wholly unpredictable from observation of the components of that unit." Cleland et al. (1996) stated that "the conditions and processes occurring across larger ecosystems affect and often override those of smaller ecosystems, and the properties of smaller ecosystems emerge in the context of larger systems." In northeast lower Michigan, Padley (1989) hypothesized that landscape-level fire disturbance regimes altered overstory and ground-flora succession to include both pyrophilic and mesophilic species in morainal landforms nested within or lying adjacent to fire-prone outwash landforms. Host and Pregitzer (1992) later suggested that similar relationships existed among landforms and local ecosystems in northwest lower Michigan. In these cases, conditions within a local ecosystem could only be explained by examining patterns and processes at a broader spatial scale, and relating local conditions to a broader spatial context.

This research involved the classification of fine scale ecological land units in northeastern Lower Michigan. The classification was nested within Districts and Subdistricts as defined by Albert et al. (1986) to accommodate broader scale influences and reduce the variability in climate and landforms affecting soil and plant relationships that were used as a basis for classification. Applications of hierarchy theory were employed in defining the sample frame at the Subdistrict scale.

The classification of ecological land units based on local soil-plant relationships was necessary in northeastern lower Michigan because classifications developed in other regions of Michigan may not be applicable in this area. The indicator value of ecological species groups varies across climatic and physiographic regions (Pregitzer and Barnes 1982), and species assemblages are likely to change with changes in macroclimate or regional physiography (Host and Pregitzer 1991). Analysis of climatic data indicated that temperatures in northeastern lower Michigan were significantly colder, and growing seasons significantly shorter, than those of northwestern Michigan (Cleland et al. 1994). Host (1987) found many of the same species described by Spies and Barnes (1985b) in the Sylvania Recreation Area in the Upper Peninsula present in northwest lower Michigan, but in different assemblages that represented responses to different environmental conditions. He reported that the usefulness of particular species groups defined for northwest lower Michigan was unknown for the finer-textured and more calcareous landforms of the northeastern Lower Peninsula (Host and Pregitzer 1992).

Multivariate methods were used in each of the research studies conducted in Michigan and Wisconsin. Pregitzer (1981) used four agglomerative clustering techniques to classify species groups, two agglomerative clustering techniques to classify samples based on environmental variables, PCA to examine relationships between sample plots and physiographic and soil variables, and discriminant analysis to test the robustness of the classification. He did not ordinate samples based on species, did not explore use of divisive clustering (TWINSPAN), and used commonly occurring species in clustering procedures.

Spies and Barnes (1985a) used TWINSPAN and DCA to classify species and samples. They reported that agglomerative clustering failed to identify meaningful species groups due to bad fusions at the initial stage of clustering. They used commonly occurring species in ordination and clustering procedures.

Host (1987) used TWINSPAN to classify species and samples, DCA to ordinate species and samples, and tabular methods to arrive at the final classification. He did not use multivariate methods to analyze soils data, used commonly occurring species in ordination and clustering procedures, and did not describe how the classification of ecological species groups was integrated with analyses of soils data to arrive at the final classification.

Hix (1988) used two agglomerative clustering techniques to classify samples based on various combinations of soils, physiographic, and vegetative variables, and TWINSPAN followed by tabular arrangements of species abundance classes to formulate ecological species groups. He did not use ordination methods to analyze soils data, used commonly occurring species in ordination and clustering procedures, and did not describe how the classification of ecological species groups was integrated with analyses of soils data to arrive at the final classification.

In this research, a series of complementary methods were used and compared to one another to derive the classification of multifactor ecological land units and their components. This contrasts in several respects with the past use of multivariate methods in research including that conducted in Michigan and Wisconsin.

OBJECTIVES

The overall objectives for this research were to classify samples and species groups in northeast lower Michigan using a combination of indirect and direct gradient analyses, clustering techniques, and graphical and tabular methods. The specific objectives for this research were to:

(1) Develop an integrated classification of local land units based on ground-flora, and soils conditions in northeast lower Michigan;

(2) Document the use of a series of complementary methods and compare results to one another to derive the final classification of multifactor ecological land units and their components; and

(3) Determine if the integrated ecological land units classified using ordination and clustering methods could be improved by eliminating ubiquitously or superfluously distributed understory and ground-flora species based on their sums-of-squared cosines in five-dimensional subspace and position within the arch of two-dimensional subspaces of a correspondence analysis.

MATERIALS AND METHODS

Sample Design and Field Methods

A random, stratified sampling design was used to locate forty-seven late successional forest stands on upland sites throughout the Huron National Forest, Michigan (Figure 2.1). Stratification was based on general landform classes (Host 1987). Only well-stocked stands with minimal evidence of recent disturbance (windthrow, logging, firewood cutting) were selected for sampling. The sample unit was defined as a relatively homogeneous area of at least one hectare (2.5 acres) within a randomly selected Forest Service stand. Four random sample points were established within each homogeneous area, and the sample points were averaged to produce summary data for analysis. Sampling methods follow those recommended by Host et al. (1993)

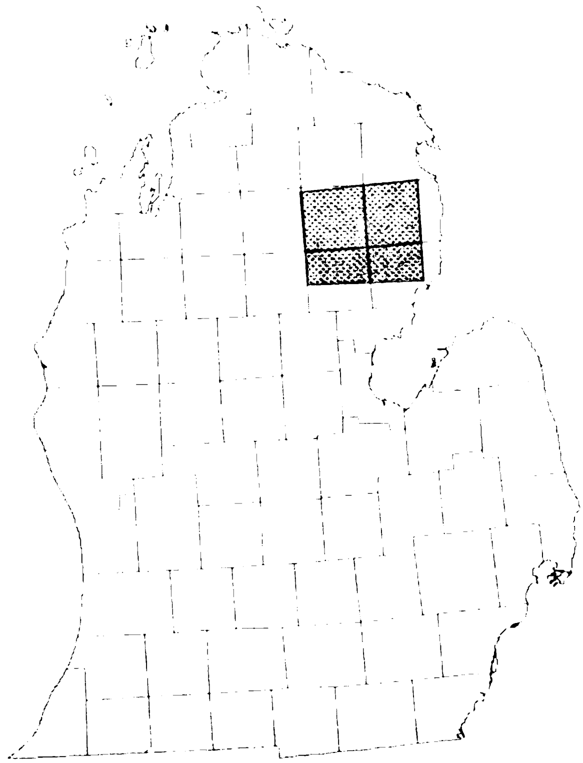


Figure 2.1 Study area on the Huron NF in Alcona, Iosco, Oscoda, and Ogemaw counties.

Selection criteria were developed and used in locating sampling locations. These criteria included:

(1) the overstory must be at least 40 years old;

(2) the canopy must be closed, as far as site conditions allow;

(3) density must be uniform throughout the stand, extensive open areas or wide age distributions (range over 10 years) are cause for rejection;

(4) stand composition must be relatively uniform;

(5) the topography must represent upland conditions;

(6) the soils must be moderately or more well-drained; mottling in the upper 40 cm. is cause for rejection;

(7) aspen must not comprise more than 30% of total stand basal area;

(8) more than 30% of the overstory consisting of multiple stems (stump sprouts) is cause for rejection; and

(9) evidence of cutting, thinning, underplanting or other disturbance within the past 40 years is cause for rejection.

Photo-interpretation of color infrared (CIR) photographs in conjunction with landform maps and Forest Service compartment maps were used to identify candidate sampling locations. Candidate sampling locations were randomly selected from each strata. Stands from each stratum were visited in the field and evaluated using the rejection/acceptance criteria. If the stand passed the acceptance criteria, a homogeneous area (minimum size one ha) was delineated and defined as the research site.

Stand Methods

Stand measurements were made on four randomly located variable radius plots using a 10 BAF prism. All live tally trees were measured for diameter at breast height (dbh), species, total height, crown ratio, and crown class. Merchantable height was estimated for all live tally trees with dbh greater than the minimum merchantable dbh (dbh over 4 inches). All borderline trees were measured to determine whether they should be tallied. Dbh was measured using a diameter tape and recorded to the nearest 0.1 inch. Total height and merchantable height were recorded to the nearest foot using a Relaskop. For cubic foot volume, merchantable height was measured from a one foot stump height to a 4-inch top diameter, or to where merchantability was limited by the bole. The Relaskop's optical dendrometer was used to determine the upper stem diameter and height.

Two dominant, uninjured, and free growing trees on each stand sample point were bored to determine average age at breast height (1.37 m). This was converted to total age and with total height was used to estimate site index. Trees off the sample point but within the homogeneous area were also measured to provide ancillary data on site index.

Secondary stand data processing included construction of stand and stock tables. Gross cubic foot volume was calculated for the preliminary sample summaries using Beers' version of the Gevorkiantz formula, a composite volume equation that has shown good performance in the Lake States (Martin 1984). Site index was estimated using the equations developed by Hahn and Carmean 1982.

Ground-flora Methods

Ground-flora composition and abundance were sampled using four five by thirty meter plots centered on the overstory sample points. In flat terrain, plots were oriented on north-south axes. In hilly terrain, plots were generally oriented perpendicular to the slope to avoid sampling across different physiographic conditions.

Average percent ground cover was determined for all moss, herbaceous, and woody species in the plot using a modified Braun-Blanquet cover-abundance rank (Mueller-Dombois and Ellenberg 1974; Table 2.1). Abundance values were determined by traversing the plot several times to record the species present, and then assigning abundance values after the species list was compiled. Relative frequencies for ground-flora species were determined by recording species presence/absence in six one m^2 frequency frames located at five m intervals along the long axis of each plot. These plots were also used to determine seedling densities in a subset of sample plots (Host et al. 1987). Nomenclature for vascular plants followed Gleason (1952); nomenclature for bryophytes followed Crum and Anderson (1981). Samples of unknown species were collected, pressed, and identified at the Michigan State University Beal-Darlington Herbarium.

Table 2.1 Cover-abundance classes and ranks used in field sampling and data analysis.

Class midpoint	Range of cover	Rank
r	Trace - 0.1	1
+	0.1 - 1.0	2
2	1 - 2	3
10	2 - 15	4
25	15 - 33	5
50	33 - 66	6
80	66 - 100	7

Soil Methods

The forest floor, soil solum, substrata and groundwater characteristics were sampled at four points in each research site. Information at each point was collected from soil pits extending into C horizons, and to depths up to 4.5 m using a 9 cm. diameter bucket auger. Forest floor and soil horizons were described based on color, texture, coarse fragments, mottles, structure, soil reaction, clay skins, uncoated particle differences, soil reaction and rooting. Soil textures estimated in the field were converted into categorical variables for numerical analyses corresponding with the centroid of the textural triangle (Table 2.2; USDA Soil Taxonomy, Padley 1989). Drainage classes were also coded into categorical variables (Table 2.3). Soil depth was defined according to Soil Taxonomy (1975) as the lower limit of biological activity, which coincides with the rooting depth of native perennial plants. The presence of deep lying textural bands has been shown to have a significant influence on tree growth and species composition (Hart et al. 1969, Hannah and Zahner 1970, Cleland et al. 1985, Host et al. 1988). It was therefore important to record the presence, absence, or intensity of deep-lying textural bands and data were collected for the upper 4.5 m in soils with stratified sandy and loamy sand upper sola.

A Banding Intensity and Continuity variable (BIC) representing substratum characteristics was described categorically for data analysis. BIC values assigned to sub-plot locations were: 0 for sands with no textural bands; 1 for loamy sand to sandy loam bands less than 5 cm. thick; 2 for sands with sandy loam bands 5 to 15 cm. cumulative thickness; 3 for sands with sandy loam bands greater than 15 cm. in thickness; and 4 for sands with sandy clay loam or finer bands greater than 10 cm. thick. Substratums were not sampled when sola of sandy clay loam or finer textures greater than 30 centimeter were encountered.

Table 2.2. Field texture codes for soil variables.

Texture	Sand%	Silt%	Clay%	Silt+Clay%
s	90	5	5	10
fs	88	6	6	12
vfs	86	7	7	14
ls	83	12	5	17
lfs	81	13	6	19
sl	65	25	10	35
fsl	63	26	11	37
l	42	40	18	58
scl	57	15	28	43
cl	33	35	32	67
sil	20	65	15	80
si	10	85	5	90
sic	6	47	47	94
sicl	10	55	35	90
c	20	20	60	80
fscl	55	16	29	45
vfsl	60	28	12	40

Table 2.3. Soil drainage class codes.

CODE	DRAINAGE CLASS
1	Excessively well drained
2	Somewhat excessively drained
3	Well drained
4	Moderately well drained
5	Somewhat poorly drained
6	Poorly drained
7	Very poorly drained

Analysis of Vegetation

Vegetative data were interrogated using ordination, agglomerative and divisive clustering, graphical and tabular methods. Vegetative data transformed based on a modified Braun-Blanquet cover-abundance rank (Table 2.1; Host et al. 1993) were ordinated using correspondence analysis (CA). Graphical displays of the first five CA axes were examined to detect sample outliers. The data set was reduced as necessary, and CA was used again to produce graphical displays of samples in species space, and species in sample space.

Samples were classified based on commonly occurring species using both agglomerative and divisive hierarchical clustering procedures. For agglomerative clustering, Ward's, flexible beta using a -0.25 beta value, and average linkage methods were used. Divisive hierarchical clustering methods included ordination space partitioning and TWINSPAN. A subjective decision that a minimum cluster size of three samples was used in interpreting dendograms. Results of these four clustering methods were compared to one another using graphical and tabular methods. Results were also used in exploratory ordination space partitioning of samples in species space based on CA.

Analysis of Soils Data

Soils data were interrogated using principal components analysis, agglomerative clustering, graphical and tabular methods. Explorative data analysis was conducted on soil variables to test for assumptions underlying PCA, and to detect intercorrelated variables for data reduction purposes. Descriptive statistics and histograms were examined, and means and variances were correlated to test the assumptions of normality, homogeneity of variance and uncorrelated errors underlying the PCA model (Appendix A).

Soils data were standardized to a mean of zero and unit variance and ordinated using PCA. Correlations among soil variables, variable weights, and factor loadings were examined to eliminate redundant or unimportant variables in clustering procedures. Variables with low weights and low loadings were removed, and the reduced soils data set was ordinated again using PCA to reassess data reduction needs.

Prior to clustering, raw data for the reduced number of soil variables were transformed using a range transformation in which individual values were divided by the maximum minus minimum values recorded for respective variables. Range transformed soils data were classified using agglomerative clustering procedures and Wards, flexible beta with a -0.25 beta value, and average linkage methods.

Tabular methods were used to compare and synthesize results of the analyses of vegetation and soils data. Relationships between soil morphological and physical characteristics and ground-flora composition within and across samples were subjectively examined, and ordinal placement of samples was adjusted. Results from tabular comparisons suggesting the need for further subdivision of sample groups were used to subset samples occurring within heterogeneous clusters.

Reanalysis of Vegetation

Analyses of ground-flora data were repeated in a second iteration on a data set for which species with low fidelity to five-dimensional ordination space were removed. The mass, inertia, and quality of display for species in each of the first five dimensions were examined, and species with less than 45% of their total variability, or sum-of-squared-cosines, accounted for in five dimensions were removed to create a more parsimonious data set for subsequent clustering procedures. The reduced vegetative data set was reclassified using ordination and clustering procedures, and results of each method were compared to one another using graphical and tabular methods. Samples were classified using Ward's, flexible beta (-0.25 beta value) and average linkage methods. Divisive hierarchical clustering methods included ordination space partitioning and TWINSPAN.

Results of these four clustering methods were compared to one another using graphical and tabular methods. Results were also used in ordination space partitioning of samples in species space based on CA.

A final set of synthesis tables was constructed based on high quality species and important soil variables. Samples were grouped according to interpretation of ordination and clustering results. Samples were then subjectively reordered using tabular methods to arrive at final groupings. Ecological unit descriptions were based on these final groupings.

RESULTS

Analysis of Commonly Occurring Understory and Ground-flora Species

Table 2.4 displays the decomposition of inertia, or variability, for the first fifteen principal coordinates of a CA of forty-six samples and 104 commonly occurring understory and ground-flora species. Fifty-one per cent of the total variability in full dimensional space was accounted for by the first five principal coordinates.

Figure 2.2 arrays samples in the first and second dimensions of commonly occurring species space based on CA. Based on initial evaluation of ground-flora composition and soil textures, the first axis is interpreted to represent a decreasing

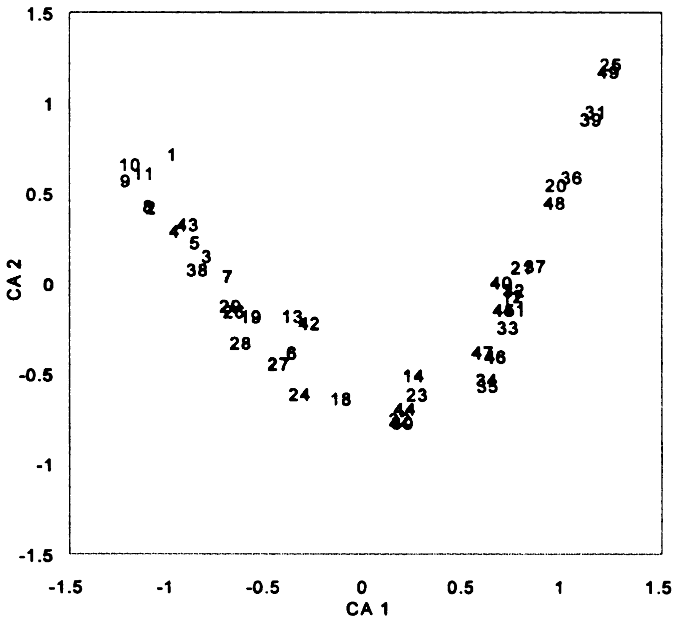


Figure 2.2. Samples in CA dimensions 1 and 2 of commonly occurring species space labeled by sample number.

moisture gradient with increasing sample scores. The second axis appears to ordinate samples along a successional stability gradient. The interpretation of gradients expressed along principal coordinates is offered in the discussion section of this chapter.

Table 2.4. Inertia and Chi-Square decomposition of the first fifteen principal coordinates.

Singular Values	Principal Inertias	Chi-Squares	Percents
0.78191	0.61138	1181.65	25.42%
0.51640	0.26666	515.40	11.09%
0.37222	0.13855	267.78	5.76%
0.35271	0.12441	240.44	5.17%
0.32661	0.10667	206.18	4.44%
0.30059	0.09036	174.63	3.76%
0.29766	0.08860	171.25	3.68%
0.27453	0.07537	145.66	3.13%
0.26933	0.07254	140.20	3.02%
0.25966	0.06742	130.31	2.80%
0.23066	0.05321	102.83	2.21%
0.22441	0.05036	97.33	2.09%
0.22113	0.04890	94.51	2.03%
0.21610	0.04670	90.26	1.94%
0.20878	0.04359	84.25	1.81%

Figures 2.3 and 2.4 display the same ordination as Figure 2.2, samples in the first and second dimensions of commonly occurring species space, with samples labeled with soil textures in the upper 30 cm., and in substrates between 150 and 250 cm., respectively. These figures show edaphic gradients in silt plus clay content in the upper 30 cm. and in the substrates of soil profiles. Silt plus clay content decreased with increasing sample scores along the first axis, with samples grading from mesic to xeric due to differences in soil textures and moisture regimes.

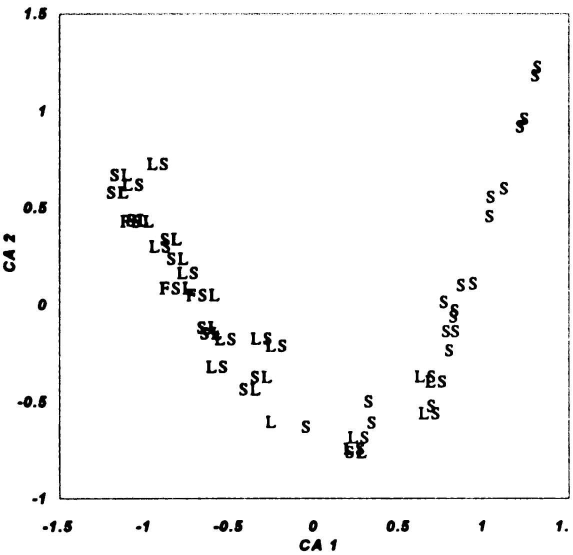


Figure 2.3. Samples in CA dimensions 1 and 2 of commonly occurring species space labeled by soil texture of upper 30 cm.

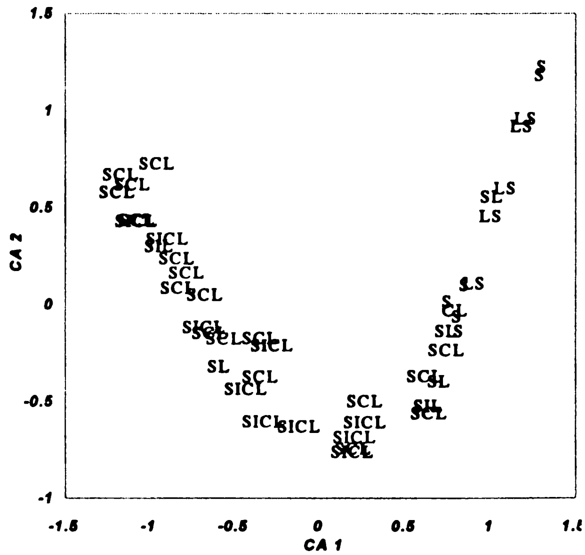


Figure 2.4. Samples in CA dimensions 1 and 2 of commonly occurring species space labeled by substrate textures at 100 to 250 cm.

Figures 2.5, 2.6, 2.7, and 2.8 display the partitioning of the first two dimensions of samples ordinated in species space based on results of three agglomerative clustering linkage methods (average, Ward's, and flexible beta linkage), and the third level of TWINSPAN divisive clustering using cut levels of 0, 0.5, 1.5, and 3.0 for rank ground-flora abundance. Results from the three agglomerative linkage methods were relatively consistent, with six clusters identified. Arrows indicating separation of sample groups at respective levels of each dendogram have been added to facilitate reader's interpretation.

Average linkage placed samples in the same clusters as flexible beta linkage method with the exception of sample 18, which was an outlier in the former. Average linkage placed samples in the same clusters as Ward's with the exception of sample 20.

Flexible beta linkage placed samples in the same clusters as Ward's linkage method with the exception of samples 14 and 48. TWINSPAN identified 5 clusters, with 3 sets of outliers consisting of 1 or 2 samples identified. Thus TWINSPAN results were somewhat different from results of agglomerative clustering procedures. Further interpretation of the classification of samples within clusters was delayed until soils data were analyzed.

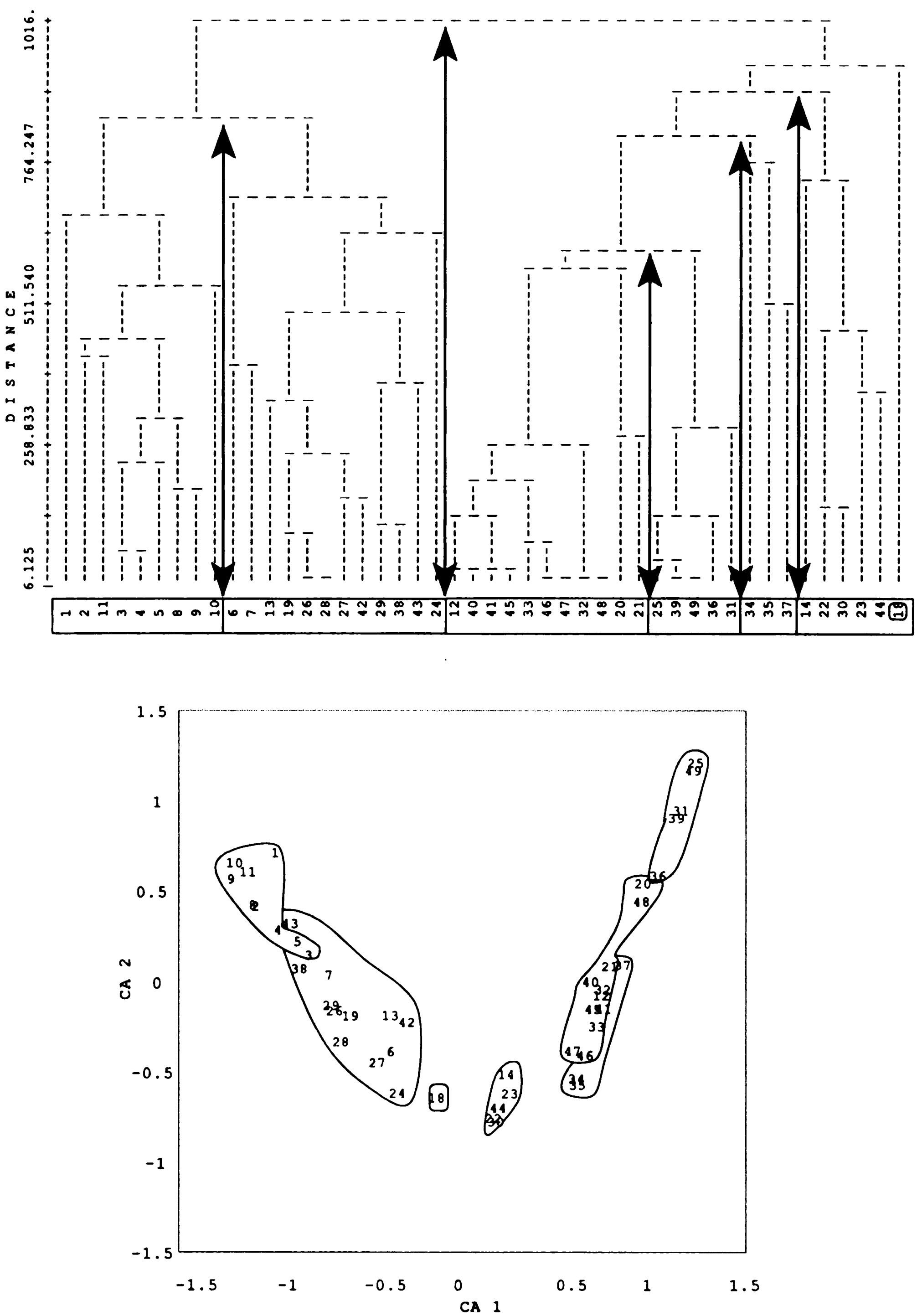
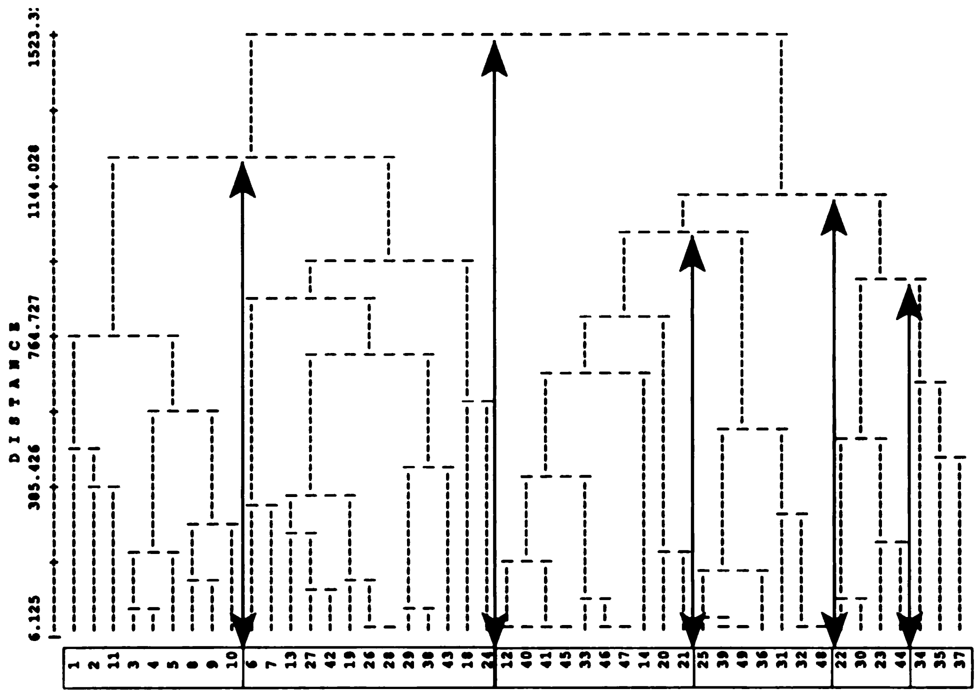


Figure 2.5. Exploratory ordination space partitioning of samples in CA dimensions 1 and 2 of commonly occurring species space based on clustering results using average linkage.



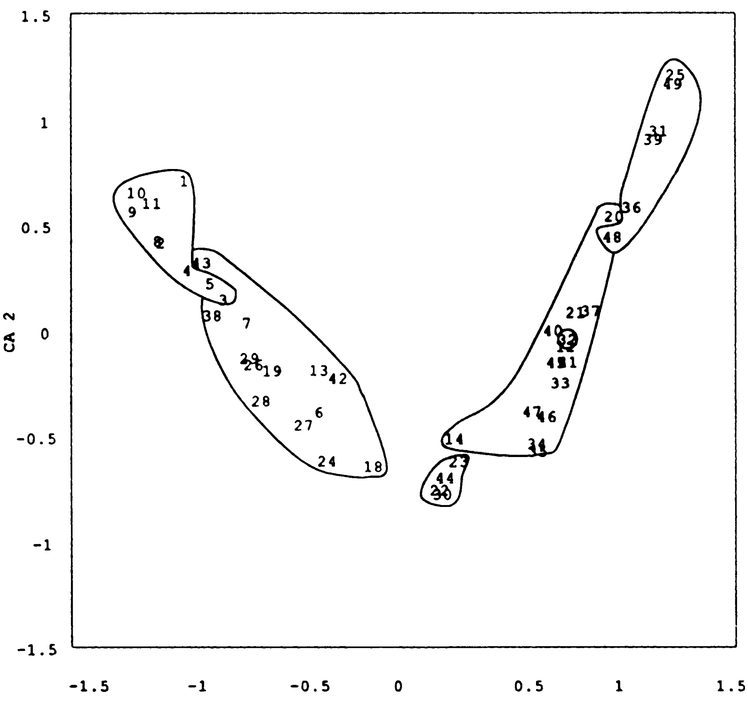


Figure 2.6. Exploratory ordination space partitioning of samples in CA dimensions 1 and 2 of commonly occurring species space based on clustering using flexible beta linkage.

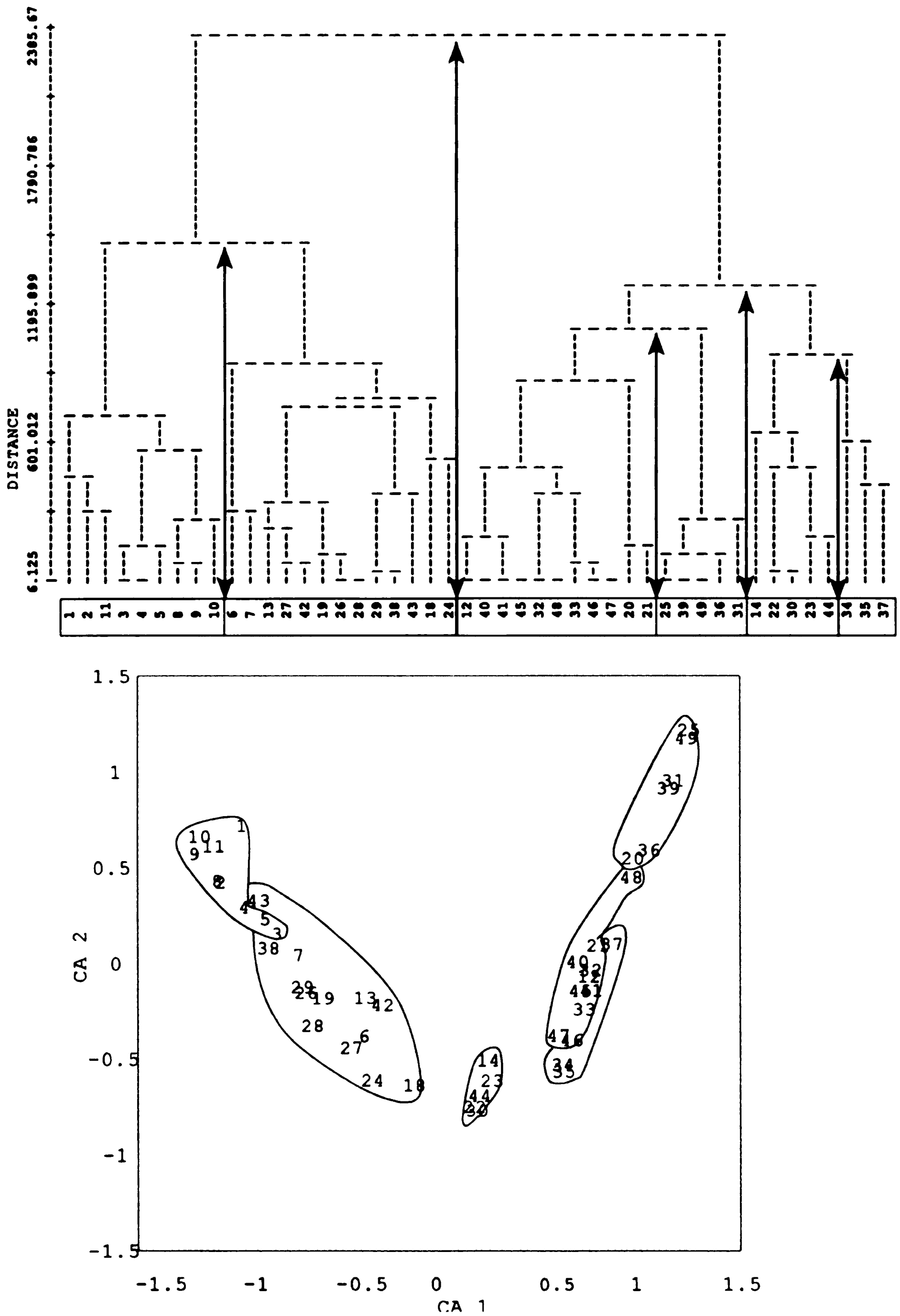


Figure 2.7. Exploratory ordination space partitioning of samples in CA dimensions 1 and 2 of commonly occurring species space based on clustering using Ward's linkage.

```
34   1      1 224222   11 1 132234 3334444 124334433 22    Sample
83 890345121 4926786739 8 452304 4236157 210198967 05    number

                                                          TWINPAN
                                                          division

00 000000000 0000000000 0 111111 1111111 111111111 11    level 1
00 000000000 1111111111 1 000000 0000000 111111111 11    level 2
00 111111111 0000000000 1 000000 1111111 000000000 11    level 3
```

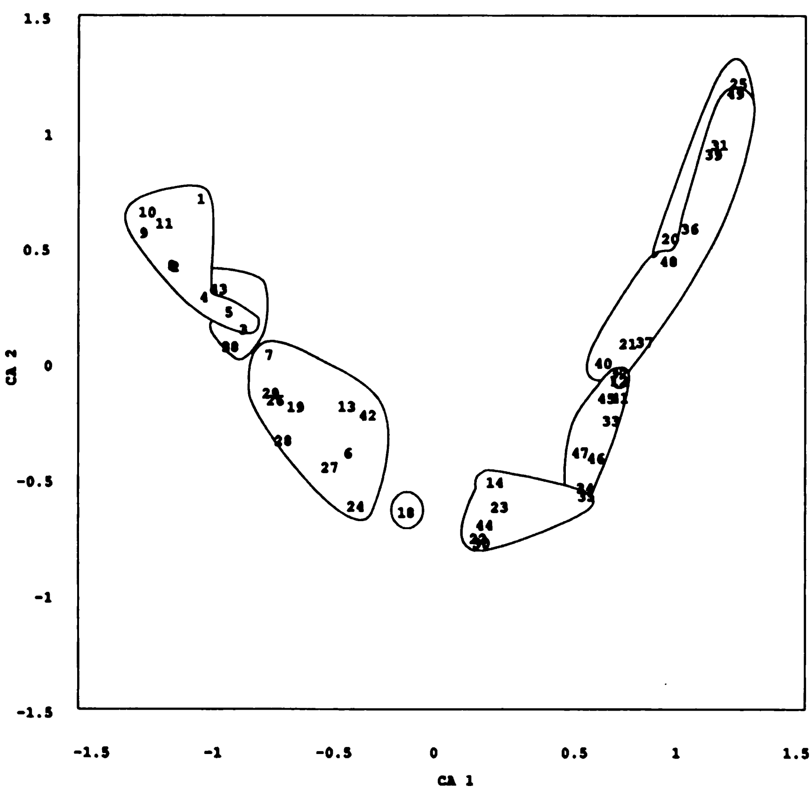


Figure 2.8. Exploratory ordination space partitioning of samples in CA dimensions 1 and 2 of commonly occurring species space based on clustering using TWINSPAN.

Analysis of Soils Data.

Soils data was interrogated using PCA, agglomerative clustering, graphical, and tabular methods. Principal component analysis is based on an assumed underlying linear model (Morrison 1976), and thus data were tested to determine if variables were normally distributed with uncorrelated means and errors. Results indicate that most variables were not normally distributed (appendix A). Means and errors were correlated ($r^2 = .416$, $p < .01$; Figures 2.9 and 2.10). The correlation matrix rather than the variance-covariance matrix was therefore used in principal component analyses of soils data

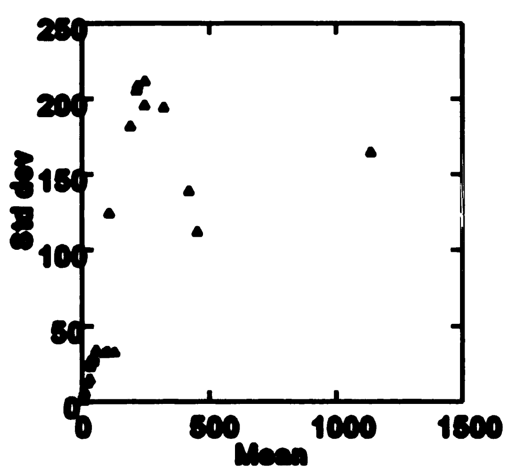


Figure 2.9. Mean and standard deviation for 35 soil variables.

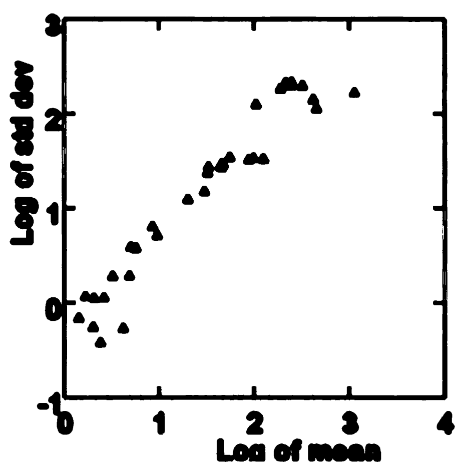


Figure 2.10. Log_{10} of mean and standard deviation for 35 soil variables.

Principal Component Analysis of Soils Data

In the decomposition of variability of the soils data using PCA (Table 2.5), sixty-eight percent of the overall variability set was accounted for in the first five dimensions, with thirty-seven percent accounted for in the first dimension, twelve percent in the second, eight percent in the third, six percent in the fourth, and five percent in the fifth. The soils data set was not summarized well in low dimensional subspaces, and patterns in the third and higher dimensions did not assist in the interpretation of samples in variable space or variables in sample space.

Table 2.5. Eigenvalues of the soil correlation matrix.

	Eigenvalue	Difference	Proportion	Cumulative
PRIN1	13.0212	8.83728	0.372035	0.37203
PRIN2	4.1839	1.40512	0.119541	0.49158
PRIN3	2.7788	0.77655	0.079395	0.57097
PRIN4	2.0023	0.15331	0.057208	0.62818
PRIN5	1.8490	0.41870	0.052828	0.68101
PRIN6	1.4303	0.20308	0.040865	0.72187
PRIN7	1.2272	0.12913	0.035062	0.75693
PRIN8	1.0981	0.18705	0.031373	0.78831
PRIN9	0.9110	0.03433	0.026029	0.81434
PRIN10	0.8767	0.08809	0.025048	0.83938
PRIN11	0.7886	0.06999	0.022531	0.86191
PRIN12	0.7186	0.10785	0.020531	0.88245

Table 2.6 arrays soil variable names and abbreviations. Table 2.7 arrays the first six eigenvectors of a PCA with soils variables ordered by variable weights in the first dimension. Important variables based on high positive first dimensional weights included soil textures in substrata, then textures in sola. Important variables based on high negative first dimensional weights included variables describing depths to textural discontinuities, thickness of sandy Bs horizons, and depths to mottles and watertables.

Important variables based on high positive second dimensional weights (Table 2.8) included thickness of O2 and E horizons, E horizon development code, depths to mottles, dominant texture of sola and substrates, dominant texture of discontinuities, and average texture of discontinuities. Important variables based on high negative second dimensional weights included B horizon thickness, depth to C horizons, A1 horizon thickness, depth to accumulation of varves, and drainage class.

The most important soil variables based on high positive first dimensional factor loadings, or variable correlations with variates derived in the first principal component, included a coded variable describing substrate textures, textures between 100 and 150 cm., and sola textures (Table 2.9). The most important soil variables based on negative factor loadings included depth to heavy textured horizons, depths to mottles and water tables, and Bs horizon thickness.

The most important soil variables based on high positive second dimensional factor loadings included depths to mottles, dominant texture of sola and substrates, textures between 100 and 250 cm., and depth to watertables (Table 2.10). The most important soil variables based on high negative second dimensional factor loadings included drainage class code, texture of the top 30 cm., and a coded variable describing substrata textures.

Table 2.6. Soil variable names and abbreviations.

VARIABLE	ABBREVIATION
Average banding intensity code	BIC8
Texture of heaviest band	MAXSIC
Texture of SCL or heavier bands	TXSICL
Texture of 150-450 cm.	LTSICL
B horizon texture	BSICL
Texture of upper 150 cm.	UTSICL
Average texture to 450 cm.	SICL
Dominant banding texture	DOMSICL
Drainage class code	DCL
Number of textural discontinuities to 150 cm.	LD150
Texture to 30 cm.	T30SICL
Depth to B horizon	BDEP
Depth to C horizon	CDEP
B horizon thickness	BTH
E horizon thickness	ETH
B intensity code[1]	BIN
A horizon thickness	A1TH
Physiographic form	PF
E horizon development code[2]	EDC
Aspect	ASP
O2 horizon thickness	O2TH
Depth to vfs accumulations > 15 cm.	ACV
Elevation	ELEV
Slope	SLOP
Depth of major rooting zone	EFFDE
A1 horizon value	A1V
Depth to LS accumulation > 15 cm.	ACLS
B horizon value	BVA
Gross water table depth	GWTDE
Bs horizon thickness	BSTH
Depth to mottles	MOTDE
Depth to till	TILLD
Depth to SCL	DEPSCL
Depth to SL accumulation > 15 cm.	ACSL
Depth to SCL accumulation > 15 cm.	ACSCL

1. B intensity code: 1 = Bw, 2 = Bs, 3 = Bh
2. E horizon code: 1 = mixed, 2 = discontinuous under <50% of pedon, 3 = discontinuous under >50% of pedon, 4 = continuous

Variable weights in the first dimension and factor loadings in the first and second dimensions identified the same important variables, and these variables primarily related to soil textures and drainage classes. These factors directly affect moisture and nutrient regimes and hence were ecologically important. Soil textures directly affect water holding capacity, and also chemical equilibria and nutrient availability. Drainage class codes, depths to mottles, and depths to water tables are measures of free water available for tree, understory, and to a lesser extent ground-flora consumption. Variable weights in the second dimension identified O2, E, B, and A1 horizon thicknesses and development codes as important variables. In addition, variable weights in the second dimension identified depth to mottles, dominant banding textures, depth to varves, and drainage class as important variables, similar to weights in the first dimension and factor loadings in the first and second dimensions.

Table 2.7. Soil variables ordered by variable weights in the first dimension of a PCA.

VAR	PRIN1	PRIN2	PRIN3	PRIN4	PRIN5	PRIN6
BIC8	0.26088	-0.07806	0.00927	0.06334	0.03260	-0.09904
MAXSIC	0.25424	0.00516	0.03327	-0.03571	-0.11722	0.08593
TXSICL	0.23284	0.18292	0.00540	-0.00074	-0.07531	0.08200
LTSICL	0.23064	0.16174	-0.05627	0.04761	-0.00824	0.06962
BSICL	0.22443	-0.02141	0.05929	-0.07258	-0.21899	0.20384
UTSICL	0.22027	0.08720	0.02322	-0.10159	-0.13309	0.13282
SICL	0.21581	0.20936	0.06652	-0.05099	-0.08636	-0.01356
DOMSICL	0.21210	0.22086	0.10450	-0.08686	0.02732	-0.03963
DCL	0.20888	-0.16096	-0.12965	0.15876	0.02534	-0.00887
LD150	0.20632	0.10888	-0.09067	-0.05569	0.01330	-0.05059
T30SICL	0.19464	-0.11219	0.00707	0.02122	-0.27743	-0.00884
BDEP	0.14638	0.02743	0.34369	-0.21280	0.26421	-0.09225
CDEP	0.13233	-0.33843	0.11880	0.06834	0.12624	-0.17767
BTH	0.12711	-0.35015	0.08038	0.13397	0.13021	-0.13616
ETH	0.12375	0.27175	0.18260	-0.06375	0.26667	-0.00151
BIN	0.08624	0.09360	0.02232	-0.24810	0.14818	0.44605
A1TH	0.07510	-0.30910	0.31817	-0.13256	0.13066	0.02937
PF	0.06737	-0.04727	-0.05953	0.17168	0.25538	0.52302
EDC	0.06550	0.26104	-0.11120	0.27689	0.28118	-0.07200
ASP	0.00905	0.17523	0.43895	0.10630	-0.07609	-0.09471
O2TH	0.00305	0.33550	0.00020	0.32585	0.00052	-0.02747
ACV	-0.01725	-0.20019	-0.00001	0.03233	-0.24902	0.27480
ELEV	-0.02741	-0.09300	0.08468	0.56457	0.05477	0.25036
SLOP	-0.03647	0.07952	0.29356	0.33608	-0.02467	-0.00813
EFFDE	-0.06888	0.03730	0.32810	0.16249	-0.04336	0.07803
A1V	-0.11272	-0.03344	0.39302	-0.16352	0.12842	0.12214
ACLS	-0.12209	-0.07776	0.21874	-0.10589	-0.16088	0.03920
BVA	-0.12257	-0.01335	0.15128	0.09865	-0.23272	0.30379
GWTDE	-0.13729	0.10503	0.17595	0.13386	-0.29512	-0.29367
BSTH	-0.14648	0.00589	-0.01535	-0.00637	0.44384	-0.02500
MOTDE	-0.15452	0.25778	0.02719	-0.14794	-0.12145	0.05268
TILLD	-0.23641	0.02516	-0.08757	0.00935	0.03171	0.04143
DEPSCL	-0.24134	0.00472	0.03789	-0.09022	0.02468	0.10390
ACSL	-0.24897	0.09003	-0.01380	-0.07362	0.01980	0.06411
ACSCL	-0.25080	0.05912	-0.03693	-0.05425	0.00285	0.03631

Table 2.8. Soil variables ordered by variable weights in the second dimension of a PCA.

VAR	PRIN1	PRIN2	PRIN3	PRIN4	PRIN5	PRIN6
O2TH	0.0030	0.3355	0.0002	0.3258	0.0005	-0.0275
ETH	0.1237	0.2717	0.1826	-0.0637	0.2667	-0.0015
EDC	0.0655	0.2610	-0.1112	0.2769	0.2812	-0.0720
MOTDE	-0.1545	0.2578	0.0272	-0.1479	-0.1215	0.0527
DOMSIC	0.2121	0.2209	0.1045	-0.0869	0.0273	-0.0396
SICL	0.2158	0.2094	0.0665	-0.0510	-0.0864	-0.0136
TXSICL	0.2328	0.1829	0.0054	-0.0007	-0.0753	0.0820
ASP	0.0091	0.1752	0.4390	0.1063	-0.0761	-0.0947
LTSICL	0.2306	0.1617	-0.0563	0.0476	-0.0082	0.0696
LD150	0.2063	0.1089	-0.0907	-0.0557	0.0133	-0.0506
GWTDE	-0.1373	0.1050	0.1760	0.1339	-0.2951	-0.2937
BIN	0.0862	0.0936	0.0223	-0.2481	0.1482	0.4461
ACSL	-0.2490	0.0900	-0.0138	-0.0736	0.0198	0.0641
UTSICL	0.2203	0.0872	0.0232	-0.1016	-0.1331	0.1328
SLOP	-0.0365	0.0795	0.2936	0.3361	-0.0247	-0.0081
ACSCL	-0.2508	0.0591	-0.0369	-0.0543	0.0028	0.0363
EFFDE	-0.0689	0.0373	0.3281	0.1625	-0.0434	0.0780
BDEP	0.1464	0.0274	0.3437	-0.2128	0.2642	-0.0923
TILLD	-0.2364	0.0252	-0.0876	0.0094	0.0317	0.0414
BSTH	-0.1465	0.0059	-0.0153	-0.0064	0.4438	-0.0250
MAXSIC	0.2542	0.0052	0.0333	-0.0357	-0.1172	0.0859
DEPSCL	-0.2413	0.0047	0.0379	-0.0902	0.0247	0.1039
BVA	-0.1226	-0.0134	0.1513	0.0986	-0.2327	0.3038
BSICL	0.2244	-0.0214	0.0593	-0.0726	-0.2190	0.2038
A1V	-0.1127	-0.0334	0.3930	-0.1635	0.1284	0.1221
PF	0.0674	-0.0473	-0.0595	0.1717	0.2554	0.5230
ACLS	-0.1221	-0.0778	0.2187	-0.1059	-0.1609	0.0392
BIC8	0.2609	-0.0781	0.0093	0.0633	0.0326	-0.0990
ELEV	-0.0274	-0.0930	0.0847	0.5646	0.0548	0.2504
T30SICL	0.1946	-0.1122	0.0071	0.0212	-0.2774	-0.0088
DCL	0.2089	-0.1610	-0.1296	0.1588	0.0253	-0.0089
ACV	-0.0172	-0.2002	0.0000	0.0323	-0.2490	0.2748
A1TH	0.0751	-0.3091	0.3182	-0.1326	0.1307	0.0294
CDEP	0.1323	-0.3384	0.1188	0.0683	0.1262	-0.1777
BTH	0.1271	-0.3502	0.0804	0.1340	0.1302	-0.1362

Table 2.9. Factor patterns for soil variables ordered by variable loadings in the first dimension of a PCA.

Var	FACTOR1	FACTOR2	FACTOR3	FACTOR4	FACTOR5	FACTOR6
BIC8	0.9414	-0.1597	0.0155	0.0896	0.0443	-0.1184
MAXSIC	0.9174	0.0106	0.0555	-0.0505	-0.1594	0.1028
TXSICL	0.8402	0.3742	0.0090	-0.0011	-0.1024	0.0981
LTSICL	0.8323	0.3308	-0.0938	0.0674	-0.0112	0.0833
BSICL	0.8099	-0.0438	0.0988	-0.1027	-0.2978	0.2438
UTSICL	0.7949	0.1784	0.0387	-0.1438	-0.1810	0.1589
SICL	0.7788	0.4282	0.1109	-0.0722	-0.1174	-0.0162
DOMSICL	0.7654	0.4518	0.1742	-0.1229	0.0372	-0.0474
DCL	0.7538	-0.3292	-0.2161	0.2246	0.0345	-0.0106
LD150	0.7445	0.2227	-0.1512	-0.0788	0.0181	-0.0605
T30SICL	0.7023	-0.2295	0.0118	0.0300	-0.3773	-0.0106
BDEP	0.5282	0.0561	0.5729	-0.3011	0.3593	-0.1103
CDEP	0.4775	-0.6922	0.1980	0.0967	0.1717	-0.2125
BTH	0.4587	-0.7162	0.1340	0.1896	0.1771	-0.1628
ETH	0.4465	0.5559	0.3044	-0.0902	0.3626	-0.0018
BIN	0.3112	0.1915	0.0372	-0.3511	0.2015	0.5335
A1TH	0.2710	-0.6323	0.5304	-0.1876	0.1777	0.0351
PF	0.2431	-0.0967	-0.0992	0.2429	0.3473	0.6255
EDC	0.2364	0.5340	-0.1854	0.3918	0.3823	-0.0861
ASP	0.0327	0.3584	0.7317	0.1504	-0.1035	-0.1133
O2TH	0.0110	0.6863	0.0003	0.4611	0.0007	-0.0329
ACV	-0.0622	-0.4095	0.0000	0.0457	-0.3386	0.3286
ELEV	-0.0989	-0.1902	0.1412	0.7989	0.0745	0.2994
SLOP	-0.1316	0.1627	0.4894	0.4756	-0.0336	-0.0097
EFFDE	-0.2485	0.0763	0.5469	0.2299	-0.0590	0.0933
A1V	-0.4068	-0.0684	0.6552	-0.2314	0.1746	0.1461
ACLS	-0.4406	-0.1591	0.3646	-0.1498	-0.2188	0.0469
BVA	-0.4423	-0.0273	0.2522	0.1396	-0.3164	0.3633
GWTDE	-0.4954	0.2148	0.2933	0.1894	-0.4013	-0.3512
BSTH	-0.5286	0.0121	-0.0256	-0.0090	0.6035	-0.0299
MOTDE	-0.5576	0.5273	0.0453	-0.2093	-0.1652	0.0630
TILLD	-0.8531	0.0515	-0.1460	0.0132	0.0431	0.0496
DEPSCL	-0.8709	0.0097	0.0632	-0.1277	0.0336	0.1243
ACSL	-0.8984	0.1841	-0.0230	-0.1042	0.0269	0.0767
ACSCL	-0.9050	0.1209	-0.0616	-0.0768	0.0039	0.0434

Table 2.10. Factor patterns for key soil variables ordered by variable loadings in the second dimension of a PCA.

Variable	FACTOR2
MOTDE	0.52728
DOMSICL	0.45176
LTSICL	0.33082
GWTDE	0.21483
ACSL	0.18414
UTSICL	0.17836
ACSCL	0.12092
DEPSCL	0.00966
BSICL	-0.04380
BIC8	-0.15967
T30SICL	-0.22947
DCL	-0.32923

The first PC axis ordinated samples along a textural and moisture gradient. Textures of the upper 30 cm. and 100 cm. graded from sands to sandy loams with increasing sample weights along the first axis (Figures 2.11 and 2.12). Textures of the lower 150 cm. graded from sands to sandy clay loam with increasing sample weights along the first axis (Figure 2.13). Soil drainage graded from excessively well drained to well drained with increasing sample weights along the first axis (Figure 2.14).

The second axis ordinated samples along a substrate silt content gradient (Figure 2.13), and along a drainage class gradient in which samples containing moderately well drained soils were separated from well drained soils (Figure 2.14). Silt content of the soil horizons at depths of 100 to 250 cm. increased somewhat with increasing sample weights along the second axis (Figure 2.13). Soil drainage graded from well drained to moderately well drained with decreasing sample weights along the second axis, although the gradient was not as distinct as that expressed along the first axis (Figure 2.14)

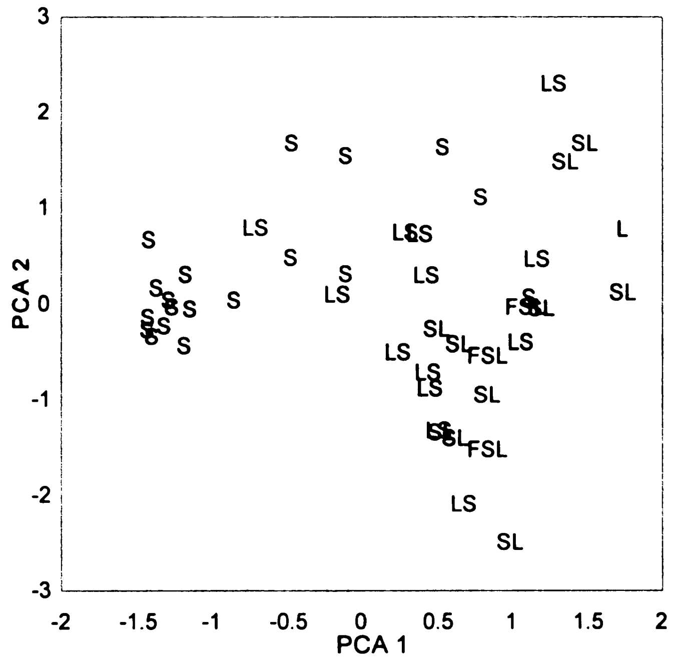


Figure 2.11. Samples in PCA dimensions 1 and 2 of soil variable space labeled by texture of upper 30 cm.

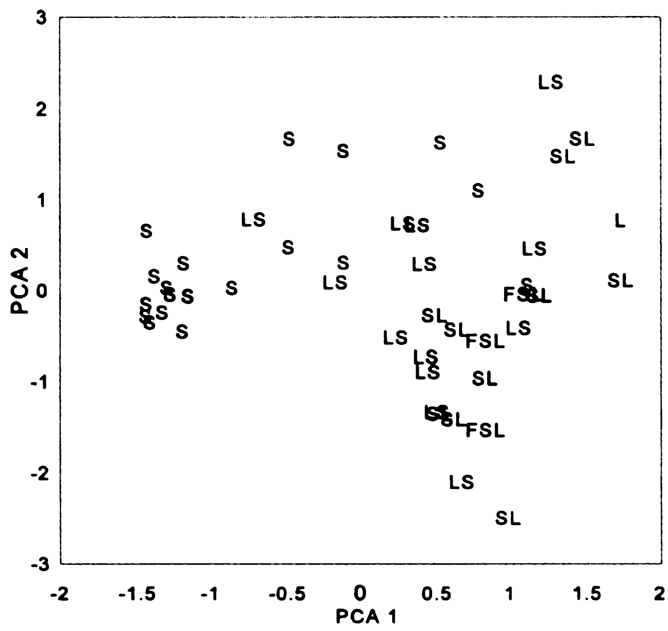


Figure 2.12. Samples in PCA dimensions 1 and 2 of soil variable space labeled by texture of upper 100 cm.

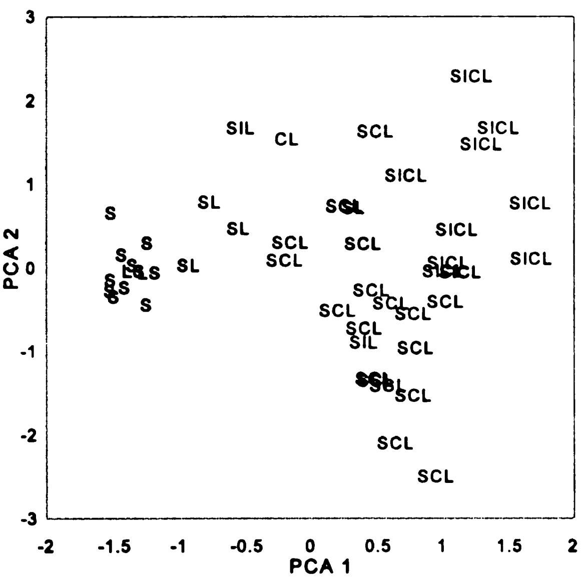


Figure 2.13. Samples in PCA dimensions 1 and 2 of soil variable space labeled by texture at 100 to 250 cm.

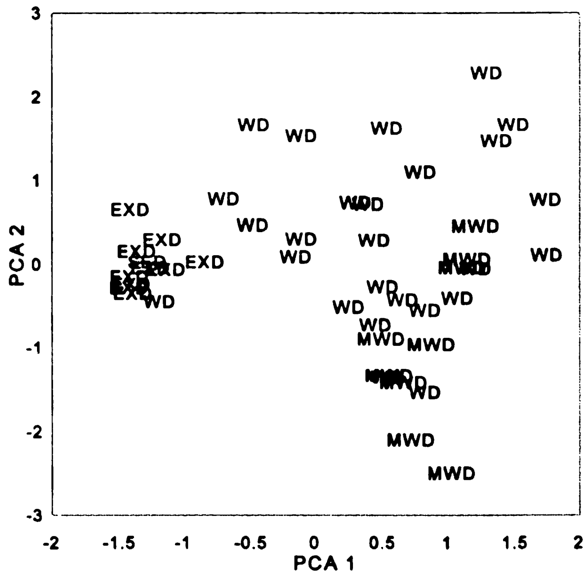


Figure 2.14. Samples in dimensions 1 and 2 of soil variable space labeled by drainage class.

Clustering of Samples Based on Soil Variables

Seven soil variables were removed for clustering analyses because of intercorrelations and low weights and loadings based on PCA. These variables included texture of heaviest band, texture of bands of sandy clay loam or heavier textures, physiographic form, aspect, elevation, slope, and depth to till.

Clustering of samples using twenty-eight soil variables based on Ward's linkage identified seven groups of samples (Figure 2.15, Table 2.11). The cluster labeled 1 consisted of samples composed of deep sandy soils. The cluster labeled 2 consisted of samples with sandy sola overlying loamy sand or sandy loam substrata. The cluster labeled 3 consisted of samples with sandy sola overlying fine loamy substrata of silty loam, sandy clay loam, or clay loam textures. The cluster labeled 4 consisted of samples with loamy sand sola overlying sandy clay loam substrata; one sample had sandy loam sola. The cluster labeled 5 consisted of samples with heterogeneously textured sola; four samples had sandy loam sola and three samples had loamy sand sola. All samples in cluster 5 had sandy clay loam substrata. The cluster labeled 6 was heterogeneous, with sola ranging from loamy sand to fine sandy loam and substrata ranging from sandy loam to silt loam to sandy clay loam. The cluster labeled 7 consisted of samples with heterogeneous sola textures and silty clay loam substrata.

Clustering of samples using twenty-eight soil variables based on average linkage identified eight groups of samples (Figure 2.16, Table 2.12). The cluster labeled 1 consisted of samples with loamy sand sola overlying sandy clay loam substrata. The cluster labeled 2 consisted of samples with sandy loam and fine sandy loam sola overlying silty clay loam substrata. The cluster labeled 3 consisted of samples with loamy sand sola overlying heterogeneous substrata with sandy loam, silt loam, and sandy clay loam textures. The cluster labeled 4 consisted of samples with sand loam sola overlying sandy clay loam substrata. The cluster labeled 5 consisted of sandy loam sola overlying silty clay loam substrata; one sample was loamy sand over sandy loam. The cluster labeled 6 consisted of heterogeneous sola textures and silty clay loam substrata. The cluster labeled 7 consisted of samples with sandy sola and sandy clay loam substrata. The cluster labeled 8 consisted of samples with sand sola and substrata.

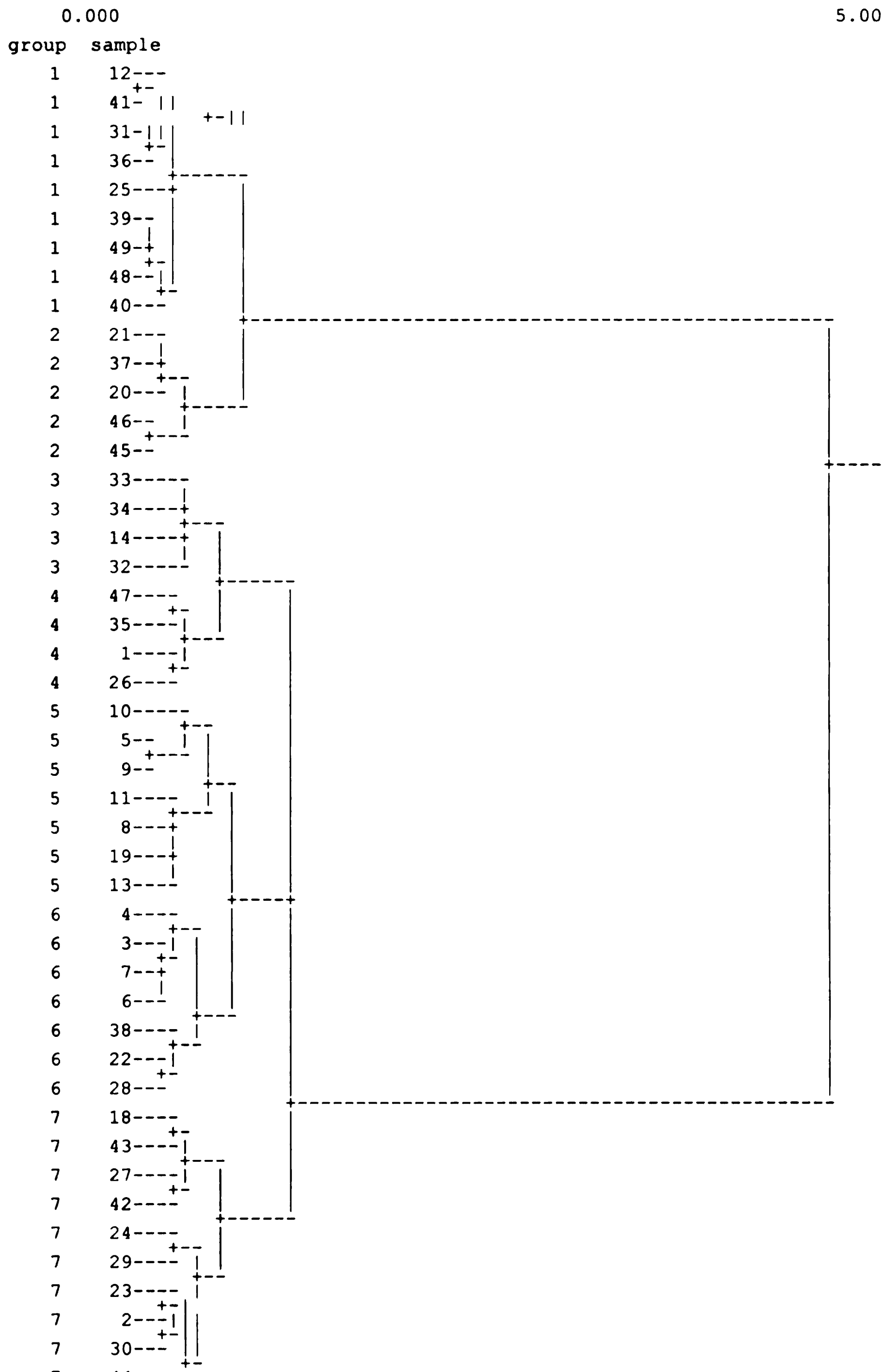


Figure 2.15. Sample clusters based on 28 soil variables using Ward's linkage.

Table 2.11. Soils table arraying key variables for samples grouped by Ward's linkage.

GROUP	STA	T30	UTEX	LTEX	BTEX	DPSCL	ACSL	ACSCL	DOMB	DCL	MOTDE	GWTDE
1	12	S	S	S	S	500	500	500	S	WD	290	500
1	41	S	S	S	S	500	500	500	S	EXD	500	500
1	31	S	S	S	S	500	500	500	S	EXD	500	500
1	36	S	S	S	S	500	500	500	S	EXD	500	500
1	25	S	S	S	S	500	500	500	S	EWD	500	500
1	39	S	S	S	S	500	500	500	S	EXD	500	500
1	49	S	S	S	S	500	500	500	S	EXD	500	500
1	48	S	S	LS	S	500	500	500	LS	EXD	500	500
1	40	S	S	S	S	500	500	500	S	EXD	442	500
2	21	S	S	S	S	500	500	500	LS	SED	500	500
2	37	S	S	LS	LS	500	500	500	LS	EWD	500	500
2	20	S	S	SL	S	500	240	500	SL	EXD	500	500
2	46	LS	S	SL	LS	244	500	500	SL	WD	500	500
2	45	S	LS	SL	LS	183	335	500	SL	WD	500	500
3	33	S	S	SCL	L	46	290	79	SICL	EXD	500	500
3	34	S	S	SIL	S	259	274	500	SIL	EXD	290	500
3	14	S	SCL	SCL	S	106	500	111	SCL	WD	380	500
3	32	S	S	CL	S	87	154	205	SICL	EXD	500	500
4	47	LS	S	SCL	SL	37	185	52	SCL	WD	500	500
4	35	LS	LS	SCL	SL	32	60	500	SCL	WD	500	500
4	1	LS	SL	SCL	LS	45	70	50	SCL	WD	500	500
4	26	SL	SCL	SCL	SCL	40	18	59	SCL	WD	500	500
5	10	SL	SL	SCL	L	88	30	93	SCL	MWD	45	82
5	5	SL	SL	SCL	SL	15	15	98	SCL	MWD	36	500
5	9	SL	L	SCL	L	52	18	57	SCL	MWD	23	500
5	11	LS	SL	SCL	L	116	61	143	SCL	MWD	55	500
5	8	SL	SL	SCL	SL	105	17	137	SCL	WD	168	500
5	19	LS	SL	SCL	SCL	45	38	69	CL	WD	161	161
5	13	LS	SCL	SCL	SL	81	17	86	SCL	WD	234	366
6	4	LS	LS	SIL	LS	179	142	185	SCL	MWD	94	203
6	3	LS	LS	SCL	SL	118	15	155	SCL	WD	45	500
6	7	FSL	SCL	SCL	SL	74	57	79	SCL	WD	129	305
6	6	SL	SCL	SCL	L	138	21	76	SCL	WD	167	366
6	22	LS	SL	SCL	SL	133	136	268	SCL	MWD	171	309
6	28	LS	S	SL	LS	125	198	244	SCL	WD	135	194
6	38	FSL	SCL	SCL	SCL	171	173	187	SCL	WD	153	411
7	18	S	L	SICL	S	133	134	140	SICL	WD	500	500
7	43	SL	SICL	SICL	L	21	110	40	SIL	WD	374	389
7	27	SL	SICL	SICL	SICL	54	34	72	SICL	WD	500	500
7	42	LS	SICL	SICL	SL	165	37	183	SICL	WD	500	500
7	24	L	SICL	SICL	SICL	48	22	60	SICL	WD	111	500
7	29	SL	SICL	SICL	SICL	32	15	47	SICL	WD	106	500
7	23	S	SCL	SICL	L	100	48	115	SICL	MWD	90	145
7	2	FSL	FSL	SICL	SL	43	25	49	SCL	MWD	24	500
7	30	SL	SCL	SICL	SCL	41	26	57	SCL	MWD	120	155
7	44	LS	SICL	SICL	SCL	28	50	44	SCL	MWD	18	101

Clustering results between the two linkage methods were not fully consistent. Cluster one of Ward's linkage was equivalent to cluster seven of average linkage. Cluster three of Ward's linkage was equivalent to cluster six of average linkage. Cluster seven of Ward's linkage was equivalent to average linkage clusters two and five combined. Four of seven samples in cluster five of Ward's linkage were the same as four of six samples in average linkage cluster four. Four of seven samples in cluster six of Ward's linkage were the same as four of six samples in average linkage cluster one.

Interpretation of clustering results indicate that soil groupings were highly variable, including a number of combinations of possible soil textures. The ecological significance of these clusters is discussed at the end of this chapter.

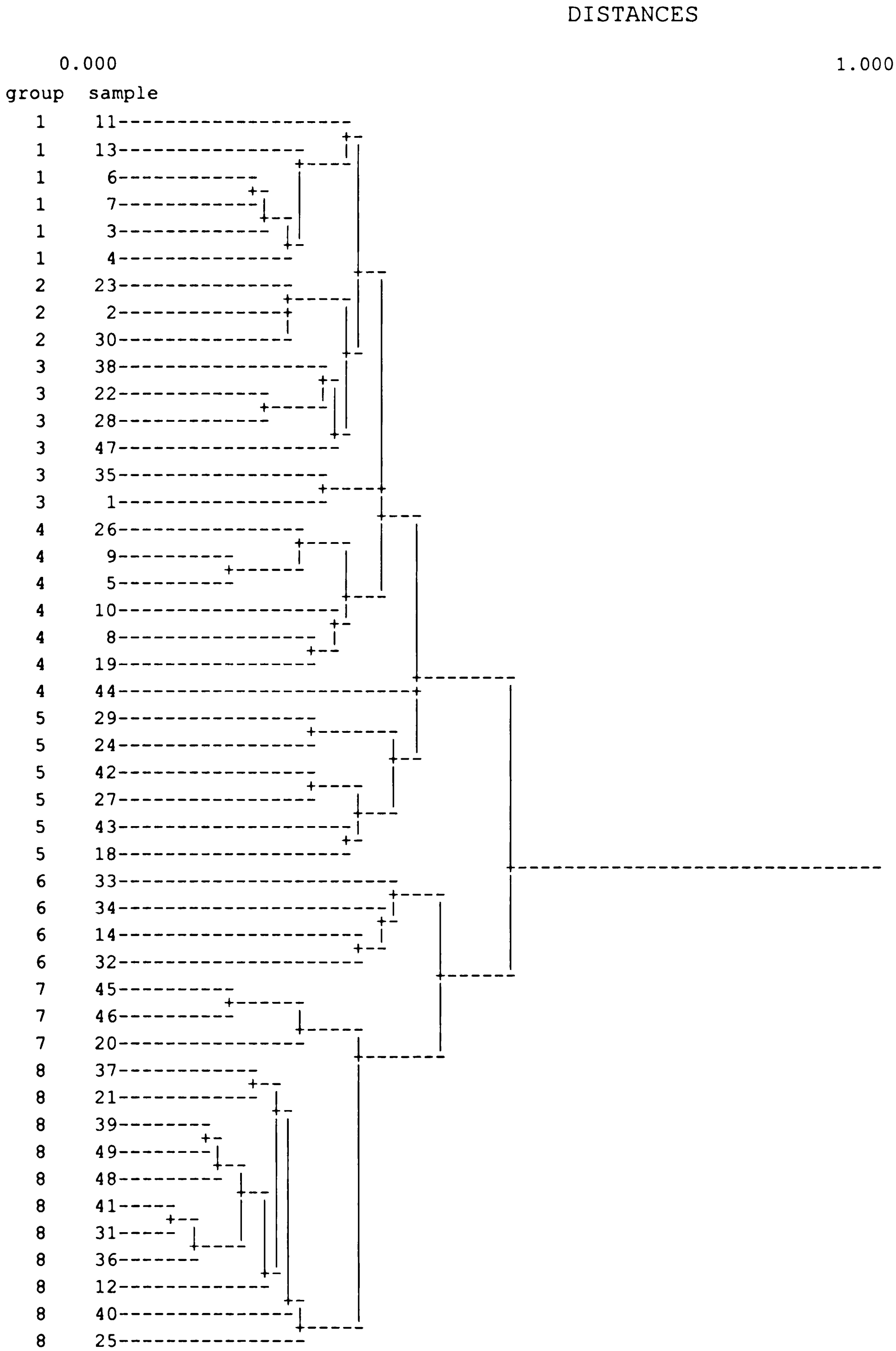


Figure 2.16. Sample clusters based on 28 soil variables using average linkage.

Table 2.12. Soils table arraying key variables for samples grouped by average linkage.

GROUP	STA	T30	UTEX	LTEX	BTEX	DPSCL	ACSL	ACSCL	DOMB	DCL	MOTDE	GWTDE
1	11	LS	SL	SCL	L	116	61	143	SCL	MWD	55	500
1	13	LS	SCL	SCL	SL	81	17	86	SCL	WD	234	366
1	6	SL	SCL	SCL	L	138	21	76	SCL	WD	167	366
1	7	FSL	SCL	SCL	SL	74	57	79	SCL	WD	129	305
1	3	LS	LS	SCL	SL	118	15	155	SCL	WD	45	500
1	4	LS	LS	SIL	LS	179	142	185	SCL	MWD	94	203
2	23	S	SCL	SICL	L	100	48	115	SICL	MWD	90	145
2	2	FSL	FSL	SICL	SL	43	25	49	SCL	MWD	24	500
2	30	SL	SCL	SICL	SCL	41	26	57	SCL	MWD	120	155
3	38	FSL	SCL	SCL	SCL	171	173	187	SCL	WD	153	411
3	22	LS	SL	SCL	SL	133	136	268	SCL	MWD	171	309
3	28	LS	S	SL	LS	125	198	244	SCL	WD	135	194
3	47	LS	S	SCL	SL	37	185	52	SCL	WD	500	500
3	35	LS	LS	SCL	SL	32	60	500	SCL	WD	500	500
3	1	LS	SL	SCL	LS	45	70	50	SCL	WD	500	500
4	26	SL	SCL	SCL	SCL	40	18	59	SCL	WD	500	500
4	9	SL	L	SCL	L	52	18	57	SCL	MWD	23	500
4	5	SL	SL	SCL	SL	15	15	98	SCL	MWD	36	500
4	10	SL	SL	SCL	L	88	30	93	SCL	MWD	45	82
4	8	SL	SL	SCL	SL	105	17	137	SCL	WD	168	500
4	19	LS	SL	SCL	SCL	45	38	69	CL	WD	161	161
4	44	LS	SICL	SICL	SCL	28	50	44	SCL	MWD	18	101
5	29	SL	SICL	SICL	SICL	32	15	47	SICL	WD	106	500
5	24	L	SICL	SICL	SICL	48	22	60	SICL	WD	111	500
5	42	LS	SICL	SICL	SL	165	37	183	SICL	WD	500	500
5	27	SL	SICL	SICL	SICL	54	34	72	SICL	WD	500	500
5	43	SL	SICL	SICL	L	21	110	40	SIL	WD	374	389
5	18	S	L	SICL	S	133	134	140	SICL	WD	500	500
6	33	S	S	SCL	L	46	290	79	SICL	XD	500	500
6	34	S	S	SIL	S	259	274	500	SIL	EXD	290	500
6	14	S	SCL	SCL	S	106	500	111	SCL	WD	380	500
6	32	S	S	CL	S	87	154	205	SICL	EXD	500	500
7	45	S	LS	SL	LS	183	335	500	SL	WD	500	500
7	46	LS	S	SL	LS	244	500	500	SL	WD	500	500
7	20	S	S	SL	S	500	240	500	SL	EXD	500	500
8	37	S	S	LS	LS	500	500	500	LS	EXD	500	500
8	21	S	S	S	S	500	500	500	LS	SED	500	500
8	39	S	S	S	S	500	500	500	S	EXD	500	500
8	49	S	S	S	S	500	500	500	S	EXD	500	500
8	48	S	S	LS	S	500	500	500	LS	EXD	500	500
8	41	S	S	S	S	500	500	500	S	EXD	500	500
8	31	S	S	S	S	500	500	500	S	EXD	500	500
8	36	S	S	S	S	500	500	500	S	EXD	500	500
8	12	S	S	S	S	500	500	500	S	WD	290	500
8	40	S	S	S	S	500	500	500	S	EXD	442	500
8	25	S	S	S	S	500	500	500	S	EXD	500	500

Tables 2.13 and 2.14 were constructed for synthesizing patterns in soil variables based on samples ordered by PC1 and CA 1. The ordering of samples according to results of PCA and CA led to different groups of observations based on soil variables.

Samples ordered by PC1 (Table 2.13) showed an interesting pattern. Samples with silty clay loam substrates occurred together in a sequence corresponding to changes in sola textures, with sandy loam sola preceding loamy sands and sands. Samples with sandy clay loam substrates followed those with silty clay loam substrates in a sequence corresponding to sola textures, with sandy loam sola preceding loamy sands and sands. Samples with sandy loam substrates followed those with sandy clay loam substrates. Finally, samples composed of deep sandy soils were grouped together. This ordering of samples along the first PC according to substrata textures then sola textures corresponded with variable weights and factor patterns for the first PC.

Samples ordered by CA1 (Table 2.14) showed a different pattern. The first group of samples sequenced in this ordination was composed of sandy loam sola overlying sandy clay loam substrates. Next samples with loamy sand and sandy loam sola over silty clay loam substrates were grouped together. Samples with sandy sola overlying finer textured substrates of sandy loam, sandy clay loam, silty clay loam, and clay loam substrates were then ordinated together. The final discernible group consisted of deep sandy soils.

Correspondence analysis of samples in species space reflected a moisture and nutrient gradient that was indirectly expressed by ground-flora composition. Groups of samples ordered based on CA of vegetation appeared more ecologically meaningful than the ordination of samples based on soil variables using PCA. The first group composed of loamy sands and sandy loams over sandy clay loam substrata would provide an optimum rooting zone, with water held above and within the fine loamy substrate. Seven of the first nine samples were moderately well drained, indicating an additional source of water beyond soil moisture holding capacities. The next group had equivalent sola, with silty clay loam substrates. The first group of samples with silty substrates were well drained, followed by samples that were moderately well drained. The next group consisted of sandy soils underlain by textural discontinuities. Host et al. (1987) and Cleland et al. (1985) reported that these types of ecosystems were more productive than ecosystems underlain by soils only containing deep sands. The final group of deep sands were typical of xeric outwash systems in terms of soil characteristics and ground-flora composition.

The ordination of samples in species space seemed to result in a more ecologically meaningful sequence of observations based on soil characteristics than the ordination of samples in soil variable space. Soil variables used in this research were principally categorical variables, and may not have adequately described subtle edaphic conditions affecting biota. Ground-flora composition and relative abundance appeared to effectively serve as phytometers of important soil conditions from a biological standpoint, moreso than soil variables themselves.

Table 2.13. Soil table arraying key variables for samples ordered by sample weights in the first dimension of a PCA of soils data.

STA	T30	UTEX	LTEX	BTEX	DPSCL	ACSL	ACSCL	DOMB	DCL	MOTDE	GWTDE
29	SL	SICL	SICL	SICL	32	15	47	SICL	WD	106	500
24	L	SICL	SICL	SICL	48	22	60	SICL	WD	111	500
27	SL	SICL	SICL	SICL	54	34	72	SICL	WD	500	500
43	SL	SICL	SICL	L	21	110	40	SIL	WD	374	389
42	LS	SICL	SICL	SL	165	37	183	SICL	WD	500	500
30	SL	SCL	SICL	SCL	41	26	57	SCL	MWD	120	155
44	LS	SICL	SICL	SCL	28	50	44	SCL	MWD	18	101
23	S	SCL	SICL	L	100	48	115	SICL	MWD	90	145
2	FSL	FSL	SICL	SL	43	25	49	SCL	MWD	24	500
19	LS	SL	SCL	SCL	45	38	69	CL	WD	161	161
10	SL	SL	SCL	L	88	30	93	SCL	MWD	45	82
9	SL	L	SCL	L	52	18	57	SCL	MWD	23	500
38	FSL	SCL	SCL	SCL	171	173	187	SCL	WD	153	411
7	FSL	SCL	SCL	SL	74	57	79	SCL	WD	129	305
18	S	L	SICL	S	133	134	140	SICL	WD	500	500
11	LS	SL	SCL	L	116	61	143	SCL	MWD	55	500
6	SL	SCL	SCL	L	138	21	76	SCL	WD	167	366
5	SL	SL	SCL	SL	15	15	98	SCL	MWD	36	500
8	SL	SL	SCL	SL	105	17	137	SCL	WD	168	500
33	S	S	SCL	L	46	290	79	SICL	EXD	500	500
3	LS	LS	SCL	SL	118	15	155	SCL	WD	45	500
26	SL	SCL	SCL	SCL	40	18	59	SCL	WD	500	500
4	LS	LS	SIL	LS	179	142	185	SCL	MWD	94	203
13	LS	SCL	SCL	SL	81	17	86	SCL	WD	234	366
22	LS	SL	SCL	SL	133	136	268	SCL	MWD	171	309
28	LS	S	SL	LS	125	198	244	SCL	WD	135	194
47	LS	S	SCL	SL	37	185	52	SCL	WD	500	500
1	LS	SL	SCL	LS	45	70	50	SCL	WD	500	500
14	S	SCL	SCL	S	106	500	111	SCL	WD	380	500
32	S	S	CL	S	87	154	205	SICL	EXD	500	500
35	LS	LS	SCL	SL	32	60	500	SCL	WD	500	500
34	S	S	SIL	S	259	274	500	SIL	EXD	290	500
45	S	LS	SL	LS	183	335	500	SL	WD	500	500
46	LS	S	SL	LS	244	500	500	SL	WD	500	500
20	S	S	SL	S	500	240	500	SL	EXD	500	500
37	S	S	LS	LS	500	500	500	LS	EXD	500	500
40	S	S	S	S	500	500	500	S	EXD	442	500
12	S	S	S	S	500	500	500	S	WD	290	500
48	S	S	LS	S	500	500	500	LS	EXD	500	500
21	S	S	S	S	500	500	500	LS	SED	500	500
25	S	S	S	S	500	500	500	S	EXD	500	500
41	S	S	S	S	500	500	500	S	EXD	500	500
49	S	S	S	S	500	500	500	S	EXD	500	500
31	S	S	S	S	500	500	500	S	EXD	500	500
36	S	S	S	S	500	500	500	S	EXD	500	500
39	S	S	S	S	500	500	500	S	EXD	500	500

Table 2.14. Soil table arraying key variables for samples ordered by sample weights in the first dimension of a CA of vegetation data.

STD	T30	UTEX	LTEX	BTEX	DEPSCL	ACSL	ACSCL	DOMB	DCL	MOTDE	GWTDE
9	SL	L	SCL	L	52	18	57	SCL	MWD	23	500
10	SL	SL	SCL	L	88	30	93	SCL	MWD	45	82
11	LS	SL	SCL	L	116	61	143	SCL	MWD	55	500
8	SL	SL	SCL	SL	105	17	137	SCL	WD	168	500
2	FSL	FSL	SICL	SL	43	25	49	SCL	MWD	24	500
1	LS	SL	SCL	LS	45	70	50	SCL	WD	500	500
4	LS	LS	SIL	LS	179	142	185	SCL	MWD	94	203
43	SL	SICL	SICL	L	21	110	40	SIL	WD	374	389
5	SL	SL	SCL	SL	15	15	98	SCL	MWD	36	500
38	FSL	SCL	SCL	SCL	171	173	187	SCL	WD	153	411
3	LS	LS	SCL	SL	118	15	155	SCL	WD	45	500
7	FSL	SCL	SCL	SL	74	57	79	SCL	WD	129	305
29	SL	SICL	SICL	SICL	32	15	47	SICL	WD	106	500
26	SL	SCL	SCL	SCL	40	18	59	SCL	WD	500	500
28	LS	S	SL	LS	125	198	244	SCL	WD	135	194
19	LS	SL	SCL	SCL	45	38	69	CL	WD	161	161
27	SL	SICL	SICL	SICL	54	34	72	SICL	WD	500	500
13	LS	SCL	SCL	SL	81	17	86	SCL	WD	234	366
6	SL	SCL	SCL	L	138	21	76	SCL	WD	167	366
24	L	SICL	SICL	SICL	48	22	60	SICL	WD	111	500
42	LS	SICL	SICL	SL	165	37	183	SICL	WD	500	500
18	S	L	SICL	S	133	134	140	SICL	WD	500	500
22	LS	SL	SCL	SL	133	136	268	SCL	MWD	171	309
30	SL	SCL	SICL	SCL	41	26	57	SCL	MWD	500	500
44	LS	SICL	SICL	SCL	28	50	44	SCL	MWD	18	101
14	S	SCL	SCL	S	106	500	111	SCL	WD	380	500
23	S	SCL	SICL	L	100	48	115	SICL	MWD	90	145
47	LS	S	SCL	SL	37	185	52	SCL	WD	500	500
34	S	S	SIL	S	259	274	500	SIL	EXD	290	500
35	LS	LS	SCL	SL	32	60	500	SCL	WD	500	500
46	LS	S	SL	LS	244	500	500	SL	WD	500	500
40	S	S	S	S	500	500	500	S	EXD	442	500
45	S	LS	SL	LS	183	335	500	SL	WD	500	500
33	S	S	SCL	L	46	290	79	SICL	EXD	500	500
12	S	S	S	S	500	500	500	S	WD	290	500
32	S	S	CL	S	87	154	205	SICL	EXD	175	500
41	S	S	S	S	500	500	500	S	EXD	500	500
21	S	S	S	S	500	500	500	LS	SED	500	500
37	S	S	LS	LS	500	500	500	LS	EXD	500	500
48	S	S	LS	S	500	500	500	LS	EXD	500	500
20	S	S	SL	S	500	500	500	SL	EXD	500	500
36	S	S	S	S	500	500	500	LS	EXD	500	500
39	S	S	S	S	500	500	500	S	EXD	500	500
31	S	S	S	S	500	500	500	S	EXD	500	500
49	S	S	S	S	500	500	500	S	EXD	500	500
25	S	S	S	S	500	500	500	S	EXD	500	500

Analysis of High Quality Understory and Ground-flora Species

Table 2.15 arrays species retained for additional analyses based on their the sums of squared cosines in five dimensional subspace. These were species with greater than forty-five per cent of their total variability in full dimensional sample space accounted for in the first five dimensions. *Allium tricoccum* and *Uvularia perfoliata* were also retained despite their relatively low five-dimensional display qualities of thirty-eight and thirty-two percent, respectively, because of their high indicator value of fine textured sola or substrates for mesic hardwood ecosystems in northwest lower Michigan (Host 1997), and corroborating field observations in northeast lower Michigan.

Table 2.16 displays the decomposition of inertia for the first fifteen principal coordinates of a CA of forty-six samples and forty-nine high quality understory and ground-flora species. Sixty-eight per cent of the total variability in forty-five dimensional space was accounted for within the first five dimensions, with thirty-seven percent of inertia accounted for by the first principal coordinate and fourteen percent accounted for by the second principal coordinate.

A higher proportion of the total inertia was decomposed along the first five principal coordinates for the high quality ground-flora data set than for the commonly occurring ground-flora data set, for which fifty-one per cent of the total variability in full dimensional space was accounted for by the first five principal coordinates.

Table 2.15. Sums of squared cosines in five dimensional subspace, mass, and inertia for high quality species.

Species	Spp Code	5DQuality	Mass	Inertia
Actaea rubra	ACPA	0.504244	0.007768	0.015550
Acer rubrum	ACRU	0.816312	0.052685	0.017437
Acer saccharum	ACSA	0.929969	0.057920	0.049944
Allium tricoccum	ALTR	0.386129	0.002026	0.011941
Amelanchier spp.	AMAR	0.633853	0.026005	0.024220
Apocynum androsaemifolium	APAN	0.736796	0.005572	0.013508
Arctostaphylos uva-ursi	ARUV	0.635972	0.003546	0.018517
Aster macrophyllum	ASMA	0.578214	0.030564	0.012989
Athyrium felix-femina	ATFE	0.481367	0.002702	0.016195
Athyrium spp.	ATSP	0.459617	0.004222	0.009350
Carex annectens	CAAN	0.845810	0.012327	0.022018
Carex deweyana	CADE	0.648147	0.007092	0.042612
Carex pennsylvanica	CAPE	0.541322	0.057413	0.025903
Carex plantaginea	CAPL	0.519425	0.008274	0.016297
Caulophyllum thalictroides	CATH	0.565080	0.005066	0.015425
Cladina spp.	CLRA	0.730446	0.002871	0.011827
Comptonia peregrina	COPE	0.927055	0.013509	0.040373
Cretaegus spp.	CRSP	0.511502	0.005066	0.010778
Dicranum polysetum	DIPO	0.636293	0.006417	0.016617
Dryopteris spinulosa	DRSP	0.590485	0.002702	0.008627
Fagus grandifolia	FAGR	0.713320	0.017562	0.022915
Fraxinus americana	FRAM	0.804374	0.054880	0.026993
Gaylussacia baccata	GABA	0.764684	0.020601	0.040150
Galium triflorum	GATR	0.718202	0.020432	0.018011
Hamamelis virginiana	HAVI	0.614521	0.022627	0.023242
Hepatica acutiloba	HEAC	0.606066	0.010469	0.017788
Lonicera canadense	LOCA	0.484476	0.013340	0.013203
Melampyrum lineare	MELI	0.778551	0.009287	0.021834
Mitella diphylla	MIDI	0.662048	0.011820	0.015562
Oryzopsis asperifolia	ORAS	0.646829	0.047957	0.015541
Osmorhiza chilensis	OSCH	0.748104	0.021783	0.023910
Ostrya virginiana	OSVI	0.718115	0.032759	0.026034
Prenanthes alba	PRAL	0.526168	0.020432	0.013604
Pteridium aquilinium	PTAQ	0.753352	0.066532	0.031056
Quercus alba	QUAL	0.745493	0.028875	0.024651
Quercus rubra	QURU	0.603897	0.036981	0.012520
Quercus velutina	QUVE	0.888014	0.017899	0.031063
Ribes cynobasti	RICY	0.619363	0.015535	0.017356
Rubus allegheniensis	RUAL	0.691570	0.008443	0.026516
Sanicula trifoliata	SATR	0.591941	0.011651	0.017899
Solidago hispida	SOHI	0.512137	0.014691	0.017461
Tilia americana	TIAM	0.728322	0.018744	0.016035
Trillium grandiflorum	TRGR	0.447832	0.011651	0.009081
Uvularia perfoliata	UVPE	0.337519	0.008105	0.010621
Vaccinium angustifoliu	VAAN	0.904778	0.045424	0.029523
Viburnum acerifolium	VIAC	0.611664	0.031577	0.019663
Viola spp.	VISP	0.783282	0.027356	0.015867

Gains in inertia accounted for by CA of the high quality ground-flora data set when compared with the CA of commonly occurring species were twelve percent for the first principal coordinate, three percent for the second principal coordinate, one percent for the third principal coordinate, and less than one percent for the fourth and fifth principal coordinates, totaling a seventeen percent increase in total variability accounted for within the first five dimensions. This increase in the overall variability accounted for in the first five dimensions was due to the inclusion of species with relatively high correlations, or fidelity, to this subspace and elimination of species more strongly associated with higher dimensions.

Table 2.16. Correspondence analysis: inertia and Chi-Square decomposition of the first fifteen principal coordinates.

Singular Values	Principal Inertias	Chi-Squares	Percents	7 14 21 28 35
0.81798	0.66909	990.586	37.37%	***************************
0.50238	0.25239	373.658	14.10%	**********
0.34035	0.11584	171.496	6.47%	*****
0.31220	0.09747	144.300	5.44%	****
0.29561	0.08738	129.371	4.88%	***
0.24810	0.06155	91.130	3.44%	**
0.23386	0.05469	80.967	3.05%	**
0.21129	0.04464	66.096	2.49%	**
0.20517	0.04209	62.320	2.35%	**
0.19614	0.03847	56.958	2.15%	**
0.18304	0.03350	49.602	1.87%	*
0.17885	0.03199	47.357	1.79%	*
0.17158	0.02944	43.585	1.64%	*
0.16319	0.02663	39.428	1.49%	*
0.15866	0.02517	37.267	1.41%	*

Figures 2.17, 2.18, and 2.19 display results of sample groups agglomerated based on high quality species using three linkage methods. There was close agreement in clusters defined and sample assignment to clusters among all clustering procedures. Clustering using beta linkage identified the same clusters and samples within clusters as clustering using average and Ward's linkage methods with the exception of samples 34, 35, and 37 that formed a discrete cluster, and sample 21. Clustering using average linkage method identified the same clusters and samples within clusters as clustering using Ward's linkage with the exception of sample 18, that was identified as an outlier in the second level. Interpreting the assignment of samples 34, 35, and 37 at one lower level of agglomeration using flexible beta linkage, however, gave identical results as the other two agglomerative linkage methods. Clustering based on TWINSPAN gave the same results as agglomerative clustering with the exception of two samples, samples 44 and 48.

The consistent recovery of the same cluster structure by three different agglomerative linkage methods and divisive clustering indicated that the derived classifications were valid. The interpretation of these groupings and final classification of samples and species was made by tabularly examining patterns in soil characteristics. This interpretation is offered in the final section of this chapter.

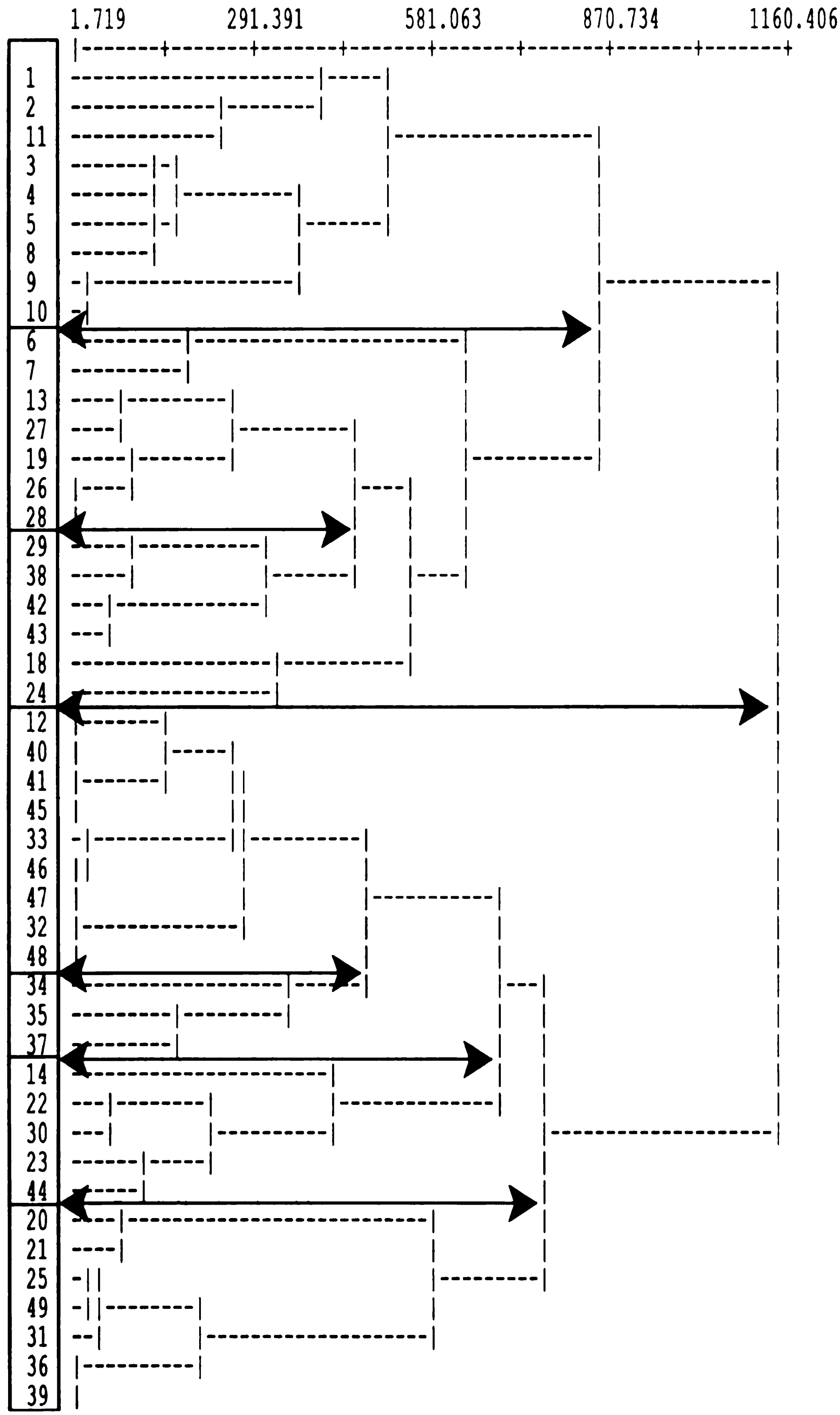


Figure 2.17. Clustering of samples based on high quality species: beta linkage.

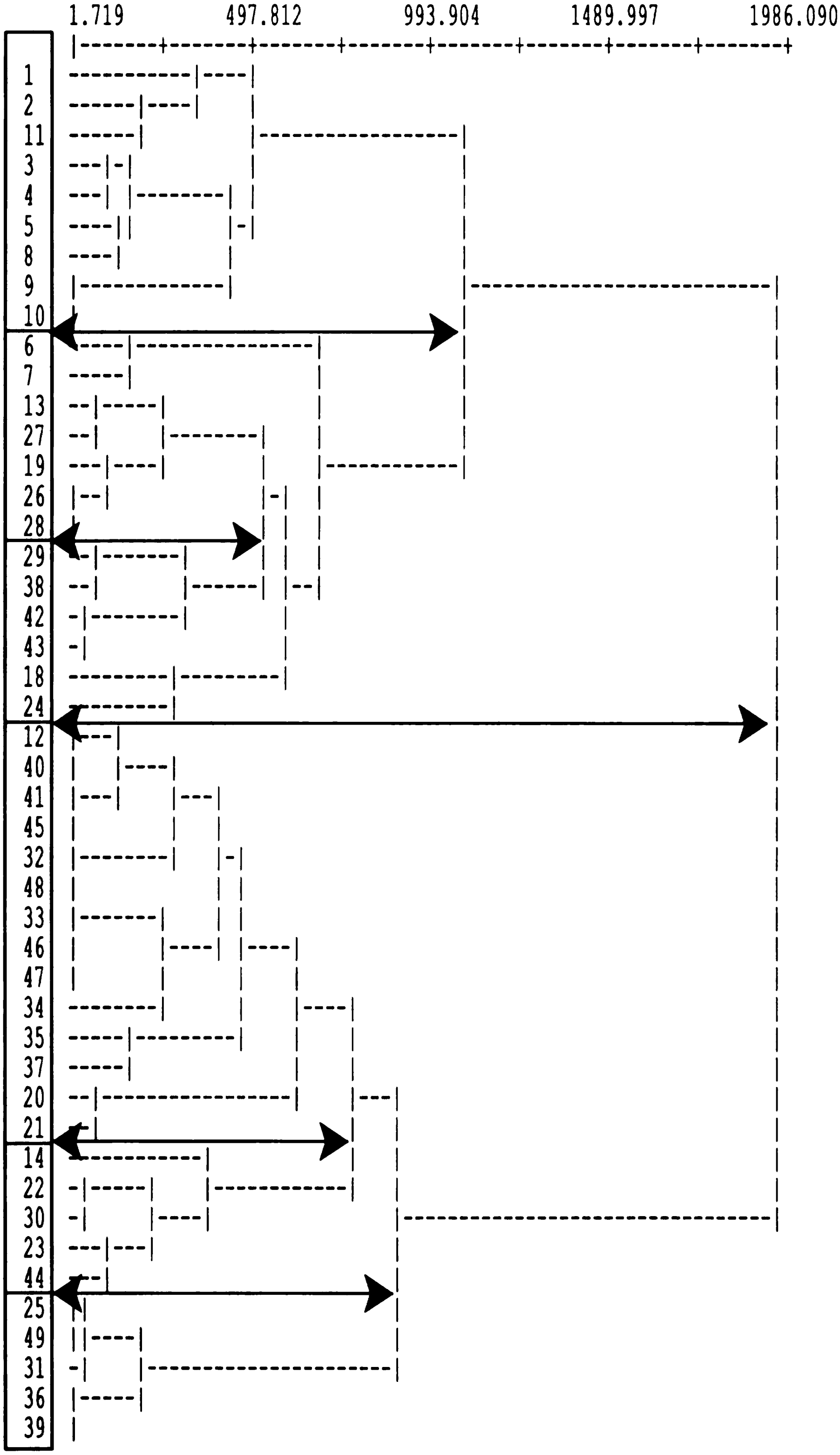


Figure 2.18. Clustering of samples based on high quality species: Ward's linkage.

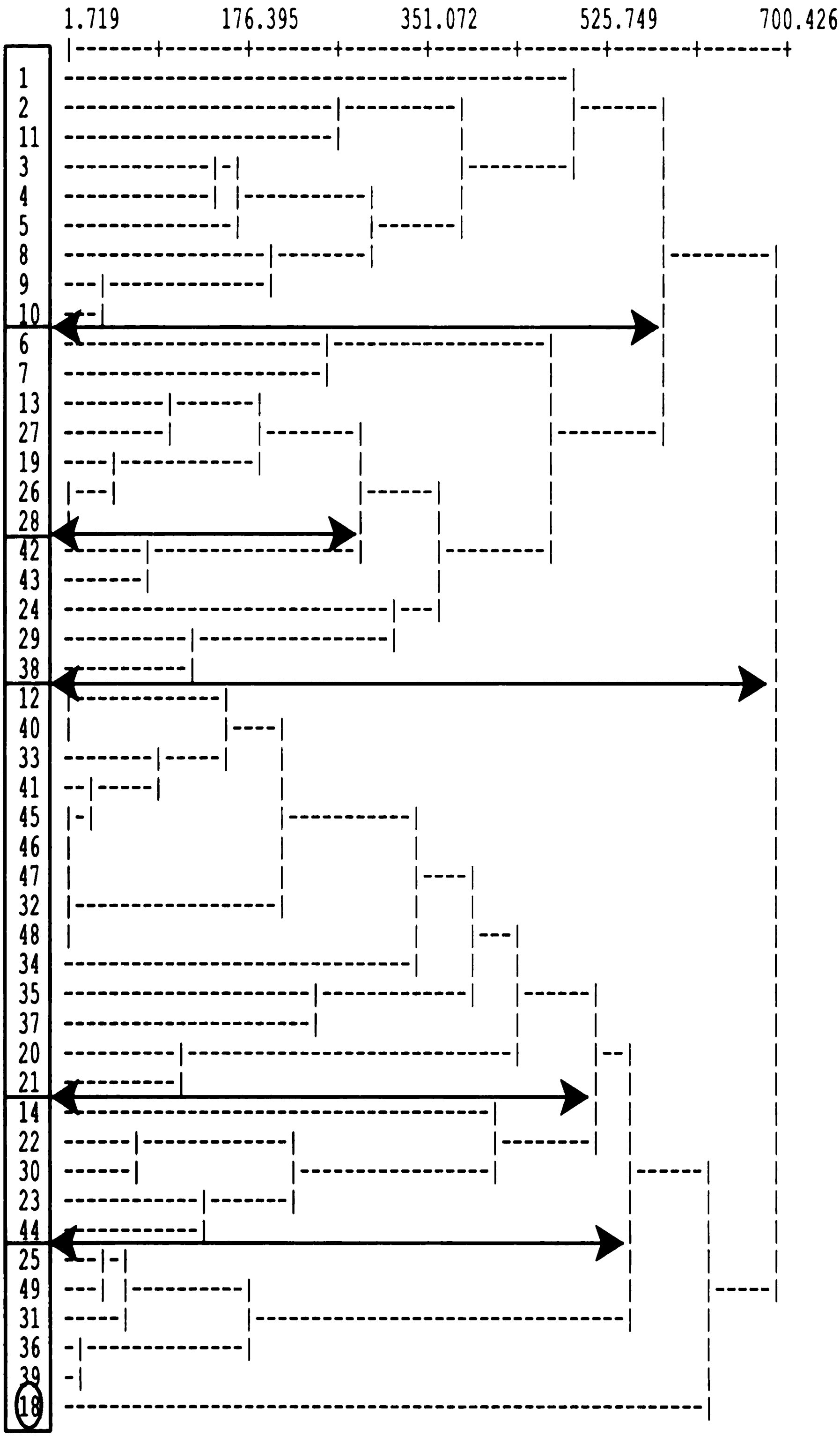


Figure 2.19. Clustering of samples based on high quality species: average linkage.

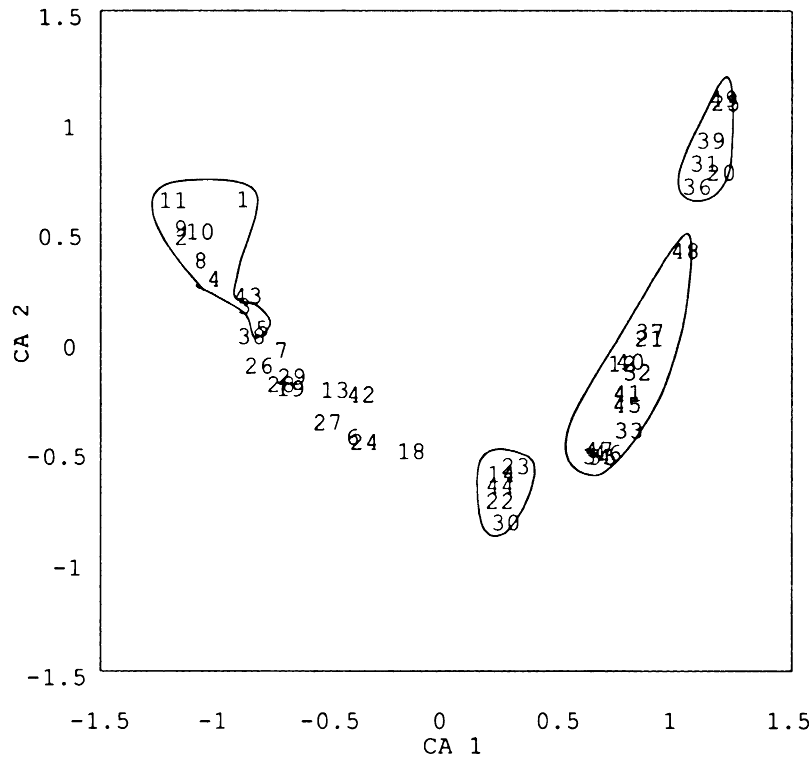


Figure 2.20. Samples in CA dimensions 1 and 2 of high quality species space partitioned by clusters identified using Ward's and average linkage methods.

Figure 2.20 shows samples in the first and second dimensions of high quality species space partitioned by clusters identified using Ward's and average linkage methods. Two clusters could not be partitioned due to intermingled placement of samples.

Figure 2.21 shows samples in the first and third dimension of high quality species space partitioned by clusters identified using Ward's and average linkage methods. All clusters could be partitioned in these two dimensions, suggesting that latent structure of the vegetative data emerged in the first and third dimensions of a CA as opposed to the first and second dimensions.

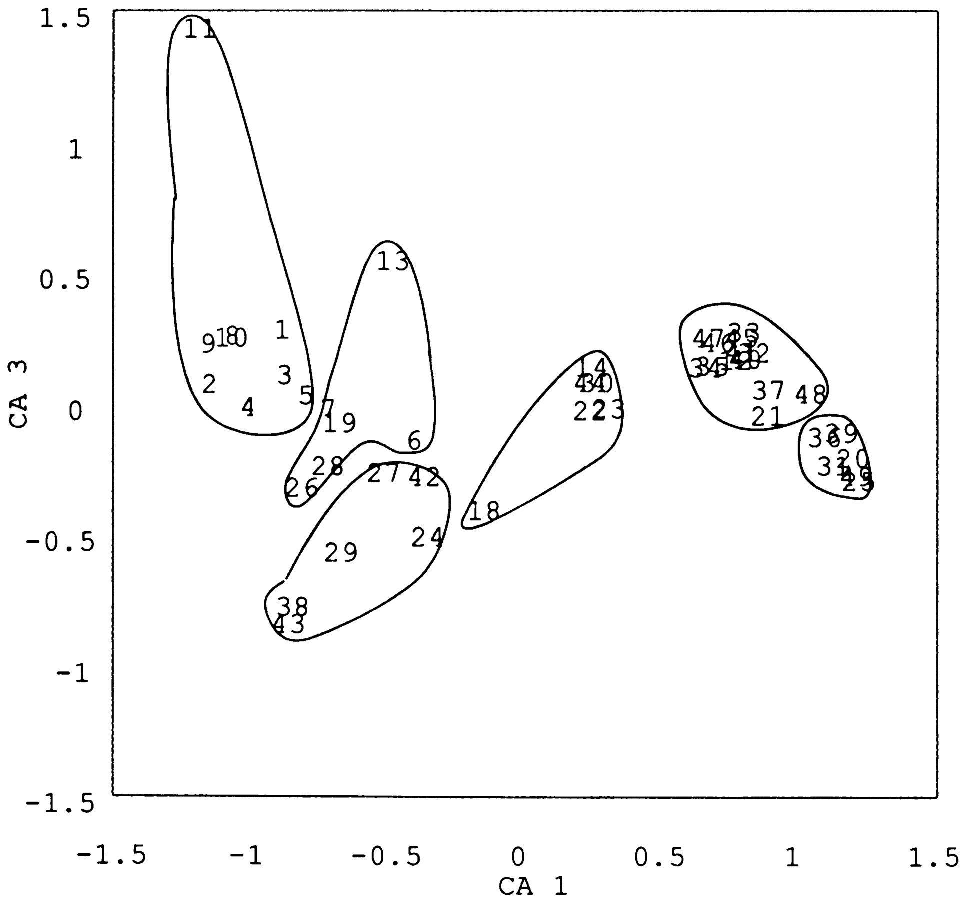


Figure 2.21. Samples in CA dimensions 1 and 3 of high quality species space partitioned by clusters identified using Ward's and average linkage methods.

Classification of Species

Ordination of species in the first two dimensions of sample space identified two species, *Carex pensylvanica* Lam. and *Athyrium spp.*, that occurred far within the arch (Figure 2.22). *Pteridium aquilinium, Trientalis borealis*, and *Acer rubrum* were also somewhat interior to the arch. Interior points in the first two dimensions of a CA indicate

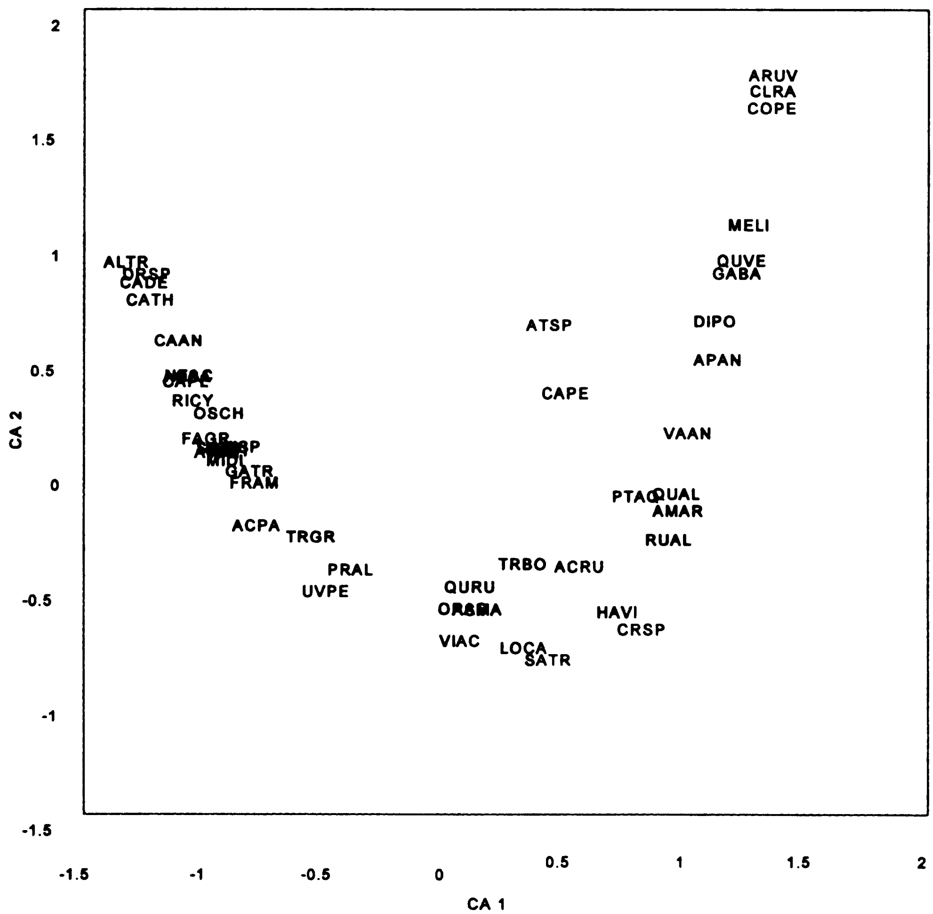


Figure 2.22. High quality species in CA dimensions 1 and 2 of sample space.

species with especially broad or undiscriminating distributions (Gauch 1982). TWINSPAN classified *Carex pensylvanica* Lam. and *Athyrium spp.* as a separate group at the forth level of division (Table 2.17). Inspection of the TWINSPAN synthesis table corroborated a ubiquitous distribution of these species, and *Rubus allegheniensis*, and *Quercus alba*, hence these seven species were removed from further consideration for use in formulating ecological species groups.

Classification of species by TWINSPAN identified eight groups and two outliers (Figure 2.23). Groups consisted of species assemblages grading from highly mesophilic species typifying northern hardwood ecosystems to pyrophilic xeric species typifying oak and pine-oak ecosystems. Interpretation of these groups, made by comparing species assemblages to sample clusters and soil variables, are offered in the final classification and synthesis of results sections of this chapter.

Classification of species using agglomerative clustering procedures produced inconsistent results. The number of clusters and species' assignment to groups varied among agglomerative procedures, and were not comparable to groups identified by TWINSPAN and ordination diagram partitioning. Data reduction based on subjective interpretation of the TWINSPAN synthesis table and subsequent agglomerative clustering also failed to identify consistent clusters. Consequently agglomerative clustering was not further used to identify ecological species groups.

Table 2.17. TWINSPAN classification of high quality species and samples.

Species Group		Sample number	
		1 1 22 1 12234241122344443343331243423432	Sample number
		1189023456873697983428423041572364572101859960	
1	ALTR	1122-2--	00000
1	CATH	-22232-22-------2-----------------------------	00000
1	DRSP	12122-22--------------------------------------	00000
1	CAAN	332332323--332--------------------------------	00001
1	CADE	4-333-------3---------------------------------	00001
2	HEAC	-23223223-------233-2-----2-------------------	0001
2	RICY	213333223--3123-332-2-----2-------------------	0001
2	ACSA	444444444334343334433-------------------------	001000
2	FAGR	3223-3333332333222----1-----------------------	001000
2	OSVI	323432433324243334323-4-----------------------	001000
2	SOHI	133-2223322313-332---1------------------------	001000
2	TIAM	22332233332332-223322-------------------------	001001
2	CAPL	-2233----222---1232-2-------------------------	00101
3	GATR	-2333-233--2-311343333-2--3----------1--------	00101
3	MIDI	--233-22212--2-2332321-2----------------------	00101
3	OSCH	244333132113---2333323-------11---------------	00101
3	ACPA	-----31--21--22233221--21---------------------	0011
3	ATFE	---2------------1232--------------------------	0011
4	FRAM	3344434444334344334444--3334--------1---------	010
4	PRAL	--2-2222323323333-322-332---212--21--1-1---12	010
4	UVPE	----22122212-3---223-2-2222-------------------	010
4	TRGR	1-3221222----222221212-1322---1--12-----------	011
4	VISP	32433334422322-333-31212222--111-1------------	011
5	VIAC	--2-2-3-3-23341331-3--443442112222 3332--------	1000
5	ASMA	-1------222233-3331333233332-2222333-2122---2-	1001
5	ORAS	2-3---32421334343-2333443443343333 33222-2---2-	1001
5	QURU	2------22333332333333-333333332233 2333322-----	1001
5	TRBO	-----------22312-2-222231--22-22----2222-2----	1001
0	CAPE	-42232333--2-2-23-323-2-413333424434 4-4444444-	101
0	ATSP	----------------22212---------1-2----2-2-2-2--	1100
6	PTAQ	--------2--233-----3343433334444434444 34444344	1100
6	ACRU	---------123332322233-3434334444444334 33332123	11010
6	LOCA	---1--2---2-2-11---22-23233212111-3211-------2	11010
6	SATR	----------------3--213--322--2222332-----2----	11010
6	CRSP	------------------------212---222231-------12-	11011
6	HAVI	----------1--22----2--13233333433423---33-----	11011
6	RUAL	-----------------------3--2-----1344-2----1-3-	11011
7	AMAR	--------------------2---232333343433-33233-323	11100
7	QUAL	----------------------13313323443-333233333222	11100
7	VAAN	-------------------1--3333333343333443444444443	11100
8	APAN	------------------------2--------322---2121-22	11101
8	DIPO	---------------1-----------21-12----2223-2221-	11110
8	GABA	---------------------------43231-2-32-2443442-	11110
8	MELI	------------------------1-----2--122-1-2332233	111110
8	QUVE	-----------------------2---1-122-23323-3343334	111110
8	ARUV	-----------------------------------2---2-3222-	111111
8	CLRA	-------------------------------------1-22222-1	111111
8	COPE	-----------------------------------3-2-4243433	111111
		0000000000000000000000111111111111111111111111	
		0000000001111111111111000000000000000111111111	
		0000011110000000011111100000111111111000111111 1	
		01111 001111100000101111000000111 0000001	

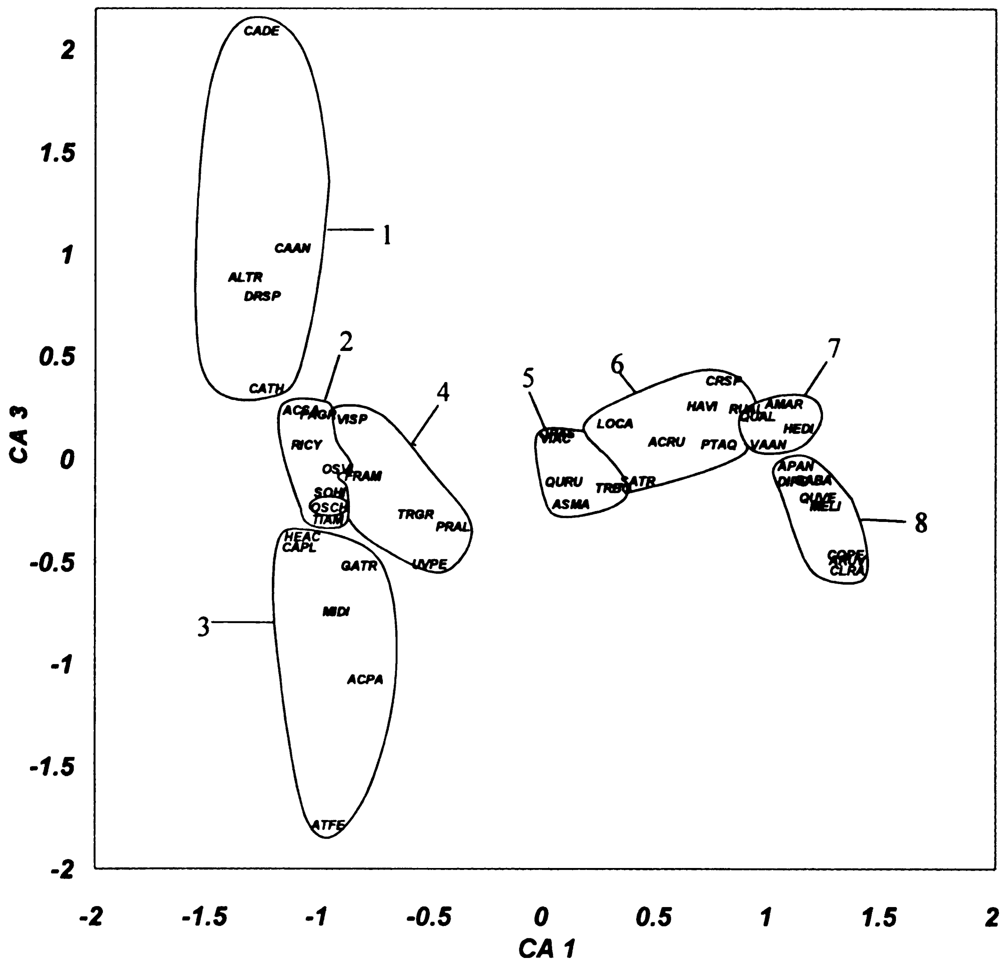


Figure 2.23. High quality species in CA dimensions 1 and 3 of sample space partitioned by TWINSPAN clusters.

Final Classification of Samples and Species based on Combined Ground-flora and Soil Factors

Seven ecological land classification units (ELU's) and ecological species groups were defined based on a series of complementary analyses of ground-flora and soils conditions. Comparisons of soils data arrayed in Tables 2.12 and 2.13 to clusters of samples defined by high quality species revealed two distinctly different soil-substrata conditions within one cluster that included samples consisting of deep sands and of sands underlain by fine loamy substrates. This cluster was subdivided into two ecological land units as a consequence. Placement of sample 38 was also changed due to similarity of soil textures to a different cluster. Sample 38 had sandy loam soil textures to a 30 cm depth overlaying sandy clay loam textures between 30 cm and 150 cm, but was originally grouped with samples containing loamy sand textures to depths of 100 cm. This large difference is soil textures was used as a basis to subjectively assign sample 38 to a group composed of equivalent soil textures. The remaining groupings of samples based on high quality understory and ground-flora species showed consistent patterns in soil characteristics. Examination of overstory composition within combined soil-ground-flora units corroborated the meaningful formulation of seven ecological land units based on congruent changes in ground-flora and soil variables. Table 2.18 arrays key soil variables, Table 2.19 arrays key species, and Table 2.20 arrays overstory composition for these classes.

The identification of seven ecological land units by comparison of clustering and tabular results was corroborated by partitioning ordinations of samples in high quality understory and ground-flora species space (Figure 2.24) and samples in soil variable space (Figure 2.25). The CA of high quality species and PCA of twenty-eight soil variables placed similar samples adjacent to one another, and dissimilar samples away from one another, with equivalent sample placement within respective ordination space groupings. These units are described in the Ecological Land Units (ELU) section of this chapter.

Table 2.18 Key soil variables for ecological land units.

ELU	STA	T30	UTEX	LTEX	BTEX	DEPSCL	ACSL	ACSCL	DOMB	BIC8	DCL	MOTDE	GWTDE
1	1	LS	SL	SCL	LS	45	70	50	SCL	4.25	WD	500	500
1	2	FSL	FSL	SICL	SL	43	25	49	SCL	5.00	MWD	24	500
1	3	LS	LS	SCL	SL	118	15	155	SCL	4.50	MWD	45	500
1	4	LS	LS	SIL	LS	179	142	185	SCL	5.00	MWD	94	203
1	5	SL	SL	SCL	SL	15	15	98	SCL	4.50	MWD	36	500
1	8	SL	SL	SCL	SL	105	17	137	SCL	5.00	WD	168	500
1	9	SL	L	SCL	L	52	18	57	SCL	5.00	MWD	23	500
1	10	SL	SL	SCL	L	88	30	93	SCL	5.00	MWD	45	82
1	11	LS	SL	SCL	L	116	61	143	SCL	4.75	MWD	55	500
2	6	SL	SCL	SCL	L	138	21	76	SCL	5.00	WD	167	366
2	7	FSL	SCL	SCL	SL	74	57	79	SCL	4.75	WD	129	305
2	13	LS	SCL	SCL	SL	81	17	86	SCL	3.75	WD	234	366
2	19	LS	SL	SCL	SCL	45	38	69	CL	5.00	WD	161	161
2	26	SL	SCL	SCL	SCL	40	18	59	SCL	5.00	WD	500	500
2	38	FSL	SCL	SCL	SCL	171	173	187	SCL	5.00	WD	153	411
2	28	LS	S	SL	LS	125	198	244	SL	4.00	WD	135	194
3	24	L	SICL	SICL	SICL	48	22	60	SICL	5.00	WD	111	500
3	27	SL	SICL	SICL	SICL	54	34	72	SICL	5.00	WD	500	500
3	29	SL	SICL	SICL	SICL	32	15	47	SICL	5.00	WD	106	500
3	42	LS	SICL	SICL	SL	165	37	183	SICL	4.00	WD	500	500
3	43	SL	SICL	SICL	L	21	110	40	SIL	4.50	WD	374	389
4	14	S	SCL	SCL	S	106	500	111	SCL	2.75	WD	380	500
4	18	S	L	SICL	S	133	134	140	SICL	5.00	WD	500	500
4	22	LS	SL	SCL	SL	133	136	268	SCL	4.50	WD	171	309
4	23	S	SCL	SICL	L	100	48	115	SICL	3.75	MWD	90	145
4	30	SL	SCL	SICL	SCL	41	26	57	SCL	5.00	MWD	120	155
4	44	LS	SICL	SICL	SCL	28	50	44	SCL	5.00	MWD	18	101
5	32	S	S	CL	S	87	154	205	SICL	3.25	WD	500	500
5	33	S	S	SCL	L	46	290	79	SICL	4.50	WD	500	500
5	34	S	S	SIL	S	259	274	500	SIL	1.50	WD	290	500
5	35	LS	LS	SCL	SL	32	60	500	SCL	2.00	WD	500	500
5	45	S	LS	SL	LS	183	335	500	SL	2.25	WD	500	500
5	46	LS	S	SL	LS	244	500	500	SL	1.25	WD	500	500
5	47	LS	S	SCL	SL	37	185	52	SCL	2.50	WD	500	500
6	12	S	S	S	S	500	500	500	S	1.00	WD	290	500
6	21	S	S	S	S	500	500	500	LS	0.75	SED	500	500
6	37	S	S	LS	LS	500	500	500	LS	1.00	EXD	500	500
6	40	S	S	S	S	500	500	500	S	0.00	EXD	442	500
6	41	S	S	S	S	500	500	500	S	0.25	EXD	500	500
6	48	S	S	LS	S	500	500	500	LS	0.75	EXD	500	500
7	20	S	S	S	S	500	240	500	SL	1.00	EXD	500	500
7	25	S	S	S	S	500	500	500	S	0.25	EWD	500	500
7	31	S	S	S	S	500	500	500	S	0.00	EXD	500	500
7	36	S	S	S	S	500	500	500	S	0.00	EXD	500	500
7	39	S	S	S	S	500	500	500	S	O.00	EXD	500	500
7	49	S	S	S	S	500	500	500	S	0.00	EXD	500	500

Table 2.19. Ecological species groups for ecological land units.

ELU	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	3	3	3	3	3	3	4	4	4	4	4	4
CATH	2	4	-	3	2	-	3	2	5	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-
DRSP	2	-	2	3	-	1	1	3	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ALTR	1	3	-	-	-	1	3	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CADE	-	-	-	-	-	6	4	4	5	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CAAN	5	3	4	3	4	5	4	4	5	2	4	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
VISP	4	5	4	6	6	5	6	5	5	3	4	4	-	2	3	4	1	4	5	4	-	3	1	4	3	3	3
PRAL	-	3	3	3	3	-	2	-	2	4	4	5	4	4	3	5	2	5	4	4	-	4	-	4	5	2	-
SOHI	4	3	3	4	5	1	4	-	3	5	5	1	-	3	3	4	-	-	5	3	-	1	-	-	-	-	-
RICY	1	4	2	3	5	4	5	5	5	3	5	1	4	-	-	-	2	-	5	5	2	-	-	-	-	-	2
FAGR	2	4	5	4	4	4	3	5	-	4	3	4	4	4	5	3	-	-	3	3	-	-	1	-	-	-	-
ACSA	6	6	6	6	6	6	6	6	6	6	6	5	4	5	5	5	5	4	4	6	6	-	-	-	-	-	-
OSVI	2	3	6	5	4	5	5	6	5	6	6	2	4	4	3	5	5	2	5	6	5	-	6	-	-	-	-
MIDI	-	-	2	3	3	-	2	4	5	2	-	-	-	1	3	2	3	5	5	5	3	1	-	2	-	-	-
OSCH	6	5	1	4	3	3	6	4	5	-	4	-	-	1	1	3	3	5	5	5	4	5	-	-	-	-	-
ATFE	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	3	1	3	4	-	-	-	-	-	-
HEAC	3	4	4	2	4	-	5	3	3	-	-	-	-	-	-	-	3	-	2	5	5	-	-	-	-	-	2
CAPL	3	-	-	-	-	-	3	5	5	-	2	-	-	2	3	1	2	-	4	4	3	-	-	-	-	-	-
ACPA	-	4	1	-	-	-	-	-	-	2	-	-	2	2	1	4	1	3	5	4	3	-	-	3	1	-	-
GATR	2	-	4	5	4	-	5	5	5	4	3	-	1	-	-	1	4	4	5	6	5	4	-	2	-	-	5
TIAM	3	2	5	5	5	2	4	4	2	4	5	4	-	4	3	4	4	4	3	5	5	-	-	-	-	-	-
UVPE	-	3	1	2	2	-	-	-	2	4	2	-	-	2	1	-	-	5	-	2	2	2	-	2	3	3	2
TRGR	-	1	2	2	2	1	4	4	3	2	-	-	2	-	-	3	1	4	3	4	1	4	-	1	4	3	2
VISP	4	5	4	6	6	5	6	5	5	3	4	4	-	2	3	4	1	4	5	4	-	3	1	4	3	3	3
FRAM	4	5	6	6	6	5	6	6	6	6	6	5	6	5	5	5	6	6	5	6	6	-	-	5	5	5	6
PRAL	-	3	3	3	3	-	2	-	2	4	4	5	4	4	3	5	2	5	4	4	-	4	-	4	5	2	-
VIAC	-	-	4	-	4	-	3	-	2	6	5	4	1	-	2	5	-	4	4	1	-	-	6	6	4	6	6
HAVI	-	-	-	-	-	-	-	-	-	3	-	-	2	-	1	-	-	3	-	-	-	-	1	5	4	4	5
SATR	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	3	4	-	-	4	-	-	5	2	3
CRSP	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1	4
ORAS	-	-	4	3	6	3	5	-	-	6	4	5	4	2	1	6	5	5	4	-	2	5	6	6	5	6	6
ASMA	1	-	-	-	3	-	-	-	-	4	3	5	-	4	3	5	5	5	5	5	1	5	2	5	5	5	5
QURU	-	-	-	2	2	3	-	-	-	5	4	4	3	5	5	5	5	4	5	5	4	-	4	5	5	5	5
LOCA	-	-	3	-	-	-	-	1	-	-	-	3	1	-	2	1	3	3	-	-	-	-	2	5	4	4	5
AMAR	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	3	5	2
VAAN	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	5	5	5	4	5
ARUV	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CLRA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
COPE	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
APAN	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-
MELI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
DIPO	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
GABA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
QUVE	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-

Values are cover rank abundance arrayed in Table 2.1.

Table 2.19 (cont). Ecological species groups for ecological land units.

ELU	5	5	5	5	5	5	5	6	6	6	6	6	6	7	7	7	7	7	7
CATH	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
DRSP	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ALTR	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CADE	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CAAN	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
VISP	-	1	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
PRAL	3	-	-	2	2	-	1	-	-	1	-	1	1	1	-	-	2	-	-
SOHI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
RICY	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
FAGR	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ACSA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
OSVI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
MIDI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
OSCH	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ATFE	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HEAC	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CAPL	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ACPA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
GATR	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
TIAM	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
UVPE	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
TRGR	2	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
VISP	-	1	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
FRAM	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
PRAL	3	-	-	2	2	-	1	-	-	1	-	1	1	1	-	-	2	-	-
VIAC	5	2	4	1	3	1	2	4	4	-	3	4	-	-	-	-	-	-	-
HAVI	2	6	5	5	4	5	6	-	5	-	-	4	5	-	5	-	-	-	-
SATR	5	5	4	3	4	-	2	-	-	-	-	2	-	-	-	-	-	-	2
CRSP	4	3	2	-	3	-	3	-	-	-	-	1	-	2	-	-	-	1	-
ORAS	5	5	5	6	5	4	4	3	5	4	3	4	3	3	-	-	-	-	-
ASMA	5	5	3	4	2	-	3	-	4	1	4	5	3	3	2	-	-	-	-
QURU	3	5	5	4	3	5	3	5	5	5	4	5	2	-	4	-	-	-	-
LOCA	5	-	1	3	1	1	1	1	3	-	1	3	-	-	-	-	3	-	-
AMAR	5	6	5	5	6	4	5	-	4	5	5	4	4	2	4	-	4	5	5
VAAN	6	5	5	5	5	5	6	5	5	6	6	6	6	6	6	6	5	6	6
ARUV	-	-	-	-	-	-	-	-	-	-	-	2	-	4	2	2	-	2	5
CLRA	-	-	-	-	-	-	-	-	-	-	1	-	2	-	4	2	1	2	3
COPE	-	-	-	-	-	-	-	-	-	-	3	4	3	5	6	5	5	6	6
APAN	3	4	-	-	-	-	-	-	-	-	-	4	1	3	2	1	3	-	4
MELI	3	1	-	-	-	-	4	-	-	-	1	3	4	4	4	3	5	3	5
DIPO	-	-	-	-	2	1	1	4	3	4	3	-	-	1	4	2	-	3	3
GABA	-	2	-	3	1	4	5	2	6	3	-	5	6	4	6	6	-	6	5
QUVE	4	2	-	1	3	-	2	2	1	-	5	5	5	5	5	5	6	4	6

Values are cover rank abundance arrayed in Table 2.1.

Table 2.20. Overstory composition within ecological land units.

STA	1	2	3	4	5	11	8	9	10	6	7	13	19	26	28	38
ELU	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2
SM	103	75	60	40	63	80	50	75	80	13	43	18	5	15	25	45
BW	15	30	48	80	45	38	30	18	28	5	10	0	0	80	20	45
WA	0	20	18	5	0	8	5	8	0	13	8	0	0	45	25	30
BE	0	3	5	3	0	10	20	13	0	10	0	13	10	5	5	5
IW	0	0	0	3	0	5	0	0	0	0	0	0	0	5	0	10
PB	0	0	3	0	0	0	0	0	0	8	3	15	5	0	0	15
RO	0	0	0	0	0	10	0	0	0	8	33	60	70	10	80	0
RM	0	0	0	0	0	0	0	0	0	23	17	10	20	0	0	0
BA	0	13	13	23	18	0	15	5	13	18	18	2	25	10	0	5
WO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

STA	27	42	24	29	43	18	14	22	23	30	44	35	34	46	47	33	45	32
ELU	3	3	3	3	3	4	4	4	4	4	4	5	5	5	5	5	5	5
SM	0	40	30	10	80	10	0	0	0	0	0	0	0	0	0	0	0	0
BW	35	0	70	15	50	0	0	0	0	0	0	0	0	0	0	0	0	0
WA	10	0	10	35	0	0	0	0	0	15	0	0	0	0	0	0	0	0
BE	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
IW	0	5	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PB	50	5	5	5	15	0	0	10	0	0	40	0	0	0	0	0	0	0
RO	65	60	35	105	15	60	83	105	55	120	45	45	100	95	63	45	105	0
RM	5	25	0	0	0	30	28	35	25	10	50	5	30	10	20	15	35	20
BA	0	0	0	0	0	5	3	0	0	5	0	0	5	10	0	0	10	25
WO	0	0	0	0	0	25	3	20	25	0	10	60	5	15	35	40	0	100
BP	0	0	0	0	0	0	0	10	0	0	0	15	0	0	0	25	0	0

STA	12	41	40	21	37	48	36	31	39	20	49	25
ELU	6	6	6	6	6	6	7	7	7	7	7	7
SM	0	0	0	0	0	0	0	0	0	0	0	0
BW	0	0	0	0	0	0	0	0	0	0	0	0
WA	0	0	0	0	0	0	0	0	0	0	0	0
BE	0	0	0	0	0	0	0	0	0	0	0	0
IW	0	0	0	0	0	0	0	0	0	0	0	0
PB	0	0	0	0	0	0	0	0	0	0	0	0
RO	53	80	80	15	23	10	3	5	0	0	0	0
RM	30	15	10	8	0	5	0	10	0	0	0	0
BA	3	0	0	8	5	10	0	0	0	13	5	0
WO	0	25	30	8	23	55	0	2	2	3	0	5
BP	0	0	0	83	15	35	55	48	65	43	70	50

Values are basal area in ft^2.

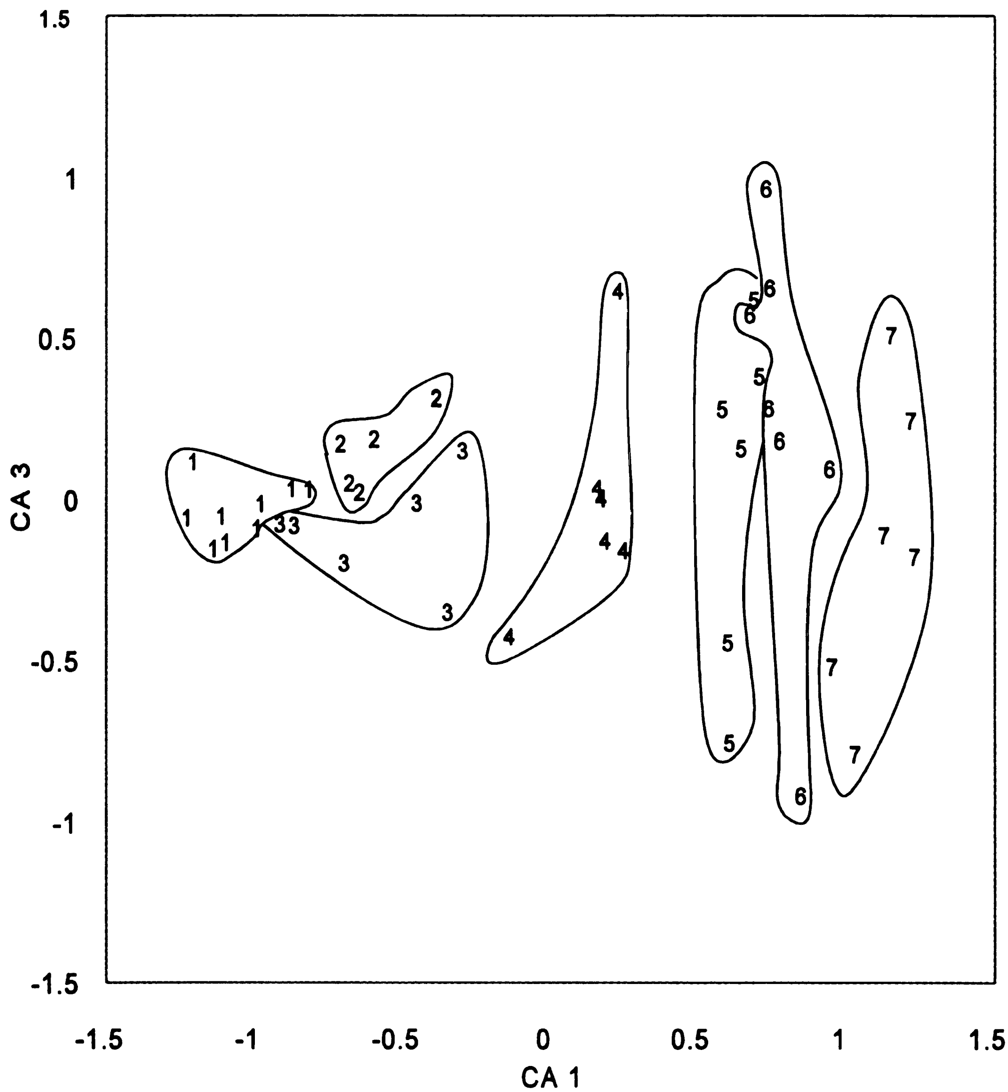


Figure 2.24. Samples in CA dimensions 1 and 3 of high quality species space labeled by ELU.

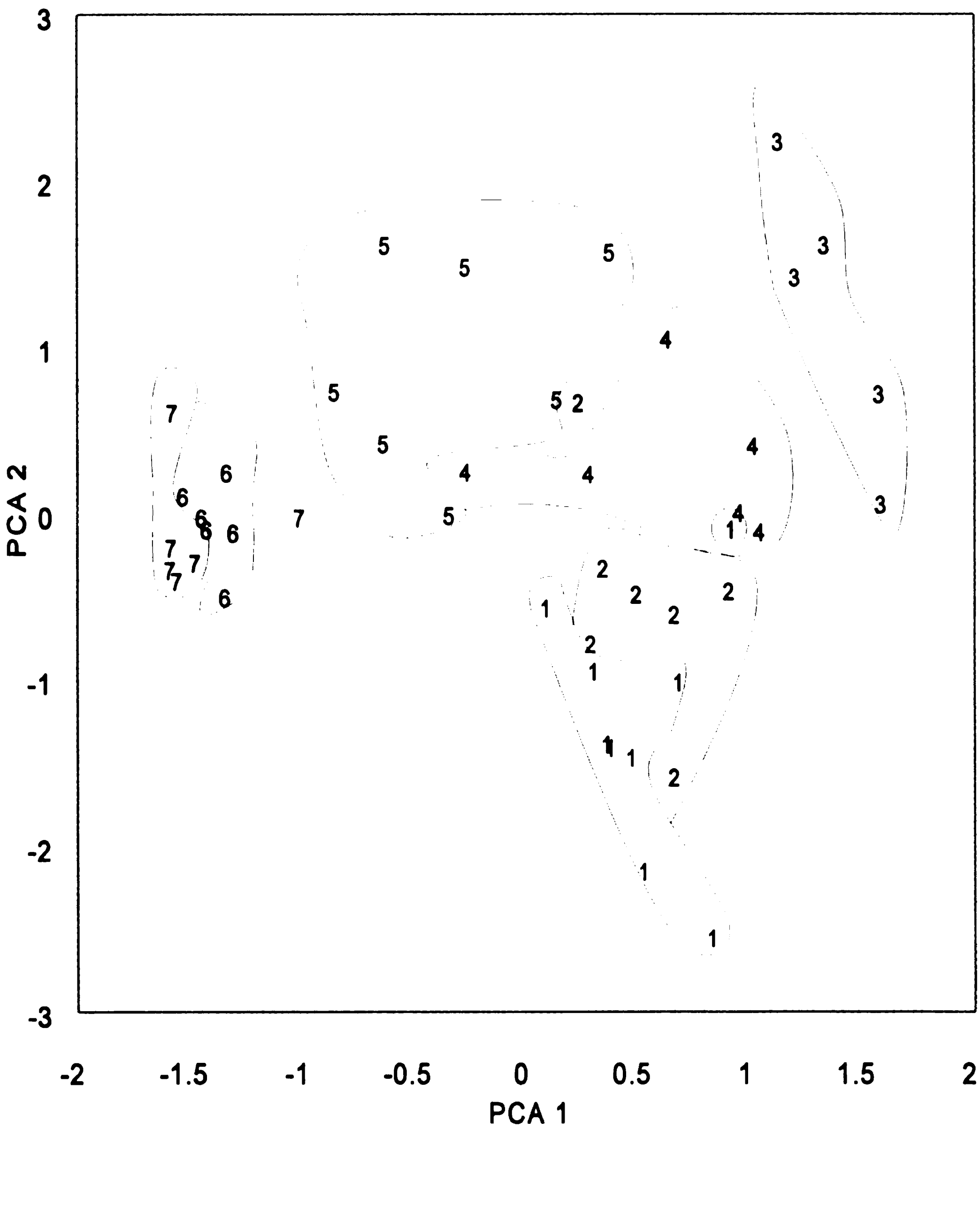


Figure 2.25. Samples in PCA dimensions 1 and 2 of soil variable space labeled by ELU.

Ecological Land Unit Descriptions

ELU 1 consists of the sugar maple-basswood-blue cohosh plant association on moderately well-drained sandy loams over sandy clay loam substratums on moraines and ground moraines; some pedons have loamy sand caps. These soils classify as coarse loamy over fine loamy, mixed, Typic Eutroboralfs and Fragiboralfs at the Subgroup level. The representative horizon sequence is O-AE-E-Bw-Bt-E&B-C1-C2. The forest floor typically consists of a 2 cm. layer of sugar maple, basswood, and white ash litter. The black A horizon averages 10 cm. in thickness. Gray E horizons average 2.8 cm. in thickness. Bhs horizons are absent. Reddish brown (5 YR 4/3) loamy sand and sandy loam Bw horizons overlie fine loamy C horizons. Mottles indicating perched watertables generally occur within the upper 50 cm.

The ground-flora of sites sampled for ELU 1 consists of *Caulophyllum thalictroides*, *Dryopteris spinulosa*, *Allium tricoccum*, *Carex deweyana*, and *Carex annectens*. These species form the *Caulophyllum* species group.

The overstories of sites sampled for ELU 1, in decreasing order of basal area, are dominantly composed of sugar maple, basswood, white ash, and beech. The average stand in this ELU was 63 years old (1988); basal area averaged 133 ft^2 per acre. Sugar maple contributed 69 ft^2 of BA per acre, basswood 37 ft^2 , white ash 7 ft^2, and beech 7 ft^2. Stand MAI averaged 49 ft^3/ac./yr., with a standard error of 3.6.

ELU 1 is similar to ELU 2 and ELU 3. ELU 1 differs from ELU 2 and 3 floristically by having *Caulophyllum thalictroides*, *Dryopteris spinulosa*, *Allium tricoccum*, *Carex deweyana*, and *Carex annectens* in the ground-flora. The soils of ELU

1 differ from ELU 2 by having dominantly sandy loam textures in the upper 100 cm., as opposed to sandy clay loam, and a moderately well drained drainage class. The soils of ELU 1 differ from ELU 3 by having dominantly sandy loam textures in the upper 100 cm., as opposed to silty clay loam, and having sandy clay loam substrates at depths greater than 100 cm. as opposed to silty clay loam substrates. The overstory of ELU 1 is similar in composition and productivity to ELU 2, but contains higher basal areas of sugar maple and lower basal areas of red oak, red maple, and paper birch.

ELU 2 consists of the red oak-sugar maple-viola plant association on well-drained sandy loams over sandy clay loam substratums on moraines and ground moraines; some pedons have loamy sand caps. These soils classify as coarse loamy over fine loamy Typic Eutroboralfs and Alfic Haplorthods at the Subgroup level. The representative horizon sequence is O-AE-E-Bs-Bt-E&B-C1-C2. The forest floor typically consists of a 2 cm. layer of red oak, sugar maple, basswood, and white ash litter. The black A horizon averages 6.6 cm. in thickness. Gray E horizons average 7.0 cm. in thickness. Bhs horizons are absent. Reddish brown (5 YR 4/3) loamy sand and sandy loam Bw and Bt horizons overlie fine loamy C horizons.

The ground-flora of sites sampled for ELU 2 consists of *Viola* species *including Viola pubescens and Viola canadensis, Prenanthes alba, Ribes cynobasti, Solidago hispida,* and a diverse assemblage of tree seedlings including *Acer saccarum, Tilia americana, Fagus grandifolia*, and *Ostrya virginiana*. These species form the *Viola* species group.

The overstories of sites sampled for ELU 2, in decreasing order of basal area, are

composed of red oak, sugar maple, basswood, white ash, red maple, beech, paper birch, and ironwood. The average stand in this ELU was 68 years old (1988); basal area averaged 137 ft^2 per acre. Red oak contributed 37 ft^2 of BA per acre, sugar maple contributed 23 ft^2, basswood 23 ft^2, white ash 17 ft^2, red maple 10 ft^2, and beech 7 ft^2. Stand MAI averaged 50 ft^3/ac./yr., with a standard error of 4.7.

ELU 2 is similar to ELU 1 and ELU 3. EL 2 differs from ELU 1 floristically by lacking *Caulophyllum thalictroides*, *Dryopteris spinulosa*, *Allium tricoccum*, *Carex deweyana*, and *Carex annectens*. EL 2 differs from ELU 3 floristically by lacking *Athyrium felix-femina* and *Hepatica acutiloba*, with *Mitella diphylla and Osmorhiza chilensis* only occasionally present in ELU 2. The soils of ELU 2 differ from ELU 3 by having dominantly sandy clay loam textures in the upper 100 cm., as opposed to sandy loam, and a well drained drainage class. The soils of ELU 2 differ from ELU 3 by having dominantly sandy clay loam textures in the upper 100 cm., as opposed to silty clay loam, and having sandy clay loam substrates at depths greater than 100 cm. as opposed to silty clay loam. The overstory of ELU 2 is similar in composition and productivity to ELU 1 and ELU 3, but contains lower basal areas of sugar maple and higher basal areas of red oak, red maple, and paper birch than ELU 1, and contains lower basal areas of red oak than ELU 3.

ELU 3 consists of the red oak-basswood- miterwort plant association on well-drained sandy loams over silty clay loam substratums on moraines and ground moraines; some pedons have loamy sand caps. These soils classify as Typic Eutroboralfs at the Subgroup level. The representative horizon sequence is O-AE-E-Bw-Bt-C1. The forest floor typically consists of a 2 cm. layer of red oak, sugar maple, basswood, red maple and white ash litter. The black A horizon averages 4.6 cm. in thickness. Gray E horizons average 10.2 cm. in thickness. Bhs horizons are absent. Reddish brown (5 YR 4/3) sandy loam Bw horizons overlie silty clay loam B and C horizons.

The ground-flora of sites sampled for ELU 3 consists of *Mitella diphylla, Osmorhiza chilensis, Athyrium felix-femina*, *Hepatica acutiloba*, *Carex plantaginea, Actaea rubra, Galium triflorum, and Tilia americana*. These species are form the *Mitella* species group.

The overstories of sites sampled for ELU 3 are composed of red oak, basswood, sugar maple, paper birch, white ash, red maple, ironwood and beech. The average stand in this ELU was 68 years old (1988); basal area averaged 144 ft^2 per acre. Red oak contributed 56 ft^2 of BA per acre, basswood 34 ft^2, sugar maple 32 ft^2, paper birch 16 ft^2, white ash 11 ft^2, red maple 6 ft^2, and beech 2 ft^2. Stand MAI averaged 57 ft^3/ac./yr., with a standard error of 6.8.

ELU 3 is similar to ELU 2 and ELU 3. ELU 3 differs from ELU 1 floristically by having *Athyrium felix-femina* present, and by lacking *Caulophyllum thalictroides*, *Dryopteris spinulosa*, *Allium tricoccum*, *Carex deweyana*, and *Carex annectens* in the ground-flora. ELU 3 differs from ELU 2 by having *Athyrium felix-femina* and *Hepatica acutiloba* present, and by having *Osmorhiza chilensis, Carex plantaginea, Actaea rubra, and Galium triflorum* present in higher coverages and frequencies. The soils of ELU 3 differ from ELU 1 by having dominantly silty clay loam textures in the upper 100 cm., as opposed to sandy clay loam, and a well drained drainage class. The soils of ELU 3 differ from ELU 2 by having dominantly silty clay loam in the upper 100 cm. and lower 100 cm., as opposed to sandy clay loam textures. The overstory of ELU 3 is similar in composition and productivity to ELU 1, but contains higher basal areas red oak and paper birch and lower basal areas of sugar maple. The overstory of ELU 3 is similar in composition and productivity to ELU 2, but contains higher basal areas red oak and paper birch.

ELU 4 consists of the red oak-red maple-bellwort plant association on well drained sands with sandy Bs to coarse to fine loamy B2t horizons overlying fine loamy substratums on ice-contact topography. These soils classify as Alfic and Entic Haplorthods. The representative horizon sequence is O-E-Bs1-Bt2-C1-C2. The forest floor typically consists of a 2 cm. layer of red oak and red maple litter. The black A horizon averages 4.6 cm. in thickness. Gray E horizons average 5.9 cm. in thickness. Bhs horizons are absent. Reddish brown (7.5 YR 4/) sandy Bs and dark reddish brown (5 YR 4/3) sandy loam to sandy clay loam Bt horizons overlie fine loamy C1 or C2 horizons.

The ground-flora of sites sampled for ELU 4 consists of *Uvularia perfoliata*, *Trillium grandiflorum*, *Viola spp.*, *Fraxinus americana*, and *Prenanthes alba*. These species form the *Uvularia* species group. The ground-flora of ELU 4 contains elements of both northern hardwood and oak ecosystems, including species within the *Uvularia* species group, and *Viburnum acerifolium*, *Hamamelis virginiana*, and *Vaccinium angustifolium*.

The overstories of sites sampled for ELU 4, in decreasing order of basal area, are

composed of red oak, red maple, white oak, paper birch, and white ash. The average stand in this ELU was 68 years old (1988); basal areas averaged 144 ft^2 per acre. Red oak contributed 78 ft^2 of BA per acre, red maple 30 ft^2, white oak 14 ft^2, paper birch 8 ft^2, and white ash 3 ft^2. Stand MAI averaged 45 ft^3/ac./yr., with a standard error of 5.7.

ELU 4 is similar to ELU 5. ELU 4 differs from ELU 5 floristically by having species typifying northern hardwood ecosystems present including *Uvularia perfoliata, Trillium grandiflorum, Viola spp., Fraxinus americana*, in addition to species characterizing ELU 5. The soils of ELU 4 differ from ELU 5 by having shallower depths to sandy clay loam textures in Bt and C horizons. The overstory of ELU 3 is similar in composition and productivity to ELU 4.

ELU 5 consists of the Redoak-red maple-viburnum plant association on well drained sands with sandy Bs overlying coarse to fine loamy substratums on ice-contact topography. These soils classify as Entic Haplorthods. The representative horizon sequence is O-E-Bs1-Bs2-C1-C2. The forest floor typically consists of a 2 cm. layer of red and white oak, and red maple litter. The black A horizon averages 2.9 cm. in thickness. Gray E horizons average 5.1 cm. in thickness. Bhs horizons are absent. Reddish brown (7.5 YR 4/4) and brown (10 YR 4/4) sandy Bs horizons overlie dark reddish brown (5 YR 4/3) sandy loam to sandy clay loam C1 or C2 horizons.

The ground-flora of sites sampled for ELU 5 consists of *Viburnum acerifolium, Hamamelis virginiana, Sanicula trifoliata, Cretaegus spp., Amelanchier spp.,and Oryzopsis asperifolia*. These species form the *Viburnum* species group.

The overstories of sites sampled for ELU 5, in decreasing order of basal area, are

composed of red oak, white oak, black oak, and red maple. The average stand in this ELU was 79 years old (1988); basal areas averaged 131 ft^2 per acre. Red oak contributed 75 ft^2 of BA per acre, white oak 26 ft^2, red maple 19ft^2, and black oak 19ft^2. Stand MAI averaged 40 ft^3/ac./yr., with a standard error of 3.5.

ELU 5 is similar to ELU 4 and ELU 6. ELU 5 differs from ELU 4 floristically by lacking species typifying northern hardwood ecosystems including *Uvularia perfoliata*, *Trillium grandiflorum*, *Viola spp*., *Fraxinus americana*. ELU 5 differs from ELU 6 floristically by having high frequencies and coverages of *Sanicula trifoliata* and *Cretaegus spp.* The soils of ELU 5 differ from ELU 4 by having greater depths to sandy clay loam textures in substrates. The soils of ELU 5 differ from ELU 6 by having deep lying coarse and fine loamy substrates, the principal criteria differentiating these two ELU's.

ELU 6 consists of the mixed oak-red maple-big leaf aster plant association on excessively well-drained sands of ice contact topography. Soils in ELU 6 classify Entic Haplorthods at the Subgroup level. Soil development is medial. Horizon sequences are O-A-AE-Bs-C. The forest floor is frequently a thin layer of oak litter. The black (10 YR 2/1) A horizon averages 4.1 cm. in thickness. Gray E horizons average 2.2 cm., and are absent in some pedons. Yellowish brown (7.5 YR and 10 YR 5/4) Bs horizons have weak spodic development, and overlie sandy substratums.

The ground-flora of sites sampled for ELU 6 consists of *Aster macrophyllum*, *Quercus rubra*, *Lonicera canadense*, and *Vaccinium angustifolium*. These species form the *Aster macrophyllum* species group.

The overstories of reference sites sampled for ELU 6 are composed of red, black, and white oak, and red maples. The average stand in this ELU was 70 years old (1988), with a basal area of 73 ft^2. Red oak contributed 37 ft^2 of basal area, white oak averaged 34 ft^2, black oak averaged 19 ft^2, and red maple averaged 11 ft^2. Stand MAI averaged 28 ft^3/ac/yr, with a standard error of 2.7.

ELU 6 is similar to ELU 5. ELU 6 differs from ELU 5 floristically by having high coverages of *Sanicula trifoliata* and *Cretaegus spp.*, and differs in soil characteristics by lacking coarse to fine loamy substratums. The overstory of ELU 6 is similar in composition to ELU 5, but is significantly less productive based on an ANOVA and Duncan's multiple range test ($p < .05$).

ELU 7 consists of the Northern pin oak-white oak-bearberry plant association on excessively well-drained sands of outwash plains. Soils in ELU 7 classify Typic Udipsamments at the Subgroup level. Soil development is minimal. Horizon sequences are O-A-Bw-C. The forest floor is frequently a thin layer of oak litter. The black (10 YR 2/1) A horizon averages 4.1 cm. in thickness. Gray E horizons average 2.2 cm., and are absent in some pedons. Yellowish brown (10 YR 5/6) Bw horizons lack spodic development, and overlie sandy substratums.

The ground-flora of sites sampled for ELU 7 consists of *Arctostaphylos uva-ursi, Cladina spp., Comptonia peregrina, Apocynum androsaemifoliumspr, Melampyrum lineare, Dicranum polysetum, Gaylussacia baccata,* and *Quercus velutina*. These species form the *Arctostaphylos* species group.

The overstories of reference sites sampled for ELU 7 are composed of upland pin, black, and white oak. The average stand in this ELU was 70 years old (1988), with a basal area of 73 ft^2. Pin and black oak contributed 55 ft^2 of basal area, and white oak averaged 2 ft^2. Red maple was absent. Stand MAI averaged 14 ft^3/ac/yr, with a standard error of 2.1.

ELU 7 is similar to ELU 6 in terms of coarse sandy soil textures. ELU 7 differs from ELU 6 by lacking red maple in the overstory, and by having high coverages of *Arctostaphylos uva-ursi, Cladina spp., Comptonia peregrina, Apocynum androsaemifoliumspr*. The productivity of ELU is significantly less than all other ELU's ($p < .05$).

Figure 2.26 displays high quality species comprising the seven ecological species groups defined in this research based on direct relationships to environmental conditions. Ecological species groups 1, 2, 4, and 8 are identical to groups 1, 2, 4, and 8, respectively, identified by TWINSPAN based on high quality ground-flora (Table 2.17, Figure 2.23). TWINSPAN identified eight species groups, whereas tabular comparisons of ground-flora distributions to samples grouped according to soil and floristic similarities only identified seven meaningful groups. Because TWINSPAN did not differentiate two important ecological land units from one another, units 5 and 6, it artificially separated species comprising these two units into three groups. Moreover, tabular inspection of the distribution of *Pteridium aquilinium* indicated that this species was too widely distributed to be of indicator value of a particular environmental condition, hence ecological unit, and was subsequently removed as a member of any ecological species group.

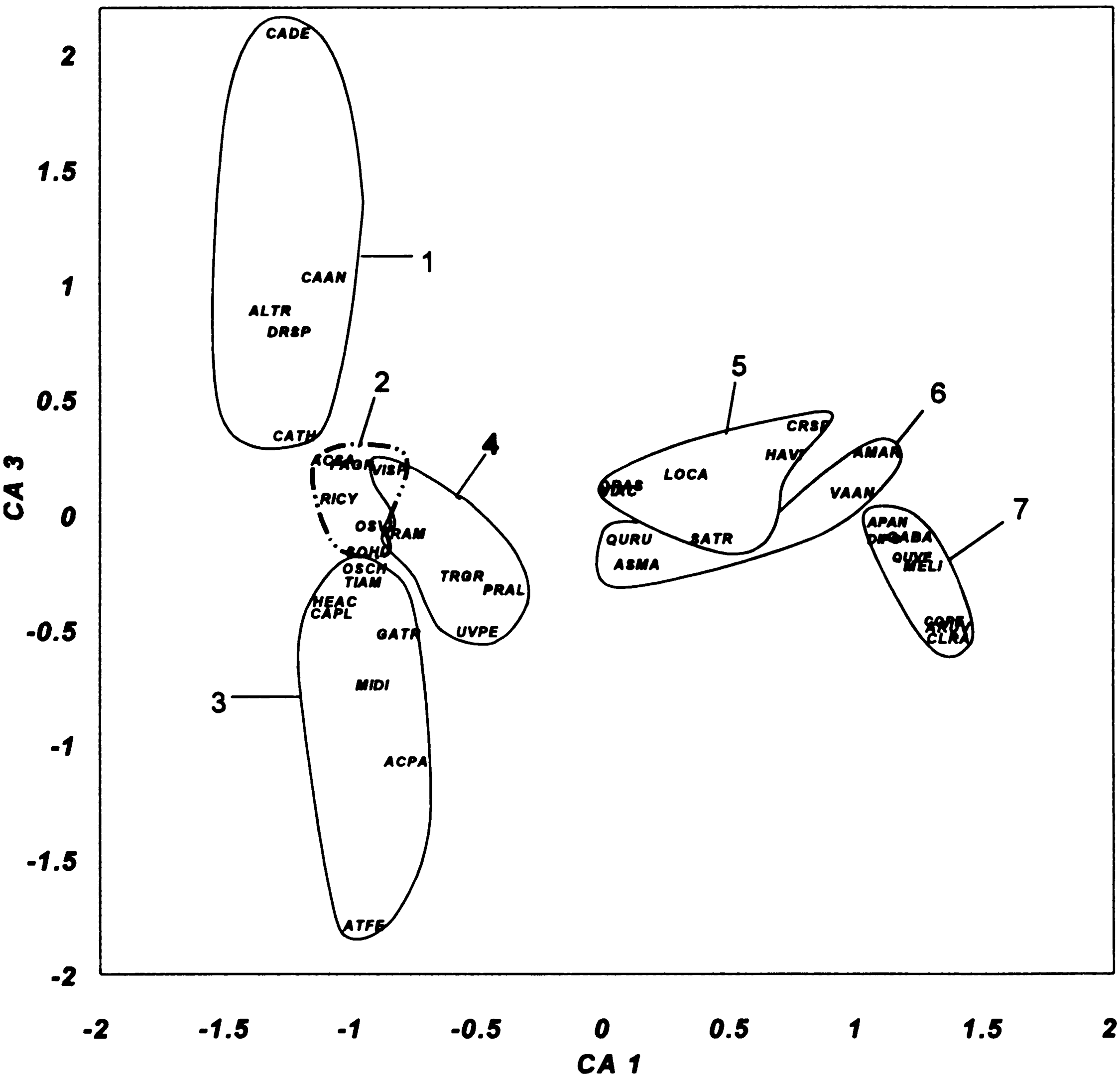


Figure 2.26. Ecological species groups in CA dimensions 1 and 3 of sample space.

Interpretation of Ordination and Classification of Samples Based on Soils Data

Principal component analysis of twenty-eight soil variables identified important soil characteristics that differentiated multifactor ecological land units and also produced ordination diagrams that grouped samples into meaningful classes of soil, ground-flora, and overstory conditions (Figure 2.25). The first PC axis ordinated samples along a textural gradient, (Figures 2.11, 2.12, and 2.13), with solas grading from sands to sandy loams with increasing sample weights, and substrates grading from sands to sandy clay loam with increasing sample weights. Soil drainage classes also graded from excessively well drained to well drained with increasing sample weights along the first axis (Figure 2.14). The second axis ordinated samples along a substrate silt content gradient (Figure 2.13), and along a drainage class gradient in which samples containing moderately well drained soils were separated from well drained soils (Figure 2.14). Silt content of soil horizons at depths of 100 to 250 cm. increased with increasing sample weights along the second axis (Figure 2.13). Soil drainage graded from well drained to moderately well drained with decreasing sample weights along the second axis (Figure 2.14).

The most important soil variables based on high positive first dimensional factor loadings, or variable correlations with variates derived in the first principal component, included a coded variable describing substrate textures, textures between 100 and 150 cm., and sola textures (Table 2.9). The most important soil variables based on negative factor loadings included depth to heavy textured horizons, and depths to mottles and water tables. The most important soil variables based on high positive second dimensional factor loadings included depths to mottles, dominant texture of sola and substrates, textures between 100 and 250 cm., and depth to watertables (Table 2.10). The most important soil variables based on high negative second dimensional factor loadings included drainage class code, texture of the top 30 cm., and a coded variable describing substrata textures.

Table 2.18 arrays key soil variables used in defining ecological land units that include sola and substrate textures, and depths to lithologic discontinuities and watertables. These were the key differentiating soil variables in the final classification that was based on all factors.

Ordinations of samples in soil variable space in the first two dimensions of a PCA distinguished all ecological land units (52.24), with only a few outliers not grouping within respective classes. With the exceptions of ELU's 6 and 7, ordinations of samples in variable space in the first and third dimensions (See Figure 2.27) failed to group, hence distinguish ELU's, however.

Ordinations of samples in soil variable space in the first two dimensions of a PCA (Figure 2.25) placed ecological land unit 3, that contained high silt content in the upper 100 cm. and in substrates, in regions with high positive sample weights in both the first and second dimensions. Ecological land units 1 and 2 differed pedologically in terms of textures in the upper 100 cm., with unit 2 containing sandy clay loam textures and unit 1 sandy loam textures; these units occurred immediately adjacent to one another in the ordination diagram. Ecological land units 4 and 5 differed from each other in depths of sandy sola overlying fine textured substrates; substrates were shallower in ecological land unit 4. These units also occurred immediately adjacent to one another in the ordination diagram. Ecological land units 6 and 7 differed from each other in terms of B horizon development, with unit 7 classifying as a udipsamment and unit 6 classifying as a spodosol. B horizon values and intensity codes were not identified as important variables in PCA, but the nevertheless the ordination of samples in variable space distinguished these units.

Agglomerative clustering of samples based on twenty-eight soil variables using Ward's and average linkage methods (Figures 2.28 and 2.29) failed to identify the same groups as ordination space partitioning of samples in soil variable space, or as the ordination and clustering of samples based on ground-flora. Clustering results between the two linkage methods were not consistent. Interpretation of clustering results indicate that soil groupings were highly variable, and simply included all possible combinations of soil textures in sola and substrata. The ecological significance of these clusters are highly limited, and are not corroborated by other ordination, graphical, and tabular analyses of soils or ground-flora data, or clustering of ground-flora.

Analyses of soils data using PCA identified key differentiating variables and assisted in defining final units. Ordination space partitioning of samples in soil variable space was effective in identifying all final units. The placement of boundaries required comparison with understory and ground-flora analyses, however. Clustering led to inconsistent results and thus had to be disregarded.

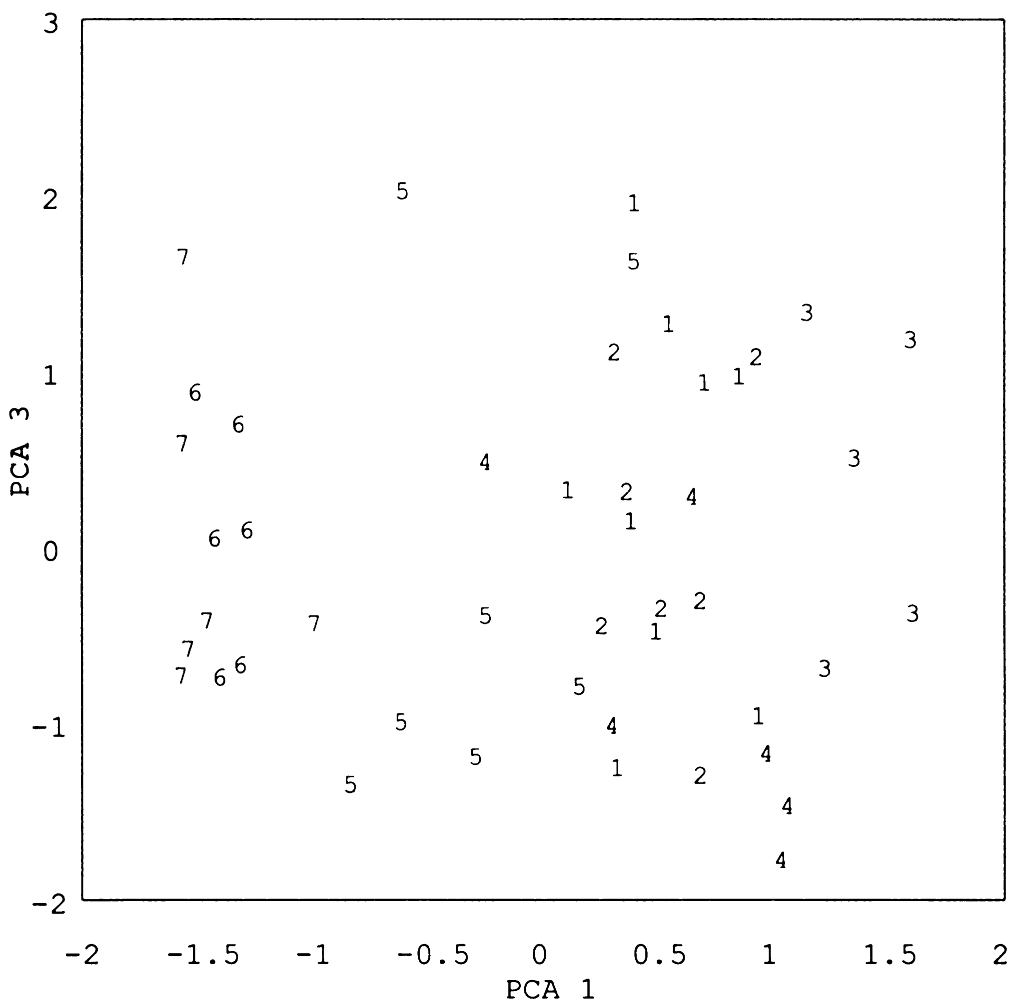


Figure 2.27. Samples in PCA dimensions 1 and 3 of soil variable space labeled by ELU.

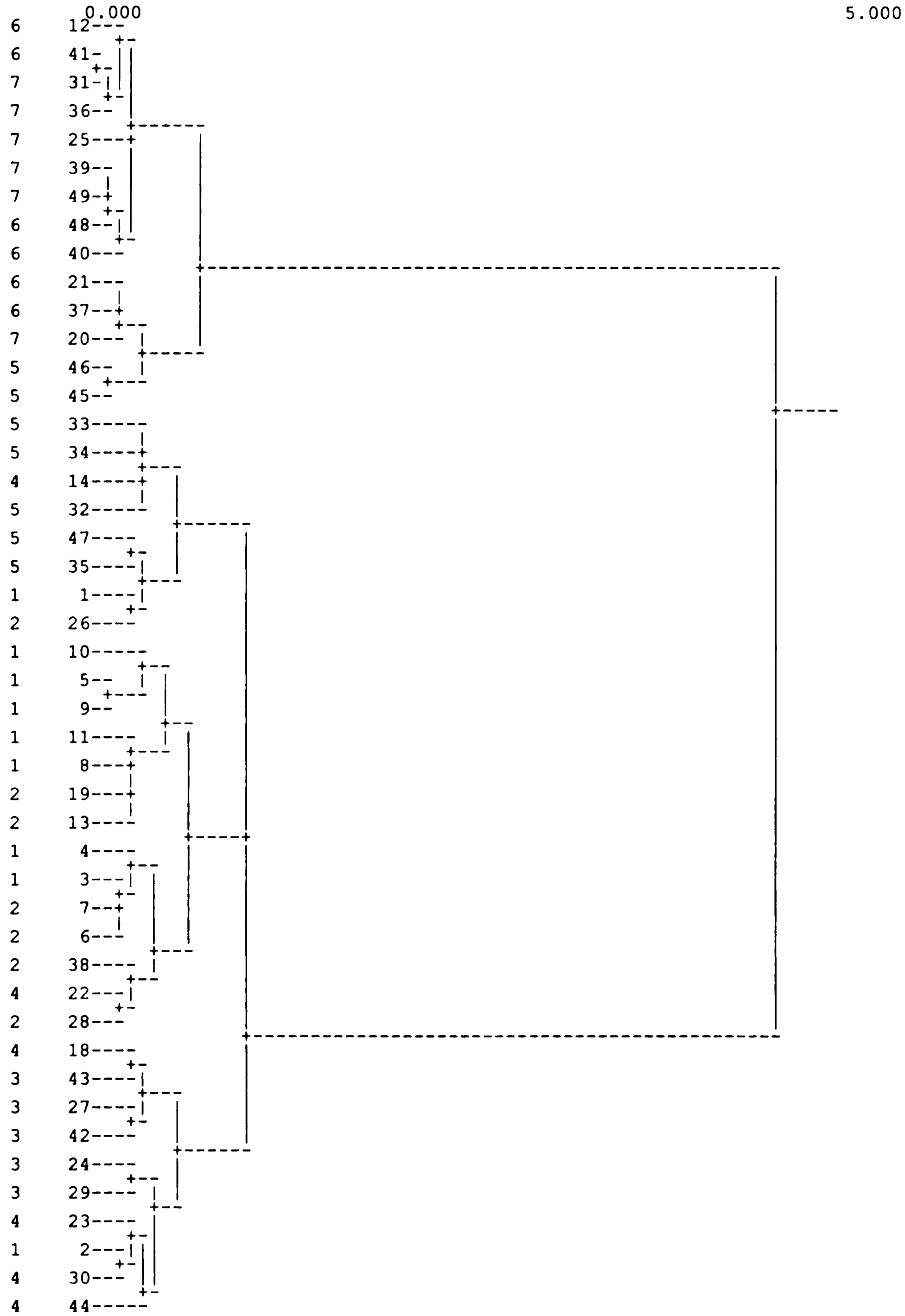


Figure 2.28. Sample clusters based on 28 soil variables using Ward's linkage labeled by ELU.

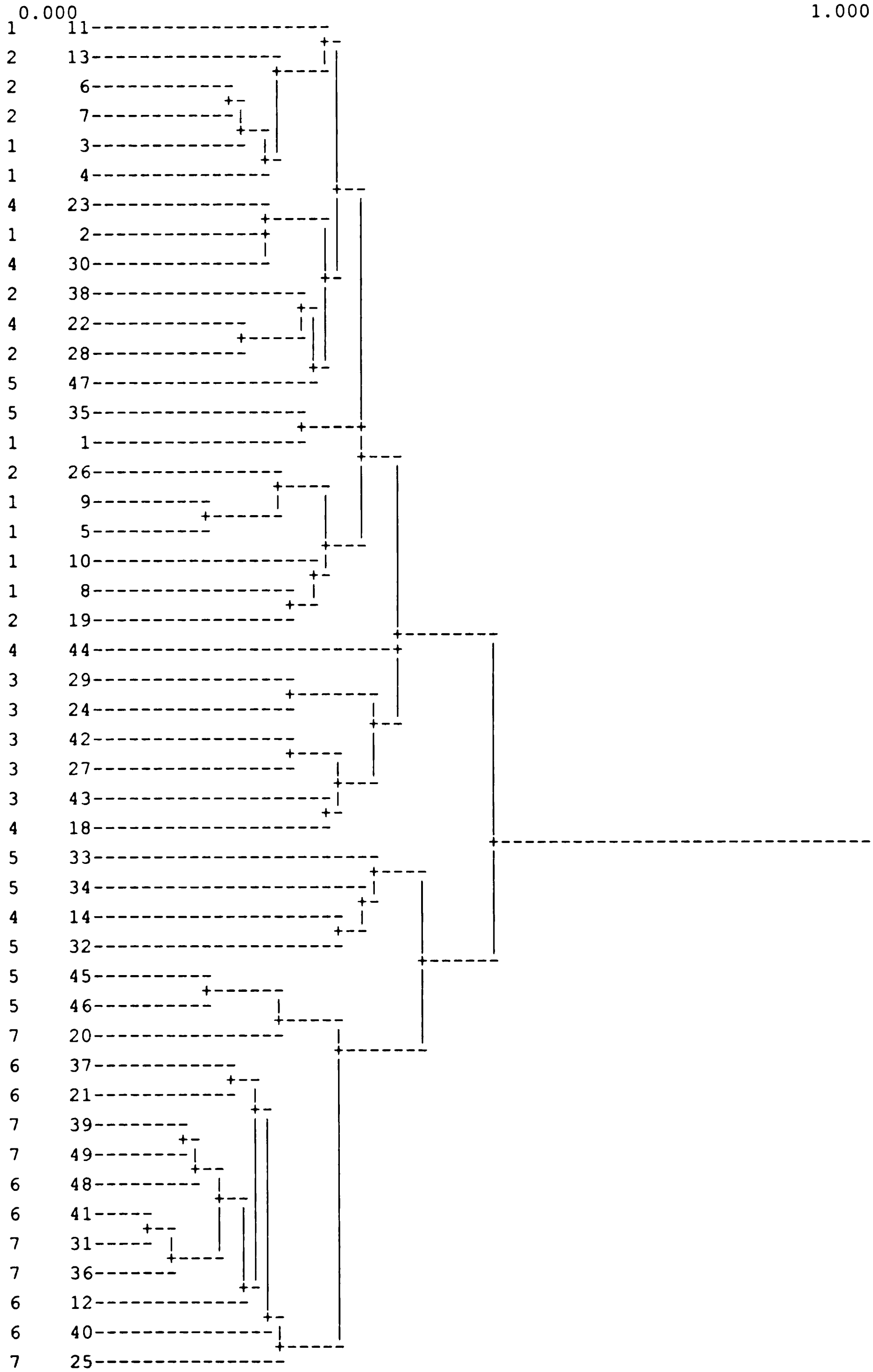


Figure 2.29. Sample clusters based on 28 soil variables using average linkage labeled by ELU.

Interpretations of ordinations of samples in understory and ground-flora species space

The first dimension of a CA of ground-flora ordinated samples along a moisture and nutrient gradient; this gradient is evident in the soils synthesis table with samples ordered by weights of the first principal coordinate (Table 2.14) and in the final soils synthesis table (Table 2.18). Figures 2.30, 2.31, 2.32, and 2.33 array samples in commonly occurring species space, with samples labeled based on soil textures in the upper 100 cm., soil textures in the lower 150 cm., and soil drainage class. These diagrams further illustrate the moisture-nutrient gradient expressed along the first axis of an ordination of vegetation.

Ground-flora integrates environmental conditions resulting from multiple soil characteristics, hence the interpretation soil characteristics in understory and ground-flora species space must consider multiple soil characteristics. ELU's graded from mesic to xeric along the first axis as sample weights graded from negative to positive. ELU 1 consisted of moderately well drained sandy loam solas to depths of 100 cm. overlying sandy clay loam substrates. ELU 2 consisted of well drained sandy loam solas to depths of 30 cm. overlying sandy clay loam substrates. ELU 3 consisted of sandy loam solas to depths of 30 cm. overlying silty clay loam substrates. ELU 4 consisted of shallow sandy caps overlying fine loamy substrates. ELU 5 consisted of deep sandy caps overlying fine loamy substrates at depths greater than 100 cm. ELU 6 consisted of deep sandy soils with moderate spodic horizon development. ELU 7 consisted of deep sandy soils lacking spodic horizon development.

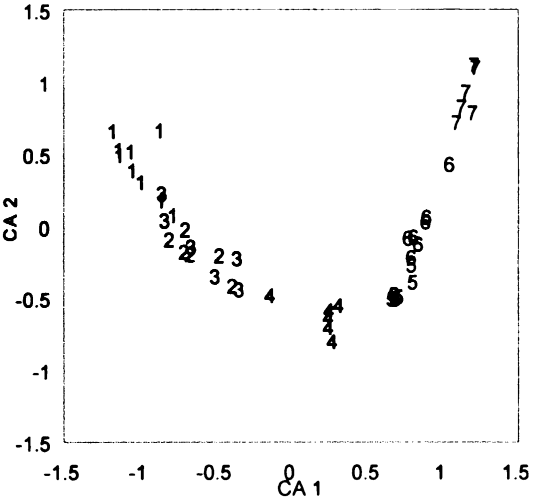


Figure 2.30. Samples in CA dimensions 1 and 2 of commonly occurring species space labeled by ELU.

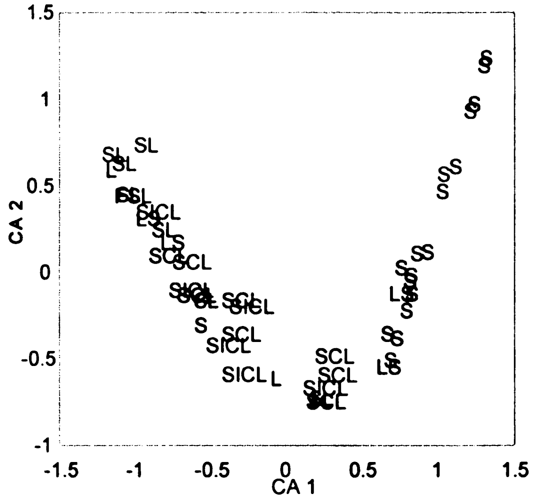


Figure 2.31. Samples in CA dimensions 1 and 2 of commonly occurring species space labeled by upper 100 cm. soil texture.

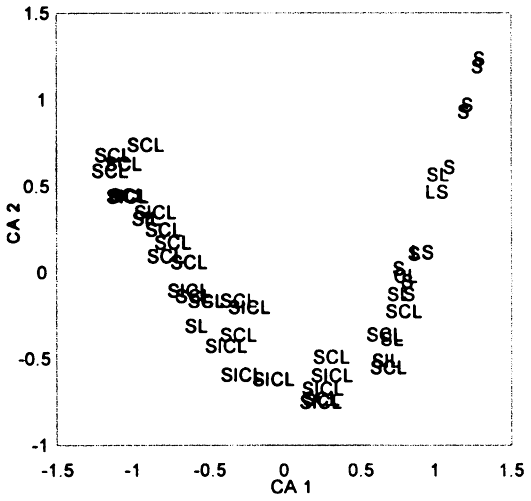


Figure 2.32. Samples in dimensions 1 and 2 of species space labeled by lower 150 cm. soil textures.

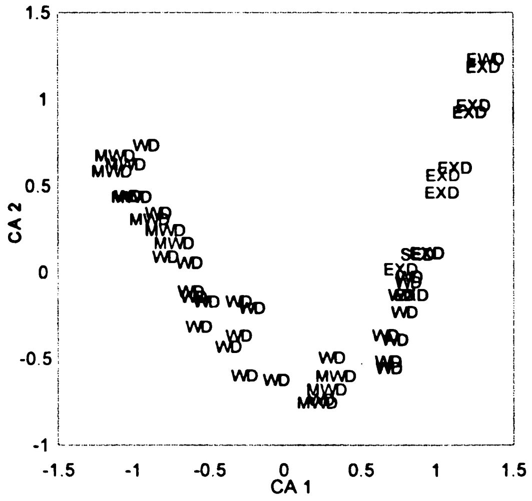


Figure 2.33. Samples in CA dimensions 1 and 2 of commonly occurring species space labeled by soil drainage class.

This gradation in soil texture-drainage class combinations of samples in understory and ground-flora species space appears to accurately represent a decreasing moisture-nutrient gradient with increasing sample weights frequently reported for indirect gradient analyses of ground-flora, corroborated with actual direct measures of soil properties.

Interpretation of the meaning of the second principal coordinate of a CA of ground-flora was less straightforward than interpretation of the first principal coordinate. Six of the seven derived ecological land unit classifications could be partitioned into discrete groupings in the first two dimensions, although sample placement in ordination space changed continuously in a horseshoe pattern (Figure 2.30). Ecological land units 2 and 3 were intermingled in this two-dimensional plane.

It appears that the second dimension separates samples based on a successional stability gradient. The idea of a successional gradient along this axis is corroborated by interpretation of the squared cosines of samples in species space. Samples classified as ecological land units 1, 6, and 7 were most strongly correlated with the first axis, whereas both ecological land units 4 and 7 were more closely associated with axis 2 (Figure 2.34).

Ecological land unit 4 consists of ground-flora typifying both mesic northern hardwood and dry-mesic and xeric oak flora. The ground-flora of sites sampled for ecological land unit 4 consists of *Uvularia perfoliata*, *Trillium grandiflorum*, *Viola spp.*, *Fraxinus americana*, and *Prenanthes alba,* but also includes high coverages of *Aster macrophyllum, Lonicera canadense*, *Hamamelis virginiana*, *Amelanchier spp.,* and *Vaccinium augustifolium,* which are understory and ground-flora species that typify more xeric ecosystems. Based on ground-flora composition and soil textures, this system has the potential to succeed to mesophilic sugar maple-white ash ecosystems, or dry-mesic oak-red maple ecosystems, depending on natural or anthropogenic disturbance regimes.

Padley (1989) discussed the effects of landscape context and exogenous disturbance through wildfire on ground-flora and overstory composition for this area of Michigan, and Host (1987) reported similar influences on overstory and ground-flora composition for northwestern lower Michigan. In these studies, local ecosystems nested within a larger landscape matrix composed of landforms and forests susceptible to fire were compositionally different from equivalent adjacent local ecosystems based on soil physical and chemical properties, and this was hypothesized as being due to fire history.

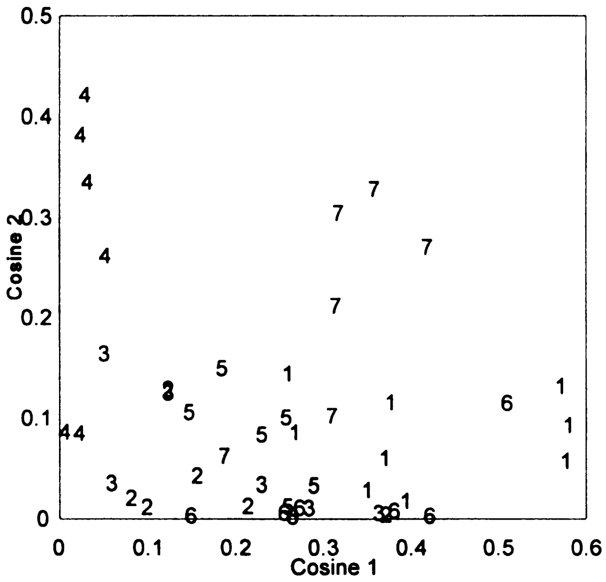


Figure 2.34. Correlation of samples labeled by ELU with dimensions 1 and 2 of CA.

Therefore, ecological land unit 4 may be a fire disclimax and successionally unstable.

Ecological land unit 7 consists of well-washed outwash sands and xeric forest types and ground-flora. This ecosystem is approaching an oak savanna condition, and is known to contain prairie remnants in parts of northeastern lower Michigan including rough fescue (*Festula scabrella*) and Hill's thistle (*Circuin hilli*). This ecosystem may have the potential to revert to savanna or prairie conditions following a significant disturbance event such as wildfire, and could also be regarded as successionally unstable.

Figures 2.35, 2.36, 2.37, and 2.38 illustrate environmental gradients expressed by the third dimension of a CA of understory and ground-flora species. The third dimension of a CA of ground-flora ordinated samples primarily along a soil textural and possibly secondary moisture gradient in which samples containing high silt content in sola (Figure 2.36) and substrates (Figure 2.37) were generally separated from samples containing sandy clay loam sola and substrates; this separation distinguished ecological land unit 2 from unit 3. Other key soil variables were not ordinated along this axis. The plane defined by dimensions 1 and 3 accentuated the separation of ecological land units, enabling all units to be differentiated from one another in ordination space.

Figures 2.39 and 2.40 display tree species in sample space based on CA. Along the first axis tree species grade from mesic northern hardwoods to dry-mesic red oak-red maple-white pine to xeric black and pin oak-pine assemblages.

Figures 2.41 and 2.42 display samples labeled by ecological land unit in tree species space. Along the first axis samples grade from the most mesic ecological unit, unit 1, to the most xeric unit, unit 7. Samples of ecological unit 1 group together in the first and third dimensions; these units are composed of high basal areas of sugar maple and basswood. Ecological units 2 and 3 group together in the first and third dimension; these units are composed of sugar maple, red oak, white ash, and red maple. Ecological units 4, 5, and 6 group together in the first and third dimension; these units are composed of red oak, red maple, and white oak. Ecological unit 7 group together in the first and third dimension; these units are composed of black and pin oak.

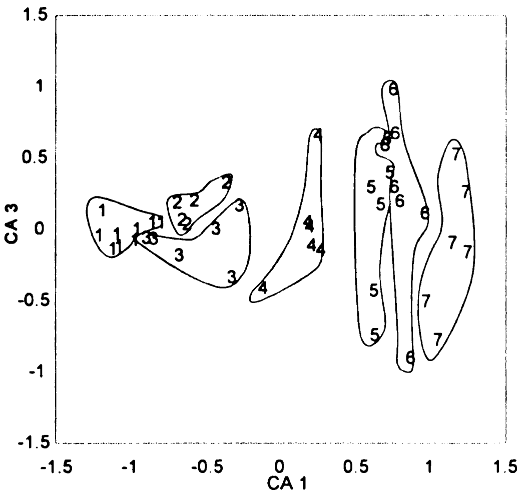


Figure 2.35. Samples in CA dimensions 1 and 3 of commonly occurring species space labeled by ELU .

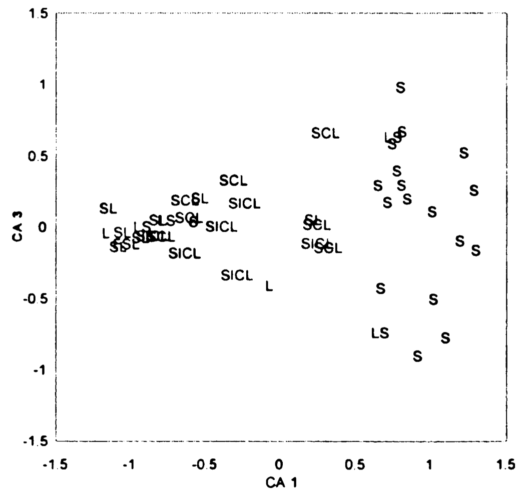


Figure 2.36. Samples in CA dimensions 1 and 3 of commonly occurring species space labeled by top 100 cm. soil texture.

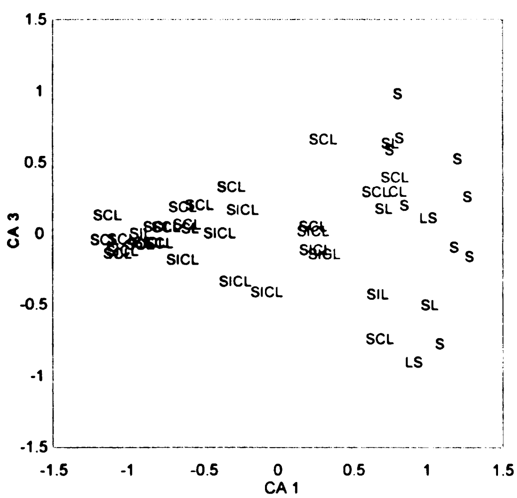


Figure 2.37. Samples in CA dimensions 1 and 3 of commonly occurring species space labeled by lower 150 cm. soil texture .

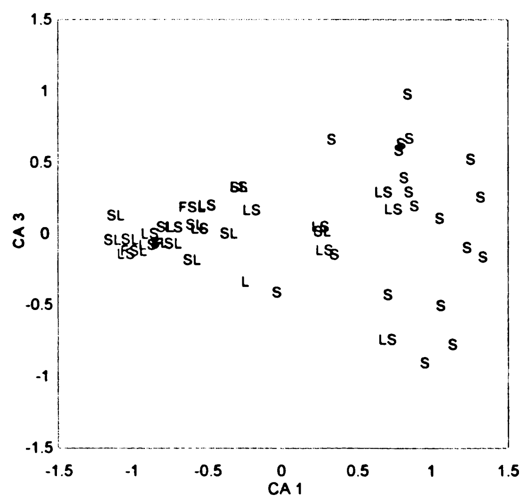


Figure 2.38. Samples in CA dimensions 1 and 3 of species space labeled by upper 30 cm. soil texture.

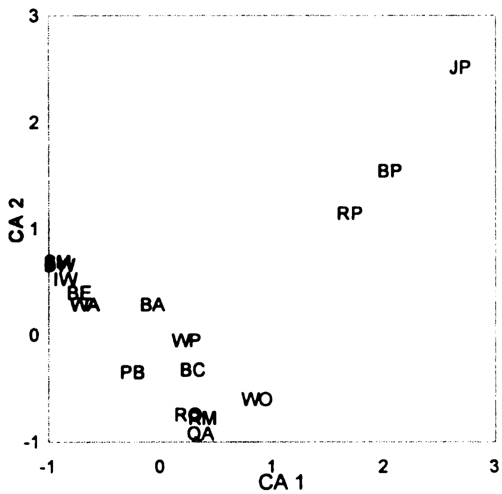


Figure 2.39. Tree species in dimensions 1 and 2 of samples space.

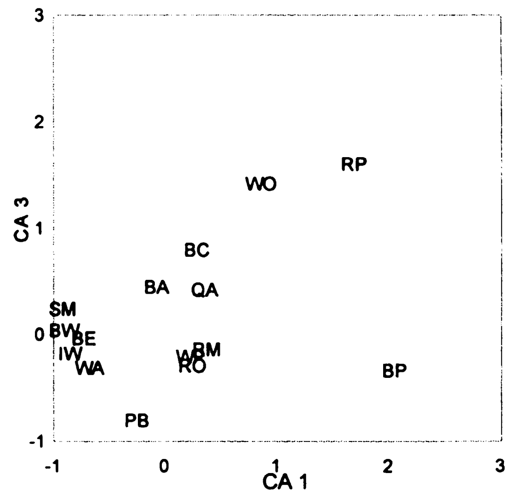


Figure 2.40 Tree species in dimensions 1 and 3 of sample space.

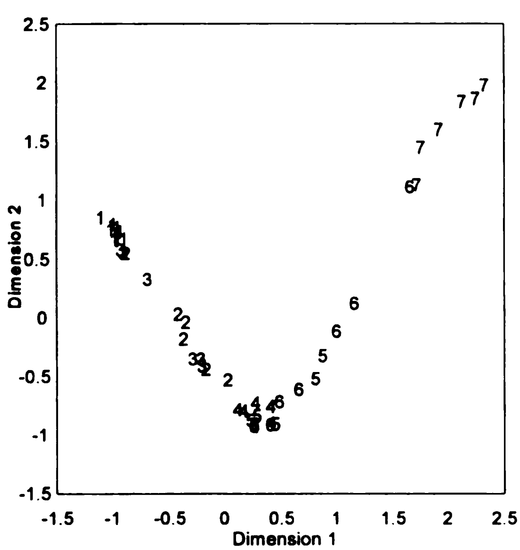


Figure 2.41. Samples in CA dimensions 1 and 2 of tree species space labeled by ELU.

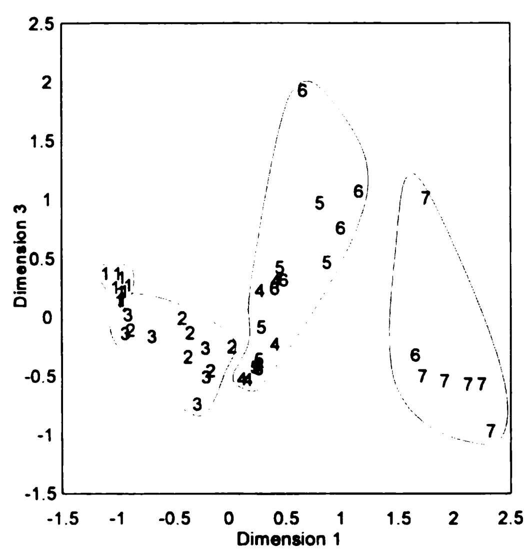


Figure 2.42. Samples in CA dimensions 1 and 3 of tree species space labeled by ELU.

COMPARISON OF ORDINATION AND CLUSTERING RESULTS

Multifactor ecological units classified in this research were used in the following sections to compare results of CA to DCA using commonly occurring and high quality ground-flora, and compare results of agglomerative clustering and TWINSPAN. To further explore differences in results of CA to DCA, and differences in clustering results, using commonly occurring and high quality ground-flora species, units published using a multifactor approach from northwest lower Michigan (Host 1987) were used as a basis for comparison. Host (1987) identified nine ecological land classification units using multivariate classification and ordination methods for upland forests of northwestern Lower Michigan based on similarities in ground-flora and overstory composition and soil characteristics among 76 sample stands. Two-way indicator species analysis (TWINSPAN) was used in conjunction with ordination space partitioning (Gauch 1982) to identify ecological species groups, and relationships between species groups and significant environmental parameters were considered to derive a multifactor ecological land classification.

Comparison of Correspondence Analysis and Detrended Correspondence Analysis for Ecological Land Units in Northeastern Lower Michigan

Figure 2.43 compares CA and DCA results for commonly occurring species in the first and second dimensions of an ordination diagram. CA displays the classic arch effect, and fails to differentiate ecological land units 2 and 3 that are intermingled. All other units are distinguished by CA. DCA differentiates all units in the first two dimensions of commonly occurring species space.

Figure 2.44 compares CA and DCA results for commonly occurring ground-flora species in the first and third dimensions of an ordination diagram. CA differentiates all units in this two-dimensional subspace. Similarly, DCA differentiates all units in this two-dimensional subspace of commonly occurring ground-flora species space.

Comparing CA for commonly occurring ground-flora species in the first and third dimensions of ordination space (Figure 2.44) to DCA results for commonly occurring ground-flora species in the first and second dimensions (Figure 2.43) reveals a nearly identical configuration of samples, with only the scale differing between ordination diagrams. Detrending removed the curved configuration of the first and second dimensions of CA, but CA revealed the same patterns in the first and third dimensions as DCA revealed in the first and second.

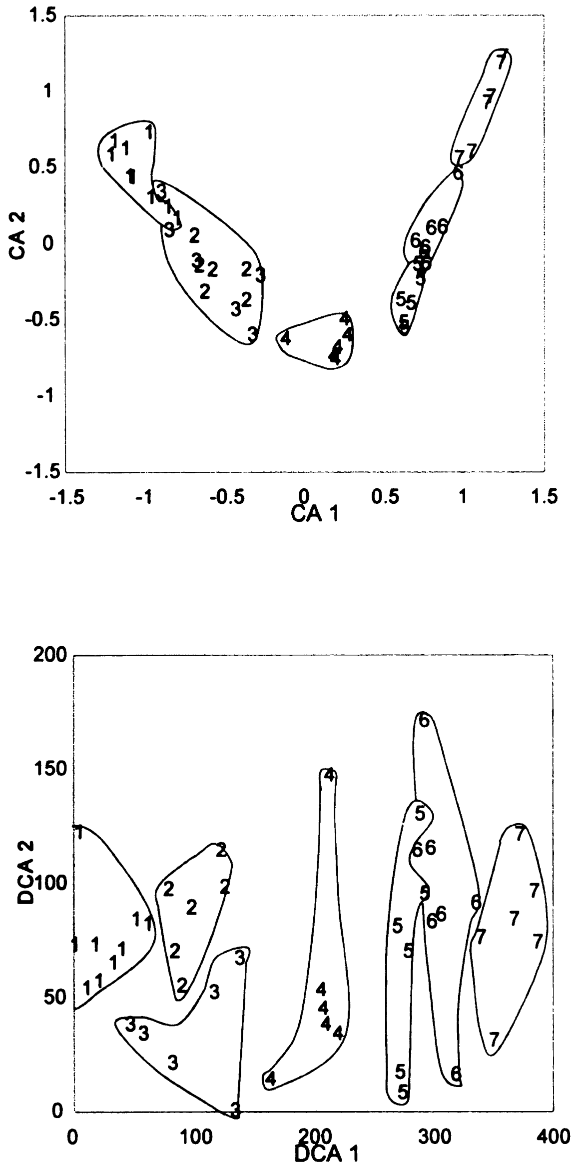


Figure 2.43. Comparison of CA and DCA for commonly occurring species in NE MI: dimensions 1 and 2.

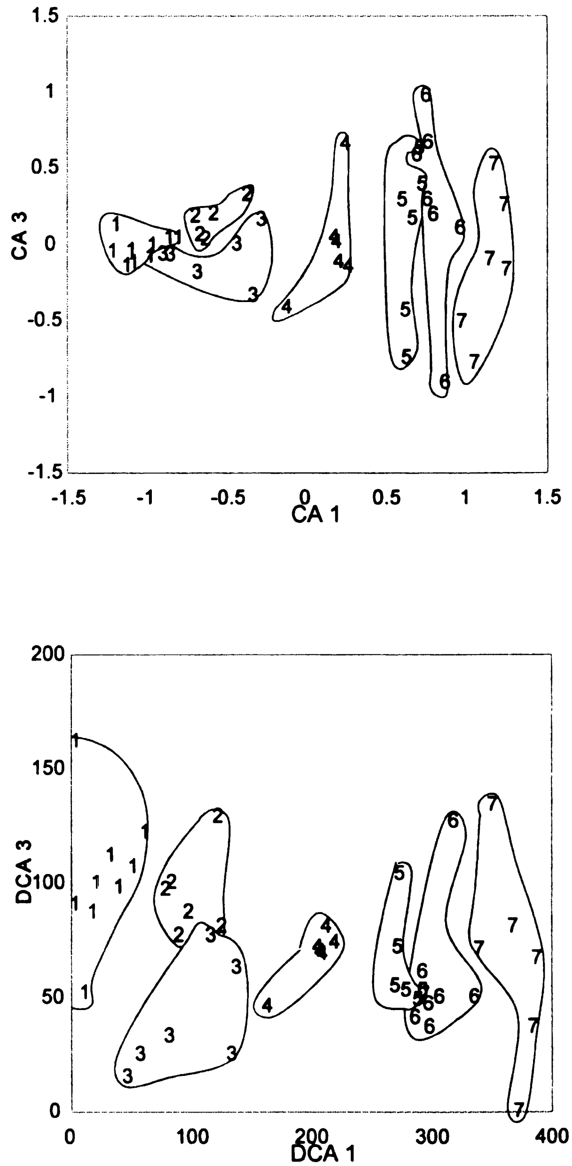


Figure 2.44. Comparison of CA and DCA for commonly occurring species in NE MI: dimensions 1 and 3.

Figure 2.45 compares CA and DCA results for high quality ground-flora species in the first and second dimensions of an ordination diagram. CA displays the classic arch effect, and fails to differentiate ecological land units 2 and 3 that are intermingled; all other units are distinguished. DCA also fails to differentiate ecological land units 2 and 3 that are intermingled, but differentiates all other units.

Figure 2.46 compares CA and DCA results for high quality ground-flora species in the first and third dimensions of an ordination diagram. Both CA and DCA differentiate all units in this two-dimensional subspace. The configuration of samples in this two-dimensional ordination are very similar, although the sign of scores in the third dimension are opposite for equivalent samples for CA as opposed to DCA, with samples and units arranged in reverse order along the third axis.

Figure 2.47 compares CA results for commonly occurring and high quality ground-flora species in the first and second dimensions of an ordination diagram. Both diagrams display the classic arch effect, and both ordinations fail to differentiate ecological land units 2 and 3 that are intermingled. All other units are distinguished by both ordinations.

Figure 2.48 compares CA results for commonly occurring ground-flora species and high quality ground-flora species in the first and third dimensions of an ordination diagram. CA differentiates all units in this two-dimensional subspace based on both data sets. CA on high quality ground-flora species identifies one sample in ecological land unit 1 as an outlier, and also places samples closer to one another, producing tighter groupings, for units 4, 5, 6, and 7.

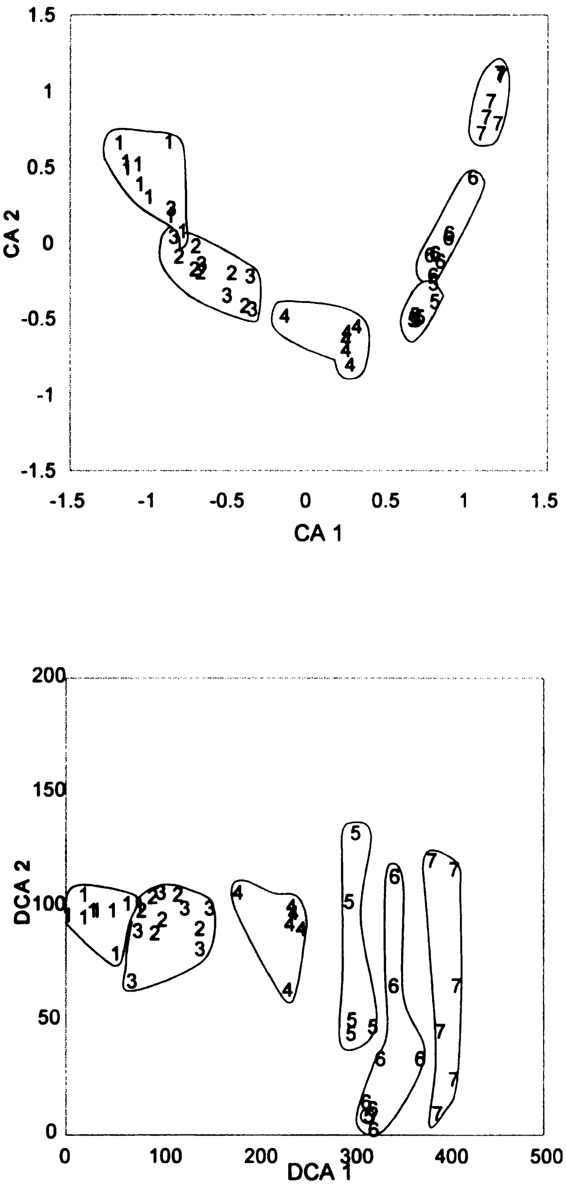


Figure 2.45. Comparison of CA and DCA for high quality species in NE MI: dimensions 1 and 2.

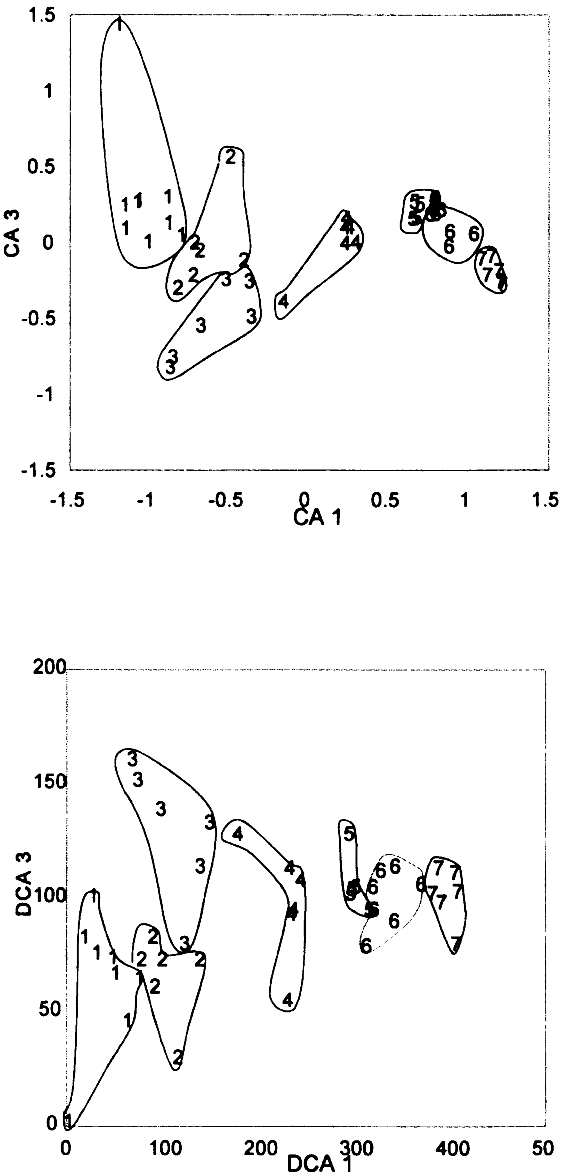
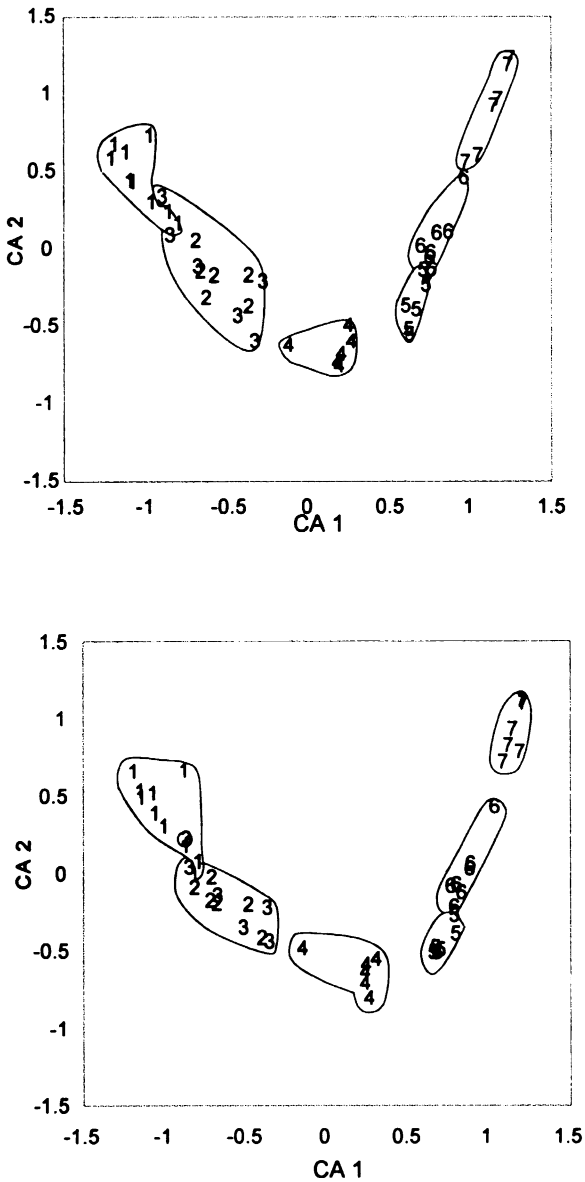


Figure 2.46. Comparison of CA and DCA for high quality species in NE MI: dimensions 1 and 3.



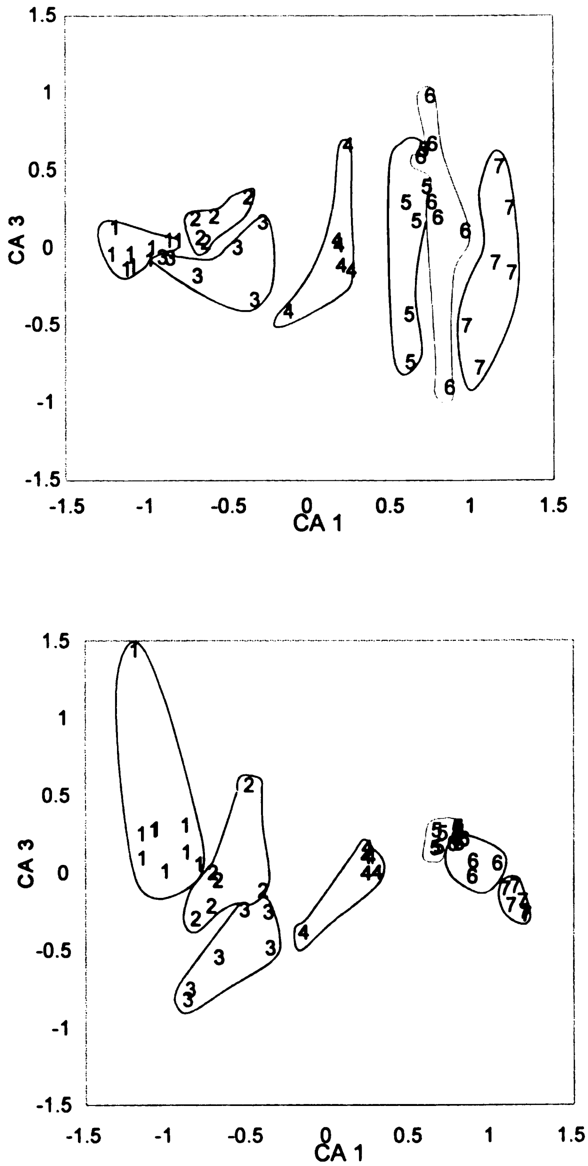


Figure 2.47. Comparison of CA of commonly occurring and high quality species in NE MI: dimensions 1 and 2.

Figure 2.48. Comparison of CA of commonly occurring and high quality species in NE MI: dimensions 1 and 3.

Figure 2.49 compares DCA results for commonly occurring and high quality ground-flora species in the first and second dimensions of an ordination diagram. DCA on commonly occurring ground-flora species identifies all units, whereas DCA on high quality ground-flora fails to differentiate ecological land units 2 and 3 that are intermingled. All other units are distinguished. Clusters of the same units are slightly more compact in high-quality ground-flora species space for all units.

Figure 2.50 compares DCA results for commonly occurring ground-flora species and high quality ground-flora species in the first and third dimensions of an ordination diagram. DCA differentiates all units in this two-dimensional subspace based on both data sets. DCA based on high quality ground-flora species places samples closer to one another than DCA on commonly occurring ground-flora species. Samples scores are reversed along the third axis for the two data sets, with equivalent samples and units arranges in reverse order along the third axis.

In summary, CA and DCA were both effective in distinguishing ecological land units classified in northeastern Lower Michigan in commonly occurring and high quality species space. Detrending removed the curved configuration of the first and second dimensions of CA, but CA revealed the same patterns in the first and third dimensions as DCA revealed in the first and second. The implication is that either method may be used to discern the underlying structure of vegetative data sets, but investigators need to interpret the first and third as opposed to the first and second dimensions of CA to arrive at the same results as DCA. Apparently information on secondary gradients expressed in DCA axis two was deferred to higher axes in CA. However, an earlier interpretation of the second principal coordinate of CA was that this axis represented a successional stability gradient. This interpretation could not be made using DCA.

The use of high quality as opposed to commonly occurring ground-flora species in DCA or CA ordination procedures provided little if any advantage based on this sample. Clusters of the same units were slightly more compact in high-quality ground-flora species space for several units for both DCA and CA. For DCA, there was a loss of efficiency in identifying latent structure of ground-flora data using high quality species, with two units that were distinguished in the first and second dimension using the commonly occurring data set intermingled using the high quality data set. Information on important secondary gradients expressed in DCA axis 2 was apparently deferred to the third axis in high quality species space.

A benefit of using CA instead of DCA lies in the geometric interpretation of a CA. Species sums of squared cosines can be added across any number of dimensions to determine the correlation of a species to that particular low dimension subspace. The fidelity of a species to reduced subspaces can be quantified and interpreted in ordination, or used to condition data for subsequent clustering procedures by eliminating ubiquitously or spuriously distributed individuals.

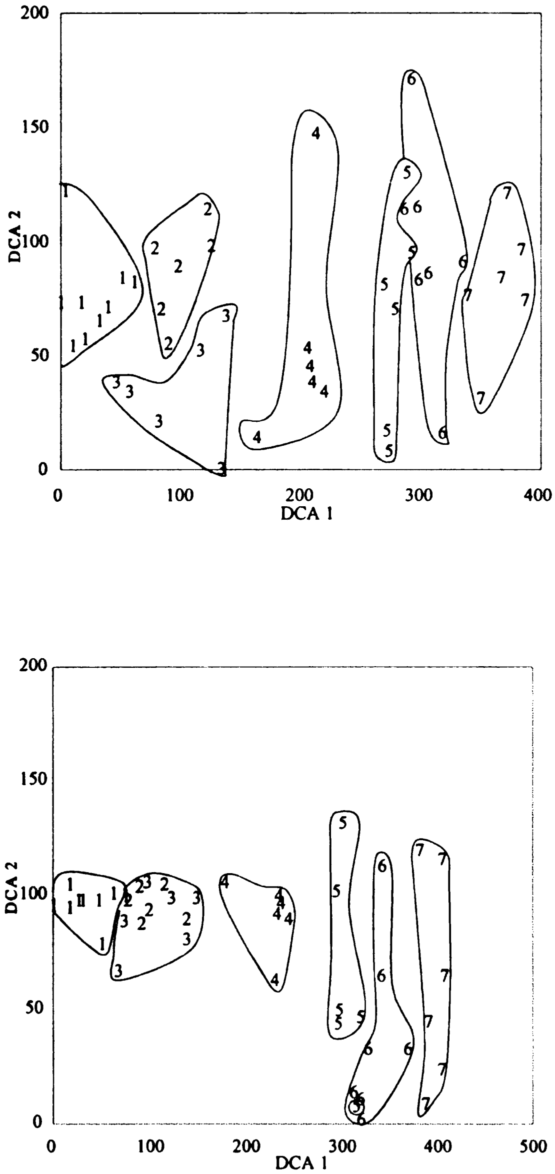


Figure 2.49. Comparison of DCA of commonly occurring and high quality species in NE MI: dimensions 1 and 2.

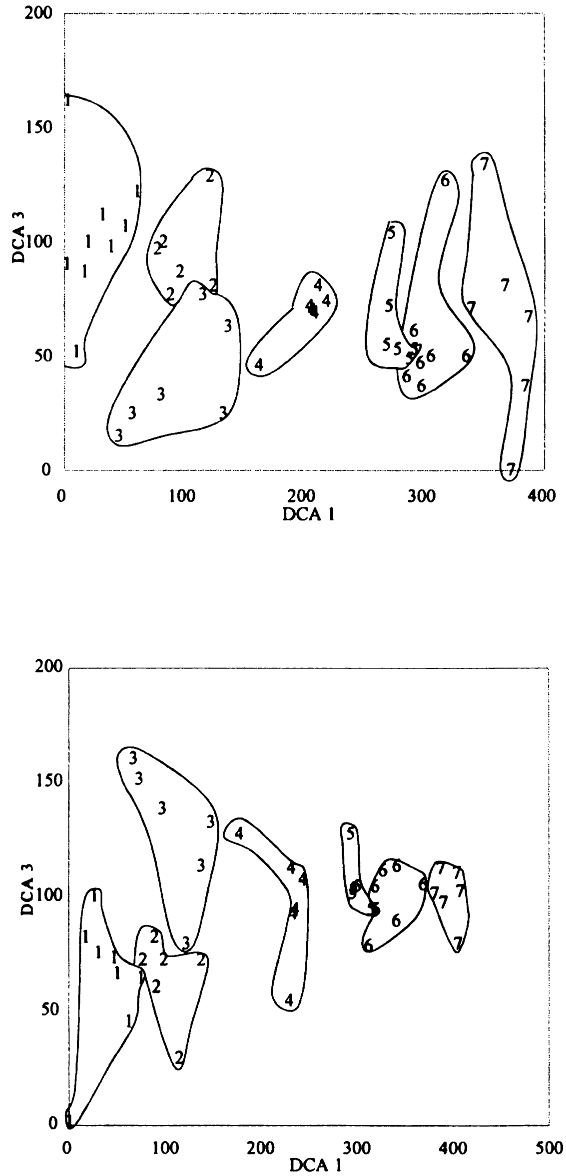


Figure 2.50. Comparison of DCA of commonly occurring and high quality species in NE MI: dimensions 1 and 3.

Comparison of Correspondence Analysis and Detrended Correspondence Analaysis for Ecological Land Units in Northwestern Lower Michigan

Figures 2.51 to 2.58 display samples in commonly occurring and high quality species space labeled by ecological units as defined by Host (1987). Figure 2.51 displays samples in dimensions 1 and 2 of commonly occurring species space based on CA. The ordination diagram displays the classic arch effect. Units 1, 2, 5, and 9 can be partitioned discretely, whereas units 3 and 4, and units 7 and 8 are intermingled in this ordination space.

Figure 2.52 displays samples labeled by ecological land unit in dimensions 1 and 2 of commonly occurring species space based on DCA. Units 1, 2, 4, 5, 6, and 9 can be partitioned discretely, whereas samples of unit 3 are scattered above and below the region occupied by unit 4, and units 7 and 8 are intermingled in this ordination space.

Figure 2.53 displays samples labeled by ecological land unit in dimensions 1 and 3 of commonly occurring species space based on CA. As in Figure 2.52, units 1, 2, 4, 5, 6, and 9 can be partitioned discretely, whereas samples of unit 3 are scattered above and below the region occupied by unit 4, and units 7 and 8 are intermingled in this ordination space.

Figure 2.54 displays samples labeled by ecological land unit in dimensions 1 and 3 of commonly occurring species space based on DCA. Units 4, 5, 6, and 9 can be partitioned discretely, whereas samples of unit 3 are scattered above and below the region occupied by unit 4. Units 1 and 2, and units 7 and 8 are intermingled in this ordination space.

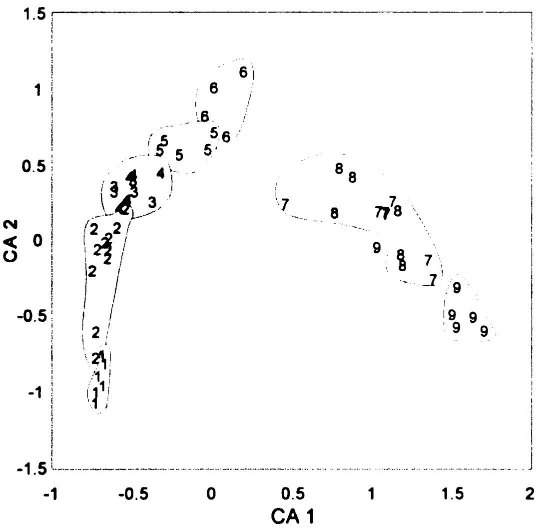


Figure 2.51. CA for commonly occurring species in NW MI: dimensions 1 and 2 labeled by ELU as defined by Host (1987).

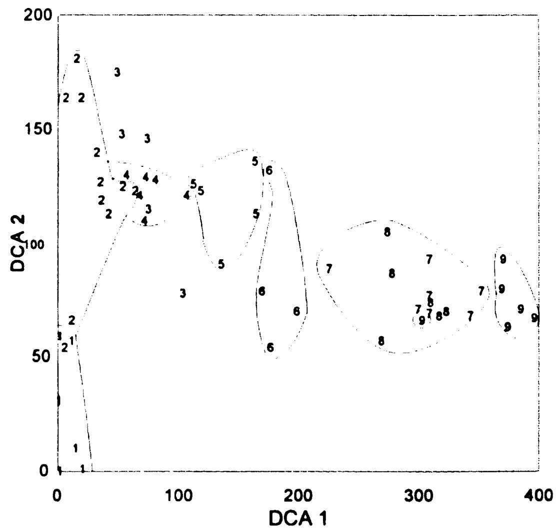


Figure 2.52. DCA for commonly occurring species in NW MI: dimensions 1 and 2 labeled by ELU as defined by Host (1987).

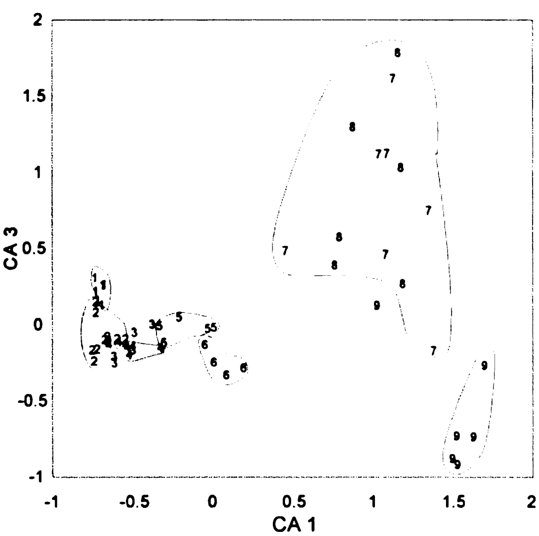


Figure 2.53. CA for commonly occurring species in NW MI: dimensions 1 and 3 labeled by ELU as defined by Host (1987).

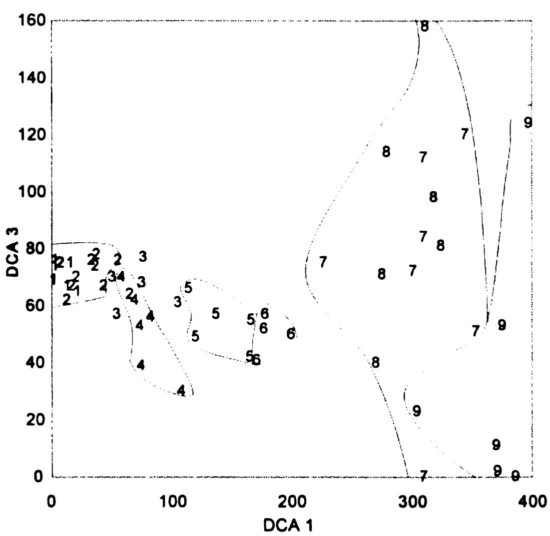


Figure 2.54. DCA for commonly occurring species in NW MI: dimensions 1 and 3 labeled by ELU as defined by Host (1987).

Figure 2.54 displays samples labeled by ecological land unit in dimensions 1 and 2 of high quality species space based on CA. The ordination diagram displays the classic arch effect. Units 1, 2, 5, 6, 7, 8, and 9 can be partitioned discretely, whereas units 3 and 4 are intermingled in this ordination space.

Figure 2.56 displays samples labeled by ecological land unit in dimensions 1 and 2 of high quality species space based on DCA. Units 1, 2, 5, 6, 7, and 9 can be partitioned discretely, whereas units 3 and 4 are intermingled in this ordination space.

Figure 2.57 displays samples labeled by ecological land unit in dimensions 1 and 3 of high quality species space based on CA. Units 1, 2, 5, 6, and 9 can be partitioned discretely, whereas units 3 and 4, and units 7 and 8 are intermingled in this ordination space.

Figure 2.58 displays samples labeled by ecological land unit in dimensions 1 and 3 of high quality species space based on DCA. Units 1, 2 5, 6, and 9 can be partitioned discretely, whereas units 3 and 4, and units 7 and 8 are intermingled in this ordination space.

In summary, CA and DCA were both effective in distinguishing most, but not all ecological units classified by Host (1987) in northwestern Lower Michigan in commonly occurring and high quality species space. Detrending removed the curved configuration of the first and second dimensions of CA, but CA revealed the same patterns in the first and third dimensions as DCA revealed in the first and second dimensions for both the commonly occurring and high quality ground-flora data sets; only the scales and compactness of groups differed. In contrast to comparisons of ordinations in northeastern

Michigan, use of high quality species improved the discriminating power of ordination space partitioning for both CA and DCA by distinguishing unit 7 from unit 8, which were intermingled in all dimensions of commonly occurring species space in CA and DCA. Use of high quality species as opposed to commonly occurring species reversed the signs of sample scores along both the second and third dimensions. Use of high quality species also produced tighter groupings of samples for both CA and DCA.

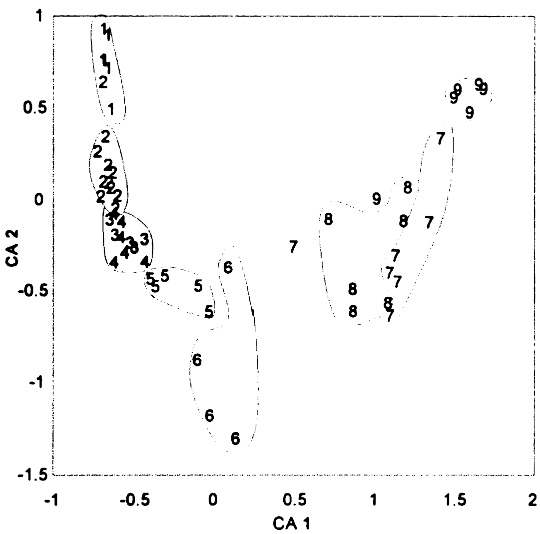


Figure 2.55. CA for high quality species in NW MI: dimensions 1 and 2 labeled by ELU as defined by Host (1987).

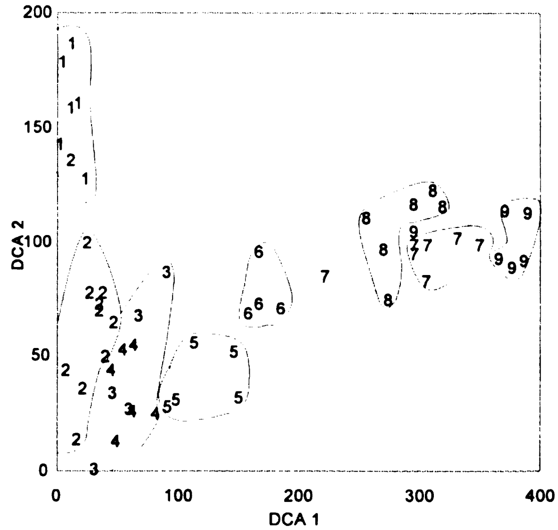


Figure 2.56. DCA for high quality species in NW MI: dimensions 1 and 2 labeled by ELU as defined by Host (1987).

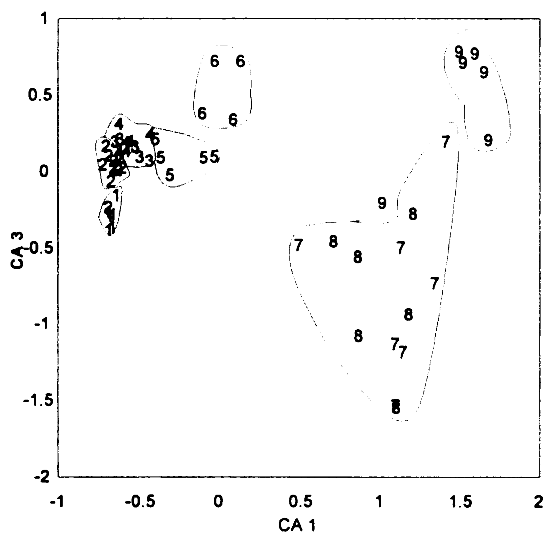


Figure 2.57. CA for high quality species in NW MI: dimensions 1 and 3 labeled by ELU as defined by Host (1987).

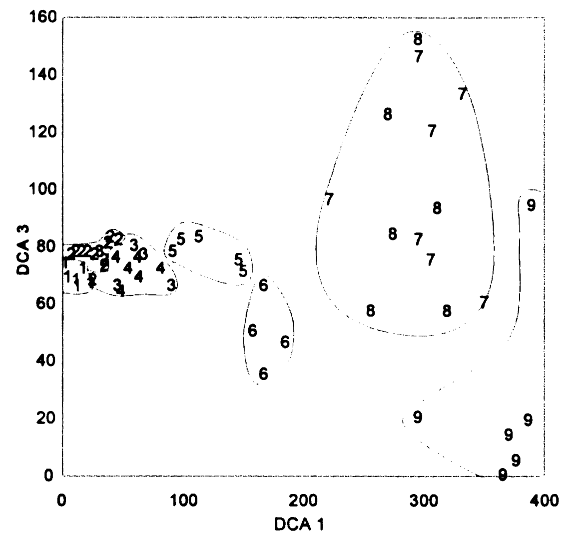


Figure 2.58. DCA for high quality species in NW MI: dimensions 1 and 3 labeled by ELU as defined by Host (1987).

Comparison of Clustering Methods for Ecological Land Units in Northeastern Lower Michigan

Figures 2.59 to 2.66 display clustering results for samples based on commonly occurring and high quality ground-flora species using three agglomerative clustering techniques and TWINSPAN divisive clustering. Agglomerative clustering of samples using average linkage (Figure 2.59) and Ward's linkage (Figure 2.61) methods for the high quality ground-flora data set produced identical results, and differed in four respects from equivalent clustering of samples based on the commonly occurring ground-flora data set (Figures 2.59 and 2.61, respectively). For both linkage methods, the high quality data set differentiated ecological land units 2 and 3 from one another, whereas the commonly occurring ground-flora data set failed to separate these units. The high quality data set also placed stand 42 adjacent to other samples that were classified as ecological land unit 2, and placed stand 20 in a cluster with other samples that were accurately classified as ecological land unit 7. Commonly occurring ground-flora identified two clusters composed of mixtures of ecological land units 5 and 6, whereas the high quality data set only identified one mixed cluster.

Agglomerative clustering of samples using flexible-beta linkage method for the high quality ground-flora data set (Figure 2.63) differed in five respects from clustering of the commonly occurring ground-flora data set (Figure 2.64). The high quality data set differentiated ecological land units 2 and 3 from one another, placed stand 42 with other samples that classified as ecological land unit 2, placed stand 20 with other samples that classified as ecological land unit 7, and misclassified one less sample in the cluster composed of ecological land unit 7. Commonly occurring ground-flora identified two clusters composed of mixtures of ecological land units 5 and 6, whereas the high quality data set only identified one mixed cluster.

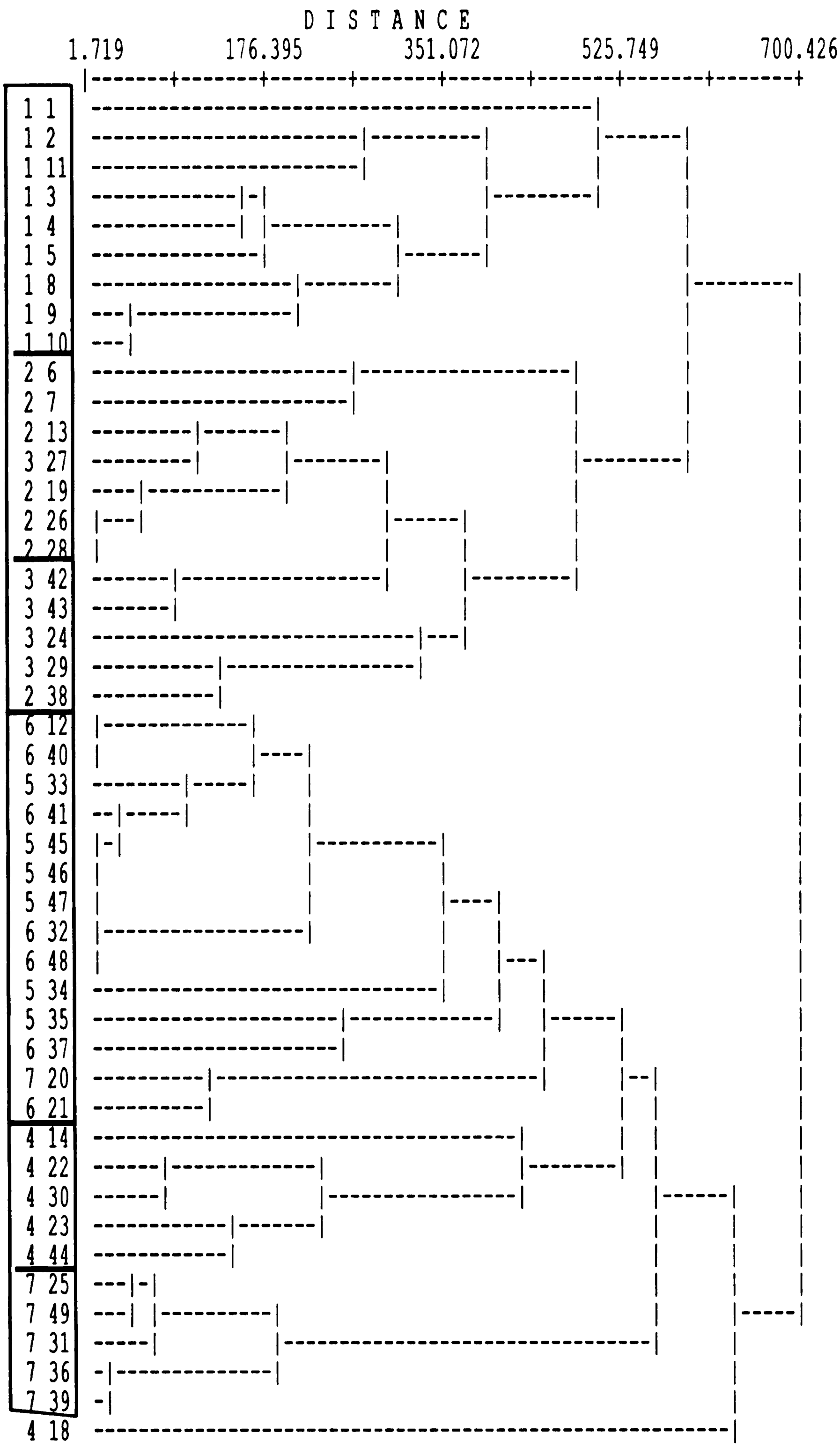


Figure 2.59. Clustering of samples labeled by ELU based on high quality species in NE MI: average linkage.

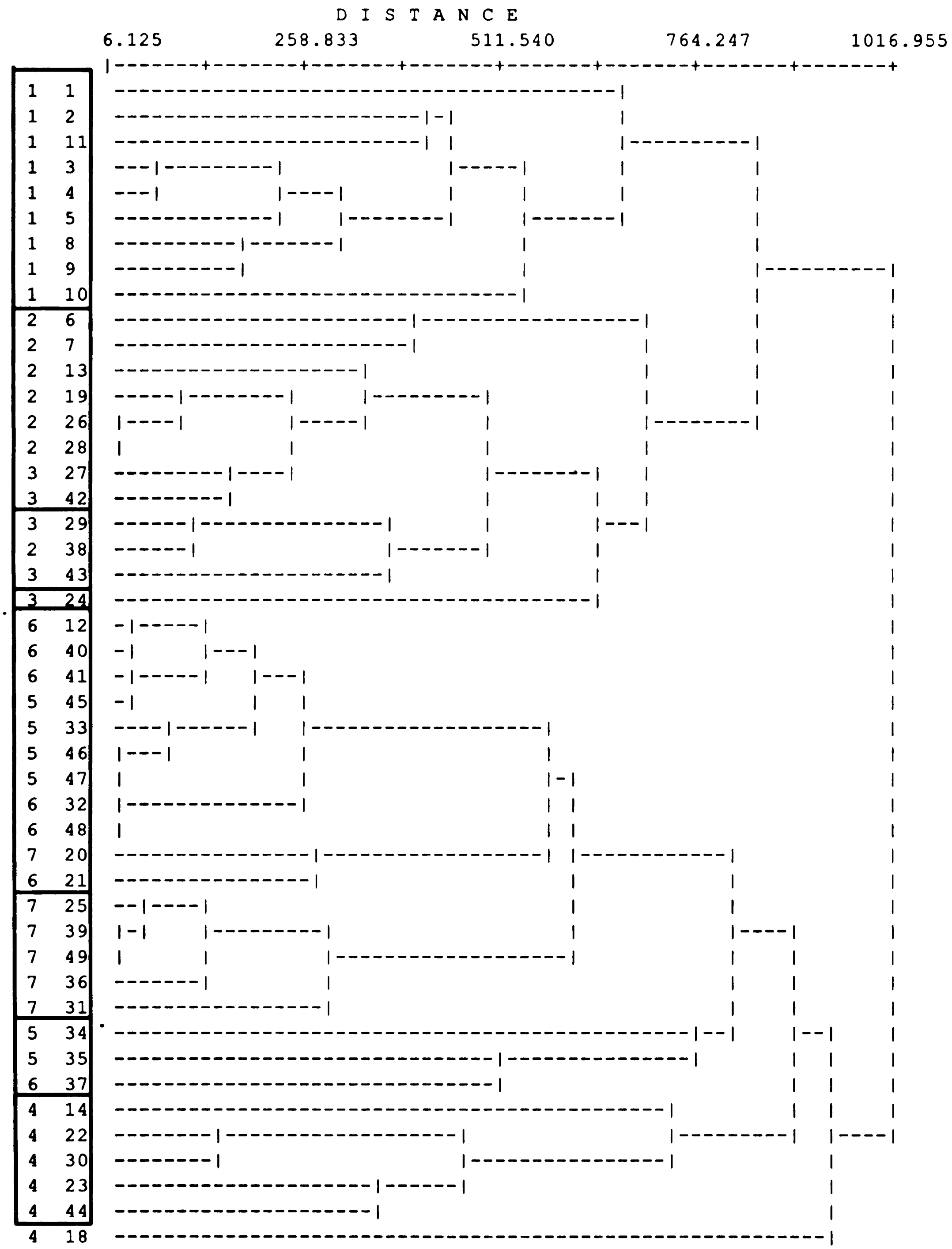


Figure 2.60. Clustering of samples labeled by ELU based on commonly occurring species in NE MI: average linkage.

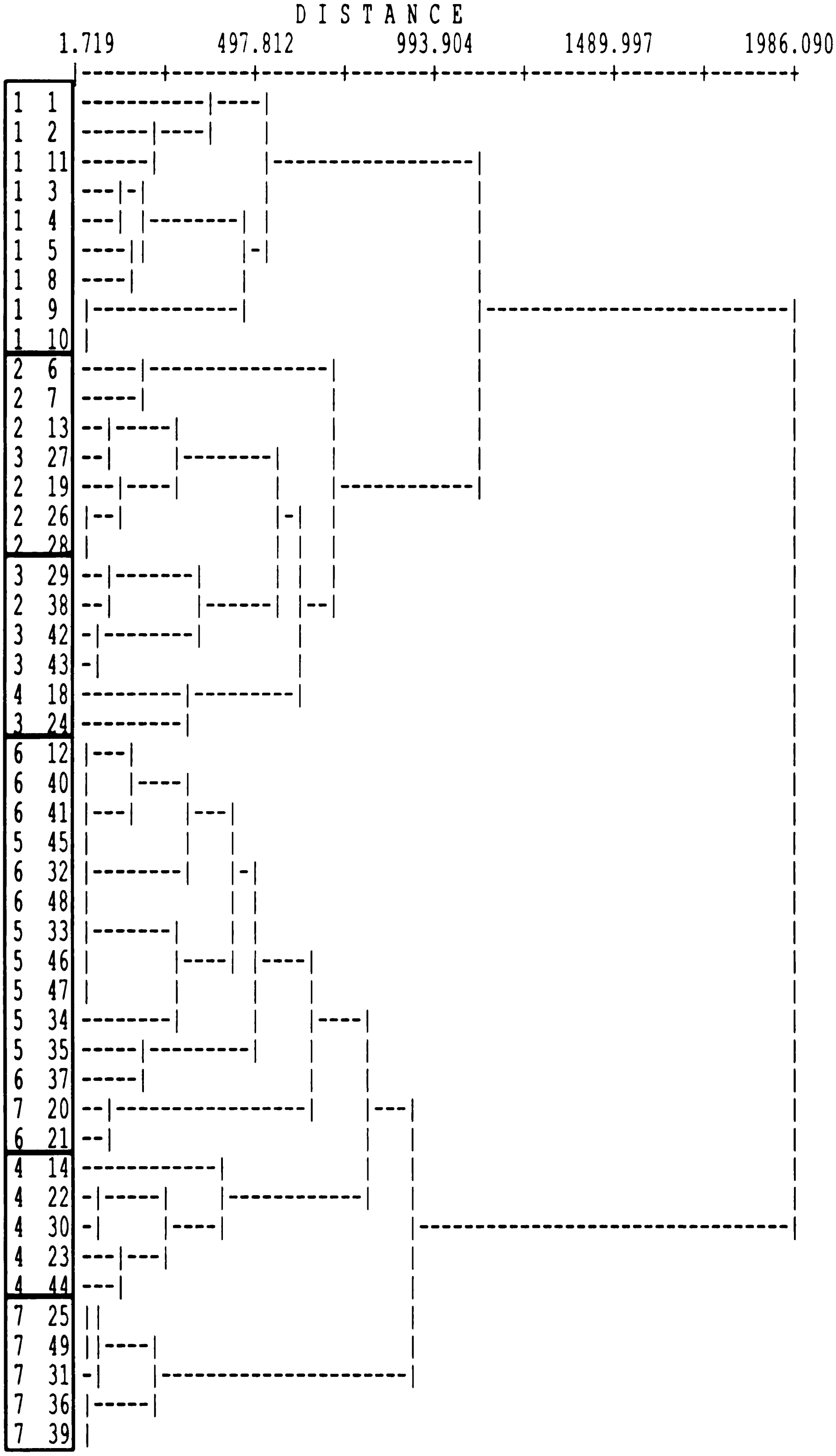


Figure 2.61. Clustering of samples labeled by ELU based on high quality species in NE MI: Ward's linkage.

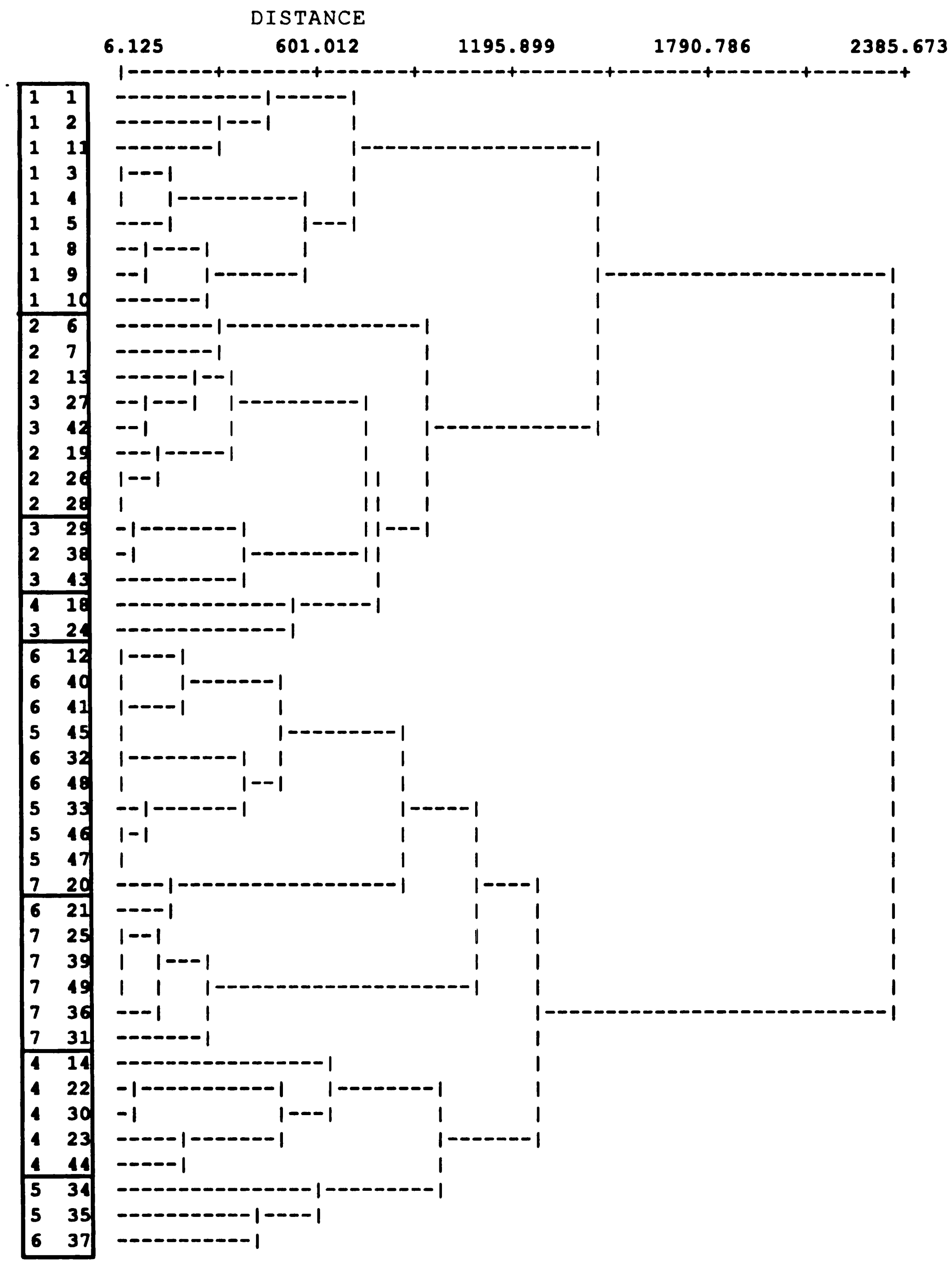


Figure 2.62. Clustering of samples labeled by ELU based on commonly occurring species in NE MI: Ward's linkage.

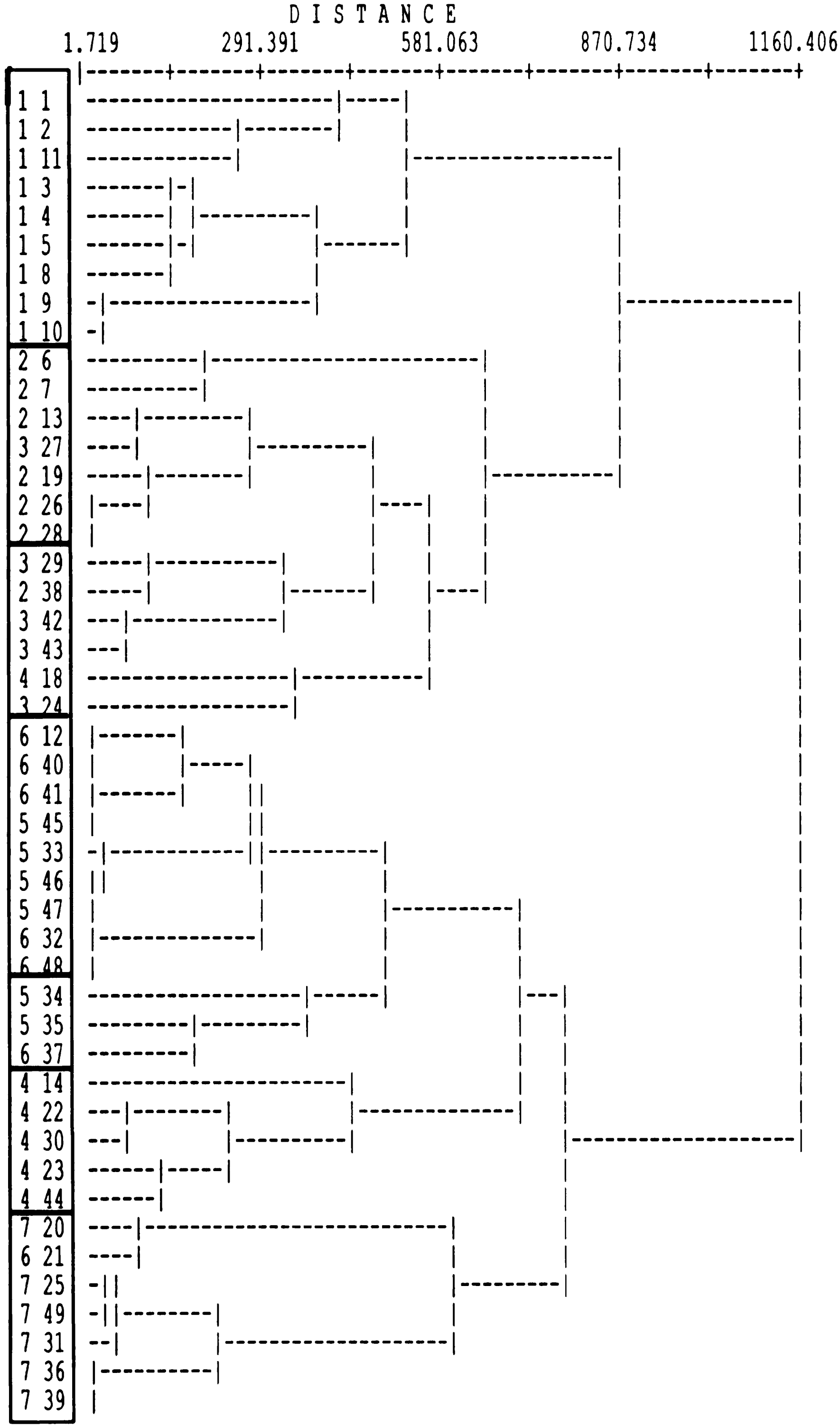


Figure 2.63. Clustering of samples labeled by ELU based on high quality species in NE MI: beta linkage.

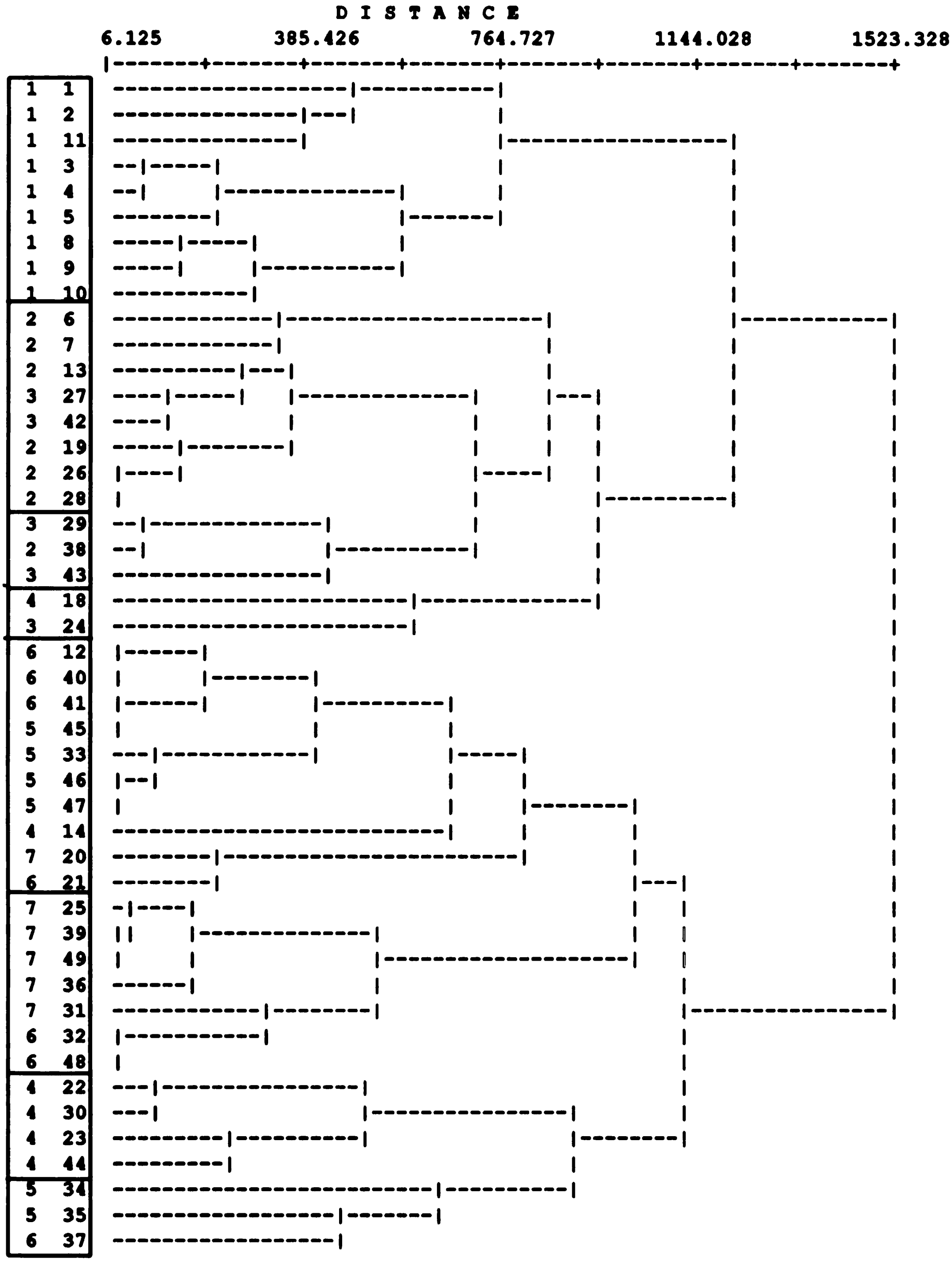


Figure 2.64. Clustering of samples labeled by ELU based on commonly occurring species in NE MI: beta linkage.

Results of divisive clustering of samples using TWINSPAN for the commonly occurring ground-flora data set (Figure 2.65) differed in five respects from divisive clustering of the high quality ground-flora data set (Figure 2.66). TWINSPAN clustering of samples based on high quality ground-flora species identified all seven ecological land units, whereas clustering based on commonly occurring ground-flora species only identified three units correctly, with units 2 and 3 mixed in one cluster, and units 6 and 7 mixed in another. TWINSPAN clustering of samples based on high quality ground-flora species misclassified two samples consisting of ecological unit 6 in the cluster composed of unit 5, whereas clustering of samples based on commonly occurring ground-flora species only misclassified one sample in this cluster. TWINSPAN clustering of samples based on high quality ground-flora species misclassified stand 18 as unit 3, whereas clustering of samples based on commonly occurring ground-flora species identified this unit as an outlier. TWINSPAN clustering of samples based on high quality ground-flora species did not erroneously cluster samples 38 and 43 as a separate cluster, although stand 38 was misclassified into the cluster composed of unit 3. TWINSPAN clustering of samples based on high quality ground-flora species misclassified a total of six samples in the seven groups identified, whereas clustering of samples based on commonly occurring ground-flora species misclassified a total of two samples in the three groups correctly identified.

```
23 111111111 3332322222 4 454444 5555655 666777776 77 ELU

34   1     1 224222  11 1 132234 3334444 124334433 22 Stand
83 890345121 4926786739 8 452304 4236157 210198967 05

00 000000000 0000000000 0 111111 1111111 111111111 11 level I
00 000000000 1111111111 1 000000 0000000 111111111 11 level II
00 111111111 0000000000 1 000000 1111111 000000000 11 level III
```

Figure 2.65. TWINSPAN classification of samples based on commonly occurring species labeled by ELU in NE MI.

```
111111111 2222223 323334 44444 655555556 666 7677777 ELU

1   1     22 1 12 234241 12234 444334333 124 3423432 Stand
118902345 6873697 983428 42304 157236457 210 1859960

000000000 0000000 000000 11111 111111111 111 1111111 level I
000000000 1111111 111111 00000 000000000 111 1111111 level II
000001111 0000000 111111 00000 111111111 000 1111111 level III
```

Figure 2.66. TWINSPAN classification of samples based on high quality species labeled by ELU in NE MI.

In summary, use of high quality ground-flora in each of the three agglomerative clustering procedures resulted in consistent classification of sample groups, ordering of groups, and assignment of samples to respective groups; six of seven units were accurately distinguished. Use of commonly occurring ground-flora also resulted in relatively consistent classification of sample groups, ordering of groups, and assignment of samples to respective groups for each of the three agglomerative clustering procedures; five of seven units were distinguished accurately. The only differences among results of the three linkage methods for commonly occurring ground-flora species was one less accurate assignment of a sample to unit 4 for beta linkage, the inclusion of one sample of unit 6 in the cluster for composed of samples of unit 7 for Ward's linkage, the inclusion of two samples of unit 6 in the cluster composed of samples of unit 7 for beta linkage, and the identification of one sample, stand 18, as an outlier by average linkage. Agglomerative clustering of commonly occurring ground-flora identified two clusters that were composed of mixtures of ecological land units 5 and 6 with each method, and was less effective in differentiating ecological land units 2 and 3 from one another. None of the agglomerative procedures for either data set were effective in distinguishing between ecological units 5 and 6.

TWINSPAN divisive clustering of samples based on commonly occurring ground-flora species (Figure 2.65) only distinguished three ecological land units, units 1, 4, and 5, with all other clusters composed of mixed groupings of ecological land units. TWINSPAN divisive clustering of samples based on high quality ground-flora species (Figure 2.66) distinguished all seven ecological land units, although there were six samples misclassified in total. In contrast, each of the three agglomerative techniques only misclassified two samples among the six clusters identified using high quality species, although samples for two ecological units, units 5 and 6, were grouped together, hence undifferentiated from one another.

Comparison of Clustering Methods for Ecological Land Units in Northwestern Lower Michigan

The data sets and nine ecological land classification units defined by Host (1987) were used as a basis for comparing agglomerative and TWINSPAN clustering results on commonly occurring and high quality ground-flora species in this section.

Figure 2.67 displays the classification as published by Host and Pregitzer (1991) based on ninety-three commonly occurring species using TWINSPAN, with samples labeled by ecological land unit. Six groups of samples were identified. The first cluster identified unit 1, with three misclassified samples consisting of unit 2. The second cluster was a mixture of units 2, 3, and 4. The third cluster was a mixture of units 3, 4, and 5. The fourth cluster was a mixture of units 5 and 6. The fifth cluster was a mixture of units 7 and 8. The sixth cluster contained only unit 9.

Figure 2.68 displays a reclassification of the same samples as used by Host based on fifty-two high quality species whose sums of squared cosines were equal to or greater than forty-five per cent in a five-dimensional subspace. The third and fourth levels of division were selected subjectively based on differences in unit membership within clusters using TWINSPAN. Samples were labeled by ecological land unit as defined by Host (1987). The first cluster grouped seven samples of unit 1, with one misclassified sample of unit 2. The second cluster grouped four samples of unit 2, with two misclassified samples of unit 1. The third cluster grouped six samples of unit 2, with three misclassified samples of unit 1, 2, and 3. The fourth cluster was a mixture of units 2, 3, and 4. The fifth cluster grouped five samples of unit 4, with one misclassified sample of unit 3. The sixth cluster grouped five samples of unit 5, with three misclassified samples of units 3 and 4. The seventh cluster grouped five samples of unit 6, and three samples of unit 5. The eighth cluster grouped three samples of unit 7, with one misclassified sample of unit 8. The ninth cluster grouped five samples of unit 8, with one misclassified sample of unit 7. The tenth cluster grouped six samples of unit 9, with two misclassified samples of unit 7.

TWINSPAN on high quality species effectively grouped samples into unit 1, 2, 4, 7, 8, and 9, and less effectively grouped samples into unit 6. There was one misclassification in the group of seven samples comprising unit 1, five misclassifications in the group of fifteen comprising unit 2, one misclassification in the group of six samples comprising unit 4, three misclassifications in the group of eight samples comprising unit 6, one misclassification in the group of four samples comprising unit 7, one misclassification in the group of six samples comprising unit 8, and two misclassification in the group of eight samples comprising unit 9. The use of ground-flora as an indirect measure of environment for multifactor units reported by Host (1987) that included criteria for soil characteristics was improved using high quality species based on these clustering results.

```
                  Oak                                 Northern Hardwoods
                   ___________________________________________
                  |                                          |
        __________|_____________                     ________|______
       |                       | Mesic              |              |
 ______|__________          ___|___                 | Low          | High
| Xeric           | Dry Mesic |      |              | Min-N        | Min-N
|                 |           |      |              |              |
5455545567  71672673  233 1113447 355667  7667811124  1167  46  3534724522432  22233 Stand
5803991468  98759318198348125956630281 83  7290036707  40024544  71750451613366  647227

1111212121  13422222222224443333322 44244  5354435554  56566665  78787587788778  999999 ELU
```

Figure 2.67. Classification of 77 samples reported by Host (1987).

```
5445555 336572 236767716   16 11344573 56776  11241168 76  1467 7 3455   234222 3 242233 Stand
0893945 385199 806831587 1391182545626 988032 43076790 74450402 4 5167 7 110356 26432767

1111211 221212 222122234 2224244323343 444443 53545554 55666656 5 8777 7 887888 99979979 ELU

0000000 000000 000000000 0000000000000 000000 00000000 00000000 1 1111 1 111111 11111111 level 1
0000000 000000 000000000 0000000000000 000000 11111111 11111111 0 0000 0 000000 11111111 level 2
0000000 000000 111111111 1111111111111 111111 00000000 11111111 0 0000 1 111111 01111111 level 3
0000000 111111 000000000 1111111111111 111111 00000011 01111111 0 1111 0 111111  0000011 level 4
0111111 000001 000000011 0000000000000 111111 011111    0000011          000111  00011   level 5
```

Figure 2.68. Reclassification of 77 samples reported by Host (1987) based on high-quality species.

Figure 2.69 displays agglomerative clustering of the samples classified by Host based on high quality ground-flora species using Ward's linkage method. Nine groups were identified, and were labeled A through I for discussion purposes.

Cluster A grouped eight samples of unit 2, one sample of unit 3, and one sample of unit 4. Cluster B was heterogeneous, and grouped two samples of unit 1, three samples of unit 2, one sample of unit 3, and one sample of unit 4. Cluster C grouped four samples of unit 4, three samples of unit 3, and three samples of unit 2. Cluster D grouped four samples of unit 4, and three samples of unit 3. Cluster E grouped seven samples of unit 1, and one sample of unit 2. Cluster F grouped five samples of unit 6 and two samples of unit 5. Cluster G grouped three samples of unit 3, and two samples of unit 4. Cluster H grouped five samples of unit 9. Cluster I grouped seven samples of unit 7, and six samples of unit 8.

Agglomerative clustering of 76 samples based on high quality species was only effective in grouping units 1, 2, 6, and 9. The procedure segregated cluster D from cluster G, however, although both were composed of units 4 and 5. Cluster D contained samples from the northern half of the Manistee National Forest, whereas cluster G contained samples from the southern half of the Manistee National Forest. Cleland et al. (1993) identified extensive climatically and physiographically uniform regions in the northern portions of Lower Michigan that distinguished the southern half of the Manistee National Forest from the northern half based on growing season. Additional analyses on data sets for commonly occurring and high quality ground-flora species that eliminated samples from the southern half of the National Forests were conducted as a consequence.

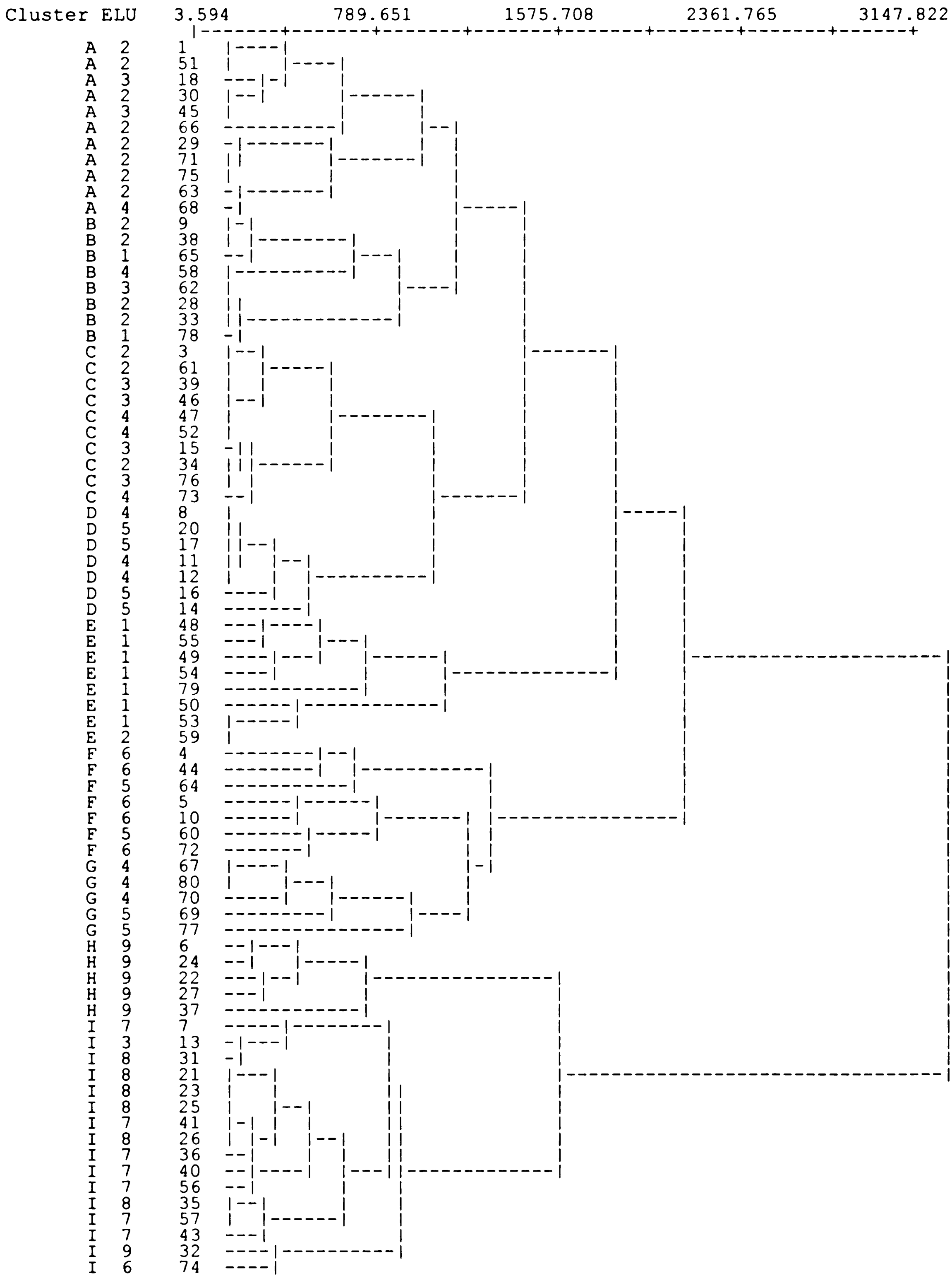


Figure 2.69. Clustering of 77 samples from NW lower MI based on high quality species with clusters labeled by letters and ELU's labeled by respective numbers: Ward's linkage.

Figure 2.70 displays agglomerative clustering of 56 samples from the northern Manistee National Forest classified by Host based on commonly occurring ground-flora species using Ward's linkage method. Eight groups were identified, and were labeled A through H for discussion purposes.

Cluster A grouped eight samples of unit ELU 2, two samples of unit 3 and one sample of unit 4. Cluster B was heterogeneous, with one sample of unit 2, one sample of unit 3, three samples of unit 5, and four samples of unit 4. Cluster C grouped three samples of unit 3 and one sample of unit 1. Cluster D grouped four samples of unit 6, and two samples of unit 5. Cluster E grouped six samples of unit 1, and one sample of unit 2. Cluster F grouped four samples of unit 9. Cluster G grouped four samples of unit 7 and six samples of unit 8. Cluster H grouped seven samples of unit 7, and six samples of unit 8 Agglomerative clustering of 56 samples within a climatically homogeneous area based on commonly occurring species was only effective in grouping units 1, 2, and 9.

Figure 2.71 displays agglomerative clustering of the samples from the northern Manistee National Forest classified by Host based on high quality ground-flora species using Ward's linkage method. Seven groups were identified, and were labeled A through G for discussion purposes.

Cluster A grouped seven samples of unit ELU 2, two samples of unit 3 and one sample of unit 4. Cluster B was heterogeneous, with two samples of unit 2, one sample of unit 4, and four samples of unit 3. Cluster C grouped four samples of unit 5 and two samples of unit 4. Cluster D grouped four samples of unit 6, and one sample of unit 5. Cluster E grouped six samples of unit 1, and one sample of unit 2. Cluster F grouped five

```
           DISTANCE
          4.625         653.198         1301.772        1950.345        2598.918
           |-------+-------+-------+-------+-------+-------+-------+-------+
A 2   1    |--------|
A 2   30   |        |---------|
A 3   45   |        |         |
A 3   18   ------|--|         |
A 2   51   ------|            |----|
A 2   9    |-----|            |    |
A 2   38   |     |------|     |    |
A 4   58   ------|      |-----|    |
A 2   28   |------|     |          |
A 2   29   |      |-----|          |
A 2   33   -------|                |
B 2   3    |--|                    |--------|
B 4   11   |  ||                   |        |
B 4   12   |  ||                   |        |
B 5   16   ---||---|               |        |
B 4   8    |   |   |               |        |
B 3   47   |   |   |--------|      |        |
B 5   20   |---|   |        |      |        |
B 5   17   |       |        |------|        |------|
B 4   52   --------|        |               |      |
C 3   15   -|--|            |               |      |
C 2   34   -|  |------------|               |      |
C 3   39   -|--|                           |      |
C 3   46   -|                              |      |
D 6   4    ----------|-----------|          |      |
D 6   44   ----------|           |----------|      |----------------------|
D 6   5    ------------|--|      |                |                      |
D 5   14   -----------||  |------|                |                      |
D 5   60   -----------|   |                       |                      |
D 6   10   ---------------|                       |                      |
E 1   48   -----|--------|                        |                      |
E 1   55   -----|        |---|                    |                      |
E 1   49   ---|----------|   |---------------------|                      |
E 1   54   ---|              |                                            |
E 1   50   ------------|-----|                                            |
E 1   53   ----|-------|                                                  |
E 2   59   ----|                                                          |
F 9   6    -------|-|                                                     |
F 9   22   -------| |-----------------|                                   |
F 9   24   --|------|                 |                                   |
F 9   27   --|                        |                                   |
G 7   7    ---|                       |                                   |
G 8   25   |  |                       |                                   |
G 7   41   || |---|                   |                                   |
G 8   26   ||||   |                   |-----------------------------------|
G 8   35   -|||   ||                  |
G 8   31   --|    ||                  |
G 8   21   |------||------|           |
G 8   23   |       |      |           |
G 7   40   -|------|      |----|      |
G 7   56   -|             |    |      |
G 8   32   ---------------|    |------|
H 7   36   --|--|              |
H 7   43   --|  |-----|        |
H 7   57   -----|     |--------|
H 9   37   -----------|
```

Figure 2.70. Clustering of 56 samples from a homogeneous climatic zone in NW lower MI based on commonly occurring species with clusters labeled by letters and ELU's labeled by respective numbers: Ward's linkage.

samples of unit 9. Cluster G grouped six samples of unit 7, seven samples of unit 8, and one sample of unit 9.

Agglomerative clustering of 56 samples within a climatically homogeneous area based on high quality ground-flora species was only effective in grouping units 1, 2, 6, and 9. Results of clustering samples based on high quality species differed from the same clustering on commonly occurring species in three respects. First, unit 6 was effectively identified using high quality species. Second, five samples of unit 9 were grouped together, as opposed to four samples using commonly occurring species. Third, four samples of unit 5 were grouped together in a cluster of six that contained two samples of unit 4.

Figure 2.72 displays TWINSPAN clustering of the samples from the northern Manistee National Forest classified by Host based on high quality ground-flora. Eight groups of three or more samples were identified, with one group of two outliers also separated. The first group consisted of six samples of unit 1 and one sample of unit 2. The second group consisted of seven samples of unit 2, one sample of unit 1, and one sample of unit 2. The third group was heterogeneous, with two samples of unit 2, four samples of unit 3, and four samples of unit 4. The fourth group consisted of five samples of unit 5. The sixth group consisted of four samples of unit 6. The consisted of three samples of unit 7. The seventh group consisted of seven samples of unit 8, and two samples of unit 7. The eight group consisted of six samples of unit 9, and one sample of unit 7.

```
         3.688         573.561        1143.434        1713.308      2283.181
           |-------+-------+-------+-------+-------+-------+-------+-------+
A 2    1   |----|
A 2    51  |    |-----------|
A 3    18  ---|-|           |
A 2    30  |--|             |
A 3    45  |                |---|
A 2    9   |-|              |   |
A 2    38  | |--|           |   |
A 2    29  --|  |------|    |   |
A 4    58  -----|      |----|   |
A 2    28  |-----------|        |
A 2    33  |                    |
B 2    3   -||                  |--------|
B 3    39  -||---|              |        |
B 3    46  | |   |              |        |
B 3    47  |-|   |-------|      |        |
B 4    52  |     |       |      |        |
B 3    15  |-----|       |      |        |
B 2    34  |             |      |        |
B 4    8   |             |------|        |-------|
C 5    20  ||            |               |       |
C 5    17  ||--|         |               |       |
C 4    11  ||  |---|     |               |       |
C 4    12  |   |   |-----|               |       |
C 5    16  ----|   |                     |       |
C 5    14  --------|                     |       |
D 6    4   ----------|-------|           |       |------------------------|
D 6    44  ----------|       |-----------|       |                        |
D 6    5   -------|--|       |                   |                        |
D 6    10  -------|  |-------|                   |                        |
D 5    60  ----------|                           |                        |
E 1    48  ---|-----|                            |                        |
E 1    55  ---|     |-----|                      |                        |
E 1    49  ----|----|     |----------------------|                        |
E 1    54  ----|          |                                               |
E 1    50  -------|-------|                                               |
E 1    53  -|-----|                                                       |
E 2    59  -|                                                             |
F 9    6   -|----|                                                        |
F 9    24  -|    |-------|                                                |
F 9    22  --|---|       |----------|                                     |
F 9    27  --|           |          |                                     |
F 9    37  --------------|          |                                     |
G 7    7   ----|---|                |                                     |
G 8    31  ----|   |--|             |                                     |
G 8    35  |--|    |  |             |                                     |
G 7    57  |  |----|  |             |-------------------------------------|
G 8    43  ---|       |             |
G 8    21  |----|     |-|           |
G 8    23  |    |     | |           |
G 8    25  |    |---| | |           |
G 7    41  ||   |   | | |           |
G 8    26  ||---|   |-| |-----------|
G 7    36  -|       |   |
G 7    40  --|------|   |
G 7    56  --|          |
H 9    32  -------------|
```

Figure 2.71. Clustering of 56 samples from a homogeneous climatic zone in NW lower MI based on high quality species with clusters labeled by letters and ELU's labeled by respective numbers: Ward's linkage.

TWINSPAN clustering of the samples from the northern Manistee National Forest based on high quality ground-flora was effective in grouping samples in units 1, 2, 5, 6, 7, 8, and 9. Only one cluster contained a heterogeneous mix of samples. Apparently TWINSPAN was efficient in identifying multifactor units classified by Host (1987) that were differentiated by combinations of soil, substrate, and floristic criteria in the original classification. The ability of ground-flora communities to serve as phytometers of important environmental conditions was improved by eliminating species with low fidelity, or species that are poorly correlated, with the first few dimensions of a CA, and retaining species most closely associated with underlying environmental gradients expressed in the first few dimensions of a CA.

```
1111112 222222132 2233444433 34 55555 6666 777 888788887 9999799 ELU

4554555 3 2233513   145 1514 34 11216   14 445 222023335 32234 2 Sample
8059439 098938154 1316282885 97 67040 4504 016 356711567 2277364

                                                                  Cluster
0000000 000000000 0000000000 00 00000 0000 111 111111111 1111111 level 1
0000000 000000000 0000000000 11 11111 1111 000 000000000 1111111 level 2
0000000 111111111 1111111111 00 00000 1111 000 000000111 0000011 level 3
0000011 000000000 1111111111 00 00011      000 111111            Level 4
```

Figure 2.72. TWINSPAN on 56 samples from a homogenous climatic zone in NW MI based on high quality species.

CUT LEVELS: 0 .00 1.00 2.00 3.00 4.00

DISCUSSION

A series of complementary multivariate, graphical, and tabular analyses was effective in classifying multifactor ELU's in northeast lower Michigan. Results of clustering of samples based on species aided in the exploratory partitioning of samples in species space. The analysis of soils data and comparison of results to ordination and clustering of samples based on species enabled an interpretation of gradients expressed along principal coordinates and the separation of samples grouped within heterogeneous clusters. The elimination of species poorly correlated with low-dimensional sample subspaces through a geometric interpretation of a CA was effective in conditioning ground-flora data sets for clustering procedures, although ordination results were not substantially improved. While clustering results of samples based on ground-flora were improved in terms of consistency in number of groups identified and assignment of samples to groups using the high quality ground-flora data set, clustering alone did not sufficiently identify final ELU's.

The utility of eliminating ground-flora species poorly correlated with the first five dimensions of a CA was validated in the analysis of a second independently derived classification by Host (1987). Samples from a different climatic region were distinguished in the clustering of 76 samples. Elimination of the samples from a different climatic region and reanalysis of 56 six samples within a homogeneous climatic zone enabled TWINSPAN to effectively identify all nine ecological units previously classified without the use of soils data that was critical to the original classification.

The determination of species with high fidelity to low-dimensional subspaces also facilitated an improved interpretation of ordination diagrams. Species that were "indicators" of the important environmental factors were included in final ordination partitions of species in sample space and in ecological species groups.

Ordination space partitioning of samples in the first and third dimensions of commonly occurring or high quality species space of a CA was effective in identifying all seven ecological land units classified in this research; these units differed in terms of both floristic and soil characteristics. Ordination space partitioning of samples in the first and second dimensions of commonly occurring or high quality species space of a DCA was also effective in identifying all seven ecological land units classified in this research. Ordination space partitioning of samples in the first and second dimensions of soil variable space was also effective in identifying ecological land units. Partitioning of continuously distributed samples in species or soil variable space required use of clustering results and tabular comparisons within and between floristic and soil data sets to locate where regions of ecological units changed. Ordination space partitioning of the seven regions occupied by ecological land unit clarifications based on either the ground-flora or soil data sets would not have been possible without the availability and analysis of both data sets.

CA and DCA were robust to the inclusion of ubiquitously distributed ground-flora species, and the use of high quality species in ordination procedures had little if any advantage over use of commonly occurring species for data collected in northeast lower Michigan, and actually obscured results for DCA the first and second dimensions. Use of high quality species in DCA for the data set from northwestern Lower Michigan improved the discriminating power of the analysis in the first and second dimension, however.

Important soil morphologic and physical characteristics were identified using PCA. The examination of factor weights and factor patterns identified soil variables primarily controlling in situ moisture and nutrient gradients that differentiated multifactor ecological land units. Ordinations of samples in soil variable space in the first two dimensions of a PCA distinguished all ecological land units, with only a few outliers not grouping within respective classes. The soils data set was not summarized well in low dimensional subspaces, and patterns in the third and higher dimensions did not assist in the interpretation of samples in variable space or variables in sample space.

The clustering of samples based on twenty-eight soil variables failed to group samples according to ecological units as defined in this research. Nonetheless, data on soil characteristics was essential in formulating ecological units in several regards. First, tabular inspection of soil variables revealed textural and drainage patterns responsible for patterns in ground-flora assemblages. Second, soil-plant relationships were used as a basis for formulating ecological species groups. Third, differences in soil characteristics were used as a basis for partitioning continuously distributed samples in species space. Fourth, differences in soil characteristics were used as a basis for subdividing one large cluster of samples objectively grouped by agglomerative and divisive clustering techniques. Fifth, the ordination space partitioning of seven groups of samples in soil variable space that matched the ordination space partitioning of samples in species space corroborated the classification of samples based on ground-flora.

Overstory composition was not a basis of classification in this research, but nonetheless units had relatively consistent composition of overstory species. These findings served as a validation of the units derived based on ground-flora and soil variables.

Management Implications of Ecological Land Classification

The units formulated in this research and the procedures applied should be useful for management in several respects. These classification units can aid in the development of map unit legends and in the interpretation of soil-plant relationships for respective units. ELU's can also serve as a basis for testing hypotheses in follow up research regarding key management concerns. Forest management information needs including rates of forest growth (Host et al. 1988), regeneration (Bruggink 1988), nutrient cycling (Zak et al 1989, Padley 1989), maintenance of long term soil productivity, and other interpretations such as wildlife forage values can be studied within the study area based on this ecological classification framework. Given positive results, findings can be extrapolated to similar areas based inventories of existing vegetation and ELU's.

The procedures used in the classification of ELU's in northeast lower Michigan can aid scientists and managers involved in multifactor ecological land classification. In particular, investigators may want to eliminate species poorly correlated with low dimensional subspaces in agglomerative clustering or TWINSPAN analysis of samples based on species, and in the interpretation of ordination diagrams of species and species' synthesis tables. Furthermore, the results of this research show that no single multivariate analysis is sufficient for multifactor ecological land classification. Iterating between environmental and floristic analyses, and careful, concurrent interpretation of ordination and clustering results is necessary.

The overall program of ecological land classification by numerous researchers in Michigan (Padley 1989, Host 1988, Spies and Barnes 1985a, Pregitzer 1981) can contribute to a larger need of understanding the basic nature and distribution of forest ecosystems. The results of research addressed in this effort, for example, corroborated the theory that plant distributions are regulated along energy, moisture, nutrient, and disturbance gradients. The separation of samples from different climatic zones in northwest lower Michigan (Albert et al. 1986) for equivalent ELU's as defined by Host (1987) based on clustering using high quality species (Figure 2.69) substantiated that even minor differences in climate can affect the composition or relative abundance of ground-flora associated with ELU's.

In this research, a random stratified sampling scheme was used to reduce the variability in vegetation due to climatic or disturbance effects. Only well stocked, minimally disturbed late successional forest stands in upland, moderately or more well drained soils were sampled. This was one of several possible sampling frames that could have been employed. Openlands, young regenerating forests, wetlands, or other combinations of forest types and soils conditions could have also comprised the sampling frame. Opportunities for quantifying relationships and conditions in these various sampling frames that affect patterns in forest ecosystem structure and function is another contribution of ecological land classification efforts.

Figure 2.73 displays a conceptual model of spatial and temporal sources of variability affecting forest ecosystem structure and function (Cleland et al. 1994). This figure shows spatial variations in environment measured at local and regional scales, and temporal variations in age and succession measured in years and centuries.

Within a local area, particular locations are wetter or drier, or more or less fertile than other locations because of differences in soil properties or hydrology. Each of these conditions supports certain assemblages of plants and animals. In Michigan's forests, this environmental-biotic gradient could include oak savannas, xeric jack pine, dry-mesic

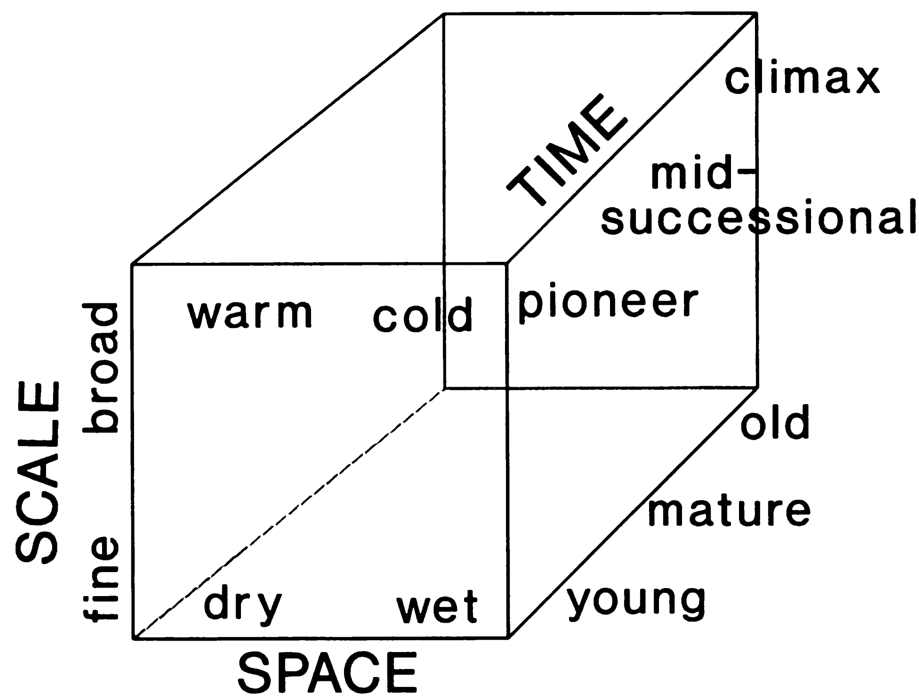


Figure 2.73. Environmental and temporal sources of variability in forest ecosystem structure and function.

pine-oak, mesic northern hardwood, and hydric hardwood or conifer communities. Fine scale ecological land units are designed to classify these general forest type - environment combinations into more precise classes. At broader spatial scales, temperature and moisture gradients vary with latitude, elevation and proximity to major bodies of water, each of which affects macroclimate. These changes at macroscales represent spatial sources of environmental variability that affect regional, landscape and local ecosystem structure and function. Meso- and macroscale ecological units are designed to classify and regionalize these regional and landscape level ecological units (Cleland et al. 1996, Albert et al. 1986).

Figure 2.73 also shows changes occurring through time. At temporal scales measured in years, a given ecosystem may be supporting vegetation that is young, mature, or old growth. These changes at finer time scales represent temporal variations that affect local ecosystem structure and function. At temporal scales measured in centuries, ecosystems undergo change such as succession. Successional developments affect the nature and complexity of food webs, ratios of net primary production to respiration, and rates of nutrient and carbon cycling (Odum 1969). From a landscape perspective, these changes form a shifting mosaic of local ecosystems at different successional stages (Borman and Likens 1979). Changes occurring at these time scales represent temporal variations affecting landscape and local ecosystem structure and function.

Figure 2.74 displays a CA of 123 samples in dimensions 1 and 3 of commonly occurring species space for a combined data set from both northwest and northeast lower

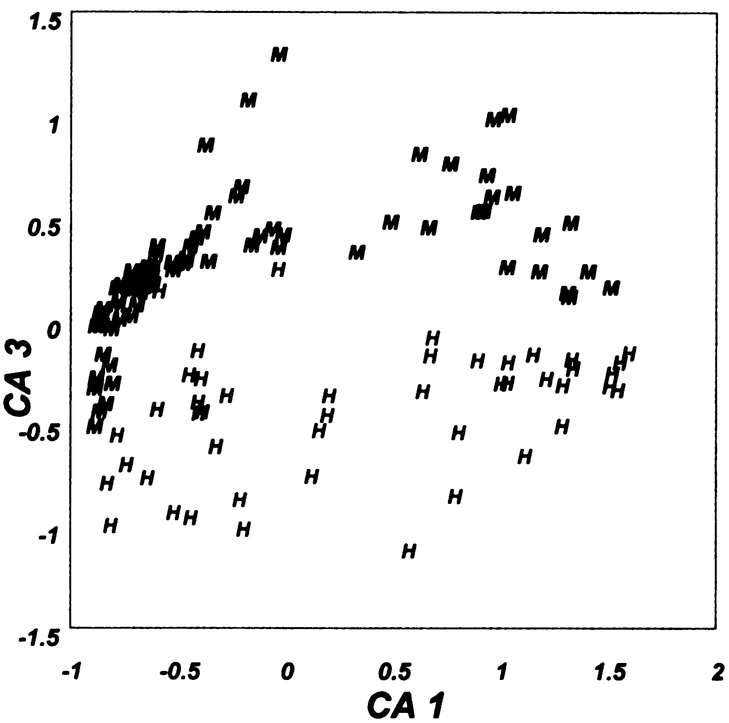


Figure 2.74. CA of 123 samples in dimensions 1 and 3 of commonly occurring species space for a combined data set from northwest and northeast lower Michigan labeled by National Forest: M denotes Manistee NF, H denotes Huron NF.

Michigan. Samples grade from xeric to mesic along the first principal coordinate with increasing sample weights. The third dimension effectively separates samples from these two different climatic zones, suggesting that subtle differences in species relative abundance reflect climatic gradients expressed along the third principal coordinate.

Figure 2.75 displays a CA of 88 samples in dimensions 1 and 2 of commonly occurring species space labeled by forest type. These samples consist of the 46 samples from northeast lower Michigan used in this research, and an additional 42 samples from the same study area measured in fully stocked aspen stands. Identical field methods were used in data collection. Figure 2.75 shows samples grading from xeric to mesic along the first principal coordinate, whereas the second dimension effectively separates samples from these two different forest types, suggesting that differences in species composition or relative abundance reflect successional gradients expressed along the second principal coordinate.

The implications of Figures 2.74 and 2.75 are that species composition and relative abundance varies along environmental and temporal gradients. Van Groenewoud (1992) recommended that the only way to get reasonable results using CA or DCA is to restrict the sampling mainly to one gradient, or pre-stratify the samples before analysis to represent mainly one gradient at a time. These preliminary analyses reported for discussion purposes support this recommendation.

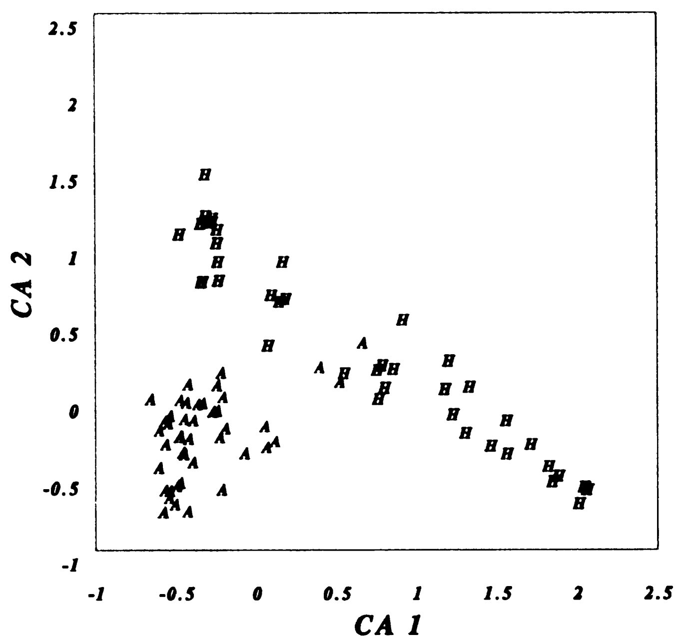


Figure 2.75. 88 samples in CA dimensions 1 and 2 of commonly occurring species space labeled by forest type: H denotes hardwoods and A denotes aspen.

The are several management implications of these findings. First, ecological land units, ecological species groups, or habitat types should be nested within and defined for different climatic zones or regions. Second, assemblages of species used as indicators of environmental conditions may need to be developed for early as well as late successional forest types. Third, extrapolation of ecological land classifications outside of the regions in which they were developed is likely unsound without verification and adjustment to local conditions.

CHAPTER III

SUMMARY AND CONCLUSIONS

The use of a series of complementary ordination, clustering, graphical, and tabular analyses of floristic and soils data was effective in defining seven multifactor ecological land units for northeastern lower Michigan. Any single analysis of any single factor would not have allowed the development of an ecologically meaningful classification of samples or species. Iterating between ordination and clustering results aided in objective exploratory partitioning of samples incommonly occurring and high quality species space. Ordination of samples in soil variable space corroborated ordination space partitioning of samples in species space, and identified important soil variables subsequently used in the interpretation of ordination and clustering of samples based on ground-flora. Reanalysis of ground-flora data composed of species with high correlation to the first five dimensions of a CA further refined the classification. Graphical and tabular methods and comparisons facilitated the interpretation of mutual changes in ground-flora and soil conditions, and these methods were essential in the development of the final classification.

Seven Ecological Land Units were classified. ELU 1 consists of the sugar maple-basswood-blue cohosh plant association on moderately well-drained sandy loams over sandy clay loam substratums on moraines and ground moraines; some pedons have loamy sand caps. The ground-flora of sites sampled for ELU 1 consists of *Caulophyllum thalictroides*, *Dryopteris spinulosa*, *Allium tricoccum*, *Carex deweyana*, and *Carex annectens*. These species form the *Caulophyllum* species group. The overstories of sites sampled for ELU 1 are dominantly composed of sugar maple, basswood, white ash, and beech.

ELU 2 consists of the red oak-sugar maple-viola plant association on well-drained sandy loams over sandy clay loam substratums on moraines and ground moraines; some pedons have loamy sand caps. The ground-flora of sites sampled for ELU 2 consists of *Viola* species *including Viola pubescens and Viola canadensis, Prenanthes alba, Ribes cynobasti, Solidago hispida,* and a diverse assemblage of tree seedlings including *Acer saccarum*, *Tilia americana, Fagus grandifolia*, and *Ostrya virginiana*. These species form the *Viola* species group. The overstories of sites sampled for ELU 2 are composed of red oak, sugar maple, basswood, white ash, red maple, beech, paper birch, and ironwood.

ELU 3 consists of the red oak-basswood- miterwort plant association on well-drained sandy loams over silty clay loam substratums on moraines and ground moraines; some pedons have loamy sand caps. The ground-flora of sites sampled for ELU 3 consists of *Mitella diphylla, Osmorhiza chilensis, Athyrium felix-femina*, *Hepatica acutiloba*, *Carex plantaginea, Actaea rubra, Galium triflorum, and Tilia americana* . These species are form the *Mitella* species group. The overstories of sites sampled for ELU 3 are composed of red oak, basswood, sugar maple, paper birch, white ash, red maple, ironwood and beech.

ELU 4 consists of the red oak-red maple-bellwort plant association on well drained sands with sandy Bs to coarse to fine loamy B2t horizons overlying fine loamy substratums on ice-contact topography. The ground-flora of sites sampled for ELU 4 consists of *Uvularia perfoliata*, *Trillium grandiflorum*, *Viola spp.*, *Fraxinus americana*, and *Prenanthes alba*. These species form the *Uvularia* species group. The ground-flora of ELU 4 contains elements of both northern hardwood and oak ecosystems, including species within the *Uvularia* species group, and *Viburnum acerifolium*, *Hamamelis virginiana*, and *Vaccinium angustifolium*. The overstories of sites sampled for ELU 4 are composed of red oak, red maple, white oak, paper birch, and white ash.

ELU 5 consists of the red oak-red maple-viburnum plant association on well drained sands with sandy Bs overlying coarse to fine loamy substratums on ice-contact topography. The ground-flora of sites sampled for ELU 5 consists of *Viburnum acerifolium, Hamamelis virginiana, Sanicula trifoliata, Cretaegus spp., Amelanchier spp.,and Oryzopsis asperifolia*. These species form the *Viburnum* species group. The overstories of sites sampled for ELU 5 are composed of red oak, white oak, black oak, and red maple.

ELU 6 consists of the mixed oak-red maple-big leaf aster plant association on excessively well-drained sands of ice contact topography. The ground-flora of sites sampled for ELU 6 consists of *Aster macrophyllum*, *Quercus rubra*, *Lonicera canadense*, and *Vaccinium angustifolium*. These species form the *Aster macrophyllum* species group. The overstories of reference sites sampled for ELU 6 are composed of red, black, and white oak, and red maples.

ELU 7 consists of the northern pin oak-white oak-bearberry plant association on excessively well-drained sands of outwash plains. The ground-flora of sites sampled for ELU 7 consists of *Arctostaphylos uva-ursi*, *Cladina spp.*, *Comptonia peregrina*, *Apocynum androsaemifoliumspr, Melampyrum lineare, Dicranum polysetum, Gaylussacia baccata,* and *Quercus velutina*. These species form the *Arctostaphylos* species group. The overstories of reference sites sampled for ELU 7 are composed of upland pin, black, and white oak.

Two secondary goals of this research met while classifying multifactor ecological land units were: (i) the documentation of a series of complementary multivariate, tabular, and graphical analyses of ground-flora, soils, and overstory data in the classification process, and (ii) the determination if the classification of samples and species into multifactor ecological land units and ecological species groups could be improved by eliminating ubiquitously distributed or superfluous ground-flora species prior to application of several ordination and clustering methods.

The display of results at each step of the classification process and in subsequent discussions provided documentation of the sequence of analyses of floristic and soil data sets. Objective numerical analyses used in conjunction with a minimum of subjective interpretation of graphical and tabular results were effective in developing the classification. Clustering results used in initial exploratory ordination space partitioning of samples in species and soil variable space provided a means of objectively subdividing continuous distributions of samples in ordination space. Interpretation of subsequent analyses by comparing initial results, diagrams, and tables were useful in deriving the final classification. A final set of synthesis tables was used to derive an integrated classification of samples and species. Results obtained could thus be repeated by other investigators with a minimum of subjective decisions affecting the final classification.

Summary of Vegetative Analyses in Northeast Lower Michigan - Ordination

The first dimension of a correspondence analysis of ground-flora ordinated samples along a moisture and nutrient gradient. ELU's graded from mesic to xeric along the first axis as sample weights graded from negative to positive. ELU 1 consisted of moderately well drained sandy loam solas to depths of 100 cm. overlying sandy clay loam substrates. ELU 2 consisted of well drained sandy loam solas to depths of 30 cm. overlying sandy clay loam substrates. ELU 3 consisted of sandy loam solas to depths of 30 cm. overlying silty clay loam substrates. ELU 4 consisted of shallow sandy caps overlying fine loamy substrates. ELU 5 consisted of deep sandy caps overlying fine loamy substrates at depths greater than 100 cm. ELU 6 consisted of deep sandy soils with moderate spodic horizon development. ELU 7 consisted of deep sandy soils lacking spodic horizon development.

Interpretation of the second principal coordinate of a CA of ground-flora was less straightforward than interpretation of the first principal coordinate. It appears that the second dimension separated samples based on a successional stability gradient. The idea of a successional gradient along this axis was corroborated by interpretation of the squared cosines of samples in species space. Samples classified as ecological land units 1, 6, and 7 were most strongly correlated with the first axis, whereas both ecological land units 4 and 7 were more closely associated with axis 2. Ecological land unit 4 consists of ground-flora typifying both mesic northern hardwood and dry-mesic and xeric oak flora. Based on ground-flora composition and soil textures, this system has the potential to succeed to mesophilic sugar maple-white ash ecosystems, or dry-mesic oak-red maple ecosystems, depending on natural or anthropogenic disturbance regimes.

CA and DCA were both effective in distinguishing ecological land units in commonly occurring and high quality species space for ecological units classified in northeastern lower Michigan. Both CA and DCA were robust to the inclusion of ubiquitously distributed ground-flora species, and the use of high quality ground flora in ordination procedures had little if any advantage over use of commonly occurring species.

For all data sets analyzed, detrending removed the curved configuration of the first and second dimensions of CA, but CA revealed the same patterns in the first and third dimensions as DCA revealed in the first and second. The implication is that either method may be used to discern underlying structure of vegetative data sets, but investigators need to interpret the first and third as opposed to the first and second dimensions of CA to arrive at the same results as DCA. Apparently information on secondary gradients expressed in the second dimension of a DCA is deferred to higher axes in CA.

A benefit to using CA instead of DCA lies in the geometric interpretation of a CA. The fidelity of a species to reduced subspaces can be quantified and interpreted in ordination diagrams, or used to condition data for subsequent clustering procedures by eliminating ubiquitously or spuriously distributed individuals based on species sums of squared cosines in respective subspaces.

Summary of Vegetative Analyses in Northeast Lower Michigan - Clustering

Agglomerative clustering of commonly occurring ground-flora using three linkage methods resulted in relatively consistent classification of sample groups, ordering of groups, and assignment of samples to respective groups for each of the three agglomerative clustering procedures. Five of seven ecological units were distinguished by clustering of commonly occurring species.

Agglomerative clustering of samples based on high quality produced more consistent results than clustering of commonly occurring species in terms of clusters defined and sample assignment to clusters among all clustering procedures. Six of seven ELU's defined in the final classification were distinguished by these clusters. None of the agglomerative procedures for either data set were effective in distinguishing between ecological units 5 and 6. The consistent recovery of the same cluster structure by three different agglomerative linkage methods and divisive clustering indicated that the derived classifications were valid. The interpretation of these groupings and final classification of samples and species was made by tabularly examining patterns in soil characteristics and vegetation.

Classification of species using agglomerative clustering procedures produced inconsistent results. Agglomerative classification of a reduced data set for which species were eliminated based on interpretation of the TWINSPAN synthesis table also failed to identify consistent clusters. Consequently agglomerative clustering was not used to identify ecological species groups.

Classification of species by TWINSPAN identified eight species groups and two outliers. Groups consisted of species assemblages grading from highly mesophilic species typifying northern hardwood ecosystems to pyrophilic xeric species typifying oak and pine-oak ecosystems. The final seven ecological species were defined by interpreting TWINSPAN clustering, ordination, and tabular results of ground-flora in conjunction with interpretations of analyses of soils data.

Summary of Analysis of Soils Data in Northeast Lower Michigan - Ordination

Principal component analysis of twenty-eight soil variables identified important soil characteristics that differentiated multifactor ecological land units and also produced ordination diagrams that grouped samples into meaningful classes of soil, ground-flora, and overstory conditions. Ordinations of samples in soil variable space in the first two dimensions of a PCA distinguished all ecological land units, with only a few outliers not grouping within respective classes. With the exceptions of ELU's 6 and 7, ordinations of samples in variable space in the first and third dimensions failed to group ELU's, however. The soils data set was not summarized well in low dimensional subspaces, and patterns in the third and higher dimensions did not assist in the interpretation of samples in variable space or variables in sample space.

Important variables based on high positive first dimensional weights included soil textures in substrata, then textures in sola. Important variables based on high negative first dimensional weights included variables describing depths to textural discontinuities, thickness of sandy Bs horizons, and depths to mottles and watertables. Important variables based on high positive second dimensional weights included depths to mottles, dominant texture of sola and substrates, soil textures in substrata, and depth to watertables. Important variables based on high negative second dimensional weights included drainage class codes, textures of the top 30 cm., a coded variable describing depths to textural discontinuities, and textures of B horizons.

The most important soil variables based on high positive first dimensional factor loadings, or variable correlations with variates derived in the first principal component, included a coded variable describing substrate textures, textures between 100 and 150 cm., and sola textures. The most important soil variables based on high negative first dimensional factor loadings included depth to heavy textured horizons, and depths to mottles and water tables. The most important soil variables based on high positive second dimensional factor loadings included depths to mottles, dominant texture of sola and substrates, textures between 100 and 250 cm., and depth to watertables. The most important soil variables based on high negative second dimensional factor loadings included drainage class code, texture of the top 30 cm., and a coded variable describing substrata textures.

The first PCA axis ordinated samples along a textural and moisture gradient. Textures of the upper 30 cm. and 100 cm. graded from sands to sandy loams with increasing sample weights along the first axis. Textures of the lower 150 cm. graded from sands to sandy clay loam with increasing sample weights along the first axis. Soil drainage graded from excessively well drained to well drained with increasing sample weights along the first axis.

The second PCA axis ordinated samples along a substrate texture and drainage class gradient. Silt content of the soil horizons at depths of 100 to 250 cm. increased with increasing sample weights along the second axis . Soil drainage graded from well drained to moderately well drained with decreasing sample weights along the second axis.

Summary of Analysis of Soils Data in Northeast Lower Michigan - Clustering

Agglomerative clustering of samples based on twenty-eight soil variables using Ward's and average linkage methods failed to identify the same groups as ordination space partitioning of samples in soil variable space, or as the ordination and clustering of samples based on ground-flora. Interpretation of clustering results indicate that soil groupings were highly variable, and simply included all possible combinations of soil textures in sola and substrata. Results were not corroborated by ordination, graphical, and tabular analyses of soils or ground-flora data, or clustering of ground-flora. Results were therefore discarded from further consideration in formulating ELU's.

Summary of Final Classifications of Ecological Land Units in Northeast Lower Michigan

Seven ecological land classification units (ELU's) and ecological species groups were defined based combinations of ground-flora, soils, and overstory conditions. Comparisons of soils data to clusters of samples defined by high quality species revealed two distinctly different soil-substrata conditions within one cluster that included samples consisting of deep sands and sands underlain by fine loamy substrates. This cluster was subdivided into two ecological land units as a consequence. The remaining groupings of samples based on high quality ground-flora species showed consistent patterns in soil characteristics.

The clustering of samples based on twenty-eight soil variables failed to group samples according to ecological units. Nonetheless, data on soil characteristics was essential in formulating ecological units in several regards. First, tabular inspection of soil variables revealed textural and drainage patterns responsible for patterns in ground-flora assemblages. Second, soil-plant relationships were used as a basis for formulating ecological species groups. Third, differences in soil characteristics were used as a basis for partitioning continuously distributed samples in species space. Fourth, differences in soil characteristics were used as a basis for subdividing one large cluster of samples objectively grouped by agglomerative and divisive clustering techniques. Fifth, the ordination space partitioning of seven groups of samples in soil variable space that matched the ordination space partitioning of samples in species space corroborated the classification of samples based on ground-flora.

Overstory composition was not a basis of classification in this research, but nonetheless units had relatively consistent composition of overstory species. Examination of overstory composition within combined soil-ground-flora units corroborated the meaningful formulation of seven ecological land units based on congruent changes in ground-flora and soil variables, and served as a validation of the ecological significance of these units.

Summary of Use of High Quality Species in the Classification of Ecological Land Units in Northwestern Lower Michigan

The utility of eliminating ground-flora species poorly correlated with the first five dimensions of a CA in cluster analysis was corroborated in the analysis of a second independently derived classification by Host (1987). CA and DCA were both effective in distinguishing ecological land units in commonly occurring and high quality species space. CA was robust to the inclusion of ubiquitously distributed ground-flora species, and the use of high quality ground flora in ordination procedures had little if any advantage over use of commonly occurring species. Use of high quality species in DCA obscured results in the first and second dimensions. DCA was as effective as CA in distinguishing units in the first and third dimensions of high quality species space.

TWINSPAN clustering of samples based on high quality ground-flora species improved the consistency of groups derived and assignment of samples to groups over clustering based on commonly occurring species. TWINSPAN clustering of 76 samples based on high quality species effectively grouped samples into six of nine units defined by Host (1987).

Agglomerative and divisive clustering of 76 samples separated samples from two different climatic regions (Albert et al. 1986). Elimination of these samples and reanalysis of 56 samples within a homogeneous climatic zone enabled divisive (TWINSPAN) clustering to effectively identify all nine ecological units previously classified by Host (1097). This was significant because soils data that was critical to the original classification was not used in the reanalysis, indicating that high quality species were effective phytometers of key soil variables.

Agglomerative clustering of 76 samples based on commonly occurring and high quality species was only effective in grouping samples into four of nine units defined by Host (1987). Agglomerative clustering of 56 samples within a climatically homogeneous area based on high quality ground-flora species was only effective in grouping four of nine units defined by Host (1987).

These results support the use of a series of complementary methods to effectively classify multifactor ecological land units. In contrast to clustering analyses of data sets from northeastern lower Michigan, agglomerative clustering failed to produce satisfactory results in northwestern lower Michigan. A full analysis of ground-flora and soils data using a series of ordination, clustering, and tabular methods iteratively for northwestern lower Michigan would have revealed these inconsistencies, enabling selection and interpretation of the most appropriate ordination and clustering procedures. Furthermore, selection of key differentiating species strongly associated with environmental gradients would have been improved if species sums of squared cosines in low dimensional subspaces had been determined and species with low fidelity eliminated from consideration for both clustering analyses and inclusion within ecological species groups.

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APPENDICES

APPENDIX A

Normality Test (Kolmogorov-Smirnov) for soil variables

O2TH	K-S Distance = 0.104	P = 0.231	Passed
A1TH	K-S Distance = 0.189	P = <0.001	Failed
A1V	K-S Distance = 0.227	P = <0.001	Failed
ETH	K-S Distance = 0.145	P = 0.016	Failed
T30SICL	K-S Distance = 0.301	P = <0.001	Failed
BDEP	K-S Distance = 0.177	P = <0.001	Failed
BIN	K-S Distance = 0.337	P = <0.001	Failed
BVA	K-S Distance = 0.170	P = 0.002	Failed
BSTH	K-S Distance = 0.105	P = 0.222	Passed
BSICL	K-S Distance = 0.204	P = <0.001	Failed
CDEP:	K-S Distance = 0.114	P = 0.138	Passed
GWT	K-S Distance = 0.415	P = <0.001	Failed
MOTDEP	K-S Distance = 0.301	P = <0.001	Failed
DCL	K-S Distance = 0.325	P = <0.001	Failed
UTSIL	K-S Distance = 0.207	P = <0.001	Failed
LTSI	K-S Distance = 0.274	P = <0.001	Failed
TXSIL	K-S Distance = 0.279	P = <0.001	Failed
MAXSICL	K-S Distance = 0.155	P = 0.007	Failed
DOMSICL	K-S Distance = 0.296	P = <0.001	Failed
ACV	K-S Distance = 0.487	P = <0.001	Failed
ACLS	K-S Distance = 0.219	P = <0.001	Failed
ACSL	K-S Distance = 0.223	P = <0.001	Failed
ACSCL	K-S Distance = 0.252	P = <0.001	Failed
LD150	K-S Distance = 0.158	P = 0.005	Failed
TILLD	K-S Distance = 0.277	P = <0.001	Failed
EFFDE	K-S Distance = 0.116	P = 0.121	Passed
SLOP	K-S Distance = 0.139	P = 0.026	Failed
ASP	K-S Distance = 0.231	P = <0.001	Failed
ELEV	K-S Distance = 0.146	P = 0.015	Failed
BTH	K-S Distance = 0.151	P = 0.010	Failed
EDC	K-S Distance = 0.076	P = 0.669	Passed
BIC8	K-S Distance = 0.225	P = <0.001	Failed
PF	K-S Distance = 0.198	P = <0.001	Failed
DEPSCL	K-S Distance = 0.242	P = <0.001	Failed
SICL	K-S Distance = 0.301	P = <0.001	Failed

A test that fails indicates that the data varies significantly from the pattern expected if the data was drawn from a population with a normal distribution.

A test that passes indicates that the data matches the pattern expected if the data was drawn from a population with a normal distribution.