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Successional Vegetation in the Jocassee Gorges, South Carolina

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SUCCESSIONAL VEGETATION IN THE JOCASSEE GORGES, SOUTH CAROLINA

A Dissertation
Presented to
the Graduate School of
Clemson University

In Partial Fulfillment
of the Requirements for the Degree
Doctor of Philosophy
Forestry and Natural Resources

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by
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Accepted by:
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ABSTRACT

Multifactor ecosystem classification systems provide a three-pronged approach to identifying site units across the landscape based on repeating patterns of vegetation, soil, and geomorphology. Ecosystem classification models have been developed for a diversity of forest landscapes throughout North America, and are beneficial as an ecosystem management tool because the outcome yields data models that can be utilized by scientists and natural resource managers alike. In contrast to the enormous amount of classification studies undertaken in relatively stable, older-aged forests in eastern North America, there have been few studies that have employed multifactor classification techniques across a successional gradient, or heavily disturbed forests of the same region. The 17,500-ha Jocassee Gorges tract in upstate South Carolina represents an ideal landscape to examine both spatial and temporal variability in vegetation-environment relationships due to its myriad of landforms and long history of intense forest management over the past century. Successional vegetation patterns across this heavily disturbed, spatially heterogeneous landscape were examined using a multifactor landscape ecosystem classification (LEC) framework developed from ecosystem types described from older-aged (> 75 years) stands. Ecosystem types for three age-classes of stand development post-timber harvest (10-25, 26-50, and 51-75 years) were determined by using environmental discriminants identified in the previous older-aged (reference) stand classification, and a total of 63 plots were established in previously logged stands between April 2003 and October 2004.

Composition of ground flora and woody stem species, along with landform and soil datasets, was compared across age-classes within and among ecosystem types using non-metric multidimensional scaling, non-metric multi-response permutation procedures, and indicator species analysis. Woody stem composition remained similar between age-classes of xeric oak-blueberry and mesic hardwood-bloodroot ecosystem types, while woody stem composition was drastically different on early successional age-classes of the xeric chestnut oak-mountain laurel, submesic oak-mixed flora, and mesic hemlock-rhododendron ecosystem types. Ground flora composition differed between successional and reference age-class for each ecosystem type. Comparisons of ecosystem types across age-classes revealed the following trends: woody stem and ground flora species composition was similar between mesophytic ecosystem types, but differed between xerophytic types; by middle succession age-class (26-50 years) ground flora composition was distinct between all ecosystem types, except the submesic oak-mixed flora type which contained species diagnostic of all others; and by late succession age-class (51-75 years), both ground flora and woody stem composition differed between all ecosystem types. When ground flora and woody stems were placed into ecological species groups, canonical correlation analysis revealed similar trends in middle to late age-classes to those exhibited in reference age-classes. Overall, forest management has not had a severe effect on the disturbance regime across the Jocassee Gorges landscape to cause a significant shift in species composition within any ecosystem type. Although composition and diversity change across temporal gradients of each type, this is to be expected in a highly disturbed landscape of the southern Appalachian Mountains due to

past natural and anthropogenic factors interrupting the process towards steady-state forests. Ecological classification systems are most effective in guiding ecosystem management processes when they are designed to document successional variation, as well as spatial heterogeneity, across landscapes. Adding a fourth (time-series) component to the LEC framework allows for a more accurate approach to documenting the biological diversity within a region, and serves as a more robust management tool because of its ability to predict vegetation across successional land units.

DEDICATION

This dissertation is dedicated to my grandfather, the late Thomas Belton Boyle, who I will always remember as “Bub”. At a young age, he introduced me to the birds, plants, and fish of South Carolina, and was responsible, more than anyone, for planting the seed of an idea which eventually grew into my career as an ecologist.

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CHAPTER ONE

INTRODUCTION

Over the past several decades there have been two major paradigm shifts with respect to the management of forestlands in North America: 1) a shift in focus from stand/unit management to landscape management and 2) a shift in concern from single resource production (timber, game wildlife) to ecosystem management that encompasses multiple interest group needs and places greater emphasis on the biological heritage of a region. The forestry and natural resource managers of the late 20th and early 21st century have been equipping themselves with the necessary education and background tools to address these shifts, resulting in a body that is more diverse in training, skills, and education from the manager of 50 years ago. Federal acts like NEPA, Federal Land Policy and Management Act, National Forest Management Act and the formation of committees like the Federal Geographic Data Committee have been put in place to ensure that land managers follow an ecosystem approach to planning. Consequently, management tools that utilize multi-use approach and integrate ecological principles are becoming increasingly important in how land is managed.

Across the United States, there has been a sea change in the forest management sector from single, economically-desirable species management to recognition of the importance of ecosystem management and maintenance of biological diversity (The Society of American Foresters 1991). As a term, biological diversity refers to the range of variation found within the hierarchical organization of biological units, beginning with the smallest unit--species--and proceeding to larger units--ecosystems and communities.

From strictly a biological perspective, putting the term to use in ecosystem management is a complicated process and difficult to implement because of a lack of information on species composition. As Roberts and Gilliam (1995) suggest, "managers need to know the potential effect of different types of treatments on diversity patterns over time in order to design environmentally sound management practices." Of particular concern is how to determine if anthropogenic "treatments", such as harvesting, mimic natural disturbance regimes. Pickett and White (1985) acknowledged that the dynamics that lead to the sorting out of vegetation composition in terrestrial ecosystems is a function of dominating disturbance regimes. Descriptions of vegetation composition and structure across both spatial and temporal gradients are required to achieve a true ecosystem-level understanding of the landscape in study.

Multifactor ecological classification systems provide a three-pronged approach to identifying units across the landscape based on repeating vegetation, soil, and geomorphology patterns (Whittaker 1962, Barnes et al. 1982). The goal of this integrated approach to landscape classification is to group interrelated sites in such a way that facilitates communication among managers, while at the same time places sites into ecologically meaningful units. Imagine a matrix of 50 study plots across a 20,000 ha terrestrial, forested landscape in the eastern United States. No two plots have the exact same vegetative composition and soil nutrient status. However, a classification that yielded 50 units based on the biotic and abiotic characteristics of each plot would be difficult for natural resource managers to implement into a landscape management plan. Conversely, assuming the plots are distributed randomly throughout the study area, a classification that yielded one unit would not be sufficient to meaningfully describe the heterogeneity of ecosystem types found throughout the landscape.

There have been numerous ecological classification systems developed for forests of the eastern United States since the work of Burton Barnes and others in the northern Michigan (Barnes et al. 1982, Pregitzer and Barnes 1984, Spies and Barnes 1985). In the Manistee National Forest of Michigan, soil and site disturbance history influenced by glacial deposits was the dominant factor in determining the distribution of ecosystems across the landscape (Host and Pregitzer 1992). In the central Green Mountains of Vermont, Smith (1995) classified seven ecological units based on elevation, parent material type, depth to soil mottling, and solum thickness. Earlier studies in New England were unsuccessful in determining site indicator species due to low richness values of species with wide ecologic amplitudes. The multi-factor approach to classifying ecosystem units, however, proved to be successful in determining ecological species groups in the Green Mountains (Smith 1995). Goebel et al. (2005) differentiated two old-growth forests in southeastern Ohio using multi-factor classification methodology in order to better describe these forest types of the Central Hardwoods Region. They found statistical differences between forest species composition of south-facing oak species (*Quercus spp*. L.) and north-facing sugar maple (*Acer saccharum* Marshall), American beech (*Fagus grandifolia* Ehrhart), and northern red oak (*Quercus rubra* L.) forests, but no differences were found in stand structure. Ecological classification research in Indiana has led to the formation of a hierarchical framework of ecosystem types based on broad and fine-scales of abiotic site characteristics (Van Kley

1993, Zhalnin 2004). An Ecological Landtype (ELT) forms the upper level of the classification, and units are distinguished by broad shifts in the landscape, such as topographic position and aspect. Lower in the hierarchy, an Ecological Landtype Phase (ELTP) units are distinguished by vegetation and soil characteristics. Although regional classifications may vary based on environmental patterns and disturbance history, the concept that ecosystem types are formed by repeating patterns of vegetation, soil, and geomorphology remains consistent.

In the southeastern United States, landscape ecosystem classification (LEC) is the preferred method of distinguishing site units in an ecological context. Early site classification studies in the southeastern US focused on soil-site index relationships (Coile 1935, Turner 1938, Baker and Broadfoot 1977) to assess the potential productivity of site types. These early attempts to delineate land units were largely unsuccessful because of the high variability of useful productivity indices within mapped soil units (Van Lear 1991). According to Jones and Lloyd (1993), LEC expresses the interrelationships 1) between vegetation and landform, 2) between vegetation and soils, and 3) between landform and soils to describe and map ecosystem site units. LEC was adopted by southeastern forest ecologists because of the incorporation of landform to describe sites and finer-scale soil variables that could be collected on LEC plots to better examine soil-vegetation relationships. LEC is similar to multifactor ecological classification models of the northern United States, except that LEC typically follows a developmental protocol that was designed by Jones (1989):

Phase I: Identification of the site units from relatively undisturbed vegetation and soil and identification of discriminating landform and soil variables.

Phase II: Identification and description of the various successional vegetation types for each site unit.

Phase III: Mapping of site units on the ground and through Geographic Information Systems (GIS) applications.

Phase IV: Development of management interpretations for each site unit.

Initially in the southeastern US, LEC was applied in the Hilly Coastal Plain Province of South Carolina (Van Lear and Jones 1987) and the Blue Ridge Physiographic Province of North Carolina (McNab 1991). Since then, LEC models have been developed for the Piedmont of South Carolina (Jones 1988), the Chauga Ridges of the Sumter National Forest, South Carolina (Hutto et al. 1999), the Wine Spring Creek Watershed of the Nantahala National Forest (McNabb et al. 1999), the Highlands Ranger District of the Nantahala National Forest, North Carolina (Carter et al. 2000), and the Jocassee Gorges of the Blue Ridge Physiographic Province, South Carolina (Abella et al. 2003).

Barnes (1989) first used the term landscape in conjunction with ecosystem classification to emphasize the horizontal distributions of ecological site units across geographic space. Critics of site unit classification point out that ecosystems do not form distinct boundaries in horizontal landscape space, because, by definition, ecosystems are viewed as more than a composite of vegetation and abiotic factors. Odum (1971) defines an ecosystem as “Any unit that includes all of the organisms (i.e. the community) in a given area interacting with the physical environment so that a flow of energy leads to a clearly defined trophic structure, biotic diversity, and material cycles (i.e., exchange of materials between living and non-living parts within the system) is an ecological system.”

Classification critics argue that because of complex interactions (i.e. Odum's "flow of energy") between ecosystems and their ability to shift over time, site units do not have ecological significance. Most ecologists support the idea that across a landscape, vegetation and environment exist, and interact, along a continuum. If Whittaker's (1978) approach to vegetation distribution across environmental gradients is taken, classification units can be formed within the context of the biotic-abiotic continuum. Because distributions of species overlap across abiotic gradients, we are able to form meaningful, interpretable ecosystem units.

Just as ecosystems vary over spatial dimensions of the landscape, they also vary over time. Ecological succession brought about by natural or anthropogenic disturbances is fairly constant in most ecological systems although the rate and scale at which it operates is in a state of flux. Kimmins (2004) defines the entire sequence of ecosystem change--from early, pioneer stages of community development to climax stages of stable forests--the sere; the seral stage is an identifiable unit of a vegetation association within the sere. Most of the multifactor classification systems developed in the past twenty years have focused on defining site units based on data collected from mature forests, and ignore the effects of anthropogenic or natural disturbance on vegetation composition. The underlying hypothesis is that site units that are relatively homogeneous in terms of vegetation composition and environment respond similarly to management techniques (e.g., harvesting) which bring about secondary disturbance (Bryce et al. 1999). There have been relatively few studies that have focused on bridging the gap between our understanding of how ecological units are distributed across landscape space and our understanding of disturbance history. In the eastern United States, where second-growth forests dominate the landscape, this paucity of data is quite remarkable.

Working in upland grasslands of the Snake River drainage in Idaho, Huschle and Hironaka (1980) instituted one of the first studies designed to examine composition of seral stage vegetation communities. They developed pyramid-shaped conceptual models of secondary succession based on Daubenmire's (1970) old-growth 'habitat typing' approach, where climax stages of vegetation represented spatially distinct units and earlier stages overlapped between habitat types. In the Land Between the Lakes region of western Kentucky and Tennessee, Franklin et al. (1993) analyzed vegetation dominance types separately between compositionally stable climax stands and early seral stage stands to determine successional pathways of community units. Similar research examining compositional differences between reference (old-growth) and clearcut (heavily disturbed) stands within an ecological classification framework has been conducted in southern Indiana (Jenkins and Parker 1999, Morrissey et al. 2010), northern Wisconsin (Scheller and Mladenoff 2002), and the western Cascade Range of Oregon (Halpern 1988). By placing ecosystem types into temporal units, successional pathways across the landscape can be better understood. As Gilliam and Roberts (1995) noted, in order for forest management to adhere to the goals of global sustainability, it must place value on all species and processes within the system, and also mimic as close as possible the natural disturbance regime that led to the development of these ecosystems. The information gathered from applying an ecological classification model across both spatial and temporal gradients can better inform forest management decisions on these ends.

The southern Appalachians represent the highest mountains in the eastern United States, and occur well south of the glacial advance during the Pleistocene. The area is composed of a multitude of landforms of differing sizes and shapes, including three-sided protected coves, two-sided stream ravines, convex toe slopes, linear high and mid-slope grades, broad and narrow ridges, and nonalluvial depressions. The distribution of these varying landforms across the southern Appalachian landscape effects soil moisture availability, and is one of the most significant factors in the determination of regional ecosystem types (McNabb et al. 1999). As Whittaker (1967) noted, ecosystem classification in the southern Appalachians must account for the complexity of the regions' topographic gradients in order to understand vegetation distribution. The forests of the southern Appalachian Mountains, like most other deciduous forests of the eastern United States, can be characterized by a historically long recurrence interval of disturbance typically occurring over a small area in relation to the large extent of surrounding forest (Delcourt and Delcourt 2000). Prior to European settlement, Runkle (1985) suggested windfall as the dominant disturbance regime of the Appalachian Mountains, causing small canopy gap and allowing for the regeneration of woody species. As Europeans settlement increased throughout the eastern United States during the nineteenth-century, so did the wide-scale conversion of natural forestland to other systems (e.g. agriculture land, human settlements). Except for a few scattered locations, most notably the Great Smoky Mountains National Park, most virgin forests of the southern Appalachians had disappeared by the early twentieth-century after a century of deforestation (Whittaker 1956). Today, the southern Appalachian landscape represents a matrix of temporal diversity and altered natural disturbance regimes brought on by hundreds of years of human-manipulated landscape practices.

This study was undertaken to develop Phase II of a LEC for the Jocassee Gorges, a significant portion of the southern Appalachian landscape of northeastern South Carolina under the management of the South Carolina Department of Natural Resources. The Jocassee Gorges represents an ideal landscape to examine both spatial and temporal variability in vegetation-environment relationships due to its myriad of landforms and history of forest management techniques over the past century. Successional documentation represents a significant challenge to forest and vegetation ecologists, due to the length of time required for most forests to develop from an early successional, pioneer to a late successional, climax seral stage. Barbour et al. (1999) described two approaches developed in the literature to overcome this obstacle: 1) use of time-series (repeated measures) analysis on permanent plots, and 2) observations made from nearby plots within distinct successional ages (i.e. chronosequence). This study in Jocassee Gorges represents the chronosequence approach, which, unlike the time-series approach, has the advantage of accounting for the variability inherent in a spatially diverse landscape. Specific objectives of this research include:

i. Describe the structural and compositional changes in vegetation and environment among age-classes of ecosystem types in a heavily disturbed landscape.

ii. Compare the structural and compositional changes in vegetation and environment independently within age-classes to determine the degree to which ecosystem types segregate in response to anthropogenic disturbance.

iii. Determine the degree to which ecological species groups respond to succession in a heavily disturbed landscape, and

iv. Evaluate the degree to which species diversity patterns and woody stem:ground flora ratios change within ecosystem type by age-class community types.

v. Provide management recommendations that can be used to guide the maintenance, form, and function of ecosystems within the Jocassee Gorges tract.

CHAPTER TWO

LITERATURE REVIEW

Introduction

Part of the human condition is to institute order in the complex, which explains the profound attempts to categorize identifiable units in all the major disciplines of life science. From the genetic to the species, and upward to the ecological level, biological objects are placed into groups in order to facilitate communication and provide a means for observations to be made and data to be rigorously tested. Classification is the process by which like individuals are arranged into similar groups, or classes, for the purpose of reducing heterogeneity within the object groups. Classification is inherently a purpose-driven procedure, and the end result of a classification is a function of the purpose statement. In other words, a different purpose statement should yield a different classification scheme. Thus, there can never be a single, best-fit classification that can acknowledge all purposes. However, in the realm of natural resources management, an ideal classification can be achieved if its predictive qualities satisfy the needs of the stated management objectives, while reducing cost and minimizing the time commitment of personnel and resources (Kimmins 2004).

Ecosystems, defined, are the composite of animals, plants, micro-organisms, and the physical environment they inhabit that are aligned in space and time. More than just structure, ecosystems are made up of the complex interactions between living organisms and their environmental substrates, i.e., soil, climate, aqueous solution (Whittaker 1975).

Furthermore, ecosystems can be represented as units in which energy is captured, stored, and utilized among trophic groups and nutrients are in circulation between organisms and the environment (Odum 1971). The plant, animal, and microbial assemblages found within ecosystems constitute their biotic community and often form--usually alone--the fundamental building blocks in classification systems. Oosting (1956) defines a community as “an aggregation of living organisms having mutual relationships among themselves and to their environment,” while Whittaker (1962) describes a community as an assemblage of spatially and temporally co-occurring species that have the ability to interact with one another. The idea that plants assemble into groups based on environmental factors is as old as the field of ecology. Early studies in plant community dynamics include Grisebach (1872), who was one of the first scientists to think about groups of plants as a unit of study and described the Earth’s vegetation based on climate zones.

Classification of natural systems can be based on several factors--e.g., climate, geomorphology, vegetation, soils--either alone or jointly. Over the years, there have been numerous approaches to classifying communities in North America. Some of these methods have emphasized a “top down” approach, whereby large-scale units based on climate or physiognomy are first defined, and subdivided to produce finer-scale units. Other methods have emphasized a “bottom up” approach, whereby fine-scale types (e.g. vegetation associations or vegetation-soil-topography units) are described for an area and upper hierarchies are described only after comparison with similar work done in adjacent areas. Kimmins (2004) recognizes four general classification types used throughout

North America: climatic, physiographic, vegetative, and ecological (Table 2.1). Some of the earliest attempts to classify vegetation utilized a climatic approach. Köppen (1923) categorized the Earth into five major climatic types based on temperature limits--tropical rainy, dry, humid mesothermal, humid microthermal, and polar. Physiographic classification uses soil and landform information, alone or in combination, to define site units, and has the advantage of providing stable classification models due to the permanence of these landscape features. This classification type also can provide valuable regional and local scale maps based on remotely sensed data, which can be used in turn by landscape managers to assess the capability of an area, regardless of the current land use, e.g., agriculture, heavily grazed lands (Barnes et al. 1998). Smalley (1991) used five hierarchical levels to classify spatial units, with the finest-scale unit (Landtype) defined by landform, within the Cumberland Plateau and Highland Rim of Virginia, Tennessee, Kentucky, and Georgia.

Both climatic and physiographic classification types utilize a “top down” approach to defining site units. Rowe (1992) argues that this type of landscape partitioning is known as *regionalization*, and is conceptually different from “bottom up” partitioning devices--*classification*. During *regionalization*, large-scale land units are mapped into homogeneous units, based on broad, measurable differences that can be detected on the landscape level. These units are further subdivided to the finest scale of available data for type differentiation. *Classification*, on the other hand, begins with building groups at the landtype scale, and is reliant on noticing similarities across the landscape, or study unit. Critics of the *regionalization* approach to classification point to

Table 2.1. Summary of Kimmins' (2004) four general classification types, including regional examples in the literature.

Classification Type	**Approach**	**Factor**	**Examples (region)**
Climatic	Top Down	single	Köppen's (1923) Climatic Classification (Earth)
Physiographic	Top Down	single	Smalley's (1991) Landtypes of the Interior Plateau (Cumberland Plateau, U.S.)
Vegetative	Bottom Up	single	Society of American Forester's Forest Cover Types (US) Daubenmire's Habitat-Type Approach (western US)
Ecological	Top Down / Bottom Up	multiple	Biogeoclimatic Classification System (British Columbia)
Ecological	Bottom Up	multiple	Multifactor Classification System (Michigan, Indiana, elsewhere) Landscape Ecosystem Classification (southeastern US)

the models' inadequacy at predicting ecologically meaningful site units, due to the fact that these models often employ only single factor physical variables. If multiple factors are used, they are typically highly correlated with each other. Another criticism of this approach is that it rarely explains the floristic component at the bottom of the hierarchy. As noted by Daubenmire (1976), the vegetation of an area provides the most ideal measurement of ecosystem characteristics--both biotic and abiotic--and key species can provide useful information about site conditions. This is why a vegetative approach to classification has often been favored by forest ecologists and natural resource managers. The vegetative classification approach and its more sophisticated offspring, the ecological approach, are discussed in detail below.

Whittaker, the Niche, and the Vegetation Approach to Classification

The earliest examples of vegetation classification are found in Europe during the 19th century, and are summarized in Kimmins (2004). These early attempts succeeded in creating broad-scale, inter-continental comparisons among vegetation types, but accomplished very little in terms of usability for small-scale ecosystem management. The next phase of vegetation classification emphasized gathering floristic composition information within specific regions, and can be broken down into three subdivisions based on specific vegetation attributes measured: ground flora only, overstory composition only, and emphasis on the entire plant community (Kimmins 2004). The ground flora subdivision was developed in Finland, and utilized only ground species due to poor distribution of site-specific tree species found in the Baltic region (Cajander 1926). The United States and Canada have incorporated the overstory composition subdivision to describe dominant forest cover types (Rowe 1972, Eyre 1980). These classifications have benefitted the forest industry by relating tree species composition to soil and ecosystem characteristics, and thereby yielding site productivity estimates.

The third subdivision, which emphasizes the entire plant community, is broken into two distinct methodologies--the Braun-Blanquet (1932) method of Central Europe and the Habitat-Type Approach of the northwestern U.S. (Kimmins 2004). The Braun-Blanquet method of vegetation classification utilizes the composition and structure of the entire plant community to form hierarchical relationships based on constancy values of diagnostic, or indicator species. This method represents an intermediate approach to the two driving concepts of species distribution in vegetation science--the ‘continuum concept' (Gleason 1926) and the 'community unit concept' (Clements 1916). The 'continuum concept' argues that species group together along environmental gradients and do not form clearly defined units (Gleason 1926, Curtis 1959). The concept is based on the 'individualistic hypothesis' of species distribution (see below) and is vastly divergent from Clements' (1916) theory that plants are distributed in repeatable combinations (i.e. community units) across the landscape. The Braun-Blanquet method accepts that species are distributed in a continuum, but also concedes that species interactions (competition, coevolutiom, dominant species alteration of the physical environment) cause discontinuities between species distributions. These spaces are represented as definable community units.

The Habitat-Type Approach of vegetation classification has been used in the northwestern U.S. for 50 years. Like the Braun-Blanquet method, it utilizes the entire plant community to organize sites into hierarchical units. Unlike the European system, the Habitat-Type Approach first defines higher-order types based on differences in overstory species composition of climax forests (Daubenmire 1952, Daubenmire and Daubenmire 1968). These types are further subdivided based on the composition of the shrub and herbaceous strata. It is important to note that this approach generally follows Clements' 'community unit concept'. However, unlike Clements' view that a climax community is an organic entity driven by regional climate conditions alone (the monoclimax theory of succession), the authors of the Habitat-Type Approach argue that multiple environmental factors (soil, fire, animal), in addition to climate, are acting on successional pathways and a region is a patchwork of unique climax types based on microsite disturbance and physical conditions (the polyclimax theory of succession).

In modern approaches, the basis for using plants to classify ecological systems can be traced to niche theory in vegetation science. The term *niche* is used to describe the suite of environmental factors that influence the distribution of species. In terms of regression modeling, the niche is analogous with species amplitude curves plotted against some environmental gradient (Whittaker 1978). The lower and upper limits of an environmental factor represent boundaries beyond which a species cannot survive (Figure 2.1). Along with popularizing this theory, Whittaker (1975, 1978) also determined seven important rules directing the distribution of plants across environmental gradients. These include:

Rule 1: *Species are individualistic in their response*

The 'individualistic hypothesis' to plant distribution was developed in the U.S. by Gleason (1926). It contends that species are distributed across an environment particular to that species' physiologic and genetic characteristics and that clear plant communities do not form. Because of

the broader scale overlap of species, communities tend to form integrades rather than displaying clear-cut boundaries. This theory is in direct contrast with Clements' view of plant succession (1916) that held repeatable combinations species yield distinct vegetation types (the 'community unit concept') and all communities are directed towards stable vegetation types ('climax communities').

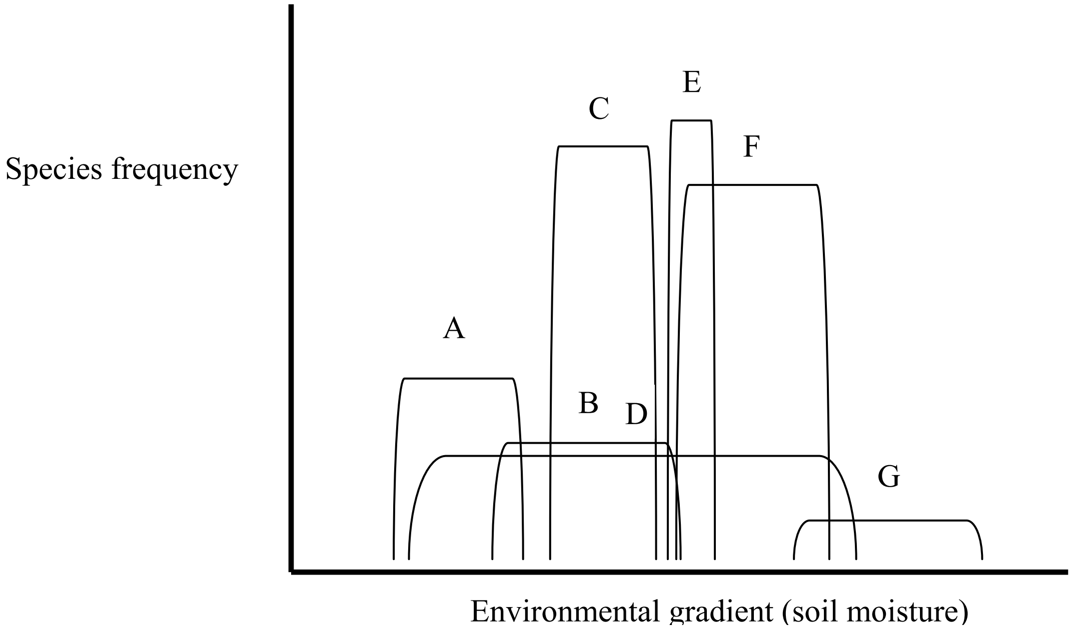

Figure 2.1. Species distribution along a hypothetical environmental gradient. The ‘individualistic hypothesis’ of species distribution suggests that clear bounded communities do not form. Instead, the broad overlaps along a gradient imply that communities intergrade gradually.

Rule 2: *Distribution of species along a gradient is Gaussian*

Species have an optimum point of growth along an environmental gradient and fall in frequency on either side of it. The lower limit of the species represents the minimum and the outer limit represents the maximum. Between these two values is the ecological amplitude of a species (Klinka et al. 1989).

Rule 3: *Species occur at different locations along a gradient*

Species curves cannot overlap because of the principle of competitive exclusion which states 1) if two species occupy the same niche in the same community, one will become extinct, and 2) no two species are directly competing for the same limited resource (Gause 1964).

Rule 4: *The shape of the curve dictates the degree of species' site fidelity*

Species with narrow curves have narrow ecological amplitudes and exhibit high fidelity to a set of certain environmental conditions (Species C and E, Figure 1.1). A species with high fidelity to certain environmental conditions, along with a high degree of constancy across communities, can be thought of as diagnostic. These species can be used as indicator plants to test an array of environmental conditions. Conversely, species with broad curves have wide ecological amplitudes and tend to occur across all communities, regardless of the environmental condition. These species are relatively useless indicators.

Rule 5: *Species of similar amplitudes on the same point of the gradient can form associations*

Species that have narrow ecological amplitudes and overlapping distributions form associations that can be used in conjunction with the indicator plant approach to predict environmental conditions. Species E and F (Figure 2.1) have formed such a relationship.

Rule 6: *Limits of associations are defined by diagnostic species*

The continuum of all species within an association across an environmental gradient is known as the coenocline. The boundaries of a coenocline are defined by the limits of the diagnostic species within an association. Typically, a complete change in species composition is four standard deviations from the optimum of one species. A standard deviation in this case is the measured horizontal gradient distance between the optimum (or peak) of one species and its +/- standard deviation.

Rule 7: *Species data can be related/correlated with the gradient if the gradient is known*

Direct gradient analysis (DGA) can be used if key environmental gradients are known. DGA displays the distributions of species along the known gradients and can be used to determine community structure and function.

The Formation of a Multifactor, Ecological Classification System

Ecosystem classification relies on a methodology of multifactor analysis to delineate larger scale areas (i.e. landscapes, ecoregions, physiographies) into smaller scale ecological site types. Multifactor classification schemes differ from component, or single-factor classification (see Daubenmire and Daubenmire 1968, Pfister and Arno 1980) in the use of a variety of ecological data and, more importantly, the ability to express interrelationships among variables. Multifactor classification uses both abiotic (soils, landform, climate,) and biotic (vegetation) variables to distinguish site types. Most ecosystem classification schemes in North America rely on a hierarchical structure both in the method of delineation (i.e. site types within landscapes, landscapes within climate zones or physiographic provinces) and in the method of site type description (i.e. soils and topography described before potential vegetation) (Barnes et al. 1982; Fralish and Franklin 2002). Over the past 25 years, multifactor classifications have been developed for areas within Michigan (Barnes et al. 1982), the southeastern US (Jones 1991, McNab 1991, Abella et al. 2003), and British Columbia (Pojar et al. 1987).

The classification of similar ecological site types based on multiple variables at multiple map scales began in the southwestern Germany state of Baden-Würtenberg in 1946 (Barnes 1984). The state was divided into major landscapes, or growth areas, based on climate, geology, and vegetation; the growth areas were further subdivided into growth districts based on similar macroclimate, landform, soils, and ground vegetation. Unique ecosystems within growth areas could then be categorized based on interrelationships of physiography, soils, and vegetation. These fine-scale areas were labeled site units and each were categorized by similar silvicultural potential, tree growth rates, disturbance regime, and degree of insect or disease attack.

The earliest ecosystem classification studies in the US that incorporated aspects of forest management were undertaken by Burton Barnes and his colleagues in Michigan in the early 1980s (Barnes et al. 1982, Pregitzer and Barnes 1984). Barnes and his colleagues borrowed extensively from the Baden-Würtenberg methodology. Regional landscape ecosystems of Michigan were classified and mapped at three hierarchical levels (Albert et al. 1986) and local ecological site units were characterized using physiography, soil, and vegetation data (Barnes et al. 1982, Pregitzer and Barnes 1984, Spies and Barnes 1985). In the McCormick Experimental Forest in upper Michigan, eleven ecosystem units were distinguished across upland landscapes based on their discriminant topographic, soil, and vegetative properties (Pregitzer and Barnes 1984). Similarly, Spies and Barnes (1985) distinguished fifteen upland and 10 wetland ecosystems within the Sylvania Recreation Area of upper Michigan using multifactor classification methods.

These early studies, which took place in the Upper Peninsula of Michigan, relied on *a priori* defined stand characteristics within old growth forests to stratify ecological site types. Critics of ecological site classification are quick to point out that a major flaw within these early studies was the introduced bias placed in the sampling technique. Instead of randomization across landscape space, sampling plots were established within areas defined as ‘unique’ based upon reconnaissance, aerial field maps, or a combination of both.

One useful component of the adapted Baden-Würtenberg methodology is the determination of ecological species groups that can be used to delineate ecosystem site units. An ecological species group is defined as an assemblage of ground-cover vegetation that is grouped together based on similar site conditions (Duvigneaud 1946). Although there were earlier studies that classified ecosystems by dominant vegetation type (Daubenmire and Daubenmire 1968; Whittaker 1956), Barnes and his colleagues were the first to apply the ecological species group methodology—which takes into account relationships between vegetation and abiotic components within an ecosystem type—in the US. Ecological species groups were determined for both old-growth forests (Spies and Barnes 1985) and moderately disturbed forests (Archambault et al. 1989) of Michigan.

Most forestry-related studies using multifactor classification methods (Barnes et al. 1982) have involved characterizing vegetative structure and composition of ecosystem types in order to provide baseline data to natural resource managers. Additionally, these studies have provided discriminant abiotic variables to further separate ecosystem types. Hix (1988) characterized 11 ecosystem units in the Kickapoo River watershed and ranked each in terms of average site productivity values for northern red oak. One of the major objectives of the study was to determine if the multifactor classification method was more or less successful in describing forest landscapes than “stand management” applications. He determined that the multifactor system was too complex and intensive for forest managers to use at the present time, but would grow in popularity along with ecosystem management. In the central Green Mountains of Vermont, Smith (1995) classified seven ecological units based on elevation, parent material type, depth to soil mottling, and solum thickness. Earlier studies in New England were unsuccessful in determining site indicator species due to low richness values of species with wide ecologic amplitudes. The multifactor approach to classifying ecosystem units, however, proved to be successful in determining ecological species groups in the Green Mountains (Smith 1995). Goebel et al. (2005) differentiated two old-growth forests in southeastern Ohio using multifactor classification methodology in order to better describe these forest types of the Central Hardwoods Region. They found statistical differences between forest species composition of south-facing mixed-oaks and north-facing sugar maple, American beech, and northern red oak forests, but no differences were found in stand structure.

Other forestry studies utilizing the multifactor classification methods of Michigan have dealt with defining ecological species groups for the purpose of easily identifying site units. In the Sylvania Recreation Area of northern Michigan, Spies and Barnes (1985) formed 16 species groups to classify 13 upland and 4 wetland ecosystem units. These species groups proved to be more reliable than using single key indicator plants to identify sites. Archambault et al. (1989) defined 13 ecological species groups in oak-dominated ecosystems of southern Michigan and were able to differentiate these groups along a soil moisture gradient.

The multifactor classification approach has also been used to test the effects of clearcutting on ecosystem characteristics. Albert and Barnes (1987) used two ecosystem site units classified from a previous study (Hix and Barnes 1984) as sample blocks to test differences in vegetation and soil factors on cut and uncut tracts. They found increased stem densities and decreased basal area of overstory trees in cut plots compared to uncut plots in both the sugar maple ecosystem type and the eastern hemlock (*Tsuga canadensis* L.) ecosystem type. There were no differences between ground-cover species richness on the cut or uncut sugar maple ecosystem type. However, there were differences in species richness values in the cut or uncut eastern hemlock ecosystem type. Similarly, Hix and Lorimer (1991) compared stand development characteristics on two distinct site types in the Kickapoo River watershed of southern Wisconsin and found minimal differences in regeneration patterns on each.

Multifactor classification methodology has been used in several studies to assess patterns of distribution and occurrence of the endangered Kirtland's warbler (*Dendroica kirtlandii* Baird) in northern Michigan. Because of the narrow nesting requirements for this species—underneath 8-20 year old jack pine (*Pinus banksiana* Lamb.) on infertile soils of the Grayling series—a hierarchical ecosystem classification which emphasizes stable abiotic components of the landscapes was thought to provide information relating warbler occurrence within ecosystem types. Kashien and Barnes (2000) examined Kirtland's warbler use of landform-level ecosystems at different elevations at Bald Hill, Michigan from 1982 to 1997. Specifically, they wanted to determine if warbler occupancy across spatial and temporal scales was at all related to physical and biotic components of the ecosystems. Results from the 16-year study indicated a shift in warbler use from high elevation landforms to low elevation landforms by 1991. Although soil characteristics were similar between the two landforms, variations in microclimate due to physiography caused faster growth in high elevation jack pines. Low elevation jack pines remained below the minimum height requirement (16 ft) for Kirtland's warbler throughout the study. Likewise, Kashian et al. (2003) used multifactor classification to describe Kirtland's warbler distribution across 12 landform types in ecosystems dominated by jack pine in northern Michigan. Landform types with favorable growing conditions for jack pine were colonized earliest and for the shortest amount of time, whereas landform types with unfavorable growing conditions were colonized later and for a longer duration. In these studies, multifactor classification proved to be a useful tool in assessing Kirtland's warbler habitat use. The hierarchical framework of ecosystem classification (physical components affect vegetative qualities, vegetative qualities affect warbler distribution) could be used by natural resource managers to assess potential sites for Kirtland's warbler habitat restoration.

There is a minimal amount of research that has employed multifactor ecosystem classification in water-related studies. Baker and Barnes (1998) compared floodplains in northern Michigan using physiography, hydrology, soil, and vegetation. They determined that physiographic position of fluvial landforms, i.e., lateral movement away from the river, was an important factor in ecosystem diversity.

Over the past two decades, multifactor ecosystem classification has been an important tool for natural resources management practice in Canada. Though distinct from province to province, there has been widespread use of classification schemes across the country (see Canadian Institute of Forestry 1992 for synopsis of nine classification methods). In British Columbia, a hierarchical classification method known as Biogeoclimatic Ecosystem Classification (BEC) has been implemented to recognize ecologically similar site units (Pojar et al. 1987; MacKinnon et al. 1992). Because of British Columbia's diverse topography and climate, site units are classified based on a unique combination of vegetation characteristics, climatic zones, and soil-landform micro-site characteristics. Initially, the province was divided into four climatic formations and seven biogeoclimatic regions based on Köppen's (1923) broad climate classification scheme. Biogeoclimatic zones were divisions of regions that represented broad vegetative and soil characteristics unique to a certain climate and subzones underwent similar, but finer divisions. Vegetation data are classified using the Braun-Blanquet (1932) approach to organizing plant communities.

Like other multi-factor ecosystem classification schemes, the BEC system incorporates a hierarchical method of describing site units (Pojar et al. 1987). The most obvious difference between the British Columbia method and U.S. method of classification is the increased emphasis that BEC places on high-order linkages such as climate, landscape vegetation, and landscape soils (top-down approach). U.S. multi-factor classifications, on the other hand, place an increased emphasis on micro-site landform and soil variables to describe ecosystem units (bottom-up approach). Because of emphasis that BEC has placed on the larger-scale definition of ecosystems, much of British Columbia has been 'ecologically' mapped. There are gaping holes in the data regarding ecosystem classification across the entire landscape of Michigan and the southeastern US because most of the studies have involved small scale (1:10,000-100,000) map units. There is a wealth of information involving forest ecosystem characteristics in a few, chosen areas of Michigan and the southeastern US. In British Columbia, ecosystem classification models may be less accurate at finer scales, but they can be applied with a fair amount of certainty across the entire province.

Classification in the Southeastern U.S

Early site classification studies in the southeastern US focused on soil-site index relationships (Coile 1935; Turner 1938; Baker and Broadfoot 1977) to assess the potential productivity of site types. These early attempts to delineate land units were largely unsuccessful because of the high variability of useful productivity indices within mapped soil units (Van Lear 1991). The landscape ecosystem classification (LEC) approach was a modified version of multifactor ecosystem classification used in Michigan in the early 1980s.

Initially in the southeastern US, LEC was applied in the Hilly Coastal Plain Province of South Carolina (Jones et al. 1984; Van Lear and Jones 1987) and the Blue Ridge Physiographic Province of North Carolina (McNab 1991). Since then, LEC models have been developed for the Piedmont of South Carolina (Jones 1988), the Chauga Ridges of the Sumter National Forest, South Carolina (Hutto et al. 1999), the Highlands Ranger District of the Nantahala National Forest, North Carolina (Carter et al.

2000), and the Jocassee Gorges tract of the Blue Ridge Physiographic Province, South Carolina (Abella et al. 2003), to name a few.

The LEC undertaken by McNab (1991) was set in the Bent Creek Experimental Forest in western North Carolina. He identified five ecosystem units that were delineated by a moisture gradient ranging from xeric to subhydric. Furthermore, units could be determined on-site using two quantifiable topographic measures--Terrain Shape Index and Landform Index. In the Savannah River Plant within the Hilly Coastal Plain Province of South Carolina, Jones et al. (1984) delineated ecosystem units along an environmental gradient (xeric to mesic) that was correlated with soil variables and topographical changes. Interrelationships between soil, vegetation, and landform were used to categorize site units. This same approach was applied to the Midlands Plateau Region of the Piedmont Province of South Carolina (Jones 1988). The gradient used to distinguish site units in this study was characterized by a combination of environmental variables such as slope position, aspect, depth to clay, and texture of subsurface horizon.

Hutto et al. (1999) developed an LEC for the Chauga Ridges Region of the Blue Ridge Mountain Province in South Carolina. This was the first study to incorporate the entire four-phase LEC protocol. First, four site units were distinguished based on landform index, slope gradient, distance to bottom, terrain shape index, and root mat thickness. Vegetation and abiotic variables used to determine site units were sampled within relatively undisturbed, old-growth stands. Afterwards, plots were chosen in early and mid successional forest communities of each site unit based on the distinguishing abiotic variables in order to characterize temporal variability within each site unit.

Finally, LEC site units were mapped using a GIS-based model. Carter et al. (2000) developed an LEC for the High Rainfall Belt of the southern Appalachian Mountains in the Highlands Ranger District of the Nantahala National Forest, North Carolina. Phase I and Phase II of the LEC modeling process were accomplished, with six ecological site units identified based on elevation, soil solum thickness, and landform index.

In 2001, a long-term study was initiated to quantify floral and faunal diversity within the Jocassee Gorges tract of the Blue Ridge Mountain Province of South Carolina. Using the LEC approach, five ecosystem site units were distinguished across the property and named according to dominant overstory and understory vegetation—xeric oak-blueberry, xeric chestnut oak-mountain laurel, submesic oak-mixed flora, mesic hardwood-bloodroot, and mesic hemlock-rhododendron (Abella et al. 2003). These site units segregated along a moisture-topographic gradient, similar to other studies in the southern Appalachian Mountains. However, no one environmental variable could be used as a discriminant. Rather, a combination of soil and geomorphic characteristics and their interactions must be used to distinguish site units.

Although LEC has been used in the southeastern US for over 15 years, there have been few attempts to incorporate the methodology into natural resource management studies. On the Clemson Experimental Forest, Waldrop et al. (2004) used the LEC model developed by Jones (1991) for the Piedmont of South Carolina to assess differences of silvicultural treatments on forest fuel loads across ecological site units. They found that burn treatments reduced the duff layer on intermediate and subxeric site units but had little effect on the duff layer of mesic sites. Overall, understanding of fuel loading characteristics was heightened by breaking the landscape into site units of differing landform positions. Jones' (1991) LEC model of the Piedmont of South Carolina was also employed to study the vegetation and herpetofaunal communities of the Clarks Hill Training Site along Lake Thurmond (Shelburne et al. 2002). Five LEC units (xeric, subxeric, intermediate, submesic, and mesic) were mapped across the tract, and data taken from intensive vegetation plots showed to correspondence to these units. This was due to the dominance of mid-successional seral stage forests across the landscape. Although reptile and amphibian surveys provided useful information about species occurrence in depression wetlands and riparian zones, survey data were not put into context with LEC site unit characteristics. Camp (2004) used the LEC model developed by Abella et al. (2003) to compare avian species diversity, richness, and abundance across ecological site units within the Jocassee Gorges. Focal species were selected and compared according to Partners in Flight (PIF) priority scores and feeding and nesting guilds. The occurrence of these species was found to differ across ecological site units and distinct environmental characteristics of each site unit were found to be useful in predicting species presence/absence.

Description of Current Research and Objectives

There have been a few studies that have employed multifactor classification techniques within seral stage, or disturbed, forests of the southern Appalachians, in spite of the tremendous amount of early and mid successional forests within the region. As noted by Carter et al. (2000) "studies that focus on seral communities in the southern Appalachians are uncommon." This is still the case ten years later. Hutto (1998) described seral communities within the Chauga Ridges of South Carolina, and found a decrease of yellow-poplar (*Liriodendron tulipifera* L.) on xeric and intermediate sites and an absence of mesophytic hardwood species--basswood (*Tilia americana* L.), American beech, and sweet birch (*Betula lenta* L.)--on early successional sites. Seral stage communities were also described in a Landscape Ecosystem Classification Framework for the Highlands Ranger District of the Nantahala National Forest (Carter el al. 2000). In this study, mid-elevation early successional (0-25 years) xeric sites were dominated by eastern white pine (*Pinus strobus* L.), mixed oaks, and black locust (*Robinia pseudoacacia* L.); intermediate sites were dominated by yellow-poplar, northern red oak, and black locust; and mesic sites were dominated by yellow-poplar, black locust, and flowering dogwood (*Cornus florida* L.)

Recent work in Indiana has employed a multifactor ecological classification framework in examining site types across disturbance regimes. Jenkins and Parker (1999) utilized such a framework when comparing vegetation composition between sites with different methods of timber harvesting. They concluded that harvesting methods on either ecological site unit has not caused enough disturbances to cause significant shifts in ground flora composition between harvested sites and reference sites. In a similar study, but one yielding drastically different results, Morrissey et al. (2010) concluded that clearcutting significantly changed overstory species composition within all ecological site types within the sampling area. Although there is merit in these types of studies involving binary (clearcut versus reference stands) disturbance types and their affect on species composition across ecological gradients, there is a need in ecosystem management for a better description of how vegetation changes over multiple seres across ecologically diverse landscapes.

The objectives of this study were to perform Phase II of the LEC process for the Jocassee Gorges, within the Blue Ridge Mountain Province of South Carolina. Specific objectives included determining how vegetation and environmental components of ecosystem types change over time in response to long-term, anthropogenic disturbances and providing managers with a description of successional communities that can be used to better understand the floristics of the Jocassee Gorges landscape.

CHAPTER THREE

METHODS

Study Area

The Blue Ridge Mountain province of South Carolina represents the extreme northwest corner of the state and makes up approximately 1.7% (133,000 hectares) of its total land area. Elevation ranges from 365 to 760 meters, and the province can be further subdivided into the Blue Ridge Mountain and Chauga Ridges Regions (Meyers et al. 1986). Within the province lies the Andrew Pickens District of the Sumter National Forest, six state parks (Oconee, Devil's Fork, Table Rock, Keowee-Toxaway, Caesar's Head, and Jones Gap), the Mountain Bridge Wilderness Area, Ellicott Rock Wilderness Area, various South Carolina Department of Natural Resources Heritage Trust Sites, two Greenville County Watersheds (Table Rock and Poinsett), and private ownership.

Jocassee Gorges occupies an area of more than 17,500 hectares within northern Oconee and Pickens counties in northwestern South Carolina along the South and North Carolina border (Figure 3.1). The majority of the property is contained along the southeastern Blue Ridge escarpment region--the abrupt transition zone between the lower-elevation Piedmont physiographic province and the Blue Ridge Mountain physiographic province (Cooper and Hardin 1970, Griffith et al. 2002). This is the section of the escarpment which parallels the west-east trajectory of the Eastern Continental Divide roughly between Hendersonville and Highlands, North Carolina. Here, the escarpment forms a prominent south-facing embankment and is characterized by heavily dissected, steep terrain with

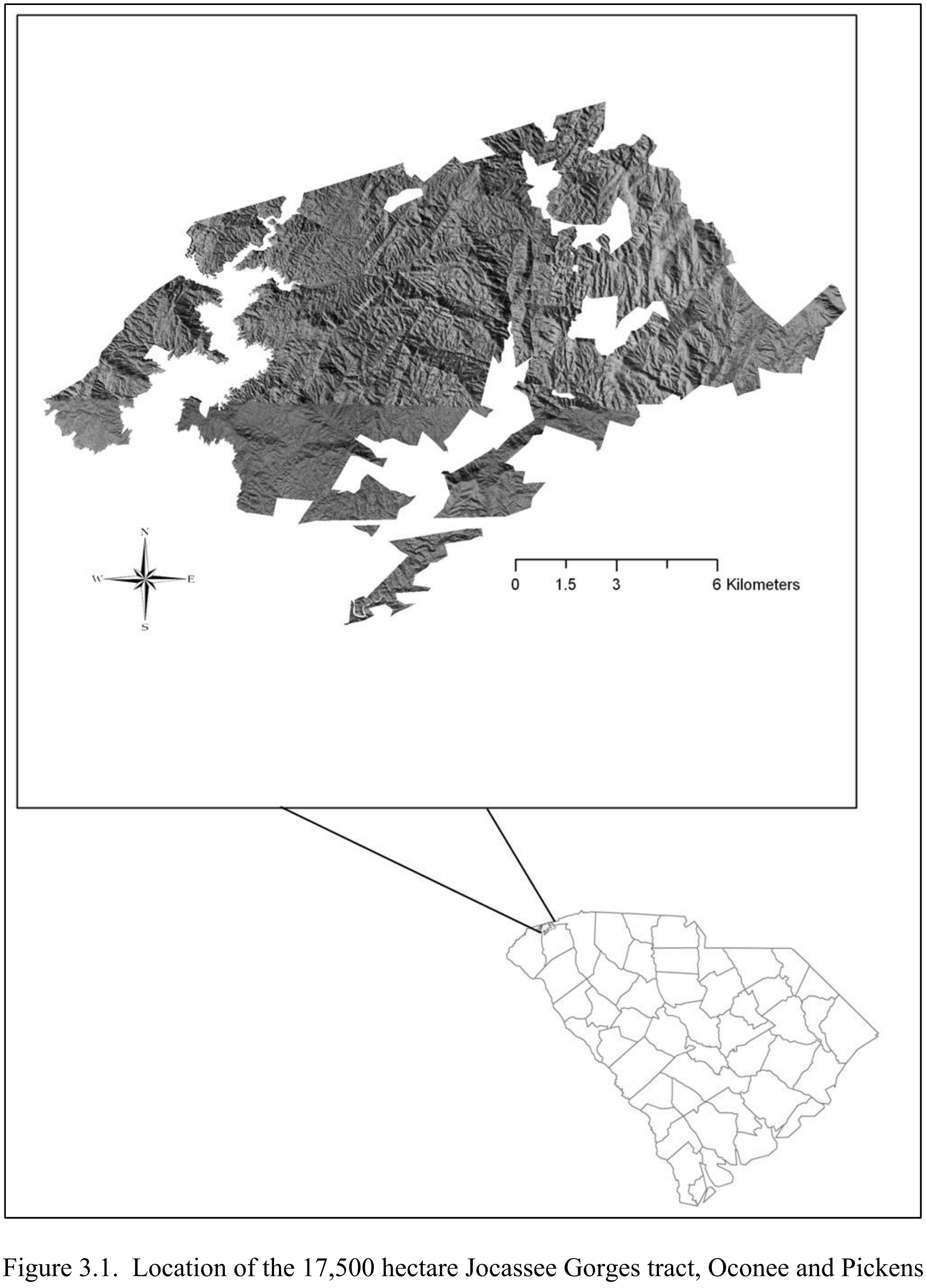

Figure 3.1. Location of the 17,500 hectare Jocassee Gorges tract, Oconee and Pickens Counties, South Carolina.

landscape elevation ranging from 350 to 800 m and localized stream-to-ridgetop elevations ranging from 180 to 250 m. The landscape is further characterized by such topographic features as ridges, stream-dissected hillslopes on side slopes and nose slopes, deep stream gorges, floodplains along flatter streams, and coves. Within the property, five major rivers form deep cutting north-south gorges that drain from North Carolina into South Carolina. These include, from east to west, Eastatoe Creek, Toxaway River, Horsepasture River, Thompson River, and Whitewater River.

The southeastern Blue Ridge escarpment region receives the highest amount of average annual rainfall within the eastern United States, due to warm Gulf Stream air currents moving up and getting trapped within north-south drainages. The gorges experience higher levels of precipitation annually than the Piedmont to the south, and have been labeled by many as a temperate rain forest. Billings and Anderson (1966) suggest mean annual rainfall between 180 and 215 cm for the area on the rim of the escarpment above the gorges, and a mean annual value of 300 cm/year within the head of Whitewater Gorge. Two spikes in rainfall occur during winter/early spring and late summer, but there is potential for precipitation throughout the year.

The Jocassee Gorges study area is bisected by the Brevard fault zone, a narrow strip of mylonitic metamorphic rock that separates the Blue Ridge and Inner Piedmont tectonic provinces. Parent material is composed of igneous and metamorphic rocks of the late Precambrian or early Paleozoic age (Stuckey 1965). Much of the area is composed of metamorphosed sedimentary and volcanic rock, such as biotite gneiss, granite, and mica schist.. Typically, the weathering of these ancient rocks yields highly acidic (pH <

6) upland soils that have shallow solum (< 70 cm) and A-horizon (< 20 cm) depths (Abella et al. 2003). However, larger-scale mapping of the area's geology reveals pockets of mafic rock, such as amphibolite (Merschat et al. 2005). According to the Natural Resources Conservation Service (NRCS) surveys of Pickens and Oconee Counties, the Jocassee Gorges are composed of coarse-loamy, mixed, mesic Typic Dystrochrepts; fine-loamy, mixed, mesic Typic Hapludults; clayey, oxidic, mesic Typic Hapludults; fine-loamy, micaceous, thermic Typic Hapludults; and fine-loamy, mixed, mesic Humic Hapludults (Byrd 1963, 1972). Typic Hapludults and Dystrochrepts occur across most slope positions and Humic Hapludults occur along larger streams or well-protected lower slope positions.

The unique climate, topography, and geology of the Jocassee Gorges have formed a landscape of diverse biological communities. As all landscapes can be defined to some extent as ecotonal to their surroundings, the Jocassee Gorges provides habitat refugium for northern temperate species left over from the Pleistocene and southern, more tropical species that persist due to the abundance of micro-habitats. Disjunct populations of several species of ferns and other cryptogams have been discovered on the property, including four rare species of filmy fern (Hymenophyllaceae) that are not found anyplace else in temperate North America. The area is also home to one of the most species rich and diverse moss flora in the United States. Billings and Anderson (1966) found 268 species of moss in the Whitewater Gorge alone. In the nearby Gorges State Park (Transylvania County, NC), Lendemer and Tripp (2008) found 218 species of lichen, including a tropical species previously not known from North America. The Jocassee

Gorges are also home to many rare and endemic vascular flora, e.g., Oconee bells [*Shortia galacifolia* Torrey and Gray], and may harbor some of the most threatened and endangered plants within the Carolinas (Sutter and Weakley 1987, Gaddy 1998).

The Jocassee Gorges is located within the southern extreme of Braun's Oak-Chestnut Forest Region (Braun 1950) and Bailey's Blue Ridge Province Level III Ecoregion and the Southern Crystalline Ridges and Mountains Level IV Ecoregion (Bailey 1976, Omernik 1987, Griffith et al. 2002). Early, pre-European settlement vegetation was dominated by a variety of oaks and American chestnut (*Castanea dentata* [Marshall] Borkh.) along hill slopes and ridges, while eastern hemlock, sweet birch, and yellow-poplar dominated cove, riparian, and wetter habitats (Ayres and Ashe 1905, Cooper and Hardin 1970). Ericaceous shrubs such as mountain laurel (*Kalmia latifolia* L.) and rhododendron species (*Rhododendron spp.* L.) were characteristic of the oak-chestnut forests, while mountain doghobble (*Leucothoe fontanesiana* [Steudel] Sleumer) and great rhododendron (*Rhododendron maximum* L.) were characteristic of riparian zones (Bartram 1791, Oosting and Billings 1939). Other common species in pre-settlement forests included hickory species (*Carya spp.* Nuttall), yellow-poplar, sourwood (*Oxydendrum arboreum* L.), and flowering dogwood. Early studies of forest communities within the study area were described for the Toxaway River (Cooper 1963), Horsepasture River (Rodgers 1965), Bearcamp Creek (Rodgers and Shake 1965), and Thompson River (Racine 1966). Forest types described in these studies included floodplain, mixed mesophytic (cove and slope), chestnut oak, mixed oak-hickory, and pine-oak (Cooper and Hardin 1970). Unlike higher mountains to the north and west, elevation does not impact the distribution of these ecosystem types throughout the Jocassee Gorges (Cooper 1963).

Post-European Settlement Land-Use History

The Jocassee Gorges landscape has been influenced by anthropogenic activities since the Pleistocene. Early botanists William Bartram and Andre Michaux, who provided the first floristic descriptions of the area in the late eighteenth century, noted the presence of Native Americans throughout the southeastern escarpment (Doyle 1935, Harper 1958). The Cherokees occupied much of the landscape of the southern Appalachians prior to European settlement, although their numbers had been reduced dramatically by the time of contact between Bartram and Michaux due to lack of resistance to European diseases and war (Van Lear and Carroll 2001). European settlers began to inhabit the escarpment of South Carolina in droves following the cession of the land to the United States in 1816 (Brown 1971). They continued the Native American practice of annual burning of forests to improve livestock grazing and maintain openings for ease of travel and hunting (Van Lear and Carroll 2001).

From the early twentieth century to 1929, the Jocassee Gorges was owned by Appalachian Timber Company and a few smaller land-holding groups (Rankin 1998). Over their thirty year ownership, most sites within the property were logged, including creek bottoms and lower, protected slopes. These groups used a combination of horse and railroad transportation to skid logs out of the forests and into the mills, and remnants of the rail system can still be observed along streambeds, e.g., Eastatoe Creek. The

Singer Sewing Machine Company purchased the land from Appalachian Timber Company in 1929, and their subsidiary, Poinsett Lumber Company, took over management in 1939 (Rankin 1998). The primary harvesting method during this period was selective removal of desired species (oaks and yellow-poplar) for Singer sewing machine cabinets. Fire typically followed logging activity on the stands of Jocassee Gorges in the early twentieth century (Van Lear and Waldrop 1989). Because of the residual slash accumulations, these were high intensity, large-scale events that usually affected areas far beyond the timbered stand and caused significant erosion events for sites downslope (Van Lear and Carroll 2001).

Duke Power Company indirectly purchased the Jocassee Gorges property in 1963, and turned the site over to its subsidiary, Crescent Land and Timber Company, for management in 1969. Immediately, they switched timber harvesting techniques from select cutting practices instituted by earlier ownership regimes like Appalachian Timber and Singer Sewing Machine Company to clearcutting in order to increase the regeneration of desirable timber species--white oak, yellow-poplar, and loblolly pine--across the property (Van Lear and Carroll 2001). Duke Power began the Keowee-Toxaway Project in 1967, overseeing the construction of a 3000 ha reservoir at the junction of the Toxaway and Whitewater Rivers. Lake Jocassee was filled in 1973. In the early 1980's, Crescent Resources began instituting wide, no-harvest buffer zones along streams throughout the Jocassee Gorges property. According to their site records, since 1964, a total of 2563 ha of the property has been clearcut and 6620 ha of the property has been selectively logged (Rankin 1998).

The state of South Carolina began acquiring property within the Jocassee Gorges in the late 1990's from cooperative acquisition efforts made by the South Carolina Department of Natural Resources, Duke Power Company, the Richard King Mellon Foundation, and the Conservation Fund. The South Carolina Department of Natural Resources currently manages the site, and the primary management objective is the maintenance of the natural character of the area. Management of the property involves input from various stakeholders, but any management decision must work in accordance with the primary management objective of the property.

Stand Selection and Plot Establishment

Stand maps of Jocassee Gorges were provided by Crescent Resources, Inc. and digitized by Abella (2002). These maps provided detailed data regarding logging history on the tract from the past 75 years, and for each stand included silvicultural treatment, e.g., select harvest cut, clearcut, and harvest year. Age-classes and ecosystem types were identified by a combination of examining stand records and field reconnaissance during April 2003 and 2004. Tree increment cores were made in certain locations of stands to corroborate logging history information and determine stand age. Stands were delineated into one of three age-classes: 5-25 years (early successional sere [ES]), 26-50 years (middle successional sere [MS]), and 51-70 years (mid-late successional sere [MLS]). These classes were chosen to ensure adequate distribution of ecosystem types across the temporal gradient.

Abella (2002, 2003) represented Phase I of the Landscape Ecosystem Classification modeling process, whereby late-successional vegetation units (late-successional sere [LS]) and significant discriminating abiotic variables were identified. Five vegetation units, or ecosystem types, were distinguished within Jocassee Gorges based on geomorphology, soil, and vegetation characteristics (Table 3.1). These ecosystem types included: xeric oak-blueberry (XOB), xeric chestnut oak-mountain laurel (XCO), submesic oak-mixed flora (SOM), mesic hardwoods-bloodroot (MHB), and mesic hemlock-rhododendron (MHR). Within the tract, these ecosystem types represent segregations along a geomorphic gradient influenced by topographic position and soil properties. The late-successional age threshold during the Phase I modeling process was 70 years. This number is arbitrary, because of the lack of general agreement between what

constitutes old growth and steady-state forests in the southern Appalachians. Zahner (1990) argues that southern Appalachian forests begin to reach steady-state conditions at age 75, while Hutto et al. (1999) used 100 years as the lower threshold for late-successional stands in the Chauga Ridges, SC. Like most of the southern Appalachian landscape, the dominant forested vegetation across the Jocassee Gorges tract is second growth forests. There is little to no mature, or old growth, forest remaining after years of intense logging practices. However, late successional forests do exist in this heavily disturbed landscape (greater than 70 years in age) and are compositionally and structurally similar to older-aged forests within the region.

Table 3.1. Characteristics of late-successional ecosystem types described by Abella et al. (2003)

	Ecosytem type				
	XOB	XCO	SOM	MHB	MHR
No. of Plots	14	7	9	3	15
Characteristic					
Topographic Features	Ridgetops, south-facing mid-upper slopes, or convex nose slopes	North-facing hillslopes, or slope gradient > 60%	Concave stream ravines, south-facing lower slopes, or coves	Coves	Concave stream ravines, north-facing, or linear lower slope positions
Soil Features	A horizon < 15 cm thick, subsoils orange-colored	Course textured soil, thick O_{e+a} horizon, rocky slopes	Dark colored A horizon, Oe+a horizon > 1 cm thick	Dark colored A horizon, Oe+a horizon < 1 cm thick, solum > 100 cm thick	Variable, Oe+a horizon > 3 cm thick
Dominant Canopy Species	*Quercus coccinea, Quercus velutina*	*Quercus montana*	*Quercus alba, Carya spp.*	*Liriodendron tulipifera*	*Tsuga canadensis, Liriodendron tulipifera*

Digitized stand data were classified into age-classes using ESRI ArcGIS 9.0 software. Although most stands in Jocassee Gorges contain multiple ecosystem types, a single type was randomly assigned to each stand and an attempt was made to establish a single 0.1 ha plot in the center of the selected type. Ecosystem types for successional plots (ES, MS, MLS) were determined in the field by using the environmental variables that distinguished LS types in Abella (2002, 2003). If the selected ecosystem type was not found within the stand, another type was chosen based on its overall dominance within the reconnaissance area. No more than one plot was established in a single stand in order to create independence among sampling units (plots) across the landscape and minimize pseudoreplication (Hurlbert 1984). Another attempt was made to sample just those stands that had undergone clearcut logging regimes. However, difficulty locating certain ecosystem types, e.g., MHB and MHR, within clearcut stands dictated that select harvest cut stands should be included in the sampling list. Plots were established in Jocassee Gorges from April - October 2003 and April - July 2004 and a total of 63 plots were used in these analyses (Figure 3.2). Not every digitized stand included a plot, due to the following factors: difficulty of access, high proportion of planted eastern white pine, high proportion of less frequent, unclassified ecosystem units, e.g., alluvial forest types, or difficulty in stand age determination.

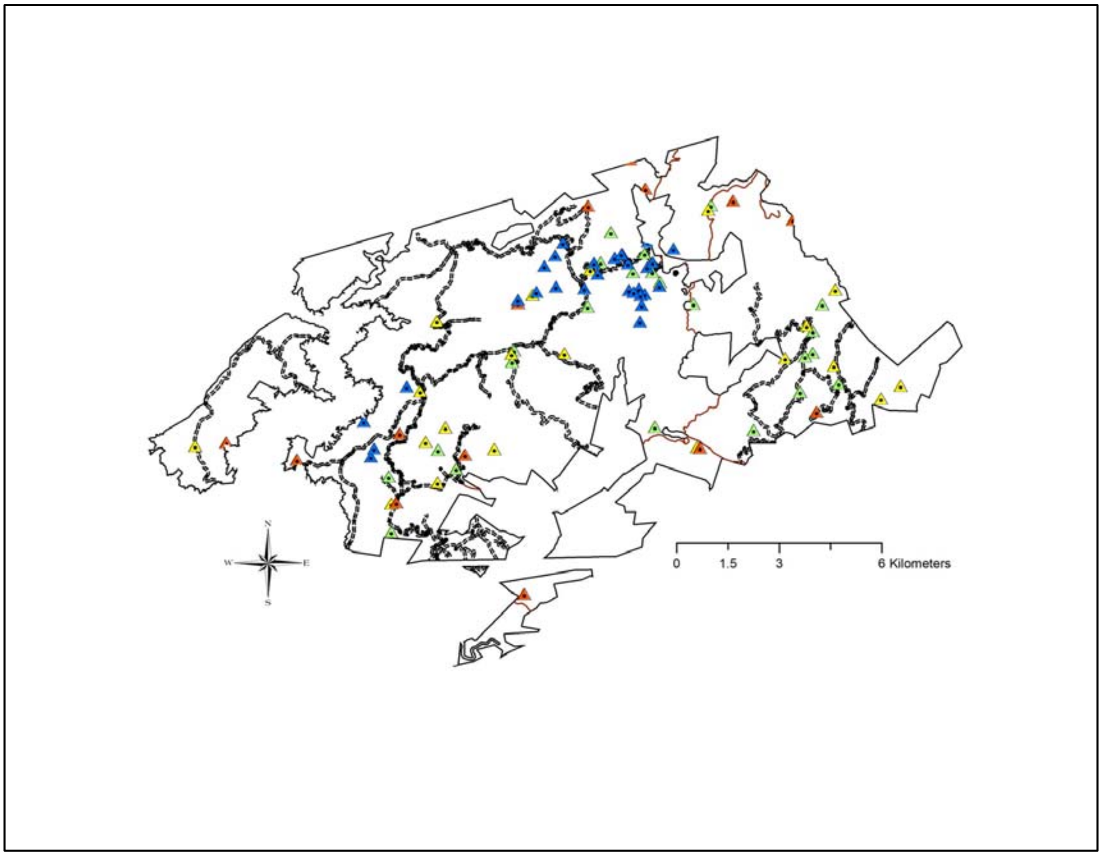

Figure 3.2. Relative location of 111 0.10 ha plots within the Jocassee Gorges property. Color codes: ES (green), MS (yellow), MLS (red), and LS (blue)

Plot Sampling

Within each established plot, vegetation, soil, and geomorphology data were sampled. To ensure that plots represented homogenous ecosystem units, site factors such as aspect, slope gradient, topographic (slope) position, and organic and A horizon depths were required to be consistent. All plot dimensions were 50 x 20 m with the long-axis established along the topographic gradient. Plots were divided into ten 10 m x 10 m subplots to inventory woody stems, ground flora, and soil variables. Geomorphology variables and plot metadata, e.g., geolocation, stand notes, etc, were taken from the center of each plot (Figure 3.3).

Woody stems were classified as trees, based on growth form definitions of Radford et al. (1968), if an individual reached and exceeded 1.37 m in height and exceeded 1 cm in diameter at that height. In the ten subplots, woody stems were tallied by species and individuals placed into 0.5 cm diameter classes. Ground flora included all species of vascular plants not recorded as woody stems, and woody stem species that failed to reach 1.37 m in height and 1 cm in diameter. Within each subplot, a complete ground flora species list was recorded. Species were assigned abundance values within a subplot by estimating areal cover class values based on Peet et al. (1998). These cover class values represent an ocular estimate of the unit area a single species' above-ground parts are projecting at all vertical positions within the 100 m^2 subplot. Cover class values include: 1 = trace, 2 = 0-1%, 3 = 1-2%, 4 = 2-5%, 5 = 5-10%, 6 = 10-25%, 7 = 25-50%, 8 = 50-75%, 9 = 75-95%, and 10 = 95-100%. Cover values of each species must be less

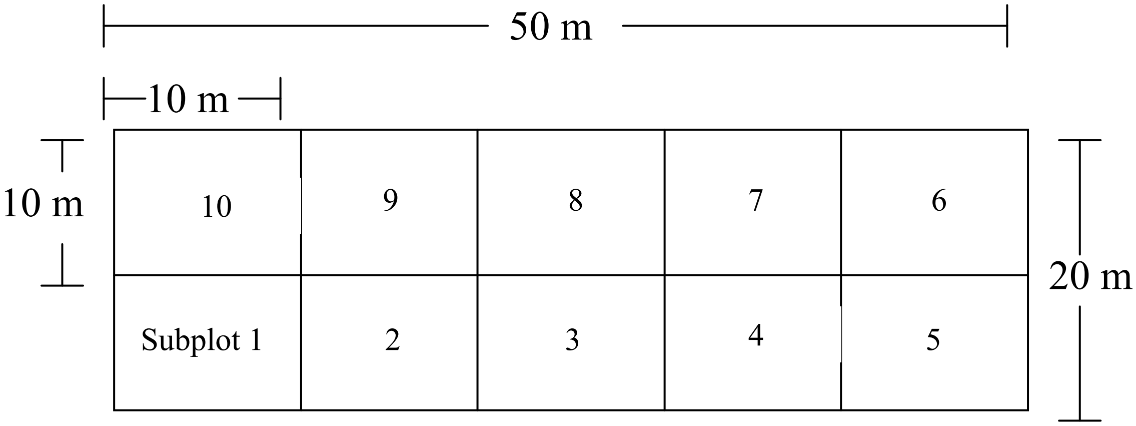

Figure 3.3. Plot design for collection of vegetation, soil, and geomorphology data in Jocassee Gorges, SC.

than or equal to 100%, although the sum of each estimate within a subplot may exceed 100%. All taxonomic concepts and authorities follow Weakley (2006).

Using a bucket auger, a complete soil profile was laid out in the center of two randomly selected subplots (Soil Survey Staff 1996). Soil variables collected at each sampling location included thickness of the Oe + Oa horizon in four cardinal directions one meter from profile hole and thickness of the A and B horizons. These data were recorded to the nearest 0.25 cm.

Geomorphology variables measured in the field included aspect, slope gradient, slope position, landform index (McNab 1993) and terrain shape index (McNab 1989). Slope position was recorded as a percentage, based on a sites relative position between ridgetops (0%) and stream bottoms (100%). Landform index is calculated by averaging eight slope gradient measurements, starting from aspect and proceeding in 45 degree increments, from plot center to skyline. Larger landform index values indicate more protection from solar radiation due to increased topographic shading, e.g., coves, deeply dissected stream ravines, while smaller values indicate increased exposure to solar radiation due to decreased topographic shading, e.g., ridgetops. Terrain shape index is a measure of the relative curvature of the site, and is calculated by averaging eight slope gradient measurements (also starting from aspect and proceeding in 45 degree increments) from plot center to a distance parallel to the ground of 20 meters. Larger terrain shape index values indicate concave sites, smaller values indicate convex sites, and values near zero indicate flat site conditions. When slope position, aspect, and slope gradient are taken into account, these indices can be used as a proxy for soil moisture units, e.g., xeric, intermediate, mesic, and hydric. Plot surface shape was also described categorically (convex, concave, or linear) for downslope and across the slope positions within the plot (Ruhe 1975). Landform values were integrated into Parker's (1982) topographic relative moisture index (TRMI), which scales values of transformed aspect, slope position, slope shape, and slope gradient into a statistic ranging from 0 (xeric) to 100 (mesic).

Data Summarization

Relative abundance values per plot were calculated for both woody stem and ground flora species and are expressed as importance value percents (IV) (Jenkins and Parker 2001, Abella et al. 2003). For woody stem species, abundance values were calculated as follows:

Abundance Value (IV) = (RD + RBA)/2

where, RD = relative density and RBA = relative basal area

RD = (Density of Species *j* / ∑ Density of All Species) x 100

RBA = (Basal Area of Species *j* / ∑ Basal Area of All Species) x 100

For ground flora species, abundance values were calculated as follows:

Abundance Value (IV) = (RCC + RF)/2

where, RCC = relative cover class and RF = relative frequency

RCC = (∑ Cover Class values of Species *j* / ∑ Cover Class values of All Species) x 100

RF = (Number of subplots with Species *j* / Subplot occurrence of All Species) x 100

All soil horizon depths were averaged from the two profiles. Slope aspect was transformed (A’) following Beers et al. (1966), resulting in values ranging from 0 - 2. Highest values indicate more northeasterly exposures (45 degrees = 2 A’), while lowest values indicate more southwesterly exposures (225 degrees = 0 A’). Geomorphic variables were integrated to produce an estimate of soil moisture availability, following Parker (1982)--the topographic relative moisture index. This index takes into account four topographic features (aspect, slope gradient, slope position, and slope shape) to produce a relative score of moisture availability. The scores range in value from 0 on mesic sites to 100 on xeric sites.

Statistical Analyses

Comparison of age-classes within ecosystem types

In order to graphically represent seral stages of ecosystem types, non-metric multidimensional scaling (NMS) was performed on XOB, XCO, SOM, MHB, and MHR datasets using PC-ORD v. 5.10 for Windows (McCune and Mefford 2006). NMS, like other ordination techniques (Principle Components Analysis, Detrended Correspondence Analysis, and Canonical Correspondence Analysis), functions as a way to arrange sample units that are distributed in complex, high-dimensional space into interpretable, low-dimensional space based on the continuum of vegetation within a dataset. The resulting 2 or 3-dimensional graphs map sample units across species space, or vice versa, whereby compositionally similar site units are close together and dissimilar site units are far apart. Unlike other ordination techniques which may unnecessarily constrain ecological datasets and lead to poor results, NMS plots sample units based on the rank order of species composition. This ordination approach does not imply that there are linear relationships among vegetation and environmental variables, and is able to illustrate gradients in datasets with high beta diversity (Minchin 1987, McCune and Grace 2002). Species importance values for both woody stem and ground flora vegetation datasets were chosen to illustrate differences in composition among age-types within site types, using Sørenson (Bray-Curtis) distance measurements. Species occurring in < 3 plots were removed for analysis. A random starting configuration was used, and the best solution was chosen among 50 runs with original data and 250 runs with randomized data (Monte Carlo significance test, p-values < 0.005). Plots and selected species were displayed against two axes that represented the highest variance within the dataset. Biplot scores for environmental variables were calculated and plotted within the ordination space. Correlations were examined between selected environmental variables and the ordination axes.

Ecosystem types were also compared using nonparametric multi-response permutation procedure (MRPP) within each site type, also using PC-ORD v. 5.10. MRPP is similar to multivariate analysis of variance and discriminant analysis in that all three can be used to test the hypothesis of no differences between two or more groups. However, MRPP performs much better with ecological data because it does not require normality or homogenous variances to meet statistical assumptions. This multivariate hypothesis testing technique provides a test statistic (*T*), measure of effect size, or "chance-corrected in group agreement" (*A*), and *p*-value (McCune and Grace 2002). The test statistic (*T*) is used to illustrate the differences between groups, with increased negative values representing stronger separation. When the effect size statistic (*A*) equals 0, group heterogeneity is no more or less than expected by chance; as *A* approaches 1, group composition becomes more similar; finally, if $A < 0$, group heterogeneity is less than expected by chance. For ecological datasets, *A* values > 0.3 are considered high (McCune and Grace 2002). MRPP was used on ground flora and woody stem vegetation datasets of each ecosystem type to determine how composition differed among age-classes.

Finally, mean values of environmental variables (soil and landform) were compared using one-way analysis of variance and Dunnett's pairwise multiple comparison test was used for comparisons between age-classes of ecosystem types ($\alpha = 0.05$). Variables that did not meet the assumptions of normality or homogeneity of variance were arcsine transformed prior to analysis. These univariate procedures were performed with SAS v. 9.2.

Comparison of age-classes across the Jocassee Gorges landscape

To assess how ecosystem types segregate across the landscape in response to long-term timber harvesting activities, NMS was performed on ES, MS, MLS, LS datasets separately using PC-ORD v. 5.10 for Windows (McCune and Mefford 2006). Species importance values for both woody stem and ground flora vegetation datasets were chosen to illustrate differences in composition among site types within age-classes, using Sørenson (Bray-Curtis) distance measurements. Species occurring in < 3 plots were removed for analysis. A random starting configuration was used, and the best solution was chosen among 50 runs with original data and 250 runs with randomized data (Monte Carlo significance test, p-values < 0.005). Plots were displayed against two axes that represented the highest variance within the dataset. Biplot scores for environmental variables were calculated and plotted within the ordination space. Correlations were examined between selected environmental variables and the ordination axes.

Ecosystem types were also compared using two multivariate grouping techniques: 1) nonparametric multi-response permutation procedure (MRPP) and 2) indicator species analysis (ISA). ISA is a technique which produces indicator values for each species in an *a priori* defined group, based on the proportional abundance and frequency of a species in relation to its abundance in all groups (Dufrene and Legendre 1997). An ideal indicator species of a group is one that is simultaneously faithful and exclusive to that group. Indicator values range from 0 (no group membership) to 100 (ideal membership). These values are tested for statistical significance using a Monte Carlo randomization technique, and only those species with a p-value < 0.05 were listed as indicator species of a certain ecosystem type (McCune and Grace 2002). MRPP and ISA were used on ground flora and woody stem vegetation datasets of each age-class to determine how composition differed among ecosystem types.

Finally, mean values of environmental variables (soil and landform) were compared using one-way analysis of variance and Tukey's multiple comparison test was used for comparisons between ecosystem types within age-classes ($\alpha = 0.05$). Variables that did not meet the assumptions of normality or homogeneity of variance were arcsine transformed prior to analysis. These univariate procedures were performed with SAS v. 9.2.

Ecological species group analysis

Species groups were developed from reference stands (LS) of Jocassee Gorges and multivariate comparison procedures yielded 11 ground flora groups (50 species) and six woody stem groups (19 species) that segregated across environmental gradients within the Jocassee Gorges landscape (Abella and Shelburne 2004). To determine if ecological species groups differed between age-classes of similar ecosystem types, the mean importance values of each group within successional age-classes were compared with the mean value of reference stands using one-way analysis of variance. Dunnett's pairwise multiple comparison tests were used to compare mean values of successional age-classes to those of reference stands within the same ecosystem type. Canonical correlation (CANCOR) techniques developed in Abella and Shelburne (2004) to explore associations between species groups were used with successional age-class datasets in order to determine the degree to which species groups shift over a temporal gradient. CANCOR is a multivariate analysis technique for analyzing the relationship between two or more sets of variables, and is similar to Principle Components Analysis (PCA) in that both techniques seek to find variation within one set of variables that are strongly correlated with a second set of variables (McGarigal et al. 2000). Linear combinations of the variables of each set are calculated, producing a range of values between -1 (a perfect negative correlation) to 1 (a perfect positive correlation) (Khattree and Naik 2000). For each age-class, CANCOR was run on a matrix of Spearman rank correlations between each pair of individual species. Similar to Abella and Shelburne (2004), only the first canonical variate was used for interpretation.

Species diversity comparisons

Diversity indices were calculated for each combination of age-class and ecosystem type and compared using univariate statistical procedures in order to provide baseline summarizations within the overall plot by vegetation dataset. Species diversity metrics are used to quantitatively express the abundance and distribution of species within and between sample units (i.e. plots, ecosystem units). Whittaker (1972) describes three levels of diversity: *alpha*, diversity within sample units; *beta*, diversity across sample units; and *gamma*, diversity in the total set of sample units. There are numerous diversity measures to choose from, each with a multitude of critics in the vegetation science literature. For the most part, diversity is a composite of the number of species per unit area (species richness) and the degree to which the species is distributed across sample units (species evenness). The two most commonly used diversity indices are Simpson's index and the Shannon-Weiner index. The Simpson index places more emphasis on abundant and less emphasis on rare species within a dataset. This index is less likely to illustrate sample unit differences because rare species are more variable across space (Barbour et al. 1999). The Shannon-Weiner index is a predictive quantifier, and measures the degree of certainty achieved by predicting which species an individual at random will belong. As the number of species and their distribution increases within a sample unit, the higher the Shannon-Weiner index. For this study, species richness (S), the Shannon-Weiner index (H'), and species evenness (E) were calculated per plot and used to compare vegetation changes across age-classes of ecosystem types and within age-classes. Formulas for each metric are as follows:

$S = \sum \text{species}$

$H' = - \sum p_i \ln p_i$

where p_i = the proportion of individuals or the abundance of each species expressed as a proportion of total importance value.

$E = H' / \ln(S)$

A one-way analysis of variance was used to determine how the vegetation of different age-classes compared within ecosystem types. To determine how the vegetation differs between age-classes (ES, MS, MLS) and LS, reference plots, Dunnett's pairwise multiple comparison tests were used on mean diversity values within each type (α = 0.05).

CHAPTER FOUR

RESULTS

A total of 280 ground flora species and 46 woody stem species were identified in 63 0.10 ha successional plots (ES, MS, MLS) and 48 0.10 ha reference plots (LS) within the Jocassee Gorges (Table A.1). The most widespread ground flora species was red maple (*Acer rubrum* L.), which occurred in 100% of the plots. Other widespread species occurring in the ground flora strata included hickory species (98%), muscadine (*Vitis rotundifolia* var. *rotundifolia* Michaux) (93%), rattlesnake orchid (*Goodyera pubescens* [Willd.] R. Brown) (86%), common greenbrier (*Smilax rotundifolia* L.) (86%), Christmas fern (*Polystichum acrostichoides* [Michaux] Schott) (83%), yellow-poplar (81%), and blackgum (*Nyssa sylvatica* Marshall) (80%). Forty seven species (< 20%) occurred only once in the ground flora dataset. The most widespread woody stem species was red maple, which also occurred in 100% of the plots. Other widespread woody stem species included yellow-poplar (89%), sourwood (89%), hickory species (87%), blackgum (80%), and flowering dogwood (79%). Five species tallied as woody stems occurred in a single plot, including yellow buckeye (*Aesculus flava* Solander), yellow birch (*Betula alleghenensis* Britton), red mulberry (*Morus rubra* L.), loblolly pine (*Pinus taeda* L.), and slippery elm (*Ulmus rubra* Muhl.). Vegetation data, summarized by species importance values and constancy across ecosystem types by age-class, are located in Appendices B and C. Ecosystem types segregated across the landscape in repeating combinations of vegetation, soils, and landform (Table 4.1). Furthermore, age-classes of

Table 4.1. Mean ± SE of selected environmental variables for successional communities of Jocassee Gorges. Mean values of ES, MS, and MLS age-classes were compared to those of reference (LS) plots using one-way ANOVA with Dunnett's multiple comparison test (row comparison); means within an age-class were compared using ANOVA with Tukey's comparison test (column comparison).

Variable	Site	ES	MS	LS	LLS
a_dep	XOB	9 ± 4 a	7 ± 2 a	8 ± 5 a	12 ± 4 a
	XCO	9 ± 4 a	8 ± 3* a	6 ± 2* a	14 ± 4 a
	SOM	11 ± 6 a	9 ± 2 a	14 ± 3 a	17 ± 5 a
	MHB	11 ± 11 a	16 ± 11 a	15 ± 6 a	30 ± 11 b
	MHR	11 ± 7 a	8 ± 8* a	10 ± 10 a	18 ± 6 a
b_dep	XOB	59 ± 19 a	28 ± 4 a	49 ± 42 a	47 ± 9 a
	XCO	39 ± 28 a	27 ± 6 a	25 ± 7 a	44 ± 9 a
	SOM	36 ± 17 a	48 ± 28 a	53 ± 6 a	46 ± 15 a
	MHB	60 ± 34 a	35 ± 29* a	43 ± 22 a	90 ± 12 b
	MHR	42 ± 32 a	37 ± 24 a	44 ± 8 a	44 ± 20 a
lfi	XOB	10 ± 1 a	11 ± 7 a	10 ± 5 a	9 ± 4 a
	XCO	15 ± 7 ab	13 ± 3 a	17 ± 3 ab	13 ± 2 ab
	SOM	16 ± 3 ab	13 ± 2 a	17 ± 3 ab	16 ± 3 bc
	MHB	14 ± 3 ab	21 ± 3 b	17 ± 6 ab	19 ± 3 bc
	MHR	19 ± 4 b	23 ± 1* b	23 ± 1* b	18 ± 3 c
o_dep	XOB	2.7 ± 1.2 ab	3.3 ± 1.1 a	3.0 ± 1.8 ab	3.0 ± 0.0 d
	XCO	5.4 ± 1.3 b	4.1 ± 1.6 a	4.9 ± 1.3 b	3.7 ± 0.0 e
	SOM	1.6 ± 1.3 a	2.6 ± 2.0 a	1.5 ± 1.3 ab	1.9 ± 0.0 b
	MHB	0.4 ± 0.0 a	0.4 ± 0.4 a	0.2 ± 0.2* a	0.8 ± 0.0 a
	MHR	2.9 ± 1.7 ab	3.7 ± 2.4 a	4.1 ± 3.4 ab	2.3 ± 0.0 c
trmi	XOB	29 ± 6 a	29 ± 11 a	27 ± 13 a	29 ± 12 a
	XCO	40 ± 7 a	42 ± 17 ab	30 ± 10 ab	40 ± 11 ab
	SOM	55 ± 8 b	59 ± 5 bc	55 ± 12 bc	51 ± 11 bc
	MHB	67 ± 11 b	68 ± 6 c	64 ± 10 c	65 ± 3 bc
	MHR	62 ± 11 b	68 ± 9 c	55 ± 10 bc	60 ± 16 c

Variable codes: a_dep (A-horizon thickness, cm), b_dep (B-horizon thickness, cm), lfi (Landform Index), o_dep (O-horizon thickness, cm), trmi (Topographic Relative Moisture Index)

* Mean significantly differs from reference plots ($p < 0.05$)

Groups within columns are significantly different without shared letters ($p < 0.05$)

each ecosystem type were distinguished due to the unique environmental conditions related to moisture status of each type.

Comparison of Age-Classes Within Ecosystem Types

NMS selected a three-dimensional solution for both xerophytic (XOB and XCO) and mesophytic (SOM, MHB, and MHR) datasets (Table 4.2). Final stress values of all ten

ordinations fell between Clarke's (1993) suggestion of between 10 and 20 for interpretability of ecological data. Species differences for both ground flora and woody stem datasets were effectively displayed in each ecosystem type (Figures 4.1-10). Typically, environmental variables were poorly correlated with ordination axes. This was an expected result due to the fact that stands were chosen to sample based on their environmental characteristics matching reference site conditions. Because of these poor correlations, species and plots separation was more likely a result of disturbance history. The most significant environmental differences between age-classes were the change in depths of both the organic and A-horizon. A-horizon depths were consistently larger in LS age-classes (Table 4.1). Although these variables were often tested *a priori* within a stand in order to define an ecosystem type, there could have been considerable soil profile variation between where a sample was taken in the stand and where a sample was taken within the plot. MRPP results suggested significant trends in ground flora species composition between age-classes of all ecosystem types (Table 4.3). Differences in

Table 4.2. Ordination results for non-metric multidimensional scaling analysis of xerophytic and mesophytic stands of distinct age-classes within Jocassee Gorges. The summary table provides eigenvalues (stress and axes variance) and Pearson Correlations of selected environmental variables for each of the ordination axes.

	Final Stress	Axis 1	Axis 2	Axis 3
XOB - ground flora	11.9	0.26	0.21	0.33
O-horizon depth	---	0.75	-0.23	-0.52
A-horizon depth	---	-0.26	0.38	0.58
TRMI	---	0.01	-0.21	0.03
XOB - woody stems	10.1	0.27	0.26	0.35
XCO - ground flora	8.4	0.46	0.19	0.17
O-horizon depth	---	-0.54	0.22	0.50
A-horizon depth	---	0.85	0.01	0.05
LFI	---	-0.29	0.47	-0.01
XCO - woody stems	8.4	0.32	0.19	0.40
SOM - ground flora	11.0	0.41	0.19	0.26
O-horizon depth	---	-0.54	0.41	0.01
A-horizon depth	---	0.18	0.33	-0.65
SOM - woody stems	14.2	0.09	0.30	0.29
MHB - ground flora	7.8	0.11	0.09	0.44
O-horizon depth	---	-0.35	0.32	-0.01
A-horizon depth	---	-0.59	0.40	-.028
MHB - woody stems	8.3	0.38	0.26	0.18
MHR - ground flora	13.1	0.37	0.28	0.18
O-horizon depth	---	0.64	0.17	0.13
A-horizon depth	---	-0.11	-0.01	0.67
LFI	---	0.54	-0.15	-0.10
MHR - woody stems	10.3	0.17	0.53	0.15

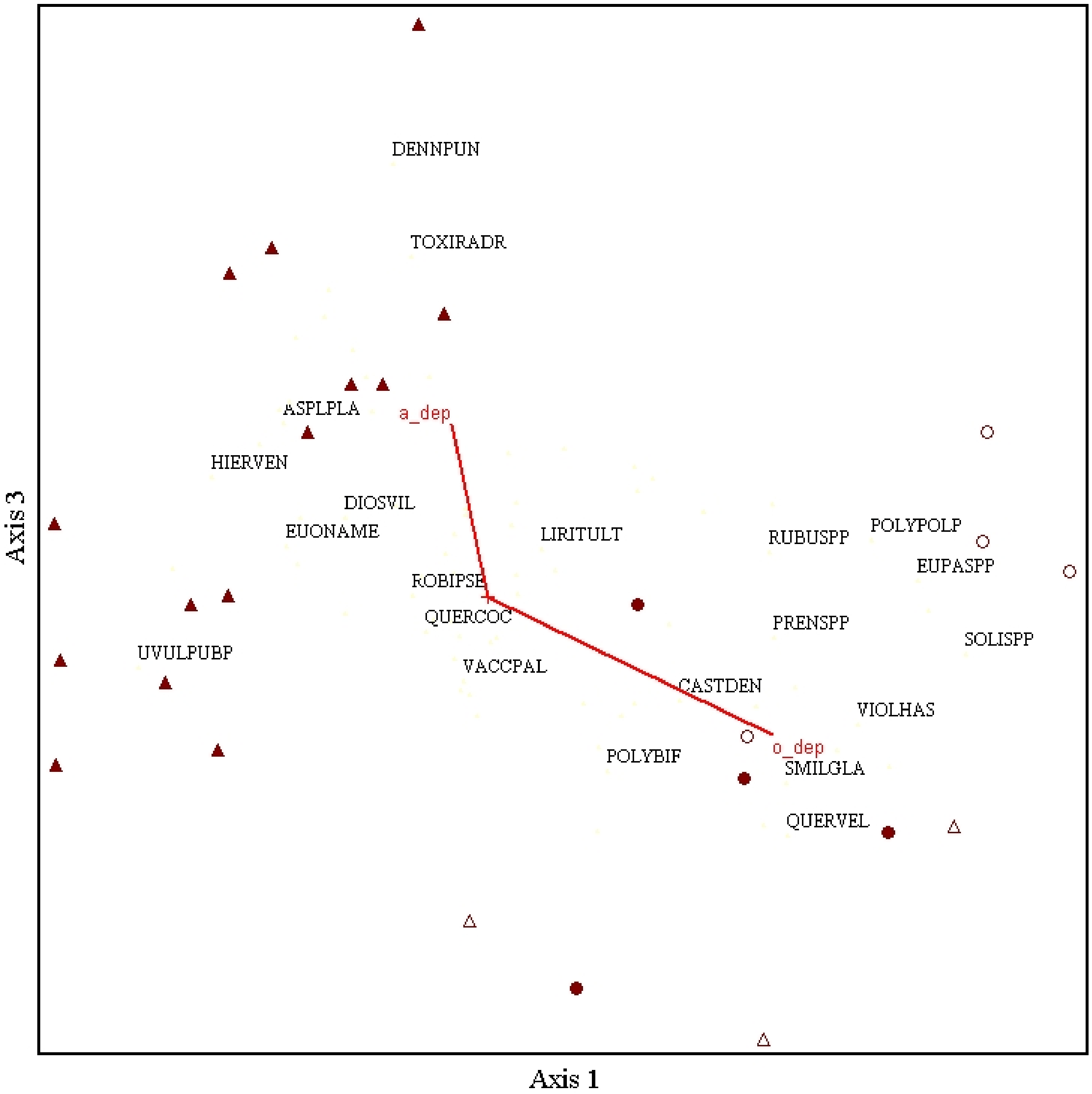

Figure 4.1: Non-metric multidimensional scaling ordination of ES (open circle), MS (open triangle), MLS (filled circle), and LS (filled triangle) xeric oak-blueberry (XOB) plots in ground flora space within Jocassee Gorges. Axis 1 and 3 are used to display plots in 2-dimensional ordination space. Designated species are also displayed. Species codes are composed of the first four letters of the genus and first three letters of the species epithet, and first letter of the variety if necessary. Environmental variables: a_dep, A horizon thickness; and o_dep, $O_e + O_a$ horizon thickness.

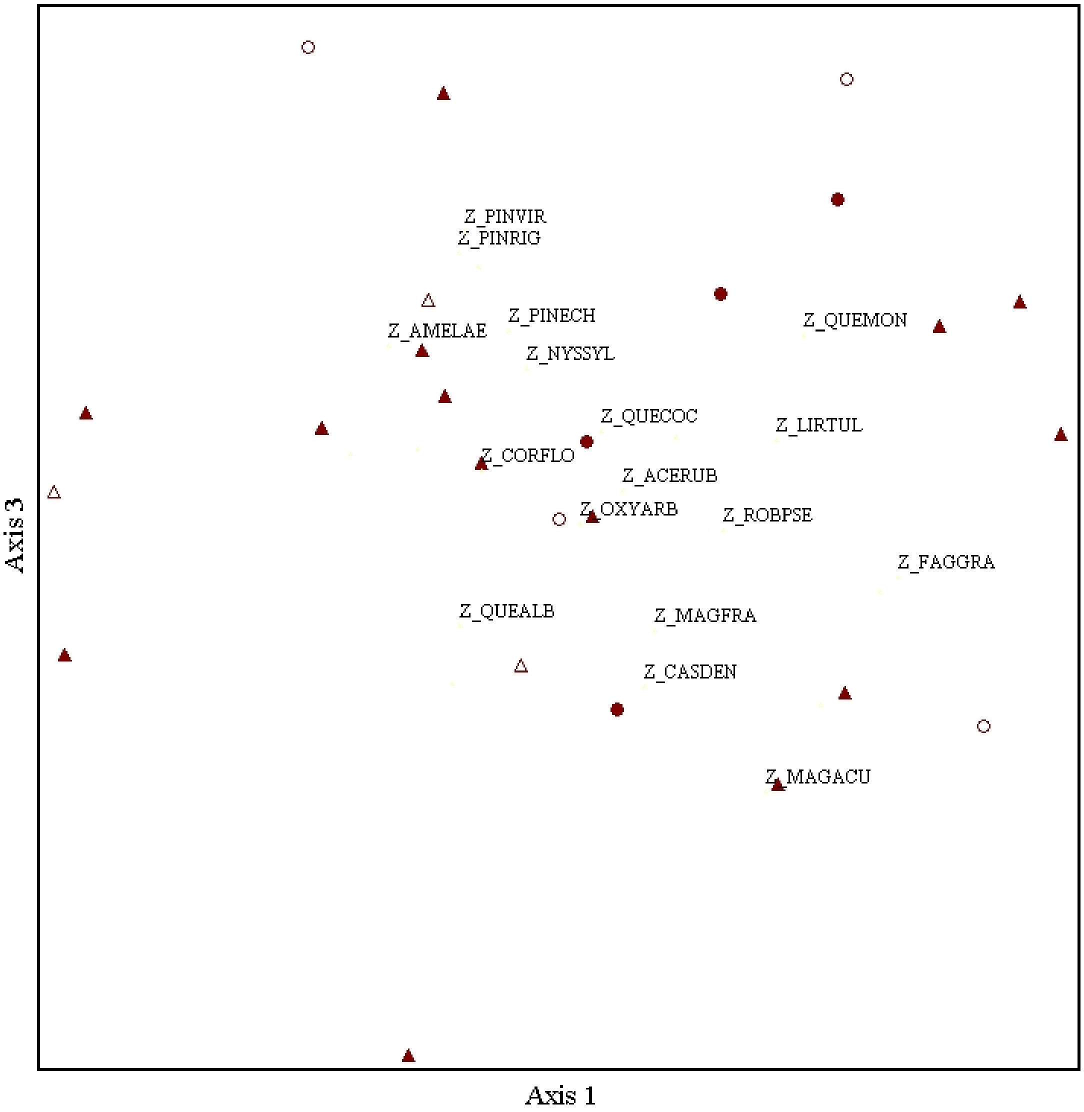

Figure 4.2: Non-metric multidimensional scaling ordination of ES (open circle), MS (open triangle), MLS (filled circle), and LS (filled triangle) xeric oak-blueberry (XOB) plots in woody stem space within Jocassee Gorges. Axis 1 and 3 are used to display plots in 2-dimensional ordination space. Designated species are also displayed. Species codes are composed of the text string "Z_", the first three letters of the genus, and first three letters of the species epithet.

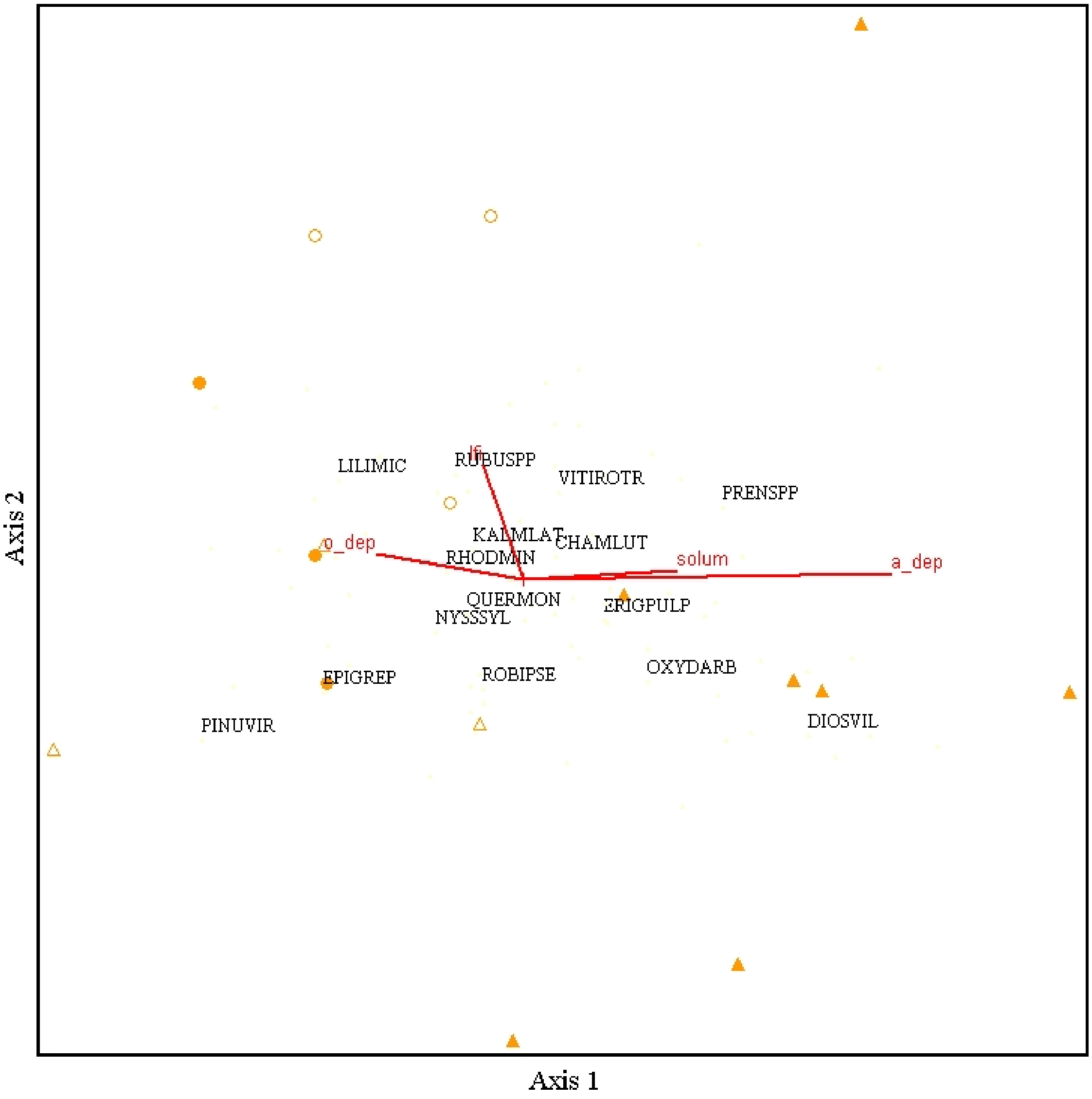

Figure 4.3: Non-metric multidimensional scaling ordination of ES (open circle), MS (open triangle), MLS (filled circle), and LS (filled triangle) xeric chestnut oak - mountain laurel (XCO) plots in ground flora space within Jocassee Gorges. Axis 1 and 2 are used to display plots in 2-dimensional ordination space. Designated species are also displayed. Species codes are composed of the first four letters of the genus and first three letters of the species epithet, and first letter of the variety if necessary. Environmental variables: a_dep, A horizon thickness; o_dep, $O_e + O_a$ horizon thickness; lfi, landform index; and solum, solum thickness.

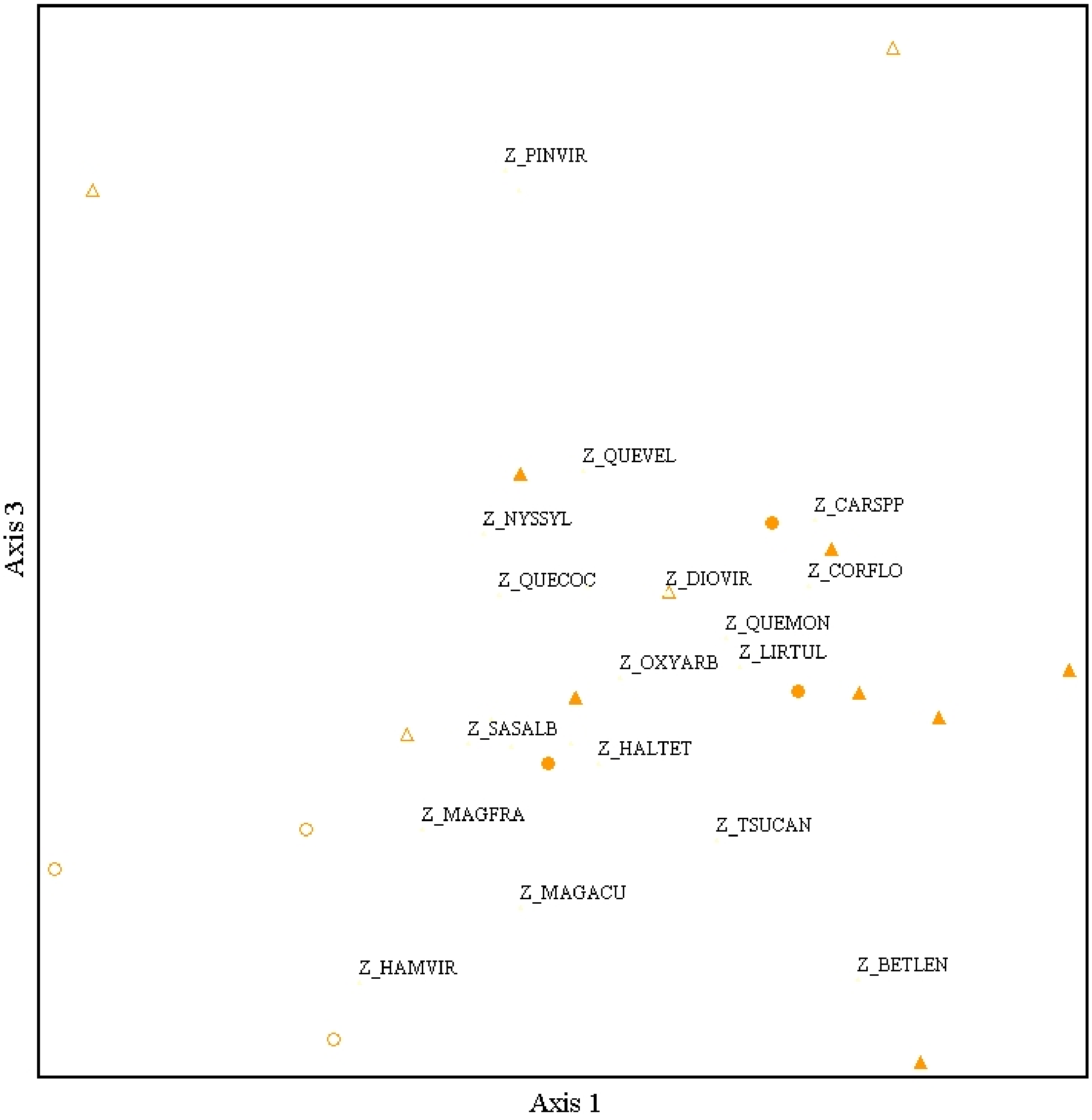

Figure 4.4: Non-metric multidimensional scaling ordination of ES (open circle), MS (open triangle), MLS (filled circle), and LS (filled triangle) xeric chestnut oak - mountain laurel (XCO) plots in woody stem space within Jocassee Gorges. Axis 1 and 3 are used to display plots in 2-dimensional ordination space. Designated species are also displayed. Species codes are composed of the text string "Z_", the first three letters of the genus, and first three letters of the species epithet.

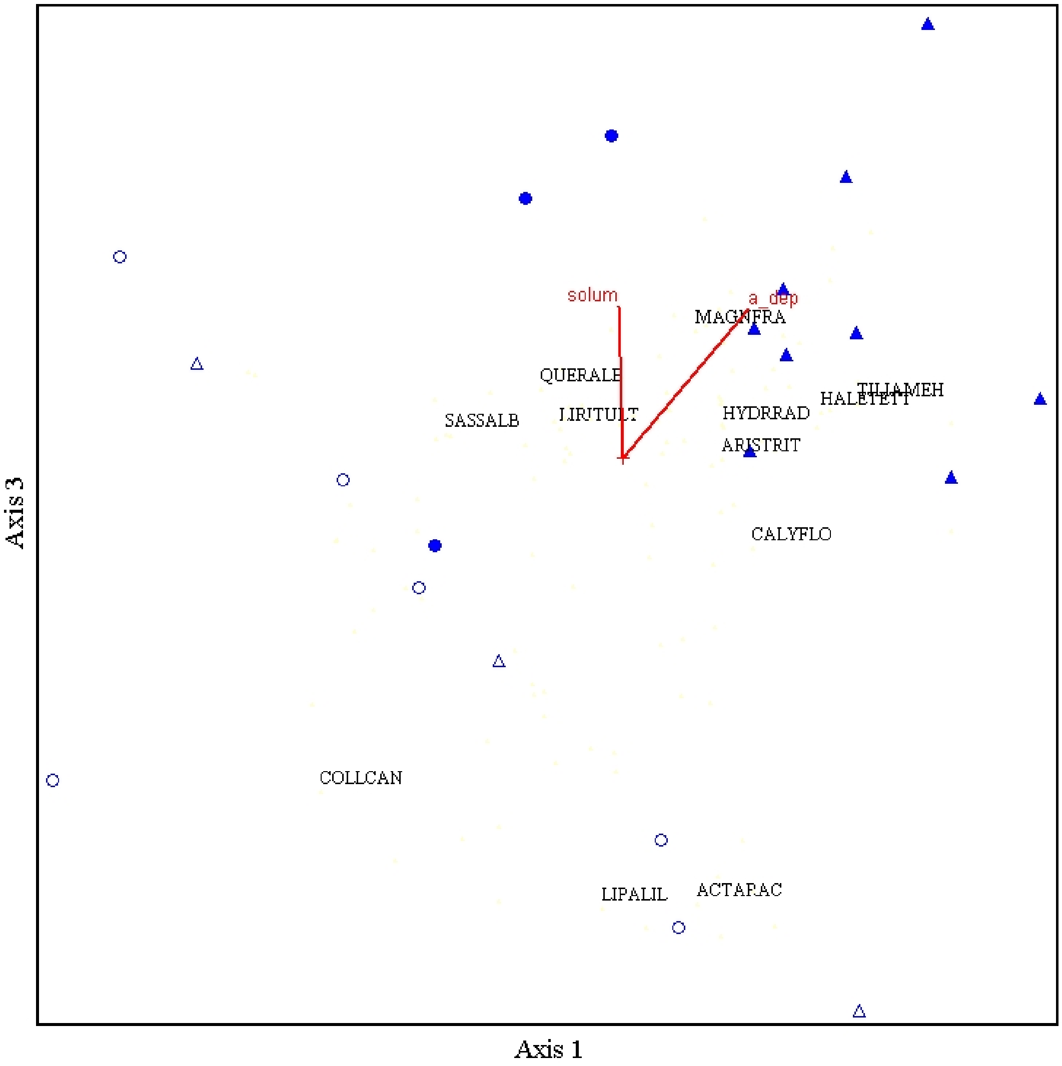

Figure 4.5: Non-metric multidimensional scaling ordination of ES (open circle), MS (open triangle), MLS (filled circle), and LS (filled triangle) submesic oak - mixed flora (SOM) plots in ground flora space within Jocassee Gorges. Axis 1 and 3 are used to display plots in 2-dimensional ordination space. Designated species are also displayed. Species codes are composed of the first four letters of the genus and first three letters of the species epithet, and first letter of the variety if necessary. Environmental variables: a_dep, A horizon thickness; and solum, solum thickness.

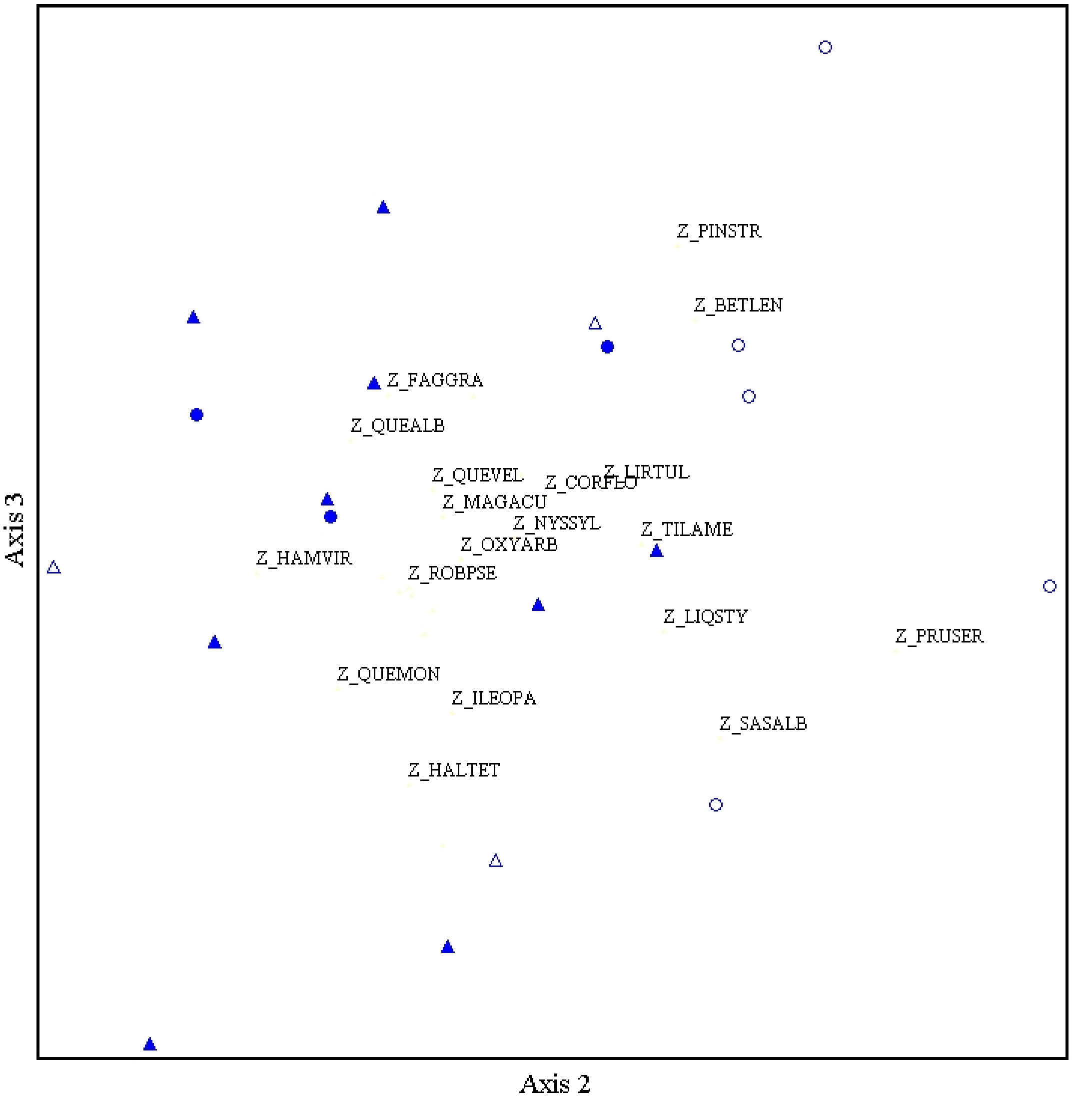

Figure 4.6: Non-metric multidimensional scaling ordination of ES (open circle), MS (open triangle), MLS (filled circle), and LS (filled triangle) submesic oak - mixed flora (SOM) plots in woody stem space within Jocassee Gorges. Axis 2 and 3 are used to display plots in 2-dimensional ordination space. Designated species are also displayed. Species codes are composed of the text string “Z_”, the first three letters of the genus, and first three letters of the species epithet.

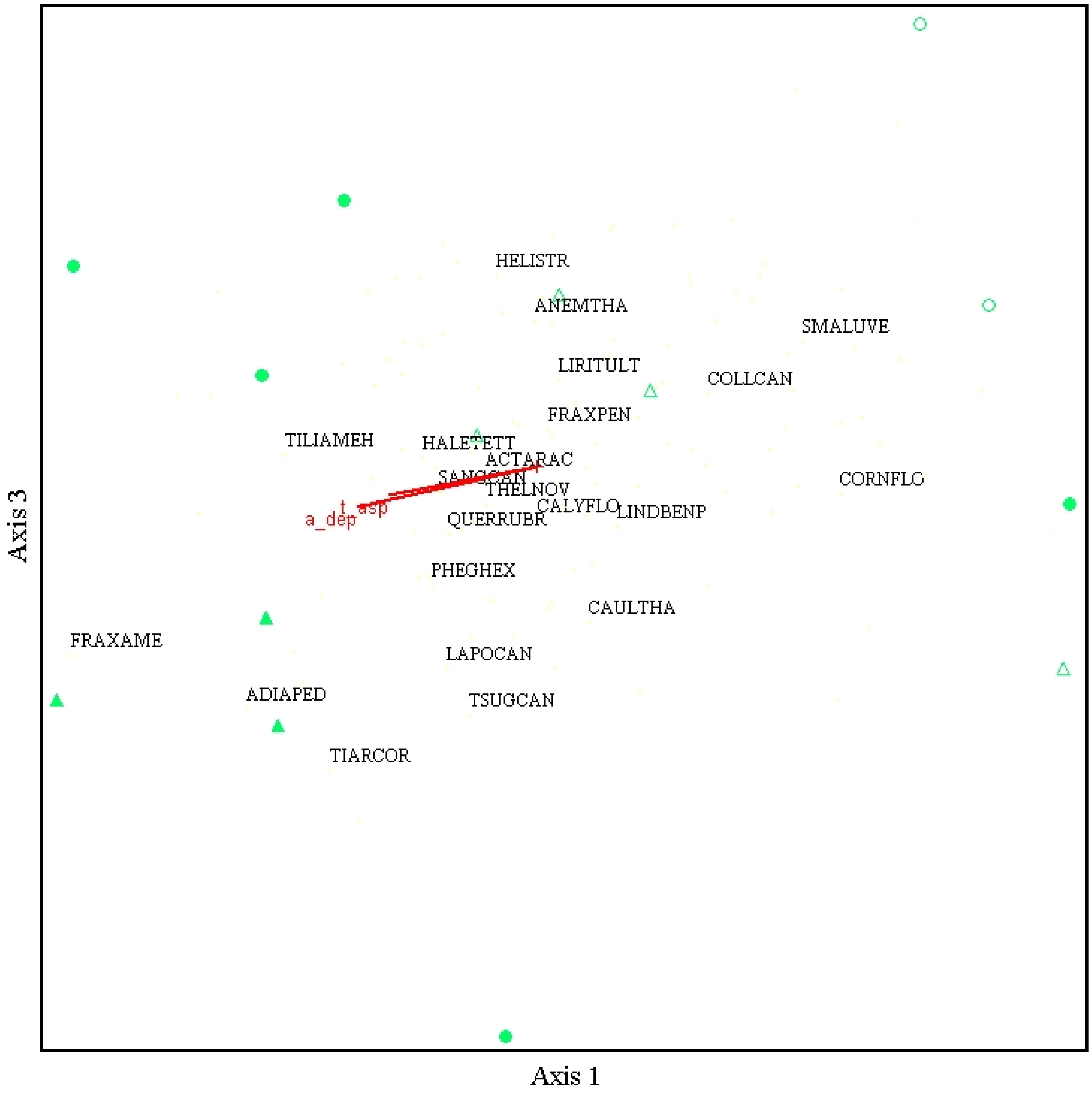

Figure 4.7: Non-metric multidimensional scaling ordination of ES (open circle), MS (open triangle), MLS (filled circle), and LS (filled triangle) mesic hardwood - bloodroot (MHB) plots in ground flora space within Jocassee Gorges. Axis 1 and 3 are used to display plots in 2-dimensional ordination space. Designated species are also displayed. Species codes are composed of the first four letters of the genus and first three letters of the species epithet, and first letter of the variety if necessary. Environmental variables: a_dep, A horizon thickness; and t_asp, transformed aspect.

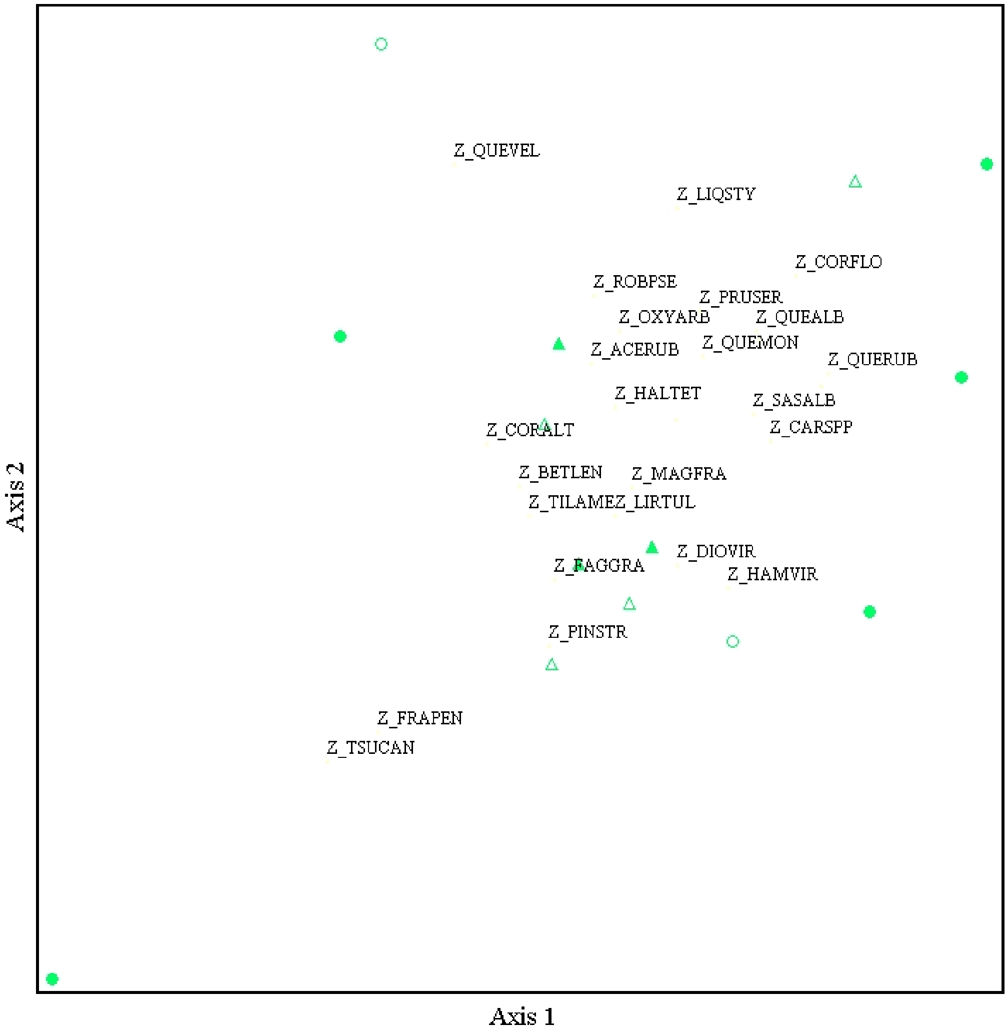

Figure 4.8: Non-metric multidimensional scaling ordination of ES (open circle), MS (open triangle), MLS (filled circle), and LS (filled triangle) mesic hardwood - bloodroot (MHB) plots in woody stem space within Jocassee Gorges. Axis 1 and 2 are used to display plots in 2-dimensional ordination space. Designated species are also displayed. Species codes are composed of the text string "Z_", the first three letters of the genus, and first three letters of the species epithet.

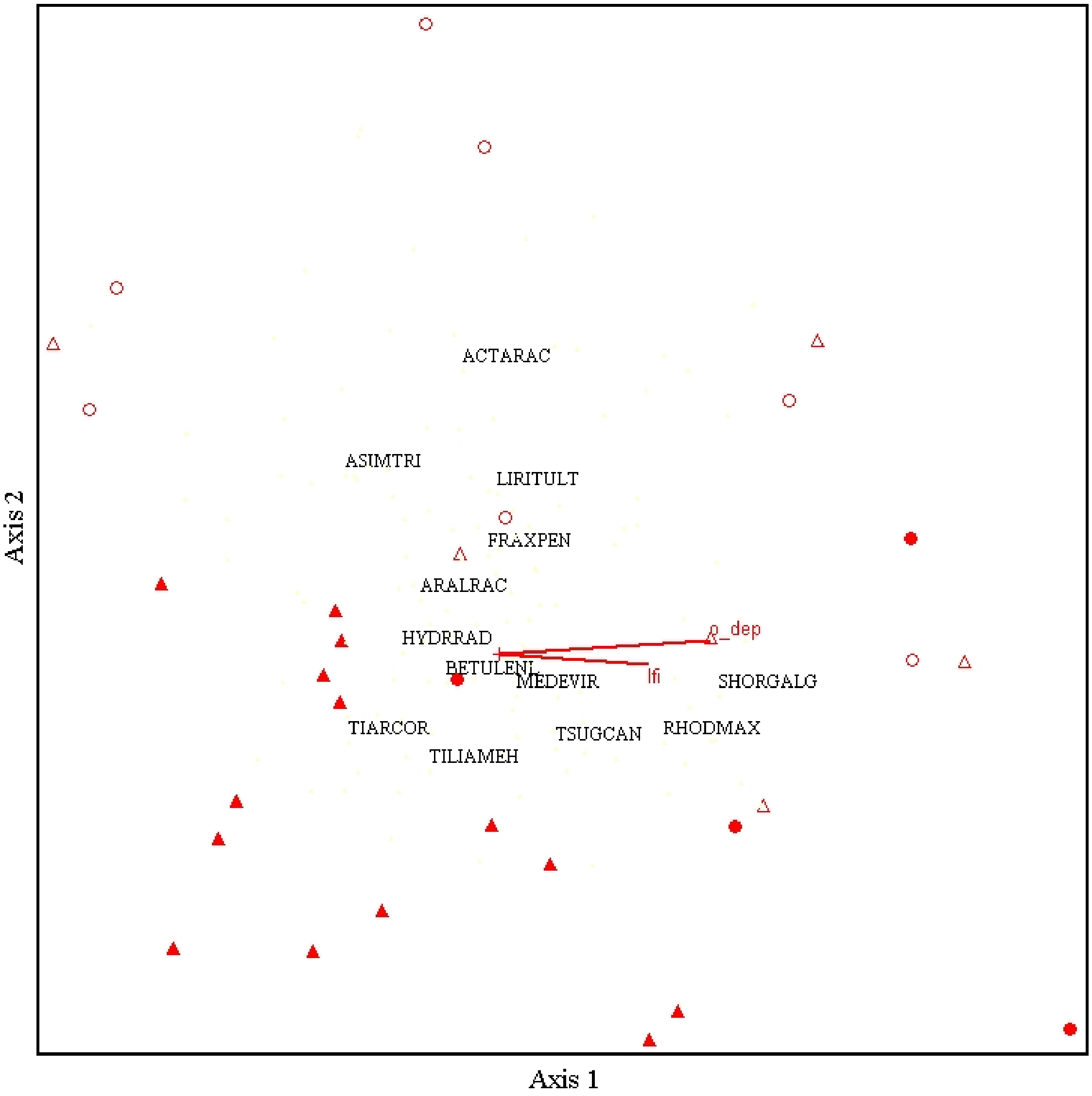

Figure 4.9: Non-metric multidimensional scaling ordination of ES (open circle), MS (open triangle), MLS (filled circle), and LS (filled triangle) mesic hemlock - rhododendron (MHR) plots in ground flora space within Jocassee Gorges. Axis 1 and 2 are used to display plots in 2-dimensional ordination space. Designated species are also displayed. Species codes are composed of the first four letters of the genus and first three letters of the species epithet, and first letter of the variety if necessary. Environmental variables: o_dep, $O_e + O_a$ horizon thickness; and lfi, landform index.

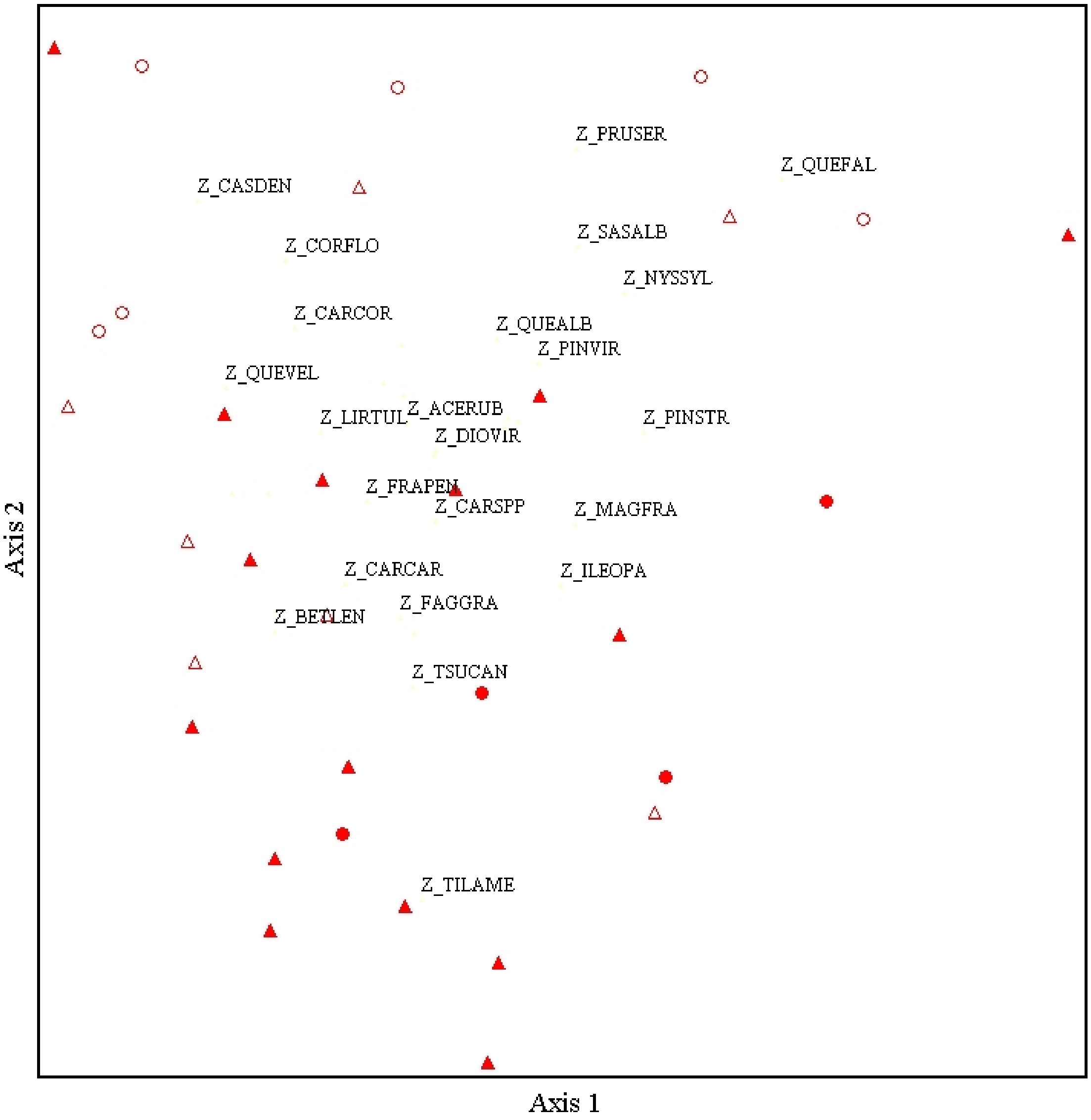

Figure 4.10: Non-metric multidimensional scaling ordination of ES (open circle), MS (open triangle), MLS (filled circle), and LS (filled triangle) mesic hemlock - rhododendron (MHR) plots in woody stem space within Jocassee Gorges. Axis 1 and 2 are used to display plots in 2-dimensional ordination space. Designated species are also displayed. Species codes are composed of the text string "Z_", the first three letters of the genus, and first three letters of the species epithet.

Table 4.3. MRPP results from comparing age-classes within Jocassee Gorges' ecosystem types.

	T	*A*	p value	Age-Class Comparison
XOB				
ground	-7.09	0.3434	< 0.0001*	ES[a] MS[a] MLS[a] LS[b]
woody	-0.19	0.0084	0.3905	ES[a] MS[a] MLS[a] LS[a]
XCO				
ground	-4.04	0.2361	0.0004*	ES[a] MS[b] MLS[ab] LS[c]
woody	-4.01	0.2654	0.0009*	ES[a] MS[b] MLS[b] LS[b]
SOM				
ground	-5.18	0.2024	< 0.0001*	ES[a] MS[ab] MLS[b] LS [c]
woody	-2.89	0.1259	0.0071*	ES[a] MS[ab] MLS[b] LS[b]
MHB				
ground	-2.36	0.1333	0.0166*	ES[a] MS[a] MLS[a] LS[b]
woody	1.35	-0.1045	0.9255	ES[a] MS[a] MLS[a] LS[a]
MHR				
ground	-4.54	0.1189	0.0003*	ES[a] MS[a] MLS[a] LS[b]
woody	-4.86	0.1686	0.0005*	ES[a] MS[b] MLS[c] LS[bc]

composition were less apparent between age-classes using the woody stem species dataset. A comparison of age-classes within individual ecosystem types follows:

Xeric oak - blueberry: NMS and MRPP results using the ground flora dataset suggested a significant separation between LS plots and successional ES, MS, and MLS plots, but no clear separation using the woody stem dataset (Figures 4.1 and 4.2, Table 4.3). Ground flora species strongly associated with LS plots included ebony spleenwort (*Asplenium platyneuron* L.), veiny hawkweed (*Hieracium venosum* L.), and Appalachian bellwort (*Uvularia puberula* Michaux var. *puberula*), while species associated with successional plots included American chestnut, blackberry (*Rubus spp.* L.), and goldenrod (*Solidago spp.* L.). All plots across each age-class were dominated by hillside blueberry (*Vaccinium pallidum* Aiton), scarlet oak (*Quercus coccinea* Muenchh.), black locust, and yellow-poplar in the ground flora strata. Woody stem composition did not favor individual age-classes within the XOB type. Dominants across all classes included scarlet oak, red maple, sourwood, and black locust. Ordination revealed a notable pattern of higher A-horizon and lower organic depths in LS stands (Figure 4.1). Landform values were constant across all age-classes.

Xeric chestnut oak - mountain laurel: NMS and MRPP results using the ground flora dataset suggested a significant separation between LS plots and successional ES, MS, and MLS plots, as well as separation between the successional age-classes (ES versus MS) (Figure 4.3, Table 4.3). Ground flora species strongly associated with LS plots included common wild yam (*Dioscorea villosa* L.), robin's-plantain (*Erigeron pulchellus* Michaux var. *pulchellus*), sourwood, and common greenbrier. Species strongly associated with ES and MLS plots included naked tick-trefoil (*Desmodium nudiflorum* L.), bear huckleberry (*Gaylussacia ursina* [Curtis] Torrey and A. Gray ex A. Gray), witch-hazel (*Hamamelis virginiana* L. var. *virginiana*), and blackberry, while Virginia pine (*Pinus virginiana* Miller), white oak (*Quercus alba* L.), and summer grape (*Vitis aestivalis* Michaux) were strong indicators for MS plots. Multivariate analysis of the woody stem dataset suggested separation between ES plots and the other age-classes (Figure 4.4, Table 4.3). Woody species associated with ES plots included red maple, witch-hazel, and cucumber magnolia (*Magnolia acuminata* L.). Older successional classes were dominated by white oak, chestnut oak (*Quercus montana* Willd.), and flowering dogwood. A pattern similar to the one detected in XOB ecosystem type was noticed between A-horizon depths of reference and earlier successional stands (Figure 4.3). Depth values were higher in reference stands than earlier successional stands.

Submesic oak - mixed flora: This ecosystem type represents an intermediate hydrological unit within the Jocassee Gorges landscape, and contains species of both xeric and mesic types. However, as noted by Abella (2002), this type does not represent merely an ecotone between the xeric and mesic sites because of the dominance of indicator species such as white oak, jack-in-the-pulpit (*Arisaema triphyllum* [L.] Schott), and common silverbell (*Halesia tetraptera* Ellis). Within this type, early and mid successional age classes were distinguished from later successional classes based on multivariate analysis of both the ground flora and woody stem species datasets (Figures 4.5 and 4.6, Table 4.3). Ground flora strongly associated with ES and MS age-classes included northern horsebalm (*Collinsonia canadensis* L.), alternate-leaf dogwood

(*Cornus alternifolia* L.), climbing hydrangea (*Decumaria barbara* L.), and black locust; ground flora strongly associated with MLS and LS age-classes included American beech, common silverbell, snowy hydrangea (*Hydrangea radiata* Walter), rattlesnake-root (*Prenanthes spp.* L.), and common greenbrier. Woody stem species strongly associated with ES and MS age-classes included yellow-poplar and sassafras (*Sassafras albidum* [Nuttall] Nees); woody stem species strongly associated with MLS and LS age-classes included Fraser magnolia (*Magnolia fraseri* Walter) and white oak.

Mesic hardwoods - bloodroot: NMS and MRPP results using the ground flora dataset suggested a significant separation between LS plots and successional ES, MS, and MLS plots, but no clear separation using the woody stem dataset (Figures 4.7 and 4.8, Table 4.3). Ground flora species strongly associated with LS plots included northern maidenhair (*Adiantum pedatum* L.), foamflower (*Tiarella cordifolia* L.), and poison ivy (*Toxicodendron radicans* [L.] Kuntze), while species associated with successional plots included northern horsebalm, purple-node joe-pye-weed (*Eutrochium purpureum* [L.] Lamont), yellow-poplar, and bearsfoot (*Smallanthus uvedalius* [L.] Mackenzie ex Small). Characteristic woody stem species of this ecosystem type included common silverbell, yellow-poplar, and basswood. Both A and B-horizon soil depths were larger in LS plots compared to successional plots (Figure 4.7).

Mesic hemlock - rhododendron: NMS and MRPP results using the ground flora dataset suggested a significant separation between LS plots and successional ES, MS, and MLS plots, and a significant separation between ES plots and older successional types using the woody stem dataset (Figures 4.9 and 4.10, Table 4.3). Ground flora species strongly associated with LS plots included common greenbrier and foamflower. Great rhododendron reached its highest importance in the MLS age-class of this ecosystem type (Table A.2). Ground flora species strongly associated with early successional types included black-cohosh (*Actaea racemosa* L.), yellow-poplar, American lopseed (*Phryma leptostachya* L.), and forest goldenrod (*Solidago arguta* Aiton). Woody stem species associated with MLS and LS age-classes included green ash (*Fraxinus pennsylvanica* Marshall), basswood, and eastern hemlock; woody stems associated with the ES age-class included flowering dogwood and yellow-poplar.

Comparison of Age-Classes Across the Jocassee Gorges Landscape

NMS selected a two-dimensional solution for MS and MLS datasets and the LS ground-flora dataset, and a three-dimensional solution for both datasets in the ES age-class and the woody stem dataset of the LS age-class (Table 4.4). Final stress values of all eight ordinations fell below or between Clarke's (1993) suggestion of between 10 and 20 for interpretability of ecological data. Species differences for both ground flora and woody stem datasets were effectively displayed in each age-class ordination (Figures 4.11-18). NMS results for all ES age-classes revealed poor separation of mesophytic ecosystem types (SOM, MHB, and MHR) in species space for both ground flora and woody stem species datasets (Figures 4.11 and 12). Xerophytic types (XOB and XCO) began to cluster individually across ground flora species space within the ES age-class (Figure 4.11). No clusters were formed by ecosystem type when plots were ordinated by woody stem species (Figure 4.12).

Table 4.4. Ordination results for non-metric multidimensional scaling analysis of distinct age-classes within Jocassee Gorges. The summary table provides eigenvalues (stress and axes variance) and Pearson Correlations of selected environmental variables for each of the ordination axes.

	Final Stress	Axis 1	Axis 2	Axis 3
ES - ground flora	9.2	0.26	0.41	0.23
TRMI	---	0.40	-0.26	0.75
O-horizon depth	---	0.14	0.72	-0.35
Slope gradient	---	0.47	0.29	0.01
ES - woody stems	10.3	0.45	0.23	0.20
MS - ground flora	9.2	0.18	0.74	---
TRMI	---	0.11	-0.72	---
A-horizon depth	---	0.48	-0.31	---
O-horizon depth	---	-0.74	0.26	---
MS - woody stems	12.9	0.65	0.20	---
MLS - ground flora	9.7	0.36	0.54	---
TRMI	---	0.79	0.69	---
A-horizon depth	---	0.36	0.50	---
O-horizon depth		-0.35	-0.70	---
MLS - woody stems	9.5	0.20	0.69	---
LS - ground flora	12.7	0.70	0.21	---
TRMI	---	-0.74	0.18	---
A-horizon depth	---	-0.54	-0.12	---
O-horizon depth		0.69	0.17	---
LS - woody stems	10.0	0.56	0.18	0.17

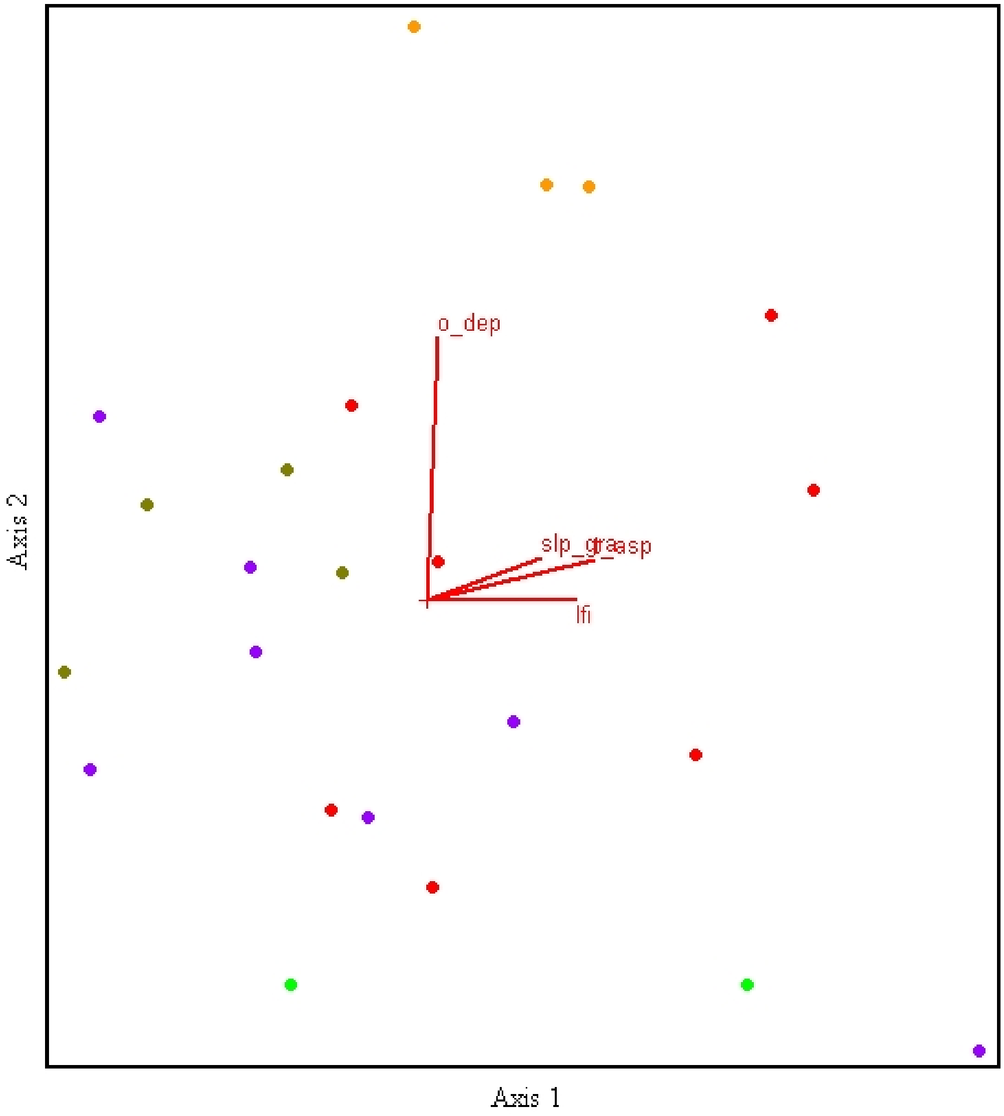

Figure 4.11: Non-metric multidimensional scaling ordination of ground flora space within ES communities for Jocassee Gorges. Ecosystem types are color-coded as follows: XOB (brown), XCO (orange), SOM (blue), MHB (green), and MHR (red). Environmental variables: o_dep, $O_e + O_a$ horizon thickness; slp_gra, slope gradient; t_asp, transformed aspect (Beers et al. 1966); and lfi, landform index.

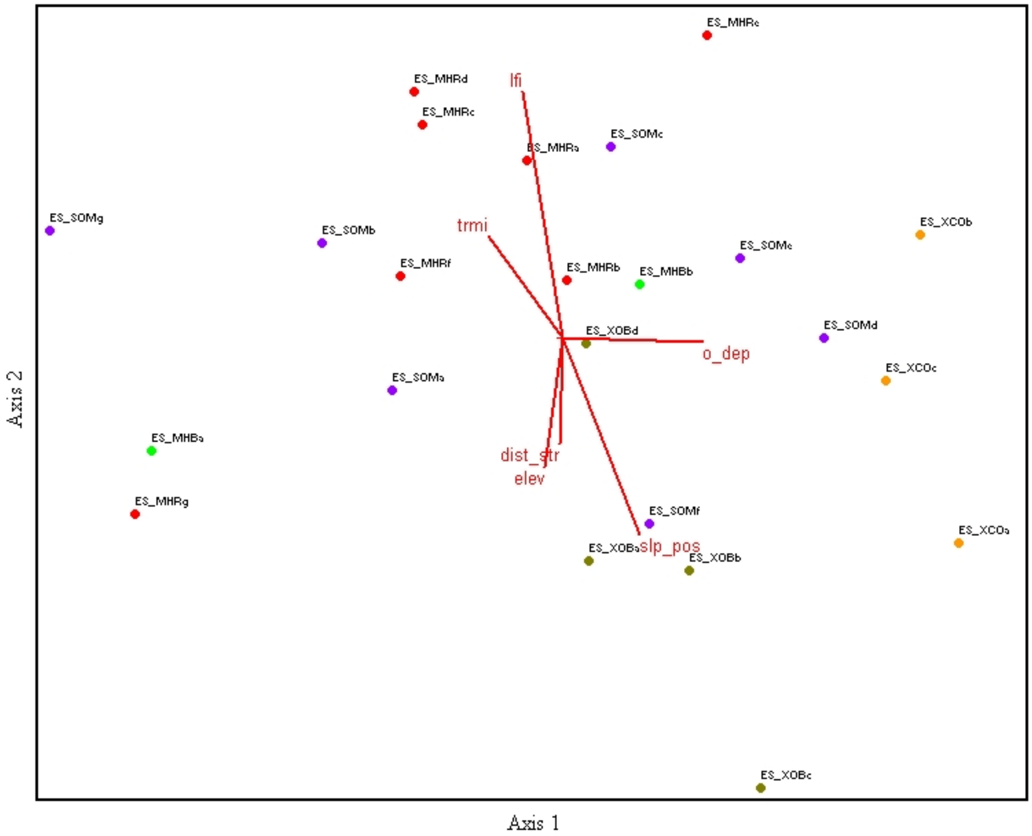

Figure 4.12: Non-metric multidimensional scaling ordination of woody stem species space within ES communities for Jocassee Gorges. Ecosystem types are color-coded as follows: XOB (brown), XCO (orange), SOM (blue), MHB (green), and MHR (red). Environmental variables: o_dep, $O_e + O_a$ horizon thickness; slp_pos, slope position; elev, elevation; dist_str, distance (m) to nearest stream; trmi, topographic relative moisture index (Parker 1982); and lfi, landform index.

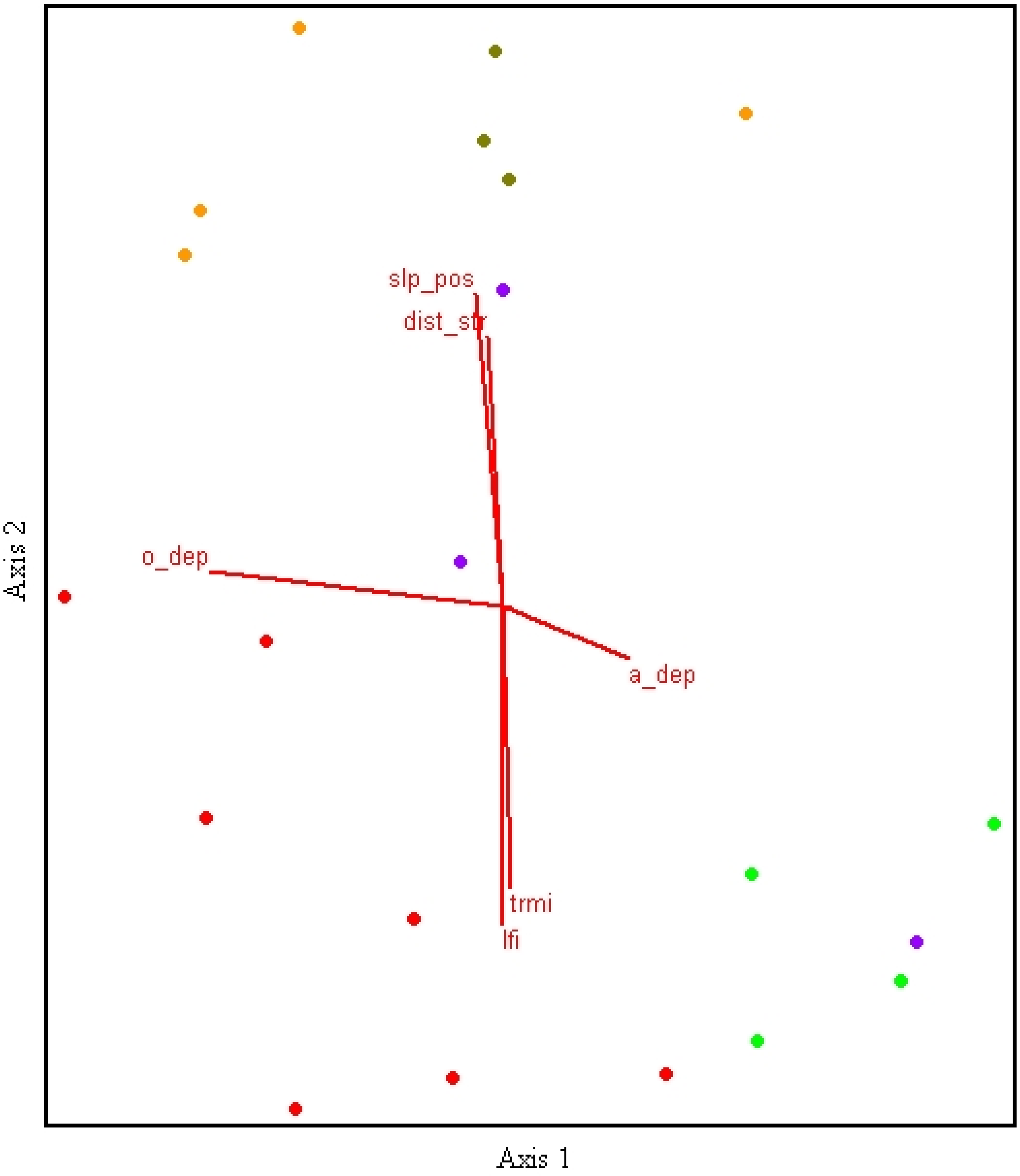

Figure 4.13: Non-metric multidimensional scaling ordination of ground flora space within MS communities for Jocassee Gorges. Ecosystem types are color-coded as follows: XOB (brown), XCO (orange), SOM (blue), MHB (green), and MHR (red). Environmental variables: o_dep, $O_e + O_a$ horizon thickness; slp_pos, slope position; dis_str, distance (m) to nearest stream; a_dep, A horizon depth; trim, topographic relative moisture index (Parker 1982); and lfi, landform index.

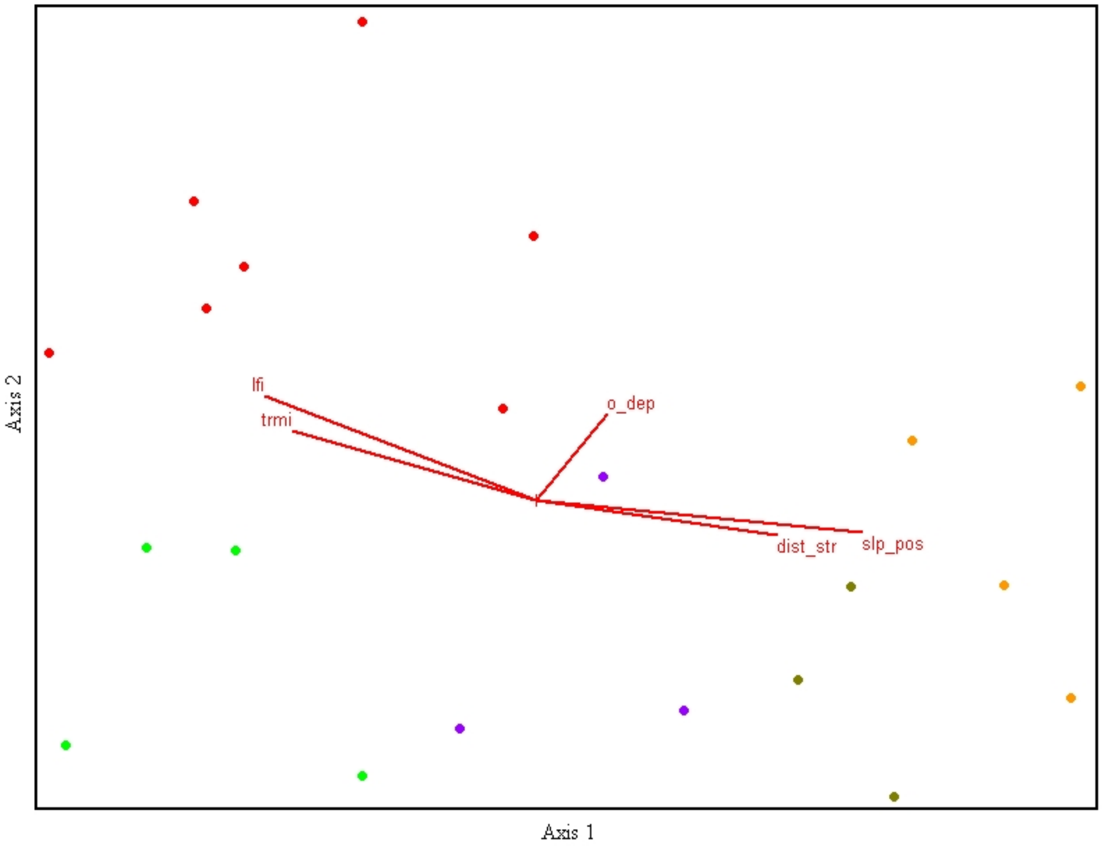

Figure 4.14: Non-metric multidimensional scaling ordination of woody stem species space within MS communities for Jocassee Gorges. Ecosystem types are color-coded as follows: XOB (brown), XCO (orange), SOM (blue), MHB (green), and MHR (red). Environmental variables: o_dep, $O_e + O_a$ horizon thickness; slp_pos, slope position; dist_str, distance (m) to nearest stream; trim, topographic relative moisture index (Parker 1982); and lfi, landform index.

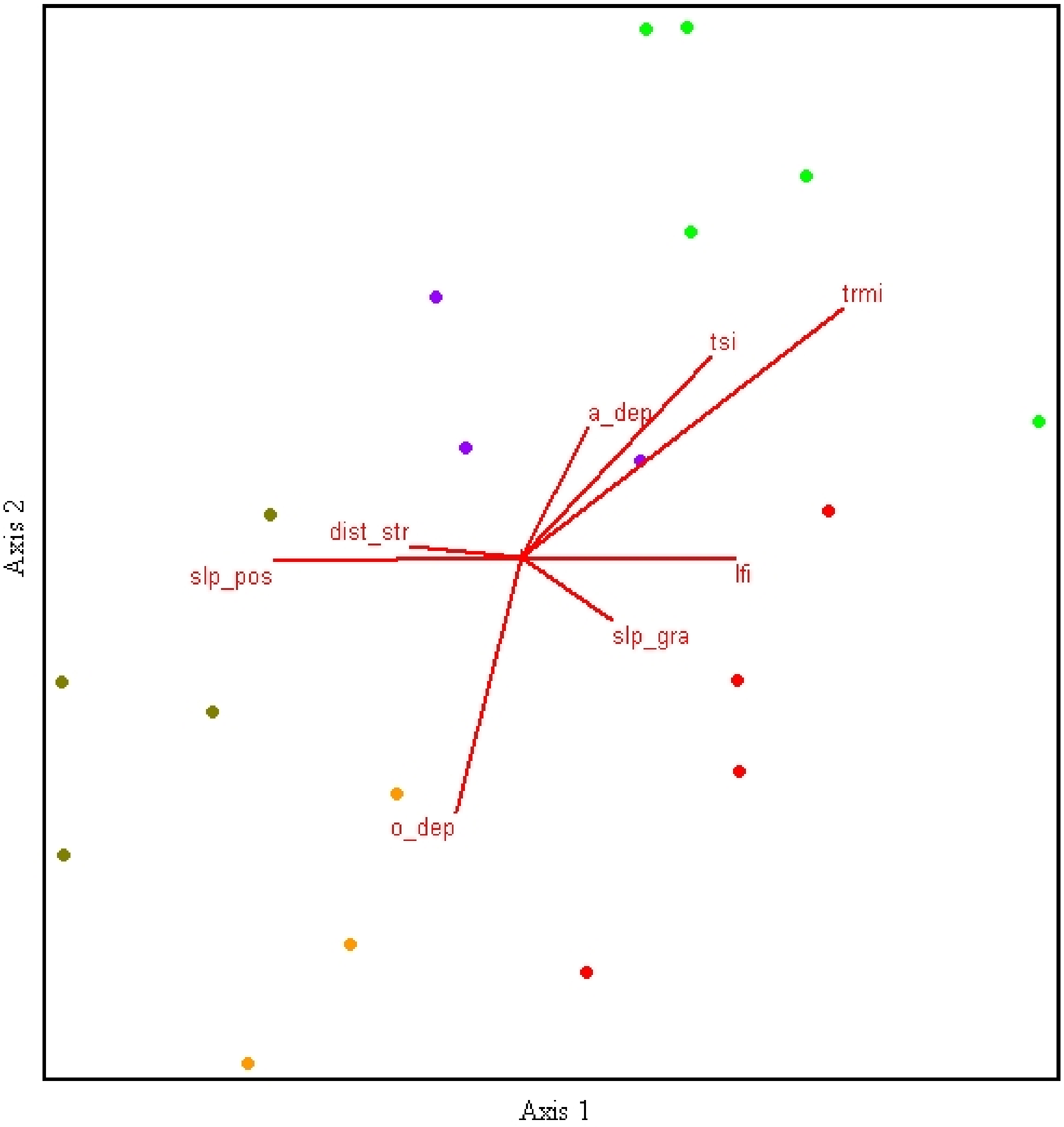

Figure 4.15: Non-metric multidimensional scaling ordination of ground flora space within MLS communities for Jocassee Gorges. Ecosystem types are color-coded as follows: XOB (brown), XCO (orange), SOM (blue), MHB (green), and MHR (red). Environmental variables: o_dep, $O_e + O_a$ horizon thickness; slp_pos, slope position; dis_str, distance (m) to nearest stream; a_dep, A horizon depth; tsi, terrain shape index; trim, topographic relative moisture index (Parker 1982); lfi, landform index; and slp_gra, slope gradient.

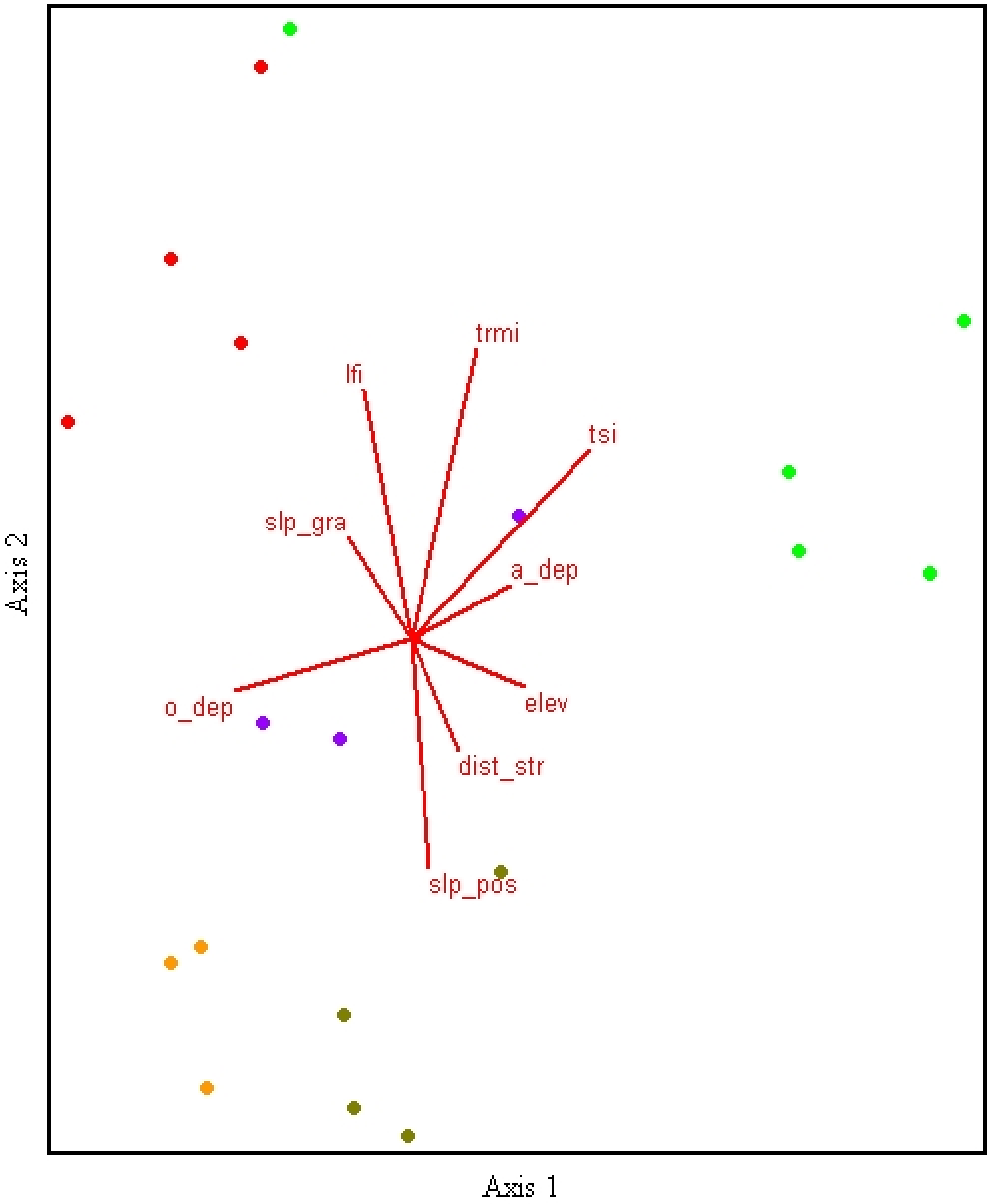

Figure 4.16: Non-metric multidimensional scaling ordination of woody stem space within MLS communities for Jocassee Gorges. Ecosystem types are color-coded as follows: XOB (brown), XCO (orange), SOM (blue), MHB (green), and MHR (red). Environmental variables: o_dep, $O_e + O_a$ horizon thickness; slp_pos, slope position; dis_str, distance (m) to nearest stream; elev, elevation (m); a_dep, A horizon depth; tsi, terrain shape index; trim, topographic relative moisture index (Parker 1982); lfi, landform index; and slp_gra, slope gradient.

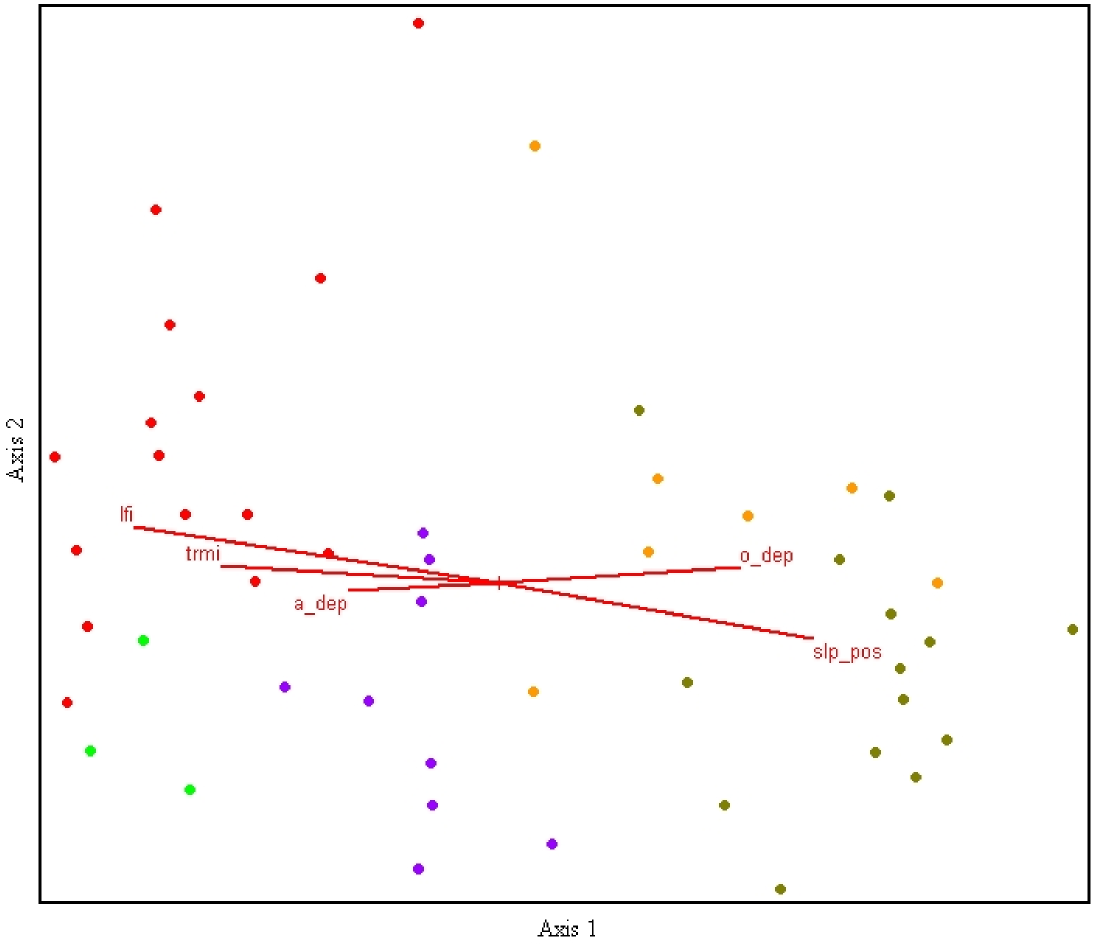

Figure 4.17: Non-metric multidimensional scaling ordination of ground flora space within LS (reference) communities for Jocassee Gorges. Ecosystem types are color-coded as follows: XOB (brown), XCO (orange), SOM (blue), MHB (green), and MHR (red). Environmental variables: o_dep, $O_e + O_a$ horizon thickness; slp_pos, slope position; a_dep, A horizon depth; trim, topographic relative moisture index (Parker 1982); and lfi, landform index.

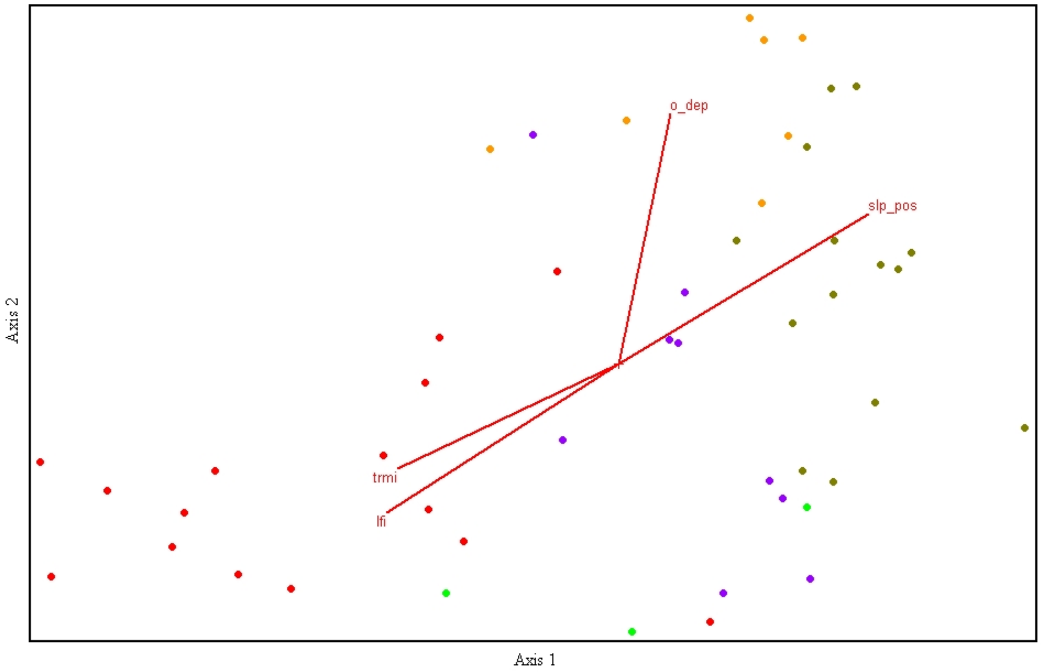

Figure 4.18: Non-metric multidimensional scaling ordination of woody stem species space within LS (reference) communities for Jocassee Gorges. Ecosystem types are color-coded as follows: XOB (brown), XCO (orange), SOM (blue), MHB (green), and MHR (red). Environmental variables: o_dep, $O_e + O_a$ horizon thickness; slp_pos, slope position; trim, topographic relative moisture index (Parker 1982); and lfi, landform index.

Landform variables used to define reference (LS) stands, like slope position and TRMI, began to show strong correlations with ecosystem type distributions in ES age-classes, and the trend continued with older age-classes (Table 4.1). Soil variables elicited varying degrees of faithfulness to ecosystem types across age-classes (Table 4.1). MHB types consistently had the highest A-horizon depths when compared to values within other ecosystem types of the same age class. However, mean depths were much lower when compared with the mean depth (30 cm) of reference MHB plots. Mean B-horizon depths for MHB reference plots was 90 cm, while mean depths for MHB successional plots was consistently less than 50 cm. The range of inconsistency between these values may have resulted from sampling error, or could represent the natural range of variation of solum depth in these rich, cove sites of Jocassee Gorges. Organic horizon thickness was consistently higher in north-facing, upper slope position XCO ecosystem types than in all other types for all age-classes (Tables 4.1 and 4.4).

MRPP analysis revealed trends similar to NMS results with respect to compositional trends in ecosystem type distribution within age-classes (Table 4.5). For all comparisons, MRPP analysis revealed significant results with very low p-values (<0.01). As expected, stronger separation (higher negative *T* values) occurred among ecosystem types of reference plots, and separation tended to increase along the temporal gradient. The relatively low *T* value (-3.66) calculated for the ES age-class woody stem dataset corresponds with the ecosystem type overlap in the ordination results (Figure 4.12). Mesophytic types in the ES age-class were not statistically distinct based on ground flora and woody stem datasets. The intermediate site type (SOM) clustered with

Table 4.5. MRPP results from comparing age-classes within Jocassee Gorges' ecosystem types.

	T	*A*	p value	Ecosystem Type Comparison
ES				
ground	-6.38	0.1249	< 0.0001*	XOB[a] XCO[b] SOM[c] MHB[c] MHR[c]
woody	-3.66	0.1048	0.0015*	XOB[a] XCO[b] SOM[c] MHB[c] MHR[c]
MS				
ground	-6.24	0.1822	< 0.0001*	XOB[a] XCO[b] SOM[abcd] MHB[c] MHR[d]
woody	-6.70	0.2376	< 0.0001*	XOB[ab] XCO[b] SOM[a] MHB[c] MHR[d]
MLS				
ground	-7.21	0.2212	< 0.0001*	XOB[a] XCO[b] SOM[c] MHB[d] MHR[e]
woody	-7.84	0.3691	< 0.0001*	XOB[a] XCO[b] SOM[c] MHB[d] MHR[e]
LS				
ground	-16.40	0.2300	< 0.0001*	XOB[a] XCO[b] SOM[c] MHB[d] MHR[e]
woody	-16.46	0.2722	< 0.0001*	XOB[a] XCO[b] SOM[c] MHB[d] MHR[e]

all ecosystem types in the MS age-class, while basic cove (MHB) composition was distinct from acidic cove (MHR) composition in this age-class. Ecosystem types were compositionally distinct, with regards to ground flora and woody stem species, by mid-late succession (51-70 years). The compositional distinctions for each ecosystem type within age-classes are described below, with emphasis placed on listing those species (followed by their indicator value) revealed in ISA.

Early Successional Age-Class (ES)

Xeric oak - *blueberry*: Ground flora species that occurred exclusively in this site included hill cane (*Arundinaria appalachiana* Triplett, Weakley, and L.G. Clark) (57.9), bracken fern (*Pteridium aquilinum* [L.] Kuhn) (61.4), and goldenrod species. (63.2). ISA revealed no faithful species to this site type. For early successional xerophytic types, saplings and small trees of red maple, blackgum, and white oak represented the dominant woody stems, regardless of specific ecosystem type, or landform position.

Xeric chestnut oak - *mountain laurel*: Ericaceous shrubs such as bear huckleberry (89.3) and gorge rhododendron (*Rhododendron minus* Michaux) (83.1), along with galax (*Galax urceolata* [Poiret] Brummitt) (75.0), dominated the ground flora within this site. Other minor ground flora species included Carolina lily (*Lilium michauxii* Poiret) (66.7), New York fern (*Thelypteris noveboracencis* [L.] Nieuwland) (51.3), and seedlings of chestnut oak (55.3). These sites contained the highest diversity (n = 10) of ground flora species of early successional ecosystem types. Saplings of chestnut oak (61) were a dominant of the woody stem species strata, along with other early successional xerophytic predictors like red maple, blackgum, and white oak.

Submesic oak - mixed flora: ISA revealed no faithful ground flora or woody stem species to these sites. This intermediate ecosystem type was composed of a composite of ground flora species from both xerophytic and mesophytic types. These sites were dominated by red maple, common silverbell, and yellow-poplar saplings and small trees.

Mesic hardwood - bloodroot: Graminoids and herbs such as common shorthusk (*Brachyelytrum erectum* [Schreber ex Sprengel] Palisot de Beauvois] (97.1), purple-node joe-pye-weed (79.2), two-flower melic (*Melica mutica* Walter) (100), and star chickweed (*Stellaria pubera* Michaux) (82.9) dominated the early successional basic coves. Yellow-poplar, the early successional woody stem dominant of all mesophytic site units, was characteristic of the sapling strata within these sites.

Mesic hemlock - rhododendron: Ground flora that occurred exclusively in these sites included strawberry-bush (*Euonymus americanus* L.) (47.6), snowy hydrangea (56.8), and seedlings/low saplings of eastern hemlock (61.5). The only woody stem species revealed as an adequate indicator species for this site was American beech (70.6). As with other mesophytic sites, yellow-poplar and red maple dominated the sapling strata in these early successional acidic coves.

Mid Successional Age-Class (MS)

Xeric oak - blueberry: Ground flora indicative of these sites included hill cane (58.9), pipsissewa (*Chimaphila maculata* [L.] Pursh) (58.6), hillside blueberry (57.3), and seedlings/low saplings of scarlet oak (46.0) and black oak (*Quercus velutina* Lamarck) (51.5).

Xeric chestnut oak - mountain laurel: These sites were dominated by seedlings/low saplings of chestnut oak (64.6) and graminoid/herbaceous species such as sedge (*Carex albicans* Willd. ex Sprengel) (66.2), galax (57.9), and Biltmore carrionflower (*Smilax biltmoreana* [Small] Norton ex Pennell) (56.9). Characteristic woody stem species included the indicator species chestnut oak (78.2) and other species of wide ecological amplitudes such as red maple, blackgum, and sourwood.

Submesic oak - mixed flora: ISA revealed no faithful ground flora or woody stem species to these sites. This intermediate ecosystem type was composed of a composite of ground flora species from both xerophytic and mesophytic types. In the overstory, these sites were dominated by a mixture of red maple, pignut hickory (*Carya glabra* [P. Miller] Sweet), mockernut hickory (*Carya alba* [L.] Nuttall ex Elliott), common silverbell, and white oak.

Mesic hardwood - bloodroot: These sites contained the highest diversity of ground flora indicator species (n = 14) of mid successional ecosystem types. Dominant ground flora included common white heart-leaved aster (*Eurybia divaricata* [L.] Nesom) (90.9), Canada lily (*Lilium canadense* L.) (75.0), two-flower melic (75.0), rattlesnake fern (*Botrypus virginianus* [L.] Holub) (65.1), and bloodroot (*Sanguinaria canadensis* L.) (48.3). The sole woody stem indicator of these sites was Fraser magnolia (56.3), but other dominant, cosmopolitan stems included yellow-poplar and red maple.

Mesic hemlock - rhododendron: Ground flora indicators of these sites included mountain doghobble (81.5), variable-leaf heartleaf (*Hexastylis heterophylla* [Ashe] Small) (70.4), partridge-berry (*Mitchella repens* L.) (62.8), and spikenard (*Aralia* *racemosa* L.) (57.1). Woody stem indicators included eastern hemlock (69.6), sweet birch (71.1), and American beech (55.3). Other dominant woody stem species included yellow-poplar and red maple.

Mid-late Successional Age-Class (MLS)

Xeric oak - blueberry: Indicator ground flora species of these sites included hillside blueberry (65.0), eastern needlegrass (*Piptochaetium avenaceum* [L.] Parodi) (75.0), and scarlet oak (67.4) seedlings/low saplings. Woody stem species with high indicator values included scarlet oak (77.4), shortleaf pine (*Pinus echinata* P. Miller) (75.0), and blackgum (47.9). The composition of ground flora and woody stem species was similar between these sites and LS sites of the same ecosystem type.

Xeric chestnut oak - mountain laurel: Indicator ground flora species of these sites included galax (72.4), mountain laurel (51.7), Biltmore's carrionflower (68.5), and chestnut oak (52.0) seedlings/low saplings. The sole woody stem indicator species was chestnut oak (65.0). This species dominated the overstory stratum of this age-class and the LS sites of this ecosystem type.

Submesic oak - mixed flora: Indicator species were eventually identified for this ecosystem type in both the ground flora and woody stem dataset in the mid-late seral stage. Although these sites still contained a mixture of xerophytic and mesophytic species, ISA revealed the following diagnostic ground flora species: New York fern (49.1*),* tick-trefoil species (*Desmodium spp*. Desvaux) (68.3), and seedlings of white oak (50.7) and American beech (66.0). Woody stem indicators included white oak (68.7) and

Fraser magnolia (61.8). Woody stem composition was similar between this age-class and LS sites of this ecosystem type.

Mesic hardwood - bloodroot: As with the mid seral stage comparison, these sites exhibited the highest indicator ground flora species diversity within mid-late seral stage ecosystem types. Ground flora indicators included black-cohosh (95.9), common white snakeroot (*Ageratina altissima* King and H.E. Robinson) (80.0), rattlesnake fern (67.9), bloodroot (60.0), and wood-nettle (*Laportea canadensis* [L.] Weddell (60.0). Woody stem indicators for these sites included common silverbell (82.3), yellow-poplar (47.8), and northern red oak (56.1). The relative dominance of northern red oak in these sites compared with LS sites of this ecosystem type suggests a possible need to refine the classification of basic mesic coves within the Jocassee Gorges landscape.

Mesic hemlock - rhododendron: Ground flora composition of these sites began to resemble the composition of LS sites of this ecosystem type in this age-class, due to the increased importance of great rhododendron (50.1) along with high indicator values for acidic-tolerant ground flora species such as partridge-berry (58.5), variable-leaf heartleaf (75.0), and mountain doghobble (58.8). Woody stem indicator species included eastern hemlock (69.1) and eastern white pine (66.0). Overstory composition was similar between these sites and LS sites of this ecosystem type.

Ecological Species Group Analysis

The full species list for each ecological species group can be found in Appendix E. Importance values of woody stem and ground flora species groups are listed in Tables

4.6 and 4.7, respectively. The *Quercus coccinea* group dominated all age-classes in the XOB ecosystem type, while the *Quercus montana* group dominated all age-classes in the XCO ecosystem type. LS stands of the SOM ecosystem type were composed of a mixture of woody stem species groups, including the *Quercus alba, Oxydendrum arboreum, Liriodendron tulipifera,* and *Quercus montana* groups. ES stands of this type were dominated by the *Liriodendron tulipifera* group, but by mid-succession (> 25 years of age), the *Quercus alba* and *Oxydendrum arboreum* groups become the dominant species groups. The *Liriodendron tulipifera* group dominated all age-classes in the MHB ecosystem type. In the MHR ecosystem type, LS age-class stands were dominated by the *Tsuga canadensis* group, with all other woody stem species groups except the *Quercus coccinea* group exhibiting minor co-dominance. ES age-classes of the MHR ecosystem type were dominated by the *Liriodendron tulipifera* group, with all other woody stem species groups except the *Quercus coccinea* group exhibiting minor co-dominance. By mid-succession (> 25 years of age), the distribution of woody stem species groups in this ecosystem type mimics the distribution of groups in the LS age-class.

Ground flora species groups that showed strong affinities for single ecosystem types in LS age-class stands included the *Vaccinium pallidum* group (XOB), *Kalmia latifolia* group (XCO), *Thelypteris noveboracensis* group (SOM), *Sanguinaria canadensis* and *Adiantum pedatum* group (MHB), and *Rhododendron maximum* group (MHR). Both the *Smilax rotundifolia* and *Vitis rotundifolia* groups exhibited broad ecological amplitudes, occurring in equal densities and frequencies within all LS ecosystem types. Other ground flora species groups showed affinities to both xerophytic

Table 4.6. Importance values (mean ± SE) of woody stem ecological species groups across successional stages of ecosystem types within Jocassee Gorges. Means from ES, MS, and MLS were compared to LS plots using one-way ANOVA with Dunnett's multiple comparison test.

Species group	Code	Ecosystem type	ES	MS	MLS	LS
Liriodendron tulipifera	ZLT	xob	12.7 ± 7.8*	4.0 ± 1.4	4.2 ± 4.6	3.9 ± 4.9
		xco	1.4 ± 1.3	1.7 ± 1.5	3.8 ± 2.4	3.8 ± 2.0
		som	20.9 ± 16.1*	7.2 ± 5.9	7.9 ± 5.6	8.3 ± 6.0
		mhb	20.1 ± 22.1	16.7 ± 21.0	15.6 ± 11.2	19.1 ± 17.8
		mhr	13.3 ± 18.1	7.9 ± 8.2	6.3 ± 6.0	6.5 ± 5.9
Oxydendrum arboreum	ZOA	xob	10.4 ± 7.9	12.5 ± 10.8	15.0 ± 10.8	12.3 ± 8.7
		xco	17.0 ± 19.1	10.8 ± 8.9	12.5 ± 11.6	12.5 ± 8.7
		som	11.9 ± 10.5	12.4 ± 13.7	12.5 ± 10.0	9.4 ± 7.4
		mhb	9.6 ± 15.5	10.4 ± 8.5	6.9 ± 7.5	10.4 ± 8.3
		mhr	8.4 ± 6.3	7.2 ± 5.4	6.4 ± 4.3	6.0 ± 6.6
Quercus alba	ZQA	xob	2.5 ± 2.1	8.2 ± 5.6	3.5 ± 2.5	6.5 ± 7.8
		xco	0.5 ± 0.5	4.9 ± 5.3	1.3 ± 0.7	5.4 ± 6.1
		som	2.7 ± 2.0*	8.7 ± 7.0	12.0 ± 8.5	9.0 ± 7.7
		mhb	2.7 ± 2.7	7.6 ± 6.7	6.6 ± 8.0	4.7 ± 5.4
		mhr	6.5 ± 4.9	4.2 ± 3.7	4.8 ± 3.2	5.3 ± 5.4
Quercus coccinea	ZQC	xob	13.2 ± 12.8	13.0 ± 8.7	13.6 ± 8.4	12.6 ± 7.4
		xco	5.5 ± 6.5	11.4 ± 10.1*	8.5 ± 4.5	4.4 ± 3.2
		som	2.9 ± 3.6	4.9 ± 5.0	4.4 ± 2.0	4.9 ± 3.5
		mhb	4.9 ± 3.0	1.2 ± 0.9	1.3 ± 1.0	1.0 ± na
		mhr	3.9 ± 3.7	1.0 ± 0.5	1.7 ± 1.2	2.6 ± 3.1
Quercus montana	ZQM	xob	5.1 ± 5.7	3.2 ± na	5.5 ± 5.5	10.5 ± 10.0
		xco	12.9 ± 2.2*	26.0 ± 9.8	38.0 ± 3.6	33.5 ± 12.4
		som	5.3 ± na	2.4 ± 3.2	13.7 ± 0.2	12.0 ± 6.5
		mhb	1.7 ± na	1.9 ± na	2.7 ± na	0.0 ± 0.0
		mhr	6.6 ± 5.6	9.5 ± 4.8	10.6 ± 1.0	6.0 ± 6.4
Tsuga canadensis	ZTC	xob	2.7 ± 4.2	0.8 ± 0.3	0.9 ± 0.8	1.5 ± 1.6
		xco	3.6 ± 5.9	1.1 ± 0.7	1.3 ± 1.4	4.9 ± 8.4
		som	6.7 ± 9.6	3.8 ± 4.2	5.1 ± 4.2	3.6 ± 4.1
		mhb	1.3 ± 0.1	4.5 ± 4.5	6.5 ± 14.6	6.5 ± 5.7
		mhr	5.7 ± 6.1	11.9 ± 13.8	15.9 ± 20.3	13.7 ± 15.5

*Cover significantly differs from LS plots ($p < 0.05$)

Table 4.7. Importance values (mean ± SE) of ground flora ecological species groups across successional stages of ecosystem types within Jocassee Gorges. Means from ES, MS, and MLS were compared to LS plots using one-way ANOVA with Dunnett's multiple comparison test.

Species group	Code	Ecosystem type	ES	MS	MLS	LS
Adiantum pedatum	ADI	xco	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.4 ± na
		mhb	1.2 ± 1.4	1.3 ± 0.7	0.9 ± 0.5	1.3 ± 0.7
		som	1.2 ± 1.1	1.5 ± 0.9	0.5 ± 0.3	0.3 ± 0.1
		mhr	0.9 ± 0.8	0.9 ± 0.6	0.9 ± 0.5	1.0 ± 0.6
Arundinaria appalachiana	ARU	xob	3.8 ± 2.5	6.1 ± 3.5*	4.5 ± 3.5	3.9 ± 2.3
		xco	2.3 ± 1.5	4.2 ± 3.0*	3.8 ± 2.1	2.5 ± 1.7
		som	2.7 ± 2.1	1.9 ± 2.0	1.5 ± 1.0	1.8 ± 1.3
		mhb	2.2 ± 1.5	0.9 ± 0.7	1.2 ± 1.0	1.2 ± 0.8
		mhr	1.4 ± 1.1	1.7 ± 1.0	1.7 ± 1.3	1.0 ± 0.8
Kalmia latifolia	KAL	xob	2.6 ± 2.3	3.0 ± 1.9	3.4 ± 3.0	3.8 ± 2.5
		xco	5.3 ± 3.2	5.4 ± 2.8	5.3 ± 3.0	3.9 ± 2.8
		som	1.9 ± 1.5	2.5 ± 1.9	2.1 ± 1.2	1.7 ± 1.4
		mhb	0.8 ± 1.7	0.7 ± 0.4	0.3 ± 0.2	0.2 ± na
		mhr	1.9 ± 1.4	3.6 ± 3.4*	2.7 ± 2.5	1.6 ± 1.5
Polystichum acrostichoides	POL	xob	1.1 ± 0.98	1.7 ± 1.7	2.7 ± 1.9	1.4 ± 1.2
		xco	1.8 ± 2.8	1.1 ± 0.9	1.7 ± 1.4	2.0 ± 1.7
		som	2.2 ± 1.6	1.8 ± 0.9	2.0 ± 1.1	2.4 ± 1.0
		mhb	2.6 ± 0.9	1.7 ± 0.9	2.2 ± 1.5	2.2 ± 1.1
		mhr	2.5 ± 1.4	3.2 ± 2.0	2.7 ± 1.9	2.9 ± 1.6
Rhododendron maximum	RHO	xob	1.0 ± na	0.7 ± na	0.6 ± na	1.4 ± 1.2
		xco	1.3 ± 1.1	1.2 ± 0.7	3.2 ± 2.9	2.3 ± 2.8
		som	1.3 ± 1.4	1.9 ± 1.2	2.0 ± 1.2	1.4 ± 1.1
		mhb	2.1 ± na	0.9 ± 0.7	2.1 ± 1.5	1.4 ± 0.8
		mhr	2.3 ± 2.2*	4.1 ± 2.6	4.4 ± 2.0	4.0 ± 3.4
Sanguinaria canadensis	SAN	som	2.9 ± 3.5	1.7 ± 0.6	0.0 ± 0.0	0.5 ± 0.3
		mhb	2.6 ± 1.5	1.3 ± 0.6	2.2 ± 0.3	1.2 ± 0.8
		mhr	0.6 ± 0.5	0.5 ± 0.2	0.0 ± 0.0	0.9 ± 0.8

Table 4.7, cont. Importance values (mean ± SE) of ground flora ecological species groups across successional stages of ecosystem types within Jocassee Gorges. Means from ES, MS, and MLS were compared to LS plots using one-way ANOVA with Dunnett's multiple comparison test.

Species group	Code	Ecosystem type	ES	MS	MLS	LS
Smilax rotundifolia	SMI	xob	2.6 ± 1.6*	3.3 ± 2.9	3.9 ± 2.7	4.3 ± 1.8
		xco	2.9 ± 2.3	2.6 ± 1.7	2.9 ± 1.9	3.6 ± 1.7
		som	2.6 ± 1.7	2.4 ± 1.5	3.2 ± 1.6	2.6 ± 1.0
		mhb	2.1 ± 1.2	1.6 ± 0.6	1.9 ± 1.2	1.6 ± 0.7
		mhr	2.3 ± 1.0	2.0 ± 1.5	2.3 ± 1.6	2.5 ± 1.3
Thelypteris noveboracensis	THE	xob	0.6 ± 0.3	1.5 ± 1.4	1.2 ± 1.0	1.0 ± 0.6
		xco	2.6 ± 1.8	1.1 ± 0.7	1.2 ± 1.2	1.6 ± 1.5
		som	1.8 ± 1.3	1.4 ± 0.8	2.2 ± 1.6	2.3 ± 1.8
		mhb	1.0 ± 0.8*	2.0 ± 1.1	1.6 ± 1.0	2.4 ± 0.9
		mhr	1.6 ± 0.9	2.3 ± 1.3	1.4 ± 0.7	1.7 ± 1.2
Tiarella cordifolia	TIA	xob	0.0 ± 0.0	0.0 ± 0.0	0.7 ± na	0.6 ± 0.3
		xco	1.3 ± 0.8	0.8 ± na	0.6 ± na	0.4 ± 0.1
		som	1.2 ± 1.4	0.9 ± 1.0	1.4 ± 1.0	1.3 ± 0.7
		mhb	2.0 ± 1.2	1.4 ± 0.8	1.8 ± 1.3	1.9 ± 0.9
		mhr	1.7 ± 1.3	1.8 ± 0.9	1.6 ± 1.1	1.9 ± 1.0
Vaccinium pallidum	VAC	xob	2.1 ± 1.4	3.5 ± 3.7	3.9 ± 2.5	3.3 ± 2.4
		xco	2.5 ± 2.1	2.9 ± 2.2	2.7 ± 1.8	2.9 ± 2.1
		som	1.2 ± 1.2	2.8 ± 2.1*	0.4 ± na	0.8 ± 0.6
		mhb	1.1 ± 1.0	0.4 ± 0.3	0.9 ± 0.6	0.2 ± na
		mhr	0.9 ± 0.7	0.6 ± 0.4	0.8 ± 0.5	0.2 ± 0.0
Vitis rotundifolia	VIT	xob	2.6 ± 1.8	4.1 ± 1.5	2.4 ± 1.2	2.6 ± 1.9
		xco	2.3 ± 1.6	2.3 ± 2.7	1.7 ± 1.2	2.0 ± 1.5
		som	3.0 ± 2.4	2.7 ± 1.0	2.6 ± 1.5	2.4 ± 1.2
		mhb	2.5 ± 1.0	1.4 ± 0.7	1.0 ± 0.8	1.7 ± 1.0
		mhr	2.6 ± 1.4	3.0 ± 1.3	2.1 ± 1.3	2.5 ± 1.3

*Cover significantly differs from LS plots ($p < 0.05$)

ecosystem types (*Arundinaria appalachiana* group) and mesophytic ecosystem types (*Polystichum acrostichoides* and *Tiarella cordifolia* groups) within LS age-classes. The ES age-class of the XOB ecosystem type is dominated by the *Arundinaria appalachiana, Vitis rotundifolia, Smilax rotundifolia,* and *Kalmia latifolia* group. Species found in these groups include the species group nominals, as well as seedlings of red maple, scarlet oak, blackgum, and sourwood. Over time, these species groups remain important within this ecosystem type, while the *Vaccinium pallidum* group increases in importance. The XCO ecosystem type is dominated by the *Kalmia latifolia* group across all age-classes, along with widely distributed groups such as *Smilax rotundifolia, Vitis rotundifolia,* and *Arundinaria appalachiana*. The *Vaccinium pallidum* group is also found throughout all age-classes of this ecosystem type, but becomes more important in the XOB type from the mid-succession seral stage and beyond. All ground flora species groups were represented and distributed evenly across all age-classes of the SOM ecosystem type, suggesting the true intermediate condition of these stands throughout the Jocassee Gorges landscape. The *Sanguinaria canadensis* group exhibited the narrowest distribution within LS stands and was largely restricted to the MHB ecosystem type. Although importance values of this group were highest in ES age-classes of the MHB and MHR ecosystem types, common blue cohosh (*Caulophyllum thalictroides* [L.] Michaux)--a member of this group--was absent from these stands. Mesophytic site types (MHB and MHR) provided environmental conditions that supported all ground flora species groups in ES age-classes. The MHR ecosystem type was dominated by both ericaceous species groups (*Rhododendron maximum* and *Kalmia latifolia*) in MS stands. The *Kalmia* group diminishes in importance over time in these acidic, mesophytic forests.

Canonical correlation analysis was used to describe relationships among ecological species groups in LS stands of Jocassee Gorges (Abella and Shelburne 2004). In this study, xeric groups, such as the *Vaccinium pallidum* group, were significantly negatively correlated with mesic groups, like the *Tiarella cordifolia* group. Subtle differences were also determined among groups with broad ecological amplitudes by using these quantitative descriptions. For instance, although widespread, the *Smilax rotundifolia* group was positively associated with xeric groups and negatively associated with mesic groups. This reflects the tendency of species within this group (common greenbrier, red maple, pignut and mockernut hickory, and Fraser magnolia) to favor xerophytic sites within the older age-class stands of Jocassee Gorges. Woody stem groups that were associated with xerophytic sites included the *Quercus coccinea* and *Oxydendrum arboreum* groups. These groups were positively correlated with xeric ground flora groups, like the *Vaccinium pallidum, Arundinaria appalachiana,* and *Kalmia latifolia* groups, and negatively correlated with mesic ground flora groups. Similarly, mesic woody stem species groups like the *Tsuga canadensis* group were positively associated with mesic ground flora species groups, like the *Rhododendron maximum* and *Tiarella cordifolia* group.

These same species groups were used to determine if similar relationships exist in seral stage communities of Jocassee Gorges (Tables 4.8-10). In ES stands, the relationships that were apparent among groups in LS stands shifted as expected. Some xerophytic ground flora groups still showed significant positive associations with xerophytic woody stem groups. For instance, the *Vaccinium pallidum* and *Arundinaria appalachiana* groups were positively associated with the *Quercus coccinea* group. However, although the xerophytic *Kalmia latifolia* group was still positively associated with the *Quercus montana* group, it was also positively associated with mesophytic groups such as the *Thelypteris noveboracensis, Rhododendron maximum,* and *Tsuga canadensis* groups. The *Sanguinaria canadensis* group was positively associated with other mesophytic ground flora groups, such as the *Adiantum pedatum* and *Tiarella cordifolia* groups. Another mesophytic indicator in LS stands, the *Polystichum acrostichoides* group, had significant positive associations with all other groups, except the *Oxydendrum arboreum* group, in ES stands. Although the *Rhododendron maximum* group exhibited negative associations in ES stands with the *Quercus coccinea* and *Oxydendrum arboreum* groups, it had positive associations with the *Quercus montana* and *Quercus alba* woody stem groups. In LS stands, the only positive associations this ground flora group had were with the *Liriodendron tulipifera* and *Tsuga canadensis* woody stem groups.

Table 4.8. Matrix of canonical correlations of ecological species groups of early successional sites of Jocassee Gorges. Values in bold-face are significant at $p < 0.05$.

	VAC	ARU	KAL	SMI	VIT	THE	POL	SAN	ADI	TIA	RHO	ZQC	ZOA	ZQM	ZQA	ZLT
ARU	**0.69**	1														
KAL	**0.76**	**0.75**	1													
SMI	**- 0.70**	**0.83**	**0.89**	1												
VIT	**- 0.59**	**- 0.69**	**0.51**	**0.79**	1											
THE	**- 0.76**	**- 0.73**	**0.83**	**0.73**	**- 0.54**	1										
POL	**- 0.84**	**0.70**	**- 0.81**	**0.62**	**0.52**	**0.76**	1									
SAN	- 0.41	**0.50**	**- 0.57**	**0.67**	0.36	**0.86**	**0.79**	1								
ADI	**0.72**	**0.69**	**- 0.83**	**0.77**	**- 0.69**	**0.89**	**0.86**	**0.81**	1							
TIA	**- 0.70**	**0.85**	**- 0.83**	**0.83**	**0.58**	**0.90**	**0.79**	**0.78**	**0.95**	1						
RHO	**0.61**	**0.69**	**0.85**	**- 0.62**	**0.69**	**- 0.67**	**0.74**	**0.56**	**0.96**	**0.98**	1					
ZQC	**0.87**	**0.76**	**- 0.72**	**0.69**	0.32	**0.74**	**0.83**	- 0.24	- 0.43	**- 0.54**	**- 0.59**	1				
ZOA	**0.68**	**0.53**	**0.75**	**0.77**	0.41	**- 0.71**	**- 0.60**	**0.58**	**0.68**	**0.75**	**- 0.60**	**0.50**	1			
ZQM	**0.40**	0.39	**0.98**	**0.62**	0.28	**0.74**	**0.60**	0.28	- 0.38	**0.40**	**0.69**	0.34	**0.52**	1		
ZQA	**0.72**	**- 0.66**	**- 0.72**	**0.59**	**0.49**	**0.52**	**0.56**	0.38	**0.72**	**0.86**	**0.88**	**0.46**	**- 0.65**	**- 0.41**	1	
ZLT	**0.49**	**0.68**	**- 0.75**	**0.77**	0.36	**0.88**	**0.80**	**0.96**	**0.79**	**0.75**	**0.72**	- 0.46	**- 0.67**	**- 0.50**	**- 0.46**	1
ZTC	**- 0 .60**	**- 0.97**	**0.78**	**0.79**	**0.67**	**0.70**	**0.66**	- 0.32	**0.86**	**0.88**	**0.98**	**0.50**	- 0.41	**0.50**	**0.86**	**- 0.67**

Table 4.9. Matrix of canonical correlations of ecological species groups of mid successional sites of Jocassee Gorges. Values in bold-face are significant at $p < 0.05$.

	VAC	ARU	KAL	SMI	VIT	THE	POL	SAN	ADI	TIA	RHO	ZQC	ZOA	ZQM	ZQA	ZLT
ARU	**0.96**	1														
KAL	**0.89**	**-0.89**	1													
SMI	**0.67**	**0.86**	**0.86**	1												
VIT	**0.63**	**0.72**	**0.69**	- 0.43	1											
THE	**0.79**	**-0.83**	**- 0.78**	**0.78**	**0.79**	1										
POL	**-0.82**	**-0.93**	**- 0.86**	**- 0.78**	**0.83**	**0.83**	1									
SAN	**-0.52**	**0.61**	**- 0.65**	**0.85**	**- 0.41**	**0.80**	**0.80**	1								
ADI	**-0.71**	**-0.70**	**- 0.73**	**0.73**	**0.63**	**0.96**	**0.89**	**0.99**	1							
TIA	**0.68**	**0.77**	**- 0.84**	**0.85**	**0.82**	**0.91**	**0.91**	**0.91**	**0.99**	1						
RHO	**0.66**	**- 0.67**	**0.93**	**- 0.81**	**0.92**	**- 0.83**	**0.96**	**0.46**	**0.80**	**0.83**	1					
ZQC	**0.94**	**0.93**	**0.80**	**0.70**	**0.59**	**0.77**	**0.75**	**0.49**	**0.62**	**- 0.63**	**- 0.60**	1				
ZOA	**0.76**	**0.70**	**0.79**	**0.87**	**0.53**	**0.75**	**0.74**	**0.67**	**0.67**	**0.73**	**0.58**	**0.72**	1			
ZQM	**0.77**	**0.76**	**0.92**	**0.62**	0.30	**0.57**	**0.47**	**0.40**	**0.50**	**0.44**	**- 0.42**	**0.46**	- 0.32	1		
ZQA	**0.63**	**0.67**	**0.70**	**- 0.82**	**0.45**	**0.76**	**0.71**	**0.80**	**0.60**	**0.80**	**0.64**	**0.55**	**0.65**	- 0.22	1	
ZLT	**-0.65**	**0.72**	**- 0.67**	**- 0.76**	**0.62**	**0.84**	**0.87**	**0.99**	**0.96**	**0.85**	**0.64**	**- 0.62**	**- 0.67**	**- 0.42**	**0.71**	1
ZTC	**-0.69**	**- 0.77**	**0.88**	**0.71**	**0.87**	**0.83**	**0.94**	0.39	**0.79**	**0.92**	**0.97**	**- 0.64**	**0.53**	- 0.35	**0.57**	**0.68**

Table 4.10. Matrix of canonical correlations of ecological species groups of mid-late successional sites of Jocassee Gorges. Values in bold-face are significant at $p < 0.05$.

	VAC	ARU	KAL	SMI	VIT	THE	POL	SAN	ADI	TIA	RHO	ZQC	ZOA	ZQM	ZQA	ZLT
ARU	**0.96**	1														
KAL	**0.94**	**0.87**	1													
SMI	**0.83**	**0.86**	**0.93**	1												
VIT	**- 0.70**	**- 0.69**	**- 0.71**	**- 0.64**	1											
THE	**- 0.81**	**- 0.79**	**- 0.72**	**- 0.70**	**0.81**	1										
POL	**- 0.80**	**- 0.78**	**- 0.81**	**- 0.70**	**0.78**	**0.84**	1									
SAN	**- 0.48**	**- 0.54**	**- 0.56**	**0.65**	- 0.34	**0.60**	**0.55**	1								
ADI	**- 0.59**	**- 0.75**	- 0.67	**- 0.73**	**0.60**	**0.92**	**0.83**	**0.99**	1							
TIA	**- 0.71**	**- 0.83**	**- 0.68**	**- 0.74**	**0.62**	**0.87**	**0.71**	**0.58**	**0.99**	1						
RHO	**- 0.59**	**- 0.58**	**- 0.92**	**- 0.67**	**- 0.62**	**0.89**	**0.90**	**0.64**	**0.90**	**0.81**	1					
ZQC	**0.99**	**0.97**	**0.86**	**0.84**	**- 0.58**	**- 0.65**	**- 0.76**	- 0.42	- 0.56	**- 0.67**	**- 0.60**	1				
ZOA	**0.86**	**0.86**	**0.92**	**0.68**	**0.54**	**- 0.81**	**- 0.85**	**0.93**	**- 0.72**	**- 0.74**	**- 0.86**	**0.86**	1			
ZQM	**0.78**	**0.60**	**0.95**	**0.58**	- 0.19	**- 0.52**	- 0.36	**- 0.38**	**- 0.50**	**- 0.46**	**- 0.85**	**0.68**	**0.47**	1		
ZQA	**0.59**	**- 0.56**	**- 0.62**	**0.77**	**0.67**	**0.57**	**- 0.75**	**0.36**	**0.87**	**0.70**	**0.75**	**- 0.49**	**- 0.54**	**- 0.38**	1	
ZLT	**- 0.64**	**- 0.68**	**- 0.75**	**- 0.73**	**- 0.46**	**0.81**	**0.84**	**0.91**	**0.99**	**0.82**	**- 0.65**	**- 0.55**	**- 0.74**	**- 0.46**	**0.93**	1
ZTC	**- 0.56**	**- 0.69**	**- 0.87**	**0.77**	**0.81**	**0.67**	**0.93**	**0.54**	**0.99**	**0.74**	**0.99**	**- 0.62**	**- 0.76**	**- 0.41**	**0.74**	**0.80**

Canonical correlation values of ecological species groups in later age-classes (MS and MLS) were similar to correlation values in late successional (LS) stands within Jocassee Gorges (Tables 4.9 and 4.10). However, there were subtle differences between these age-classes and

LS age-classes. There was a positive association between the xerophytic *Arundinaria appalachiana* group and all woody stem species groups (except the *Tsuga canadensis* group) in the MS age-class stands. This ground flora group was significantly negatively associated with

mesophytic woody stem groups such as the *Liriodendron tulipifera* and *Quercus alba* group in LS stands. Correlation values between the *Arundinaria appalachiana* group and all woody stem groups are nearly identical between MLS and LS stands. Other species groups that had weaker associations in LS stands appeared to have stronger associations within MS and MLS stands. Both the *Adiantum pedatum* and *Polystichum acrostichoides* groups was more strongly associated with mesophytic woody stem groups in both MS and MLS stands than in LS stands. However, in MLS stands xerophytic species group association values were nearly identical with LS stands.

Species Diversity and Successional Trends in Ecosystem Types

Species richness (S) and diversity (H’) was higher in mesophytic ecosystem types (SOM, MHB, MHR) than xerophytic ecosystem types (XOB, XCO) across all age-classes except the ES class (Table 4.11, Figure 4.19). In these sites, richness and diversity were highest in the MHB and MHR ecosystem types, and similar between XOB

Table 4.11. Mean ± SE of species richness (S), evenness (E), and Shannon-Weiner diversity (H') values for successional communities of Jocassee Gorges. Mean values of ES, MS, and MLS age-classes were compared to those of reference plots using one-way ANOVA with Dunnett's multiple comparison test (row comparison); means within an age-class were compared using ANOVA with Tukey's comparison test (column comparison).

Species	Ecosystem type	ES	MS	LS	LLS
Richness	xob	51.7 ± 7.9*	35.7 ± 1.5c	37.0 ± 6.3b	39.6 ± 5.4c
	xco	47.3 ± 5.0	39.0 ± 6.7c	40.0 ± 9.0b	43.4 ± 9.2bc
	som	58.0 ± 17.9	66.3 ± 17.6ab	48.3 ± 14.4ab	57.3 ± 9.8a
	mhb	76.0 ± 2.8	85.8 ± 14.9*a	72.6 ± 12.7a	58.0 ± 2.0ab
	mhr	73.6 ± 18.9*	52.1 ± 11.2bc	56.7 ± 12.8ab	49.2 ± 7.9ab
Evenness	xob	0.8 ± 0.0	0.8 ± 0.0	0.8 ± 0.0ab	0.8 ± 0.0
	xco	0.8 ± 0.0	0.8 ± 0.0	0.8 ± 0.0ab	0.8 ± 0.0
	som	0.8 ± 0.0*	0.8 ± 0.0	0.9 ± 0.0a	0.8 ± 0.0
	mhb	0.8 ± 0.0	0.8 ± 0.0	0.8 ± 0.0ab	0.8 ± 0.0
	mhr	0.8 ± 0.0	0.8 ± 0.0	0.8 ± 0.0b	0.8 ± 0.0
Diversity	xob	3.2 ± 0.2	2.9 ± 0.2b	3.0 ± 0.1bc	3.0 ± 0.1b
	xco	3.0 ± 0.0	3.0 ± 0.1b	2.9 ± 0.1c	3.0 ± 0.2b
	som	3.2 ± 0.3	3.4 ± 0.3ab	3.3 ± 0.2ab	3.4 ± 0.2a
	mhb	3.5 ± 0.0	3.5 ± 0.3a	3.4 ± 0.2a	3.2 ± 0.2ab
	mhr	3.5 ± 0.2*	3.2 ± 0.2ab	3.2 ± 0.1ab	3.2 ± 0.2ab

* Value significantly differs from reference (LS) plots ($p < 0.05$)
Value significantly differs within a column without shared letters ($p < 0.05$)

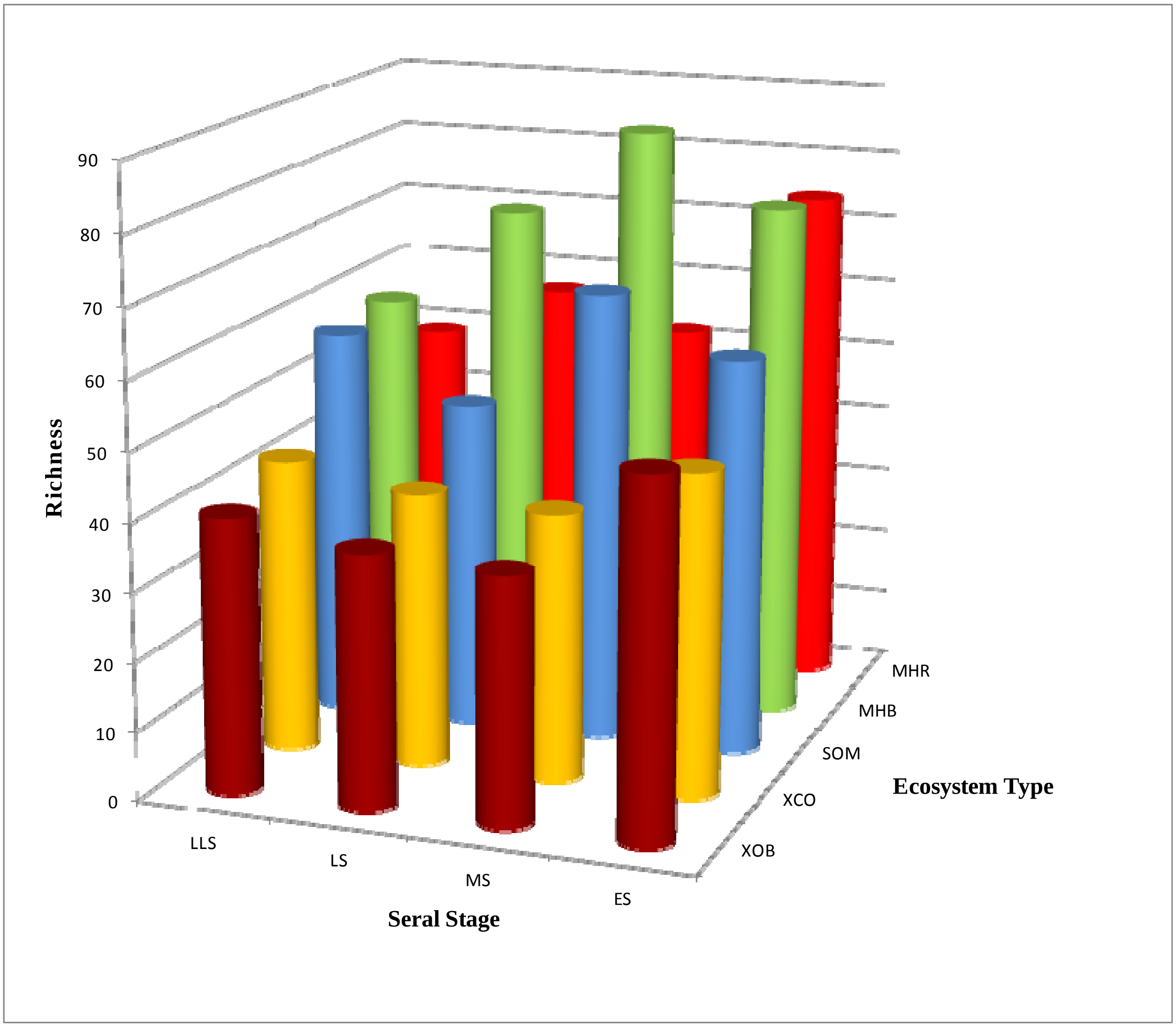

Figure 4.19. Patterns of species richness during succession of ecosystem types within Jocassee Gorges.

and SOM ecosystem types. Within all ecosystem types except SOM, richness and diversity were highest for the ES age-class. No difference in species evenness (E) was significant between ecosystem types or age-classes. Richness and diversity patterns were similar between MS, MLS, and LS age-classes, where the lowest values were consistently found in XOB and XCO ecosystem types, and the highest values were found in the MHB and SOM types. Higher richness values in the MLS age-class of the MHR ecosystem type were attributed to a decrease in great rhododendron cover in one of these plots. Dense canopies of this ericaceous shrub are common in this ecosystem type, and typically result in a decrease of species richness within these sites (Baker and Van Lear 1998).

Figures 4.20-24 document the relative compositional change of woody stems and ground flora of the same species between age-classes of each ecosystem type, in order to determine if species recruitment is changing across temporal gradients within Jocassee Gorges. Ground flora of these species can include either seedlings or saplings failing to reach breast height. Summaries of age-class comparisons by ecosystem type are given below.

Xeric oak - blueberry: Woody stem species composition and ratios between woody stems and ground flora did not significantly change between age-classes of this ecosystem type (Figure 4.20). These sites were consistently composed of an even distribution of xerophytic (scarlet oak, chestnut oak, shortleaf pine, and Virginia pine) and cosmopolitan species (red maple, blackgum, and sourwood).

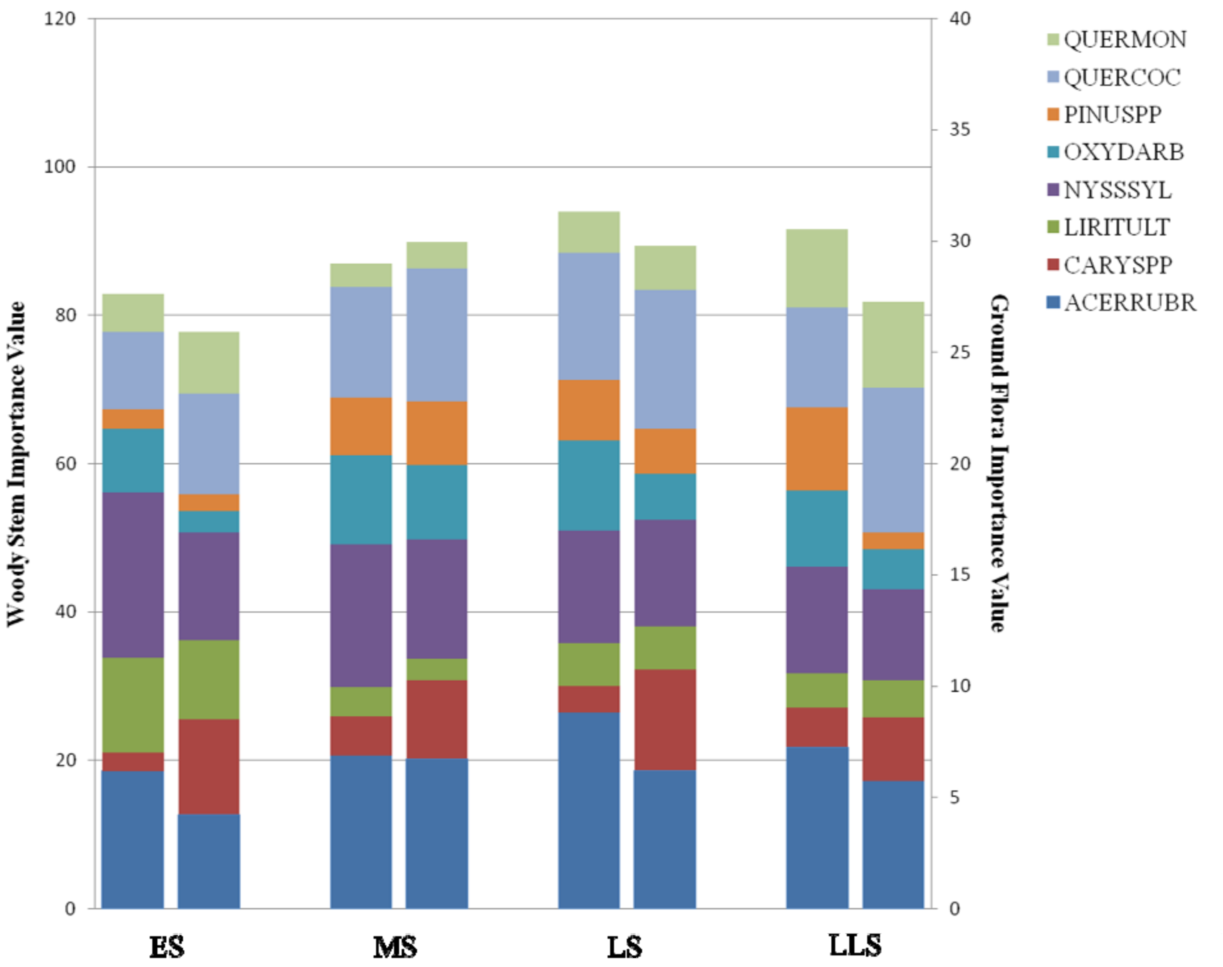

Figure 4.20. Mean importance values of selected woody stem (left stacked-bar of a pair) and ground flora (right) species for five age-classes in the xeric oak-blueberry ecosystem type of Jocassee Gorges, SC. Species codes are composed of the first four letters of the genus and first three letters of the species epithet, and first letter of the variety, if necessary.

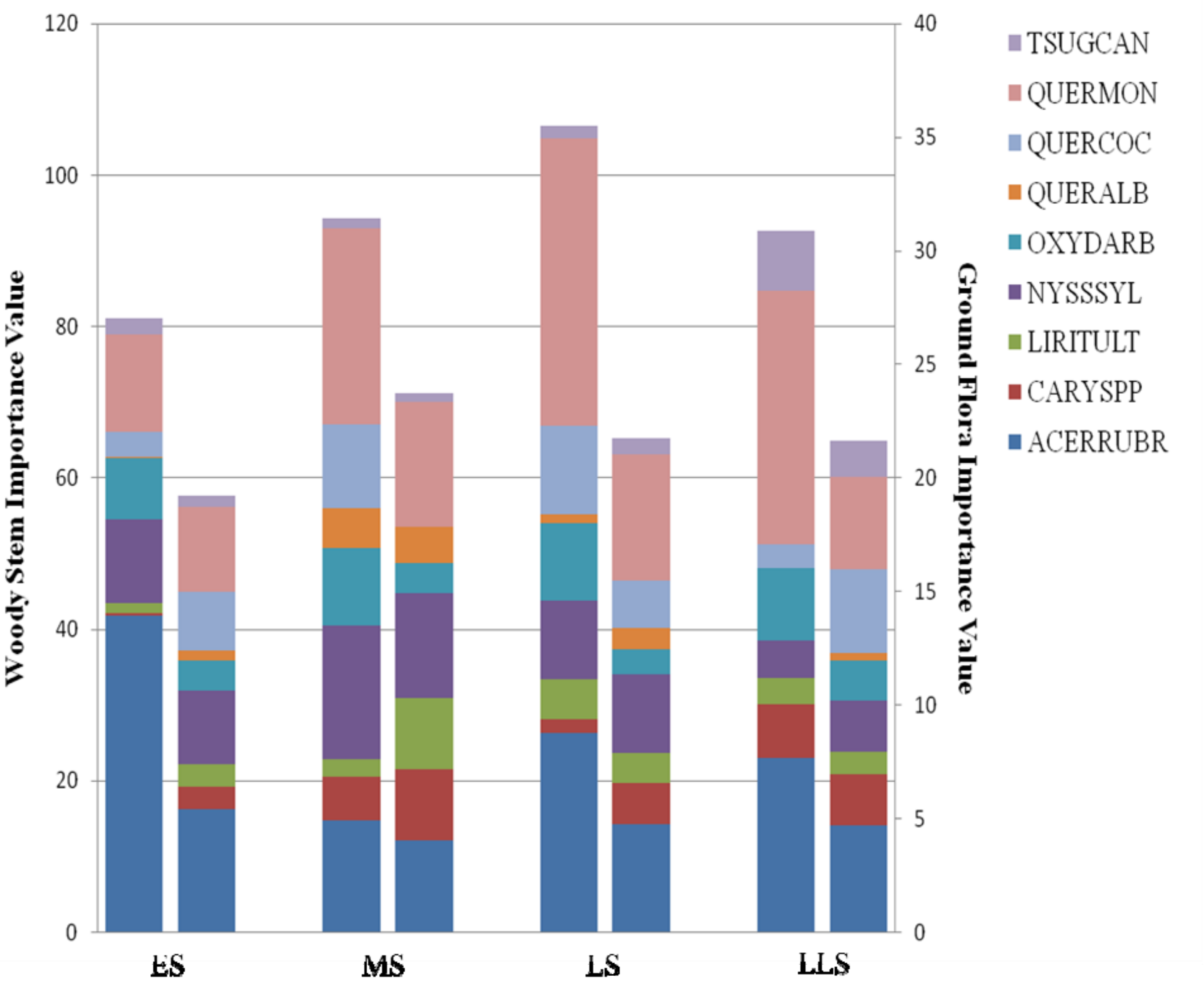

Figure 4.21. Mean importance values of selected woody stem (left stacked-bar of a pair) and ground flora (right) species for five age-classes in the xeric chestnut oak-mountain laurel ecosystem type of Jocassee Gorges, SC. Species codes are composed of the first four letters of the genus and first three letters of the species epithet, and first letter of the variety, if necessary.

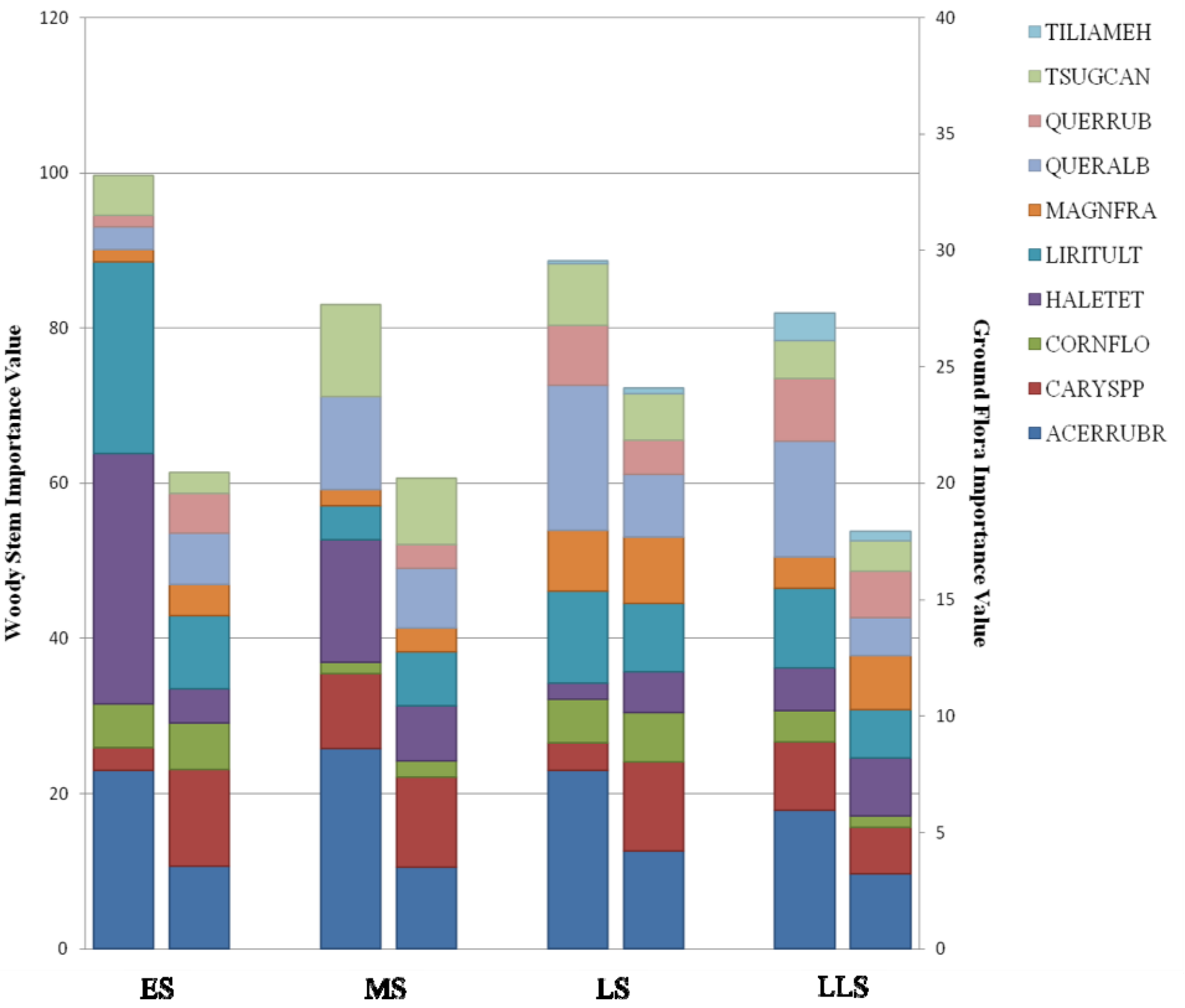

Figure 4.22. Mean importance values of selected woody stem (left stacked-bar of a pair) and ground flora (right) species for five age-classes in the submesic oak-mixed flora ecosystem type of Jocassee Gorges, SC. Species codes are composed of the first four letters of the genus and first three letters of the species epithet, and first letter of the variety, if necessary.

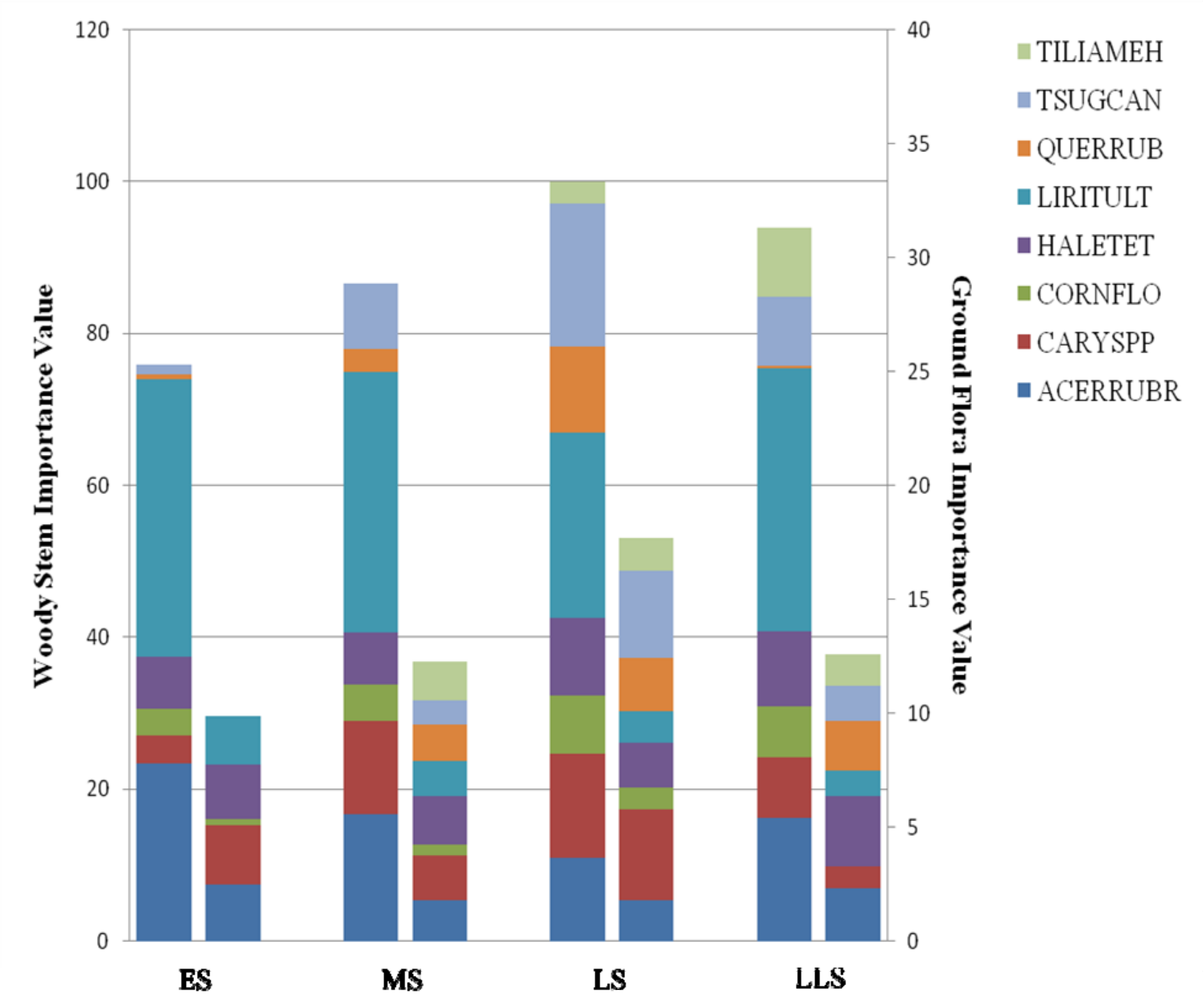

Figure 4.23. Mean importance values of selected woody stem (left stacked-bar of a pair) and ground flora (right) species for five age-classes in the mesic hardwood-bloodroot ecosystem type of Jocassee Gorges, SC. Species codes are composed of the first four letters of the genus and first three letters of the species epithet, and first letter of the variety, if necessary.

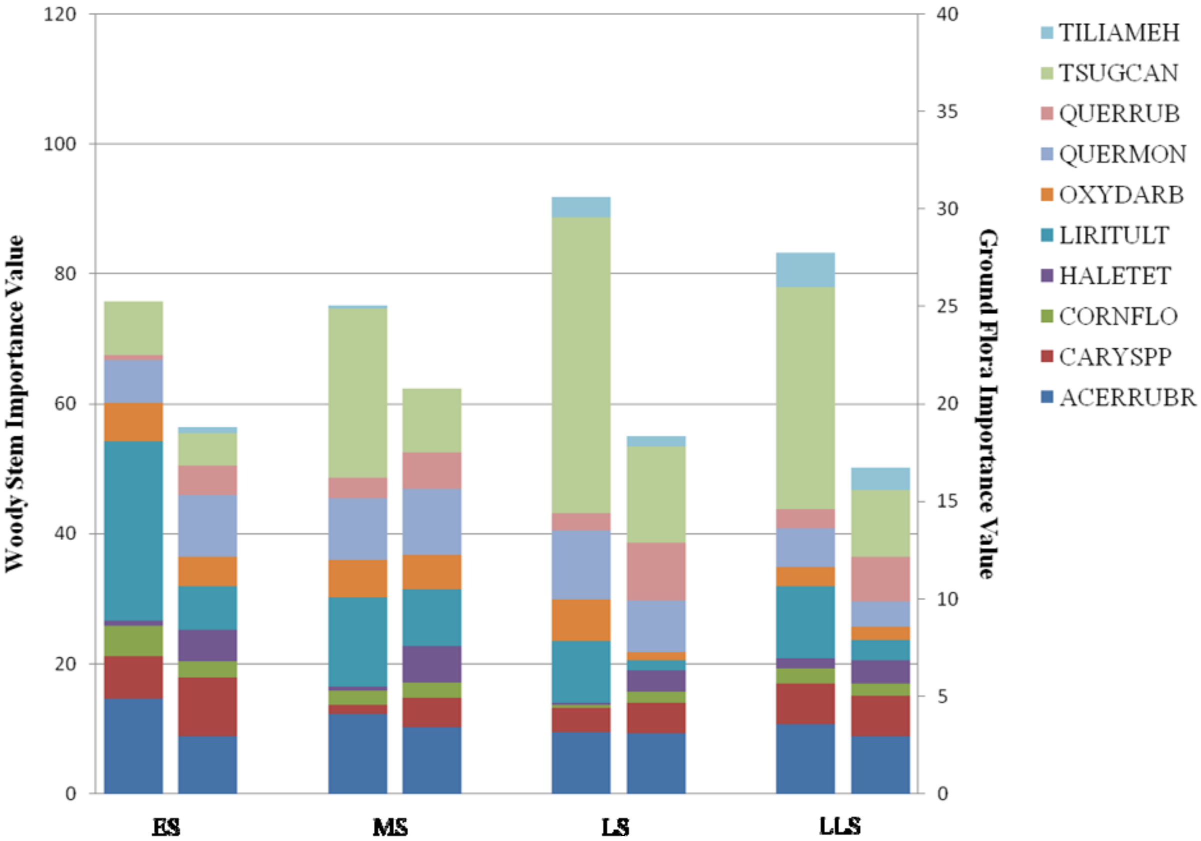

Figure 4.24. Mean importance values of selected woody stem (left stacked-bar of a pair) and ground flora (right) species for five age-classes in the mesic hemlock-rhododendron ecosystem type of Jocassee Gorges, SC. Species codes are composed of the first four letters of the genus and first three letters of the species epithet, and first letter of the variety, if necessary.

Xeric chestnut oak - mountain laurel: Early successional sites of this ecosystem type were dominated by regenerating red maple, with lesser amounts of chestnut oak, blackgum, and sourwood (Figure 4.21). Over time, chestnut oak increased in relative importance in the woody stem stratum, while ratios between woody stem and ground flora values for this species remained consistent among later age-classes (MS, MLS, and LS). Red maple declines in relative importance in these later age-classes.

Submesic oak - mixed flora: Early successional sites if this intermediate ecosystem type were dominated by regenerating red maple, common silverbell, and yellow-poplar (Figure 4.22). Over time, yellow-poplar declined in relative importance and was replaced by white oak, Fraser magnolia, and pignut and mockernut hickory. Ratios of white oak woody stems to ground flora declined in the LS age-class of this ecosystem type.

Mesic hardwood - bloodroot: Importance values of yellow-poplar were consistently high across age-classes in this ecosystem type (Figure 4.23). In MLS and LS age-classes, mesophytic species such as basswood, eastern hemlock and northern red oak were minor canopy dominants. There was a significant decline in woody stems of northern red oak between MLS and LS age-classes, although ground flora importance of this species remained constant.

Mesic hemlock - rhododendron: Early successional sites of this ecosystem type were dominated by yellow-poplar and red maple saplings (Figure 4.24). Over time, these species declined in relative importance in the woody stems, while eastern hemlock importance increased. Although only a minor canopy component, northern red oak woody stem to ground flora ratios remained similar in later successional age-classes (MS, MLS, and LS).

CHAPTER FIVE

DISCUSSION

Changes in Woody Stem Species

Examination of results from an array of multivariate and univariate analysis techniques on woody stem species datasets revealed certain trends in temporal and spatial dynamics of ecosystem types within Jocassee Gorges. Woody stem composition did not separate plots in age-classes of the XOB and MHB ecosystem type. These ecosystem types represent the two ends of the fertility gradient within Jocassee Gorges. Results were consistent with the examination of woody stem to ground flora ratios (Figure 4.20 and 4.23). In the other three ecosystem types, woody stem species composition distinguished ES age-class seres from older seres and reference stands. Woody stem richness was highest in early successional age-classes within the Jocassee Gorges landscape and remained the same in later successional classes. Elliott et al. (1997) found that woody stem species richness increased over time in the cove hardwood and xeric hardwood-pine sites within the Coweeta Basin. In the Jocassee Gorges, woody stem richness declines across temporal gradients (early succession to late succession seres) within all ecosystem types except the intermediate SOM. Vigorous resprouting species such as red maple and yellow-poplar were abundant on all early successional age-classes (except for yellow-poplar on XCO types), but did not always decline across temporal gradients. Complex interactions between environmental conditions and disturbance history caused varying responses of these woody colonizers. For instance, although initially abundant on early successional sites, yellow-poplar declined over time within MHR ecosystem types. However, on MHB ecosystem types, yellow-poplar was consistently abundant across all age-classes. Red maple, undoubtedly having the broadest ecological amplitude of any woody species in the eastern United States, also exhibited broad temporal amplitude within the Jocassee Gorges landscape. This species was abundant in all ecosystem types of all age-classes, but it did decline in relative abundance in older age-classes of xerophytic ecosystem types.

Over the past twenty years, there has been much research and speculation paid to possible oak decline in eastern North American forests (Healy et al. 1997, Brose et al. 2001). Many researchers currently agree that oak regeneration has been impeded on mesic to intermediate forest sites due to poor regeneration and an increase in dominance of red maple, sugar maple and yellow-poplar (Loftis and McGee 1993). Declines in regeneration on these productive sites seem to correspond with the increasing absence of fire beginning in the early 20th century (Lorimer 1993). Most oaks have intermediate shade intolerance and cannot maintain a positive carbon balance under dense canopies (Hodges and Gardiner 1993). These canopies can be composed of both a rich herbaceous layer and a dense mid-canopy layer of relative shade tolerant species like red maple. Historically, frequent low intensity surface fires would have top-killed these mid-canopy trees and allowed oaks to build up sufficient amounts carbohydrate to outcompete faster growing plants in the future. Oak regeneration does not seem to be a problem on dry, exposed sites because these sites tend to have higher light levels and soils are xerified and more adequate for acorn germination. Furthermore, oaks are better competitors on drier, nutrient-stressed sites than many other species. Oak regeneration and maturation seem to closely follow the initial floristics model of forest succession proposed by Egler (1954). In contrast to the original relay floristics model of succession (Clements 1916), which proposes that well-defined seral-stage plant communities follow a disturbance, i.e., pioneer shade intolerants succeed to intermediates, which succeed to climax shade tolerant species, the initial floristics model argues that succession is a function of life history traits of species that are present on a site at the time of disturbance. This model applies well to the shifting mosaic of mature oaks and immature oak seedlings that dominated historical eastern United States hardwood forests and was brought on by early human cuttings, windstorms, ice damage, disease, and lastly, fire. There does not appear to be a lack of oak regeneration on mesophytic oak sites (SOM) within the Jocassee Gorges landscape, based on similar ratios between woody stem (trees and tall saplings) and ground flora (seedlings and low saplings) across age-classes. The absence of northern red oak as a canopy dominant within the LS age-class of the fertile MHB ecosystem type is probably a function of logging history rather than problems with oak regeneration on mesic sites. Although fire has been historically absent from the Jocassee Gorges for almost a century, early successional patches created by intense timber practices over the same time period have created a similar landscape that favors oak regeneration.

Changes in Ground Flora Species

When comparisons were made between age-classes of individual ecosystem types, ordination and MRPP results indicated compositional differences in ground flora species between earlier successional seres (ES, MS, and MLS) and reference stands (LS) (Table 2.4). There were no significant trends in changes of species diversity within xerophytic or mesophytic communities. In other words, ground flora responded uniquely to disturbance history based on ecosystem type. Grime's (1977) model of succession, which accounts for certain plant life history traits (R, ruderal; C, competitive, and S, stress tolerant), predicts that higher species change will occur on fertile, more productive soils. In contrast to this model, Tilman proposed the resource-ration hypothesis (1988). This model of succession assumes that each species is able to outcompete others at a level of optimum environmental condition. Unlike Grime's model, Tilman's model predicts that minimal species change will occur on fertile, more productive sites and greater species change will occur on less productive sites. Ground flora data from these early successional communities suggested that both hypotheses are at work in the Jocassee Gorge landscape. Like Grime's model suggests, productive site composition experienced high species change between early and later successional stages. However, the unproductive XOB ecosystem type also experienced high species change across the temporal gradient, following the Tilman model. Except for the XCO ecosystem type, all sites within Jocassee Gorges experienced significant shifts in ground flora composition across the temporal gradient. Typically these shifts pointed downward over time. The XCO ecosystem, which occupied north-facing, upper slope positions and tended to have more coarse-texture soil, experienced very little ground flora composition change over time.

The debate over ground flora responses to human manipulated disturbances (logging and agriculture) in the southern Appalachian landscape has often been heated (Duffey and Meier 1992, Elliott and Loftis 1993). Although the woody stem composition and structure of these forests may quickly return to old growth function and conditions once canopy closure has been achieved, many herbaceous species may be slow to recover after decades of significant logging pressure. Species that are thought to be disturbance-sensitive in the southern Appalachians include Dutchman's britches (*Dicentra cucullaria* [L.] Bernh.), dwarf ginseng (*Panax trifolius* L.), mountain black-cohosh (*Actaea podocarpa* de Candolle), sharp-lobed hepatica (*Anemone acutiloba* [de Candolle] Lawson), and common blue-cohosh (Bratton and Meier 1998). In light of this paper, and other papers with similar datasets, results were varied in Jocassee Gorges, with respect to the distribution of ground flora species throughout recently disturbed versus older-aged stands. Disturbance-sensitive species such as Dutchman's britches, dwarf ginseng, and mountain black-cohosh were not encountered in any of the 111 plots sampled during this study. Common blue-cohosh was found in this study, but only in older-aged (> 50 years) stands. Other species restricted to older-aged stands included hay-scented fern (*Dennstaedtia punctilobula* [Michaux] T. Moore), white ash (*Fraxinus americana*), wood-nettle, Canada lily, hairy northern spicebush (*Lindera benzoin* [L.] Blume var. *pubescens*), bluegrass (*Poa autumnalis* Muhl. ex Elliott), foamflower, and basswood. In their study of rich cove forests within the southern Appalachians, Jackson et al. (2009)

determined that presence-absence of species did not differ between old and second growth forests, but that density of certain cove indicator species, e.g., umbrella-leaf [*Diphylleia cymosa* Michaux], white ash, and wood-nettle, was higher in older forests.

Overall, the results of this study indicate that forest management practices have not significantly shifted the ground flora species composition of ecosystem types within Jocassee Gorges. As noted in the last paragraph, there have been shifts in importance of individual species over time, and the absence of several key disturbance-sensitive species on the Jocassee Gorges landscape is probably a function of the lack of true southern Appalachian 'old growth' (> 200 years) stands within the property. Unlike other studies that have compared species composition between stand initiation phase, i.e., recent clearcuts, and older forests (Elliott et al. 1997, Jenkins and Parker 1999), this study's earliest age-class occurred in stands that had begun to exhibit canopy closure. As a result, true early successional species of the Jocassee Gorges landscape were not found in this dataset. On young sites that achieved canopy closure, ground flora species were distributed in pattern indicating broad distinctions between mesophytic and xerophytic forests. As these stands matured, species segregated into identifiable ecological units across the landscape, representing finer-scale differences in environmental condition.

Changes in Environmental Condition

Although the sampling design employed in this research set out to minimize environmental variation across age-classes of each site type, there were significant differences in a few of the abiotic discrimating variables. As expected, topographic position and relative moisture status of ecosystem types did not vary across site types of any age-class. However, there was a positive trend between A-horizon soil thicknesses across age-classes of all ecosystem types. Furthermore, multivariate analysis of vegetation and environmental datasets revealed A-horizon thickness as a significant explanatory variable with respect to compositional differences in early versus later successional age-classes of ecosystem types. These results are consistent with Jenkins and Parker (2000), who found significant positive correlations between A-horizon thickness and tree-age on anthropogenic disturbed forests of southern Indiana. Soil properties in the Jocassee Gorges were secondary to geomorphology with respect to distinguishing ecosystem site types in later successional forests. However, deep and fertile A-horizons characterized the soils of the MHB type, and distinguished it from other mesophytic forests.

Ecological Species Groups

The results suggest that most ecological species groups defined from later successional age-class stands remain intact even in early successional stands. The importance value of the *Liriodendron tulipifera* group was two to three times greater in ES stands than in LS stands except in the XCO ecosystem type. The increased importance of yellow-poplar stems in ES stands is related to its ability to respond quickly to increased resources brought on by small- and large-scale canopy openings (Runkle 1998, Hart and Grissino-Mayer 2009). As these forests mature, yellow-poplar--a significant shade intolerant species--is replaced by woody tree species indicative of later successional age-classes that are able to outcompete for resources on most sites. The constant high importance of yellow-poplar on fertile, mesic sites (MHB) could be a function of the high two-fold resource (nutrient, light) availability on these sites during early succession and the high nutrient availability throughout later successional phases. Most rich cove forests in the southern Appalachian Mountains dominated by yellow-poplar have experienced a large-scale disturbance to allow for this species to colonize the site and over time out-compete slower growing mesophytic canopy species more typical of undisturbed conditions. It should be noted that yellow-poplar is one of the few tree species in eastern U.S. forests that is both long-lived and shade intolerant. Successful regeneration of this species requires significant canopy gaps which allow for enough light to penetrate the forest floor.

Species group correlations in MS and MLS stands of all ecosystem types were similar to correlations in LS stands, further suggesting that long-term timber management practices in Jocassee Gorges have not significantly shifted woody stem or ground flora composition away from later successional age-class conditions. The positive correlations in ES stands between the xeric *Vaccinium pallidum* group and more mesophytic groups, such as the *Adiantum pedatum, Rhododendron maximum,* and *Quercus alba* group, are due to the increased importance of *Vaccinium pallidum* group species on mesic sites. These results are consistent with similar studies that have found that early successional mesophytic forest sites are composed of a mixture of ground flora from off-site conditions and species more indicative of later successional stage conditions (Jenkins and Parker 1999).

Species Diversity and Successional Trends in Ecosystem Types

In this study, there were no overall trends in species richness and diversity across age-classes. Rather, richness and diversity trends were unique to each ecosystem type. In xeric, exposed ridgetops (XOB), species diversity was highest in early successional stands, and was relatively stable in stands older than 25 years. Alternatively, diversity remained stable across all age-classes in xeric, north-facing (XCO) sites. Trends were also unique within mesophytic forests of Jocassee Gorges. In fertile sites with intermediate moisture status (SOM), diversity trends across age-classes were highest in mid-successional and late-successional age-classes. Diversity was highest in mid-successional stands and declined over time past 50 years within fertile sites of mesic moisture status (MHB). In mesic sites with less fertile, acidic soils (MHR), diversity trends were similar to XOB sites. In the Chauga Ridges region of South Carolina, Hutto (1998) did not detect significant differences in species richness between early (7-25 years) and late (51-84 years) age-classes across any hydrological unit, although he did detect an overall trend of increasing species richness across all units. Observations made in the Piedmont (Peet and Christensen 1988) and mountains (Elliott and Swank 1994) of North Carolina suggest that species diversity is highest at the earliest stages of stand development, decreases after canopy closure, and increases at later successional stages due to openings caused by tree fall.

Patterns of species diversity have often been sought by vegetation ecologists and observations have yielded wildly variable results. Some researchers have shown that diversity peaks in late succession and then declines over time in the climax forest

(Whittaker 1972), while others have shown both steady declines (Peet 1978) and increases (Glenn-Lewin 1980) in diversity from early succession to climax conditions. As these studies, this study, and countless others have suggested, there are no general rules that lead to a unifying model of documenting diversity through succession. However, as Peet (1992) suggests "where a few environmental gradients dominate the vegetation pattern, it is often possible to interpret diversity as a region-specific multidimensional response." The results illustrated in this study justify utilizing a multifactor ecological classification framework when examining species diversity trends and vegetation composition across both spatial and temporal gradients within forest landscapes, such as the Jocassee Gorges.

The Landscape Ecosystem Classification Framework and Dynamics of Succession

Early theories of succession can be broken down into two distinct schools: 1) Clements' Theory, where autogenic processes (within the system, e.g., nitrogen fixation, increased organic matter) take over and communities develop into noticeable seres; and 2) Cowles' Theory, where allogenic processes (outside the system, e.g., climate, wind, fire) influence community structure, resulting in more dynamic, shifting end points. Other theories have evolved from these two (Egler 1954, Grime 1977, and Tilmann 1988), each with distinct approaches as to how autogenic versus allogenic processes affect community change. As noted by Carter et al. (2000) "studies that focus on successional communities in the southern Appalachians are uncommon." This is still the case ten years later. Hutto (1998) described seral communities within the Chauga Ridges of South Carolina, and found a decrease of yellow-poplar on xeric and intermediate sites and an absence of mesophytic hardwood species (basswood, American beech, and sweet birch) on early successional sites. Similar trends were noticed in this study of the Jocassee Gorges. Seral stage communities were also described in a Landscape Ecosystem Classification Framework for the Highlands Ranger District of the Nantahala National Forest (Carter el al. 2000). In that study, mid-elevation early successional (0-25 years) xeric sites were dominated by eastern white pine, mixed oaks, and black locust; intermediate sites were dominated by yellow-poplar, northern red oak, and black locust and mesic sites were dominated by yellow-poplar, black locust, and flowering dogwood. In spite of the relative close proximity between the Highlands Ranger District and Jocassee Gorges, species composition between the two study sites was decidedly distinct on all scales (plot, community type). Climate, elevation, and disturbance history function together to affect the composition and structure of vegetation within each landscape. With this said, it is important to note that the landscape ecosystem framework developed for successional communities within Jocassee Gorges is applicable within that landscape and that landscape alone. Beyond in either direction, changes in topography, climate, physiographic province, and disturbance history result in a matrix of distinct ecosystem types.

The forest landscapes of Jocassee Gorges have undergone significant, large-scale shifts in vegetation composition for centuries. In the recent past, the loss of *Castanea dentata* brought on by the introduced chestnut blight (*Cryphonectria parasitica*) of the early twentieth-century has been linked to an increase in importance of red maple and eastern hemlock in Appalachian forests (Vandermast and Van Lear 2002, McEwan and Muller 2006). The decline of flowering dogwood from dogwood anthracnose (caused by the fungus *Discula destructive*) across eastern deciduous forests has resulted in a change in understory species composition, particularly in mesophytic sites (Jenkins and White 2002). Because of flowering dogwood's high foliar concentrations of calcium (Ca), many ecologists have speculated that the loss of this species in eastern forests could have drastic consequences in ecosystem function by significantly disrupting Ca cycling on the forest floor (Jenkins et al. 2007). Examining vegetation, environment, and successional sequences in an ecological classification framework can be used to better monitor and predict changes in ecosystem types brought on by large-scale disturbance regimes such as forest clearing and insect/pathogen outbreaks. Currently, eastern hemlock faces extirpation throughout its range because of the introduced hemlock woolly adelgid (*Adelges tsugae* Annand.) (Ford and Vose 2007). Understanding the present compositional and structural status of not only old growth, but seral stage, stands dominated by eastern hemlock within Jocassee Gorges provides baseline information for the documentation of change that is sure to occur because of this insect outbreak. The landscape ecosystem classification approach proved to be highly useful for documenting communities in early stages of stand development and describing the autogenic and allogenic processes driving these movements. Gathering more environmental data would be helpful to test hypotheses that early and mid sere communities may be defined by a different set of environmental discriminants. Understanding successional pathways of ecological units described from a multifactor classification model is a critical aspect to the management of Jocassee Gorges.

CHAPTER SIX

MANAGEMENT IMPLICATIONS

For millennia, the forest landscapes of eastern North America have undergone periodic, natural disturbances (wind throw, fire, disease/insect outbreaks) that have shaped current distribution and successional pathways of the regional vegetation. Woody species found in these landscapes are well-suited for these events that open significant portions of the forest canopy. Most woody species have the ability to regenerate and resprout following disturbance. These adaptations have led many researchers to describe eastern deciduous forests as ‘resilient’ in response to decades of anthropogenic disturbance (Thompson et al. 2009). Shifts in composition and structure of ground flora have been more profound in response to large-scale forest clearing for timber production or agriculture (Bratton and Meier 1998). However, ground flora in earlier successional age-class stands of the Jocassee Gorges have recovered to later age-class (reference) composition by 26 years following forest disturbance in all ecosystem types. This is particularly the trend when species are lumped into ecological groups and examined across age-class by ecosystem type. Undoubtedly, some disturbance-sensitive ground flora species have yet to recover following intense timber harvesting practices. Species that inhabit mesophytic forests, for instance, may be more prone to decreased survival in heavily disturbed stands due several factors, such as soil/site desiccation brought on by large-scale canopy openings, and inadequate competitive or dispersal ability of plants in an environment experiencing a resource switch from low-light to high-light.

In the southern Appalachians, the three primary causes of disturbance are human manipulation, fire, and ice storms (Copenheaver et al. 2006). Small-scale, natural disturbances are thought to be the driving force of succession in most old-growth forests of eastern North America (Runkle 1982), but large-scale, anthropogenic disturbances have also had a recent effect on community structure and temporal dynamics (Christensen 1989). The upland forests of the Jocassee Gorges tract represents a scattered mosaic of spatial patterns influenced by these natural and anthropogenic disturbance regimes. The complex interactions of environmental site conditions and long-term disturbance history weave together to influence vegetation distribution patterns across the Jocassee Gorges landscape. Furthermore, spatial and temporal heterogeneity patterns are influenced by large-scale geomorphologic boundaries occurring within the property. The southern section of the tract occurs in the Piedmont physiographic province and is characterized by lower elevations, lesser dissected topography, and an increased frequency of human-disturbed stands. The remote northern section of the Jocassee Gorges represents a low elevation, montane landscape typical of other sites within the southern Blue Ridge Mountain physiographic province. This northern unit, which represents the majority of the Jocassee Gorges landscape, is characterized by higher elevations, a heavily dissected topography, and a decreased frequency of human-disturbed stands. Management strategies employed by the South Carolina Department of Natural Resources (SCDNR) should take into consideration the major distinctions of these two broad landscape units. The inherent qualities of these landscape units coupled with the temporal model of ecosystem units is used to discuss management options within the Jocassee Gorges landscape, and follows below.

The results from this study indicate that long-term timber harvesting practices have had minor effects on the composition and structure of ground and woody stem species, but may have significant effects on overall ecosystem integrity due to such factors as the decrease of A-horizon soil depths across all early successional ecosystem types and a shift in importance from a small-scale / long-term frequency to a large-scale / short-term frequency disturbance regime. The management options that are presented here focus on implications of vegetation diversity along the continuum of environmental conditions within Jocassee Gorges, and ignore other ecosystem attributes such as wildlife diversity, soil and water resources, human recreation, and timber harvesting for financial gain. However, it is expected that management activities within the Jocassee Gorges operate under ever-shifting economic and political constraints within the state of South Carolina.

Option 1: Succession Management (Oak Regeneration)

The three basic causes of succession are site availability, differential species availability, and differential species performance (Pickett et al. 1987). Luken (1990) extrapolated how these ecological processes could be applied to ecosystem management, and developed three corresponding anthropogenic techniques designed to mimic each cause. The techniques include plant and plant part removal, e.g., timber harvesting, mowing, grazing, and prescribed fire, shifting resource availability, e.g., soil fertilization, and changing propagule availability, e.g., seedling/mulching, topsoiling, planting. If these techniques, alone or in combination, are applied in Jocassee Gorges, timing of successional pathways between early successional and stable-state conditions can be reduced in certain ecosystem types. For instance, prescribed fire within xerophytic and intermediate sites will favor oaks over red maple and yellow-poplar. It is important to note that results from this study do not suggest that oak regeneration is a problem on any site type within Jocassee Gorges, and that use of the Succession Management Option to increase yield of oak species should be applied only if it is the desire of resource managers to reduce competition and density of mesophytic or disturbance-driven species. Silvicultural techniques can be applied to stands dominated by off-site pine species or disturbance-driven yellow-poplar in order to promote regeneration of early successional species. If the desired outcome is to perpetuate oak forests, a shelterwood harvest technique followed by prescribed fire should be used to lessen the importance of unwanted species, e.g., yellow-poplar, red maple (Brose et al. 1999).

Option 2: Succession Management (Current Conditions)

The distribution of successional and reference stands is well-documented herein within the Jocassee Gorges. Management datasets, such as stand and roadways, can be integrated into a geographic information system (GIS) along with spatially mapped environmental datasets in order to produce predictive and actual maps of vegetative condition throughout the tract. Succession Management can then be applied to maintain the current spatial and temporal landscape matrix. This will involve an intense timber harvesting regime that is designed to promote early successional conditions in some areas, while other areas are left to proceed along natural successional pathways.

Option 3: Succession Management (Natural State, Active)

In order to promote composition and structure conditions of regional steady state forests, planting of disturbance-sensitive ground flora species can be applied in the early successional seres of each ecosystem type. Species lists and microsite conditions from old growth sites within the surrounding landscape (both Mountain and Piedmont) can be compared with vegetation and abiotic data from permanent plots in Jocassee Gorges and absent species can be planted in sites with similar environmental conditions. However, it should be noted that the vegetation and abiotic conditions inventoried in this study are unique to the Jocassee Gorges landscape, and that care should be given when making extrapolations on species-site attributes outside the study area. This management approach should be used if the desired outcome is to reduce encroaching thickets of great rhododendron on riparian sites and their adjacent upland forests. As noted by Vandermast and Van Lear (2002), American chestnut decline in riparian areas of the southern Appalachian Mountains is a significant cause of increased prevalence of great rhododendron. Baker and Van Lear (1998) speculate that rhododendron encroachment could seriously affect the ability of trees to regenerate on sites shaded out by the dense ericaceous canopy. The thick duff component found underneath areas of significant rhododendron could also affect recruitment and survival of ground flora.

Option 4: No Management (Natural State, Passive)

If current upland forest stands are left to succeed without any intervention from humans, they will eventually reach steady-state conditions similar to a landscape encountered by European settlers in the eighteenth century. Some of these forests will become dominated by oaks (xerophytic and intermediate sites) and other forests will become dominated by a variable mixture of oak and non-oak species (mesophytic sites). Stands that are dominated by off-site, planted species, e.g., eastern white and loblolly pine, will eventually return to compositional conditions reflected in older age-class stands of particular site types. External environmental processes will have both negative and positive effects on the Jocassee Gorges landscape, just as they have had for hundreds of years, e.g., collapse of American chestnut. In the MHR ecosystem type, eastern hemlock caopy trees will succumb to the destructive, exotic pest, hemlock wooly adelgid (*Adelges tsugae)*. In these acidic coves and streamsides, other species such as yellow-poplar, sweet birch, hickory, red maple, and eastern white pine (not natural to the Jocassee Gorges) will become canopy dominants. Although coves that were dominated by a pure canopy of eastern hemlock under a dense tangle of great rhododendron were not sampled during this study, it is thought that these stands will lose total canopy species following hemlock mortality. Another on-going external factor influencing vegetation dynamics within the Jocassee Gorges is mortality of flowering dogwood brought about by the fungal disease dogwood anthracnose. Results from this study did not show a significant decline in dogwood across age-classes or site types. However, continued monitoring of these plots could be established in order to document species decline.

Option 5: Combination Approach (Recommended)

A management approach that utilizes components of each of the first four options can be applied within the Jocassee Gorges because of its large size, diversity of forests in different phases of stand development, composition of natural, naturalized, and planted stands, and location along a major physiographic boundary. This approach is recommended by the author. Much of the northern section of Jocassee Gorges occurs in a remote, difficult to access location composed of extremely rugged terrain. Active management techniques that require heavy equipment should be withheld from these stands. Old growth, steady state forests are scarce in the southern Appalachian Mountains and southeastern Piedmont and scarcity will increase as landscapes shift towards providing resources for urban settings (real estate development, short-rotation timber harvesting regimes). Furthermore, by limiting timber harvests throughout this mountainous portion of the Jocassee Gorges tract, regional ecosystem processes can return due to the connectivity of the Jocassee Gorges between other minimally anthropogenic disturbed sites--Ellicott Rock Wilderness Area to the west and the Greenville Watershed to the east. Finally, internal ecological processes could be harmed by increased harvesting efforts, e.g., continued depletion of mineral soil. If financial constraints are placed by the state of South Carolina on the management of Jocassee Gorges, revenue can be generated from timber harvesting on heavily disturbed southern portions of the tract dominated by stands of loblolly pine. These stands can undergo shifts in planting regimes between fully-stocked pine and a mixture of pine-hardwood in order to maintain desired conditions that maximize revenue based on market timber needs.

Succession (without timber harvesting) and passive management techniques from options described above can be applied to stands within Jocassee Gorges based on desired resource outcome. However, cost analysis should be applied before undertaking expensive programs designed to either restore certain species (oaks) or remove certain others (yellow-poplar). As the data presented suggest, successional pathways do not appear significantly altered due to historical timber management regimes and most woody stem species have adequate representation in the seedling, sapling, and tree strata across spatial and temporal units of the Jocassee Gorges landscape.

Results of this study alone should not guide the overall management of the Jocassee Gorges. Certain ecosystem types that were either too small, e.g., nonalluvial wetlands, or not widely abundant, e.g., xeric pine-oak heathlands, are not represented in this study; neither are unique landforms within the Jocassee Gorges tract, e.g., Wadakoe Mountain). Management activities should take into account these units as well, since together they represent the spatial diversity across the whole landscape entire. Nonalluvial wetlands, like forested seeps or sphagnum bogs, should be identified and mapped to reduce potential disturbance from trail building activities. Sites that support xeric pine-oak heathlands will need to be managed with respect to their current condition, and may require an active approach that utilizes harvesting and prescribed fire techniques to restore these sites to their natural condition.

CHAPTER SEVEN

SUMMARY AND CONCLUSIONS

The LEC approach used to describe temporal variation in ecosystem units provided an ecological framework that can be used to facilitate the organization and communication of vegetation and environmental conditions within a spatially diverse landscape. This study highlighted the importance of documenting successional trends within the context of abiotic site conditions and supported the premise that a quantitative approach utilizing data from fixed-area plots is critical to the interpretation of relationships between species, environment, and time. Other detailed findings included:

1) A landscape ecosystem classification was developed for successional forests across a spatial model developed by Abella (2002) within the Jocassee Gorges, SC.

2) A total of 63 0.1 ha plots were established across the Jocassee Gorges tract within early successional (10 - 25 year), mid-successional (26-50 year), and mid-late successional (51-75 year) stands. Vegetation, soil, and geomorphology data were taken from each plot.

3) Multivariate analytical techniques, including nonmetric multidimensional scaling, multi-response permutation procedure, indicator species analysis, and canonical correlation analysis, were used to describe successional pathways of each ecosystem type and overall age-class dynamics of stands within the Jocassee Gorges. A total of 280 ground flora species and 46 woody stem species identified from the 111 0.10 ha plots were used in these analyses.

4) Vegetation within early successional age-classes of xerophytic and mesophytic stands was less useful at discerning ecosystem types than older successional age-classes, although late-successional indicator species are still an important component of these younger forests.

5) Environmental discriminants typically remained constant across age-classes of an ecosystem type. There was a significant inverse trend between stand age and A-horizon thickness.

6) Species richness and diversity values were highest in the early successional age-class of all ecosystem types, except the submesic oak-mixed flora type. Diversity and richness patterns were similar across ecosystem types for all age-classes.

7) Seedling, sapling, and tree importance values for selected species of woody stems were evaluated to determine if certain species are being replaced along the temporal gradient within the Jocassee Gorges landscape. Results indicated that woody stem composition remains stable across age-classes of all ecosystem types.

8) Ecological species groups were developed from woody stem and ground flora datasets and compared across age-classes. The results suggested that most ecological species groups defined from later successional age-class stands remain intact even in early successional stands.

9) Techniques that promote a diversity of management options were described. The overall management of the Jocassee Gorges should emphasize development of stands into later successional age-classes due to the regional conservation significance, and to minimize continued soil disturbance brought about by excessive timber harvesting regimes.

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APPENDICES

Appendix A: Vascular plants of the Jocassee Gorges Tract identified in 111 0.10-ha plots of early, mid, mid-late and late successional upland forests. Taxonomy follows “Flora of the Carolinas, Virginia, Georgia, and surrounding areas; Working Draft of 6 January 2006” by Alan S. Weakley, University of North Carolina Herbarium (NCU), North Carolina Botanical Garden. Distribution of a species is given for the three physiographic provinces of South Carolina, based on data compiled from the NCU Atlas (). * indicates a southern Appalachian endemic. **indicates a Blue Ridge Escarpment endemic. NR indicates a species has not been recorded for that physiographic province in South Carolina. ? indicates uncertainty in the range of that species.

Trees

Taxon Concept	Common Name	Family	Distribution
Acer rubrum var. *rubrum*	Eastern red maple	Sapindaceae	Mt, Pd, Cp
Aesculus flava	Yellow buckeye	Sapindaceae	Mt, Pd
Amelanchier laevis	Smooth serviceberry	Rosaceae	Mt?, Pd?, Cp?
Betula alleghaniensis	Yellow birch	Betulaceae	Mt
Betula lenta var. *lenta*	Sweet birch	Betulaceae	Mt, Pd
Carpinus caroliniana var. virginiana	American hornbeam	Betulaceae	Mt, Pd
Carya alba	Mockernut hickory	Juglandaceae	Mt, Pd, Cp
Carya cordiformis	Bitternut hickory	Juglandaceae	Mt, Pd, Cp
Carya glabra	Pignut hickory	Juglandaceae	Mt, Pd, Cp
Carya ovalis	Red hickory	Juglandaceae	Mt, Pd, Cp
Carya pallida	Sand hickory	Juglandaceae	Mt, Pd, Cp
Carya spp.	Hickory	Juglandaceae	Mt, Pd, Cp
Castanea dentata	American chestnut	Fagaceae	Mt
Cercis canadensis var. *canadensis*	Eastern redbud	Fabaceae	Mt, Pd, Cp
Cornus alternifolia	Alternate-leaf dogwood	Cornaceae	Mt, Pd
Cornus florida	Flowering dogwood	Cornaceae	Mt, Pd, Cp
Crataegus spp.	Hawthorn	Rosaceae	Mt, Pd, Cp
Diospyros virginiana	American persimmon	Ebenaceae	Mt, Pd, Cp
Fagus grandifolia var. *caroliniana*	American beech	Fagaceae	Mt, Pd, Cp
Fraxinus americana	White ash	Oleaceae	Mt, Pd, Cp
Fraxinus pennsylvanica	Green ash	Oleaceae	Mt, Pd, Cp
Halesia tetraptera var. tetraptera	Common silverbell	Menyanthaceae	Mt, Pd, Cp
Hamamelis virginiana var. virginiana	Witch-hazel	Hamamelidaceae	Mt, Pd, Cp
Ilex opaca var. opaca	American holly	Aquifoliaceae	Mt, Pd, Cp

Trees, continued

Taxon Concept	Common Name	Family	Distribution
Juglans nigra	Black walnut	Juglandaceae	Mt, Pd, Cp
Juniperus virginiana var. *virginiana*	Eastern red cedar	Cupressaceae	Mt, Pd, Cp
Liquidambar styraciflua	Sweet gum	Altingiaceae	Mt, Pd, Cp
Liriodendron tulipifera var. *tulipifera*	Yellow-poplar	Magnoliaceae	Mt, Pd, Cp
Magnolia acuminata var. *acuminata*	Cucumber magnolia	Magnoliaceae	Mt, Pd
Magnolia fraseri	Fraser magnolia	Magnoliaceae	Mt*, Pd
Morus rubra	Red mulberry	Moraceae	Mt, Pd, Cp
Pinus rigida	Pitch pine	Pinaceae	Mt, Pd
Pinus strobus	Eastern white pine	Pinaceae	Mt, Pd, Cp
Pinus taeda	Loblolly pine	Pinaceae	Mt, Pd, Cp
Pinus virginiana	Virginia pine	Pinaceae	Mt*, Pd, Cp
Prunus serotina var. *serotina*	Black cherry	Rosaceae	Mt, Pd, Cp
Quercus alba	White oak	Fagaceae	Mt, Pd, Cp
Quercus coccinea	Scarlet oak	Fagaceae	Mt, Pd, Cp
Quercus falcata	Southern red oak	Fagaceae	Mt, Pd, Cp
Quercus montana	Chestnut oak	Fagaceae	Mt, Pd
Quercus rubra var. *rubra*	Northern red oak	Fagaceae	Mt, Pd, Cp
Quercus velutina	Black oak	Fagaceae	Mt, Pd, Cp
Robinia pseudoacacia	Black locust	Fabaceae	Mt, Pd, Cp
Sassafras albidum	Sassafras	Lauraceae	Mt, Pd, Cp
Tilia americana var. *heterophylla*	Mountain basswood	Malvaceae	Mt, Pd, Cp
Tsuga canadensis	Eastern hemlock	Pinaceae	Mt
Tsuga caroliniana	Carolina hemlock	Pinaceae	Mt*, Pd
Ulmus rubra	Slippery elm	Ulmaceae	Mt, Pd, Cp

Shrubs and Subshrubs

Taxon Concept	Common Name	Family	Distribution
Alnus serrulata	Tag alder	Betulaceae	Mt, Pd, Cp
Amorpha fruticosa	Tall indigo-bush	Fabaceae	Mt, Pd, Cp
Aralia spinosa	Devil's-walking-stick	Araliaceae	Mt, Pd, Cp
Asimina parviflora	Small-flowered pawpaw	Annonaceae	Mt, Pd, Cp
Asimina triloba	Common pawpaw	Annonaceae	Mt, Pd, Cp
Calycanthus floridus	Sweet-shrub	Calycanthaceae	Mt, Pd, Cp
Castanea pumilla	Common chinqapin	Fagaceae	Mt, Pd, Cp
Chimaphila maculata	Pipsissewa	Ericaceae	Mt, Pd, Cp
Clethra acuminata	Mountain sweet pepperbush	Clethraceae	Mt
Corylus cornuta var. cornuta	Beaked hazelnut	Betulaceae	Mt, Pd
Epigaea repens	Trailing arbutus	Ericaceae	Mt, Pd, Cp
Eubotrys recurva	Mountain fetterbush	Ericaceae	Mt*, Pd
Gaylussacia baccata	Black huckleberry	Ericaceae	Mt, Pd
Gaylussacia ursina	Bear huckleberry	Ericaceae	Mt*
Hydrangea radiata	Silverleaf hydrangea	Hydrangeaceae	Mt*, Pd
Hypericum hypericoides	St. Andrew's cross	Hypericaceae	Mt, Pd, Cp
Ilex montana	Mountain holly	Aquifoliaceae	Mt
Kalmia latifolia	Mountain laurel	Ericaceae	Mt, Pd, Cp
Leucothoe fontanesiana	Mountain doghobble	Ericaceae	Mt*, Pd
Ligustrum sinense	Chinese privet	Oleaceae	Mt, Pd, Cp
Lindera benzoin var. *pubescens*	Hairy northern spicebush	Lauraceae	Mt, Pd, Cp
Philadelphus inodorus	Appalachian mock-orange	Hydrangeaceae	Mt, Pd, Cp
Pyrularia pubera	Buffalo-nut	Santalaceae	Mt, Pd
Rhododendron maximum	Great rhododendron	Ericaceae	Mt, Pd
Rhododendron minus	Gorge rhododendron	Ericaceae	Mt, Pd, Cp
Rhododendron spp.	Rhododendron	Ericaceae	Mt, Pd, Cp
Rhus copallinum var. copallinum	Winged sumac	Anacardiaceae	Mt, Pd, Cp
Rhus glabra	Smooth sumac	Anacardiaceae	Mt, Pd, Cp
Rubus spp.	Brambles	Rosaceae	Mt, Pd, Cp
Sambucus canadensis	Common elderberry	Adoxaceae	Mt, Pd, Cp
Symplocos tinctoria	Horsesugar	Symplocaceae	Mt, Pd, Cp
Vaccinium arboreum	Sparkleberry	Ericaceae	Mt, Pd, Cp
Vaccinium pallidum	Hillside blueberry	Ericaceae	Mt, Pd, Cp
Vaccinium stamineum var. *stamineum*	Common deerberry	Ericaceae	Mt, Pd, Cp
Vaccinium	Blueberry	Ericaceae	Mt, Pd, Cp
Viburnum acerifolium	Mapleleaf viburnum	Adoxaceae	Mt, Pd, Cp

Shrubs and Subshrubs, continued

Taxon Concept	Common Name	Family	Distribution
Viburnum rufidulum	Southern black haw	Adoxaceae	Mt, Pd, Cp
Xanthorhiza simplicissima	Yellowroot	Ranunculaceae	Mt, Pd, Cp
Yucca filamentosa	Curly leaf yucca	Agavaceae	Mt, Pd, Cp

Vines

Taxon Concept	Common Name	Family	Distribution
Bignonia capreolata	Cross-vine	Bignoniaceae	Mt, Pd, Cp
Decumaria barbara	Climbing hydrangea	Hydrangeaceae	Pd, Cp
Dioscorea villosa	Common wild yam	Dioscoreaceae	Mt, Pd, Cp
Ipomoea pandurata	Wild sweet potato	Convolvulaceae	Mt, Pd, Cp
Ipomoea spp.	Morning-glory	Convolvulaceae	Mt, Pd, Cp
Lonicera japonica	Japanese honeysuckle	Caprifoliaceae	Mt, Pd, Cp
Matelea carolinensis	Carolina spinypod	Apocynaceae	NR
Menispermum canadense	Moonseed	Melastomataceae	Pd, Cp
Parthenocissus quinquefolia	Virginia-creeper	Vitaceae	Mt, Pd, Cp
Smilax biltmoreana	Biltmore carrionflower	Smilaceae	Mt, Pd
Smilax bona-nox	Catbrier	Smilaceae	Mt, Pd, Cp
Smilax glauca	Whiteleaf greenbrier	Smilaceae	Mt, Pd, Cp
Smilax rotundifolia	Common greenbrier	Smilaceae	Mt, Pd, Cp
Toxicodendron pubescens	Poison oak	Anacardiaceae	Mt, Pd, Cp
Toxicodendron radicans var. *radicans*	Eastern poison ivy	Anacardiaceae	Mt, Pd, Cp
Vitis aestivalis	Summer grape	Vitaceae	Mt, Pd, Cp
Vitis cinerea var. *baileyana*	Possum grape	Vitaceae	Mt, Pd, Cp
Vitis rotundifolia var. *rotundifolia*	Muscadine	Vitaceae	Mt, Pd, Cp
Vitis spp.	Grape	Vitaceae	Mt, Pd, Cp

Graminoids

Taxon Concept	Common Name	Family	Distribution
Arundinaria appalachiana	Hill cane	Poaceae	Mt, Pd
Brachyelytrum erectum	Common shorthusk	Poaceae	Mt, Pd, Cp
Carex digitalis	Slender woodland sedge	Cyperaceae	Mt?, Pd?, Cp?
Carex laxiflora	Broad looseflower sedge	Cyperaceae	Mt, Pd, Cp
Carex lucorum var. *austrolucorum*	Appalachian woodland sedge	Cyperaceae	Mt*
Carex nigromarginata	Black edge sedge	Cyperaceae	Mt, Pd, Cp
Carex radfordii	Radford's sedge	Cyperaceae	Mt**
Carex scabrata	Eastern rough sedge	Cyperaceae	Mt
Carex striatula	Lined sedge	Cyperaceae	Mt, Pd, Cp
Carex swanii	Swan's sedge	Cyperaceae	Mt
Carex virescens	Ribbed sedge	Cyperaceae	Mt
Carex spp.	Sedge	Cyperaceae	Mt, Pd, Cp
Danthonia sericea	Silky oat-grass	Poaceae	Mt, Pd, Cp
Dichanthelium boscii	Bosc's witch grass	Poaceae	Mt, Pd, Cp
Dichanthelium commutatum var. commutatum	Variable witch grass	Poaceae	Mt, Pd, Cp
Dichanthelium spp.	Witch-grass	Poaceae	Mt, Pd, Cp
Juncus coriaceus	Leathery rush	Juncaceae	Mt, Pd, Cp
Juncus effusus ssp. solutus	Common rush	Juncaceae	Mt, Pd, Cp
Leersia virginica	White cutgrass	Poaceae	Mt, Pd, Cp
Luzula echinata	Hedgehog wood-rush	Juncaceae	Mt, Pd, Cp
Melica mutica	Two-flower melic	Poaceae	Mt, Pd, Cp
Piptochaetium avenaceum	Eastern needlegrass	Poaceae	Mt, Pd, Cp
Poa autumnalis	Autumn bluegrass	Poaceae	Mt, Pd, Cp
Scleria oligantha	Few-flowered nutrush	Cyperaceae	Mt, Pd, Cp
Scleria triglomerata	Tall nutrush	Cyperaceae	Mt, Pd, Cp

Ferns and Fern Allies

Taxon Concept	Common Name	Family	Distribution
Adiantum pedatum	Northern maidenhair	Pteridaceae	Mt, Pd
Asplenium platyneuron	Ebony spleenwort	Aspleniaceae	Mt, Pd, Cp
Asplenium spp.	Sleenwort	Aspleniaceae	Mt, Pd, Cp
Athyrium asplenioides	Southern lady fern	Woodsiaceae	Mt, Pd, Cp
Botrypus virginianus	Rattlesnake fern	Ophioglossaceae	Mt, Pd, Cp
Cystopteris protrusa	Lowland bladder fern	Dryopteridaceae	Mt, Pd
Dendrolycopodium obscurum	Common ground-pine	Lycopodiaceae	Mt, Pd, Cp
Dennstaedtia punctilobula	Hay-scented fern	Dennstaedtiaceae	Mt, Pd, Cp
Diphasiastrum digitatum	Common running-cedar	Lycopodiaceae	Mt, Pd, Cp
Dryopteris marginalis	Marginal wood-fern	Dryopteridaceae	Mt, Pd, Cp
Huperzia lucidula	Shining firmoss	Lycopodiaceae	Mt
Onoclea sensibilis var. *sensibilis*	Sensitive fern	Onocleaceae	Mt, Pd, Cp
Osmunda cinnamomea var. cinnamomea	Cinnamon fern	Osmundaceae	Mt, Pd, Cp
Osmunda regalis var. spectabilis	Royal fern	Osmundaceae	Mt, Pd, Cp
Phegopteris hexagonoptera	Broad beech fern	Thelypteridaceae	Mt, Pd, Cp
Pleopeltis polypodioides ssp. michauxiana	Resurrection fern	Polypodiaceae	Mt, Pd, Cp
Polystichum acrostichoides	Christmas fern	Dryopteridaceae	Mt, Pd, Cp
Pteridium aquilinum	Bracken fern	Dennstaedtiaceae	Mt, Pd, Cp
Sceptridium dissectum	Dissected grapefern	Ophioglossaceae	Mt, Pd, Cp
Thelypteris noveboracensis	New York fern	Thelypteridaceae	Mt, Pd, Cp

Herbs

Taxon Concept	Common Name	Family	Distribution
Actaea pachypoda	White baneberry	Ranunculaceae	Mt, Pd
Actaea racemosa	Common black-cohosh	Ranunculaceae	Mt, Pd
Ageratina altissima var. *altissima*	Common white snakeroot	Asteraceae	Mt, Pd, Cp
Agrimonia pubescens	Downy agrimony	Rocaceae	Mt
Amphicarpaea bracteata	Hog-peanut	Fabaceae	Mt, Pd, Cp
Amsonia tabernaemontana	Wideleaf-bluestars	Apocynaceae	Mt, Pd, Cp
Anemone acutiloba	Sharp-lobed hepatica	Ranunculaceae	Mt
Anemonella thalictroides	Windflower	Ranunculaceae	Mt, Pd, Cp
Antennaria plantaginifolia	Plantain pussytoes	Asteraceae	Mt, Pd, Cp
Aralia racemosa	Spikenard	Araliaceae	Mt
Arisaema triphyllum ssp. triphyllum	Common jack-in-the-pulpit	Araceae	Mt, Pd, Cp
Asclepias variegata	White milkweed	Apocynaceae	Mt, Pd, Cp
Asteraceae	Aster Family	Asteraceae	Mt, Pd, Cp
Caulophyllum thalictroides	Common blue cohosh	Berberidaceae	Mt, Pd
Chamaelirium luteum	Devil's-bit	Melanthiaceae	Mt, Pd, Cp
Clintonia umbellulata	Speckled wood-lily	Liliaceae	Mt
Collinsonia canadensis	Northern horsebalm	Lamiaceae	Mt, Pd, Cp
Collinsonia tuberosa	Stoneroot	Lamiaceae	Pd
Conopholis americana	Squawroot	Orobanchaceae	Mt, Pd, Cp
Coreopsis major	Woodland coreopsis	Asteraceae	Mt, Pd, Cp
Cynoglossum virginianum var. *virginianum*	Wild comfrey	Boraginaceae	Mt, Pd, Cp
Cypripedium acaule	Pink lady's-slipper	Orchidaceae	Mt, Pd, Cp
Desmodium nudiflorum	Naked tick-trefoil	Fabaceae	Mt, Pd, Cp
Desmodium rotundifolium	Roundleaf tick-trefoil	Fabaceae	Mt, Pd, Cp
Desmodium spp.	Beggar's-ticks	Fabaceae	Mt, Pd, Cp
Doellingeria infirma	Appalachian flat-topped white aster	Asteraceae	Mt, Pd
Doellingeria umbellata	Tall flat-topped white aster	Asteraceae	Mt
Elephantopus tomentosus	Elephant's-foot	Asteraceae	Mt, Pd, Cp
Endodeca serpentaria	Turpentine-root	Aristolochiaceae	Mt, Pd, Cp
Epifagus virginiana	Beechdrops	Orobanchaceae	Mt, Pd, Cp
Erigeron pulchellus var. *pulchellus*	Robin's-plantain	Asteraceae	Mt, Pd, Cp
Eryngium yuccifolium var. *yuccifolium*	Northern rattlesnake-master	Apiaceae	Mt, Pd, Cp
Euonymus americanus	Strawberry-bush	Celastraceae	Mt, Pd, Cp
Eupatorium spp.	Eupatorium	Asteraceae	Mt, Pd, Cp

Herbs, continued

Taxon Concept	Common Name	Family	Distribution
Euphorbia corollata	Eastern flowering spurge	Euphorbiaceae	Mt
Eurybia divaricata	Common white heart-leaved aster	Asteraceae	Mt, Pd
Eutrochium fistulosum	Hollow-stem joe-pye-weed	Asteraceae	Mt, Pd, Cp
Eutrochium maculatum var. *maculatum*	Spotted joe-pye-weed	Asteraceae	NR
Eutrochium purpureum var. *purpureum*	Purple-node joe-pye-weed	Asteraceae	Mt,Pd,Cp
Galax urceolata	Galax	Diapensiaceae	Mt,Pd,Cp
Galearis spectabilis	Showy orchis	Orchidaceae	Mt
Galium circaezans var. *circaezans*	Southern forest bedstraw	Rubiaceae	Mt, Pd, Cp
Galium latifolium	Wideleaf bedstraw	Rubiaceae	Mt
Galium spp.	Bedstraw	Rubiaceae	Mt, Pd, Cp
Gillenia trifoliata	Mountain Indian-physic	Rosaceae	Mt, Pd
Goodyera pubescens	Downy rattlesnake-orchid	Orchidaceae	Mt, Pd, Cp
Helianthus divaricatus	Spreading sunflower	Asteraceae	Mt, Pd, Cp
Helianthus glaucophyllus	Whiteleaf sunflower	Asteraceae	Mt*, Pd
Helianthus spp.	Sunflower	Asteraceae	Mt, Pd, Cp
Helianthus strumosus	Roughleaf sunflower	Asteraceae	Mt, Pd, Cp
Hexastylis arifolia var. *arifolia*	Little brown jug	Aristolochiaceae	Mt, Pd, Cp
Hexastylis heterophylla	Variable-leaf heartleaf	Aristolochiaceae	Mt*, Pd
Hieracium venosum	Veiny hawkweed	Asteraceae	Mt, Pd, Cp
Houstonia purpurea var. purpurea	Summer bluet	Rubiaceae	Mt, Pd, Cp
Hypoxis hirsuta	Common stargrass	Hypoxidaceae	Mt, Pd, Cp
Iris cristata	Dwarf crested iris	Iridaceae	Mt, Pd, Cp
Iris verna var. smalliana	Upland dwarf iris	Iridaceae	Mt
Laportea canadensis	Wood-nettle	Urticaceae	Mt, Pd, Cp
Ligusticum canadense	American lovage	Apiaceae	Mt, Pd
Lilium canadense var. editorum	Red Canada lily	Liliaceae	Mt, Pd
Lilium michauxii	Carolina lily	Liliaceae	Mt, Pd, Cp
Liparis liliifolia	Large twayblade	Orchidaceae	Mt
Lobelia puberula	Downy lobelia	Campanulaceae	Mt, Pd, Cp
Lysimachia quadrifolia	Whorled loosestrife	Myrsinaceae	Mt, Pd, Cp
Maianthemum canadense	Canada mayflower	Ruscaceae	NR

Herbs, continued

Taxon Concept	Common Name	Family	Distribution
Maianthemum racemosum ssp. racemosum	False Solomon's-seal	Ruscaceae	Mt, Pd, Cp
Medeola virginiana	Indian cucumber-root	Liliaceae	Mt, Pd, Cp
Mitchella repens	Partridge-berry	Rubiaceae	Mt, Pd, Cp
Monarda clinopodia	Basil bergamot	Lamiaceae	Mt, Pd
Monotropa uniflora	Indian pipes	Ericaceae	Mt, Pd, Cp
Obolaria virginica	Pennywort	Gentianaceae	Mt, Pd
Oxalis dillenii	Yellow wood-sorrel	Oxalidaceae	Mt, Pd, Cp
Packera aurea	Golden ragwort	Asteraceae	Mt, Pd
Panax quinquefolius	American ginseng	Araliaceae	Mt, Pd
Parthenium integrifolium	Wild quinine	Asteraceae	Mt, Pd, Cp
Passiflora lutea	Yellow passionflower	Parnassiaceae	Mt, Pd, Cp
Pedicularis canadensis	Eastern lousewort	Orobanchaceae	Mt, Pd, Cp
Phyrma leptostachya var. *leptostachya*	American lopseed	Phrymaceae	Mt, Pd, Cp
Physalis virginiana var. *virginiana*	Virginia ground-cherry	Solanaceae	Mt, Pd, Cp
Podophyllum peltatum	May-apple	Berberidaceae	Mt, Pd, Cp
Polygala curtissii	Appalachian milkwort	Polygalaceae	Mt, Pd, Cp
Polygala polygama var. polygama	Southern bitter milkwort	Polygalaceae	Mt, Pd, Cp
Polygonatum biflorum	Solomon's-seal	Ruscaceae	Mt, Pd, Cp
Potentilla canadensis var. canadensis	Running five-fingers	Rosaceae	Mt, Pd, Cp
Prenanthes serpentaria	Gall-of-the-earth	Asteraceae	Mt, Pd, Cp
Prenanthes spp.	Rattlesnake-root	Asteraceae	Mt, Pd, Cp
Pycnanthemum incanum var. *puberulum*	Hoary mountain-mint	Lamiaceae	Mt
Pycnanthemum pycnanthemoides	Southern mountain-mint	Lamiaceae	Mt, Pd
Pycnanthemum spp.	Mountain-mint	Lamiaceae	Mt, Pd, Cp
Sanguinaria canadensis	Bloodroot	Papaveraceae	Mt, Pd, Cp
Sanicula canadensis var. *canadensis*	Black snakeroot	Apiaceae	Mt, Pd, Cp
Sanicula smallii	Southern sanicle	Apiaceae	Mt, Pd, Cp
Scutellaria elliptica var. *elliptica*	Hairy skullcap	Lamiaceae	Mt, Pd, Cp

Herbs, continued

Taxon Concept	Common Name	Family	Distribution
Shortia galacifolia var. *galacifolia*	Oconee bell	Diapensiaceae	Mt**
Silene stellata	Starry campion	Caryophyllaceae	Mt, Pd, Cp
Silphium asteriscus var. dentatum	Rosinweed	Asteraceae	Pd, Cp
Sisyrinchium mucronatum	Needletip blue-eyed grass	Iridaceae	Mt, Pd
Smallanthus uvedalius	Bearsfoot	Asteraceae	Mt, Pd, Cp
Soildago arguta var. *caroliniana*	Vasey's goldenrod	Asteraceae	Mt, Pd, Cp
Solidago caesia var. *caesia*	Axillary goldenrod	Asteraceae	Pd, Cp
Solidago curtisii	Curtis's goldenrod	Asteraceae	Mt
Solidago spp.	Goldenrod	Asteraceae	Mt, Pd, Cp
Spigelia marilandica	Pinkroot	Loganiaceae	Mt, Pd
Stachys latidens	Broad-toothed hedge-nettle	Lamiaceae	Mt, Pd
Stellaria pubera	Star chickweed	Caryophyllaceae	Mt, Pd, Cp
Symphyotrichum cordifolium	Common blue wood aster	Asteraceae	Mt, Pd, Cp
Symphyotrichum lanceolatum var. latifolium	White panicle aster	Asteraceae	Mt, Pd, Cp
Symphyotrichum patens	Common clasping aster	Asteraceae	Mt, Pd, Cp
Taraxacum officianale	Common dandelion	Asteraceae	Mt, Pd, Cp
Thaspium trifoliatum	Meadow-parsnip	Apiaceae	Mt, Pd, Cp
Tiarella cordifolia	Foamflower	Saxifragaceae	Mt, Pd, Cp
Tipularia discolor	Cranefly orchid	Orchidaceae	Mt, Pd, Cp
Tradescantia spp.	Spiderwort	Commelinaceae	Mt, Pd, Cp
Trillium discolor	Pale yellow trillium	Trilliaceae	Mt**, Pd
Trillium spp.	Trillium	Trilliaceae	Mt, Pd, Cp
Uvularia perfoliata	Perfoliate bellwort	Colchicaceae	Mt, Pd, Cp
Uvularia puberula var. *puberula*	Appalachian bellwort	Colchicaceae	Mt, Pd
Veratrum latifolium	Crisped bunchflower	Melanthiaceae	Mt, Pd, Cp

Herbs, continued

Taxon Concept	Common Name	Family	Distribution
Viola palmata var. *palmata*	Wood violet	Violaceae	Mt?, Pd?, Cp?
Viola sororia	Dooryard violet	Violaceae	Mt, Pd, Cp
Viola tripartita var. tripartita	Three-parted violet	Violaceae	Mt?, Pd?, Cp?
Viola walteri	Walter's violet	Violaceae	Mt, Pd, Cp
Zizia trifoliata	Mountain golden-alexanders	Apiaceae	Mt, Pd, Cp

Appendix B: Average importance value (IV) and constancy for ground flora species in each ecosystem type. Values are given for each age-class, and each class is represented by its abbreviated code (ES: 5-25 years, MS: 26-50 years, MLS: 51-70 years, and LS: > 70 years). Number of plots for each age-class are listed in parentheses following the abbreviated code. Only prevalent species are listed. Prevalence was determined by ranking species by the sum of IV across all age-classes, and selecting those species with a total IV of greater than 2 for display.

Xeric oak/blueberry, 1 of 2											
	ES (4)			**MS (3)**			**MLS (4)**			**LS (14)**	
Species	IV	Constancy	x	IV	Constancy	x	IV	Constancy	x	IV	Constancy
Acer rubrum var. rubrum	4.2	100		6.7	100		6.2	100		5.8	100
Vaccinium pallidum	3.3	100		7.8	100		6.2	100		5.2	100
Quercus coccinea	3.4	75		6.0	100		6.2	100		6.5	100
Smilax glauca	5.5	100		7.5	100		6.5	100		---	---
Nyssa sylvatica	4.8	100		5.4	100		4.8	100		4.1	100
Arundinaria appalachiana	4.2	100		4.4	100		3.2	75		3.8	93
Kalmia latifolia	3.9	100		3.3	100		3.3	100		4.5	86
Vitis rotundifolia var. rotundifolia	4.2	100		4.7	100		2.4	75		3.1	93
Chimaphila maculata	1.0	75		5.7	100		2.6	100		2.9	100
Quercus velutina	2.8	100		5.9	100		2.8	50		---	---
Robinia pseudoacacia	2.3	100		3.0	100		1.7	75		3.0	100
Quercus alba	2.5	100		2.3	100		1.5	50		2.4	86
Gaylussacia ursina	0.3	25		1.8	33		3.8	50		2.5	71
Carex spp.	1.8	75		3.3	100		0.4	25		2.9	100
Smilax rotundifolia	1.2	100		1.6	67		---	---		5.4	100
Oxydendrum arboreum	0.7	75		3.4	100		2.0	100		1.8	100
Quercus montana	1.4	50		0.8	67		2.0	100		3.0	79
Symplocos tinctoria	3.0	100		1.2	100		2.1	75		0.8	36
Carya glabra	2.5	100		2.2	100		1.9	100		---	---
Sassafras albidum	1.7	100		0.4	67		1.8	50		2.6	100
Dichanthelium spp.	2.5	100		1.1	33		0.8	75		1.9	79
Liriodendron tulipifera var. tulipifera	2.7	75		0.6	67		1.4	75		1.3	79
Magnolia fraseri	0.6	50		1.4	100		1.2	75		2.5	86
Rubus spp.	3.9	100		---	---		0.6	25		0.2	29
Pinus strobus	1.5	50		0.7	67		1.5	50		1.0	57
Polystichum acrostichoides	1.3	75		1.0	33		1.1	50		0.8	50
Dioscorea villosa	1.0	75		0.3	33		0.8	25		2.1	86
Euphorbia corollata	0.9	75		1.1	100		0.7	25		1.4	71

Xeric oak/blueberry, 2 of 2											
		ES (4)			**MS (3)**			**LS (4)**			**LLS (14)**
Species	IV	Constancy	x	IV	Constancy	x	IV	Constancy	x	IV	Constancy
Parthenocissus quinquefolia	0.6	100		0.2	33		2.3	75		1.0	64
Desmodium spp.	1.2	75		0.7	67		0.9	25		1.2	71
Viola spp.	0.1	25		1.8	33		0.3	25		1.8	79
Cornus florida	1.2	100		0.4	33		1.5	75		0.8	50
Goodyera pubescens	1.0	75		0.7	33		1.1	75		0.8	79
Carya pallida	1.1	75		1.1	33		1.2	75		---	---
Vaccinium arboreum	0.5	50		0.4	33		2.1	50		0.4	36
Smilax biltmoreana	1.1	50		0.9	67		1.0	75		---	---
Maianthemum racemosum ssp. racemosum	1.4	75		---	---		1.1	75		0.3	21
Piptochaetium avenaceum	0.4	25		---	---		1.1	75		1.2	43
Potentilla canadensis var. canadensis	1.3	100		0.2	33		0.5	25		0.6	43
Lysimachia quadrifolia	0.7	75		1.4	33		0.1	25		0.4	29
Iris verna var. smalliana	1.4	100		0.2	33		0.1	25		0.9	57
Viola hastata	1.1	75		1.0	67		0.4	50		---	---
Castanea dentata	0.3	50		---	---		1.8	50		0.3	36
Carya alba	0.7	75		0.2	33		1.4	50		---	---
Amelanchier laevis	---	---		0.7	67		0.9	75		0.6	36
Polygonatum biflorum	0.4	75		1.0	67		0.5	50		0.2	29
Solidago spp.	1.3	100		0.7	67		---	---		---	---

Xeric chestnut oak/mountain laurel, 1 of 2								
		ES (3)		**MS (4)**		**LS (3)**		**LLS (7)**
Species	IV	Constancy	IV	Constancy	IV	Constancy	IV	Constancy
Kalmia latifolia	9.5	100	7.1	75	9.5	100	7.5	100
Smilax glauca	6.5	100	6.5	100	6.2	100	---	---
Acer rubrum var. rubrum	5.4	100	4.0	100	4.8	100	4.7	100
Quercus montana	3.7	100	5.5	100	5.6	100	4.1	100
Gaylussacia ursina	8.6	100	2.7	75	2.6	33	2.9	100
Galax urceolata	4.9	100	3.7	75	4.9	100	2.4	71
Nyssa sylvatica	3.3	100	4.6	100	3.5	100	1.9	86
Quercus coccinea	2.6	100	4.5	100	2.1	100	3.1	86
Vaccinium pallidum	2.0	67	3.0	75	3.1	100	3.7	86
Rhododendron maximum	2.1	100	0.8	50	5.5	100	3.1	71
Smilax rotundifolia	1.9	67	1.3	50	3.0	100	4.7	100
Rhododendron minus	3.0	100	3.7	75	1.7	100	1.0	57
Vitis rotundifolia var. rotundifolia	3.0	100	2.2	75	1.7	67	1.9	100
Polystichum acrostichoides	3.0	100	0.3	25	1.3	33	3.6	100
Sassafras albidum	1.4	67	2.4	100	2.3	100	1.4	71
Arundinaria appalachiana	0.9	67	0.4	25	3.2	67	2.7	86
Chimaphila maculata	0.5	67	2.1	100	2.8	67	1.9	100
Quercus velutina	0.8	100	3.4	75	2.8	67	---	---
Thelypteris noveboracensis	4.1	100	---	---	1.5	67	1.2	43
Smilax biltmoreana	1.5	67	2.4	100	2.3	100	---	---
Robinia pseudoacacia	0.9	100	2.1	100	0.8	67	1.7	86
Viola hastata	2.0	67	0.9	25	2.6	67	---	---
Carex albicans	1.5	33	1.5	75	2.3	67	---	---
Castanea dentata	0.6	33	1.3	75	2.0	67	1.2	71
Goodyera pubescens	1.9	100	0.8	50	1.1	100	1.4	100
Viola spp.	1.2	33	0.1	25	0.4	67	3.5	100
Symplocos tinctoria	1.2	33	1.6	25	1.7	100	0.6	14
Carex spp.	---	---	1.0	25	1.2	67	2.3	100
Liriodendron tulipifera var. tulipifera	1.0	100	2.3	75	---	---	0.7	71

Xeric chestnut oak/mountain laurel, 2 of 2

	ES (3)		MS (4)		LS (3)		LLS (7)	
Species	IV	Constancy	IV	Constancy	IV	Constancy	IV	Constancy
Dioscorea villosa	---	---	1.5	25	---	---	2.2	71
Rubus spp.	2.7	100	0.8	50	---	---	0.2	43
Oxydendrum arboreum	0.4	33	0.7	50	0.7	67	1.8	100
Magnolia fraseri	0.4	67	0.1	25	1.6	67	1.5	71
Dichanthelium spp.	0.6	67	1.3	100	0.3	33	1.2	71
Carya pallida	0.5	67	2.2	75	0.6	67	---	---
Epigaea repens	0.2	33	1.0	25	1.7	67	0.4	43
Pyrularia pubera	1.2	67	---	---	---	---	1.3	29
Parthenocissus quinquefolia	0.5	67	0.8	50	0.6	67	0.4	43
Magnolia acuminata var. acuminata	0.8	100	0.3	25	0.9	67	0.4	29
Uvularia puberula var. puberula	0.9	33	---	---	---	---	1.3	57
Halesia tetraptera var. tetraptera	0.9	67	0.5	25	0.2	33	0.5	29
Quercus alba	0.1	33	1.6	100	0.3	33	0.0	14
Maianthemum racemosum ssp. racemosum	0.2	33	1.2	50	---	---	0.6	29
Vaccinium arboreum	0.8	33	1.2	50	---	---	---	---
Desmodium spp.	0.2	33	0.3	25	---	---	1.5	86

Submesic oak/mixed flora, 1 of 2								
		ES (7)		**MS (3)**		**LS (3)**		**LLS (9)**
Species	IV	Constancy	IV	Constancy	IV	Constancy	IV	Constancy
Acer rubrum var. rubrum	3.5	100	3.5	100	4.2	100	3.2	100
Vitis rotundifolia var. rotundifolia	4.1	86	3.4	100	2.5	67	3.0	100
Polystichum acrostichoides	3.4	100	1.6	67	3.4	100	3.4	100
Smilax glauca	4.1	100	3.5	100	3.1	100	---	---
Liriodendron tulipifera var. tulipifera	3.1	100	2.4	100	3.0	100	2.1	100
Quercus alba	2.2	100	2.6	100	2.7	100	1.6	100
Thelypteris noveboracensis	1.2	86	0.7	67	3.4	100	3.5	89
Kalmia latifolia	2.1	71	3.2	67	1.3	67	2.2	89
Parthenocissus quinquefolia	2.8	100	1.0	33	1.5	100	2.6	100
Rubus spp.	3.0	100	0.8	33	2.2	100	1.7	89
Desmodium spp.	1.0	57	0.7	100	2.8	100	2.7	100
Nyssa sylvatica	2.6	86	1.6	100	1.6	100	1.5	100
Magnolia fraseri	0.8	57	1.0	100	2.9	100	2.3	100
Smilax rotundifolia	1.0	86	1.5	67	1.3	67	3.1	100
Dichanthelium spp.	1.8	100	0.6	67	2.3	100	2.0	100
Carex spp.	2.2	57	1.5	67	1.0	33	2.0	100
Arundinaria appalachiana	0.4	29	0.9	100	2.6	100	2.7	89
Viola spp.	0.2	29	2.0	100	2.0	67	2.3	89
Carya glabra	1.9	100	1.9	100	2.6	100	---	---
Quercus coccinea	1.8	86	2.0	67	0.5	33	2.1	78
Prenanthes spp.	1.5	71	0.4	67	2.7	100	1.1	100
Goodyera pubescens	1.4	86	1.4	67	1.2	100	1.3	89
Halesia tetraptera var. tetraptera	0.4	29	0.8	33	1.1	67	2.2	89
Pyrularia pubera	0.4	29	0.5	33	2.4	67	1.1	33
Arisaema triphyllum ssp. triphyllum	1.2	71	0.2	33	1.5	67	1.6	100
Quercus rubra var. rubra	0.2	14	0.7	67	1.5	100	2.0	100
Cornus florida	1.1	57	0.7	100	2.1	100	0.3	56
Mitchella repens	1.4	57	1.4	100	0.3	33	1.2	89
Quercus velutina	2.2	86	1.6	100	0.4	67	---	---

Submesic oak/mixed flora, 2 of 2

	ES (7)		**MS (3)**		**LS (3)**		**LLS (9)**	
Species	IV	Constancy	IV	Constancy	IV	Constancy	IV	Constancy
Vaccinium pallidum	0.8	71	2.8	67	---	---	0.4	44
Dioscorea villosa	0.5	71	0.5	67	1.7	100	1.3	100
Tsuga canadensis	0.4	43	0.9	33	2.0	100	0.6	44
Quercus montana	0.6	29	1.0	67	1.1	67	1.3	100
Fagus grandifolia	0.4	43	0.2	33	2.8	100	0.4	44
var. caroliniana								
Gaylussacia ursina	0.2	14	0.3	33	1.8	67	1.4	44
Castanea dentata	0.4	14	0.2	67	2.3	67	0.9	100
Robinia pseudoacacia	1.0	86	2.3	100	---	---	0.5	67
Pinus strobus	0.9	57	2.2	67	---	---	0.6	56
Rhododendron maximum	0.2	43	1.2	33	1.1	33	1.1	56
Chimaphila maculata	0.7	43	1.3	67	0.5	33	1.0	78
Toxicodendron radicans	1.3	57	0.7	67	---	---	1.5	78
var. radicans								
Hydrangea radiata	0.3	43	0.5	67	1.5	100	1.2	78
Oxydendrum arboreum	1.2	86	0.8	67	0.5	100	0.8	100
Xanthorhiza simplicissima	0.2	14	0.1	33	---	---	3.0	100
Carya alba	1.6	71	0.7	100	1.0	100	---	---
Euonymus americanus	0.5	71	1.2	67	0.3	33	1.2	78
Sassafras albidum	1.0	86	1.4	33	0.1	33	0.7	89
Maianthemum racemosum	0.3	43	0.8	100	1.2	33	1.0	78
ssp. racemosum								
Polygonatum biflorum	1.4	71	0.6	33	0.5	67	0.6	89
Vitis aestivalis	1.6	86	0.5	67	0.9	33	---	---
Liquidambar styraciflua	0.8	43	1.5	67	---	---	0.5	33
Symplocos tinctoria	0.8	43	0.6	67	0.9	33	0.4	22
Phegopteris hexagonopter	0.2	29	0.8	33	0.8	100	0.7	67
Solidago spp.	0.4	57	1.0	100	1.0	33	---	---
Galium circaezans	0.9	29	0.8	33	0.8	33	---	---
var. circaezans								
Ilex opaca var. opaca	0.6	57	0.3	33	0.7	33	0.8	67
Lysimachia quadrifolia	1.1	86	0.1	33	0.6	33	0.5	44
Bignonia capreolata	0.7	43	1.4	67	0.2	33	---	---
Phryma leptostachya	1.1	71	0.7	33	0.4	33	---	---
var. leptostachya								
Iris verna var. smalliana	0.5	57	0.6	67	1.1	33	---	---
Potentilla canadensis	1.2	86	0.5	100	---	---	0.4	67
var. canadensis								

Mesic hardwoods/bloodroot, 1 of 3

	ES (2)		MS (4)		LS (5)		LLS (3)	
Species	IV	Constancy	IV	Constancy	IV	Constancy	IV	Constancy
Parthenocissus quinquefolia	2.9	100	2.4	100	2.3	80	3.1	100
Polystichum acrostichoides	2.2	100	2.0	100	3.0	100	3.2	100
Prenanthes spp.	3.1	100	1.8	75	2.5	100	2.2	100
Arisaema triphyllum ssp. triphyllum	2.5	100	1.8	100	2.4	100	1.8	100
Acer rubrum var. rubrum	2.5	100	1.8	100	1.8	100	2.3	100
Vitis rotundifolia var. rotundifolia	3.1	100	1.9	100	0.9	80	2.2	100
Halesia tetraptera var. tetraptera	1.2	50	1.6	75	2.0	100	3.1	100
Smilax rotundifolia	2.2	100	1.4	100	1.6	100	2.1	100
Dioscorea villosa	2.4	100	1.7	100	1.6	80	1.6	100
Thelypteris noveboracensis	0.1	50	2.7	100	1.7	100	2.2	100
Viola spp.	---	---	1.5	75	2.0	80	3.1	100
Sanguinaria canadensis	1.8	50	1.4	75	1.4	60	1.9	100
Quercus rubra var. rubra	---	---	1.6	100	2.4	100	2.2	100
Liriodendron tulipifera var. tulipifera	2.1	100	1.5	100	1.1	80	1.2	100
Rubus spp.	1.1	100	1.6	100	1.5	80	1.5	100
Calycanthus floridus	0.9	50	2.0	100	0.4	40	2.1	100
Dichanthelium spp.	2.1	100	1.4	100	1.0	60	0.9	100
Phegopteris hexagonoptera	0.5	50	1.2	75	1.2	100	2.2	100
Smilax glauca	3.3	100	1.0	100	0.8	80	---	---
Mitchella repens	1.1	50	0.7	100	1.6	60	1.7	100
Euonymus americanus	1.5	50	0.9	100	1.0	80	1.4	100
Toxicodendron radicans var. radicans	0.2	50	1.0	75	0.8	80	2.6	100
Eurybia divaricata	1.4	100	1.6	100	1.4	100	---	---
Botrypus virginianus	1.4	50	1.1	75	0.7	80	1.1	100
Desmodium nudiflorum	0.9	50	1.9	75	1.5	60	---	---
Desmodium spp.	0.3	50	1.0	25	0.3	40	2.5	100

Mesic hardwoods/bloodroot, 2 of 3								
		ES (2)		**MS (4)**		**LS (5)**		**LLS (3)**
Species	IV	Constancy	IV	Constancy	IV	Constancy	IV	Constancy
Arundinaria appalachiana	1.2	50	1.0	75	0.9	40	1.1	67
Carya alba	1.0	100	0.9	100	1.9	100	---	---
Sanicula canadensis var. canadensis	0.3	50	1.3	100	0.6	40	1.6	100
Phryma leptostachya var. leptostachya	1.3	100	0.9	75	1.6	80	---	---
Quercus alba	1.0	50	1.3	100	0.5	40	0.9	67
Carya glabra	1.6	100	1.0	100	1.2	100	---	---
Goodyera pubescens	0.6	50	1.2	100	1.1	100	0.8	100
Nyssa sylvatica	2.1	100	0.5	75	0.1	20	0.9	100
Tiarella cordifolia	---	---	0.1	25	1.2	40	2.2	100
Hydrangea radiata	---	---	1.2	75	1.2	80	1.1	100
Actaea racemosa	0.2	50	1.6	100	1.7	100	---	---
Lysimachia quadrifolia	1.3	100	0.9	100	1.1	60	---	---
Magnolia fraseri	0.2	50	1.5	100	0.6	80	1.0	100
Eutrochium purpureum var. purpureum	2.4	100	0.6	50	0.2	40	---	---
Polygonatum biflorum	0.9	100	0.3	25	1.1	60	0.9	67
Galium circaezans var. circaezans	1.5	50	1.2	50	0.5	40	---	---
Carex spp.	0.9	50	0.8	50	0.5	40	1.0	100
Maianthemum racemosum ssp. racemosum	0.4	100	0.5	75	1.5	80	0.8	67
Vitis aestivalis	1.0	100	1.2	100	1.0	80	---	---
Brachyelytrum erectum	1.9	100	0.4	25	0.6	40	---	---
Solidago curtisii	1.2	100	0.3	50	1.4	60	---	---
Tsuga canadensis	---	---	1.1	100	0.8	20	1.0	67
Erigeron pulchellus var. pulchellus	1.3	100	0.6	75	0.7	60	0.3	33
Viola canadensis var. canadensis	1.9	50	0.9	25	---	---	---	---
Robinia pseudoacacia	0.7	100	0.9	100	0.8	80	0.5	67
Ageratina altissima var. altissima	0.7	50	0.5	75	1.6	80	---	---

Mesic hardwoods/bloodroot, 3 of 3

		ES (2)		MS (4)		LS (5)		LLS (3)
Species	IV	Constancy	IV	Constancy	IV	Constancy	IV	Constancy
Monarda clinopodia	---	---	1.4	100	1.4	80	---	---
Iris cristata	0.8	50	1.0	75	0.3	20	0.6	67
Trillium spp.	---	---	1.0	75	1.0	80	0.7	100
Quercus coccinea	1.2	100	0.0	25	---	---	1.4	100
Symplocos tinctoria	0.8	50	0.7	75	1.2	40	---	---
Tilia americana var. heterophylla	---	---	0.8	50	0.9	60	0.9	67
Sanicula smallii	1.6	50	0.4	50	0.4	80	---	---
Medeola virginiana	---	---	0.1	25	1.0	80	1.4	100
Galium spp.	---	---	0.9	75	1.5	80	---	---
Actaea pachypoda	0.2	50	0.4	25	0.6	80	1.2	67
Xanthorhiza simplicissima	---	---	0.1	25	---	---	2.2	100
Stellaria pubera	0.9	100	0.5	50	0.9	60	---	---
Quercus velutina	1.1	50	0.6	75	0.5	40	---	---
Fraxinus pennsylvanica	0.4	50	1.2	100	0.6	40	---	---
Smallanthus uvedalius	1.2	50	0.7	50	0.2	20	---	---
Spigelia marilandica	0.7	50	0.9	50	0.5	40	---	---
Carex digitalis	1.2	50	0.5	75	0.3	40	---	---

Mesic hemlock/rhododendron, 1 of 2

	ES (7)		MS (7)		LS (4)		LLS (15)	
Species	IV	Constancy	IV	Constancy	IV	Constancy	IV	Constancy
Rhododendron maximum	3.0	57	5.2	86	6.8	100	5.5	100
Polystichum acrostichoides	4.2	100	5.0	100	4.6	100	4.3	93
Mitchella repens	2.4	100	4.0	100	3.8	100	3.3	100
Vitis rotundifolia var. rotundifolia	3.6	100	3.3	86	3.1	100	3.2	100
Tsuga canadensis	1.4	86	2.8	86	4.9	100	3.4	100
Acer rubrum var. rubrum	3.0	100	3.4	100	3.1	100	3.0	100
Kalmia latifolia	2.1	100	3.1	57	4.2	100	1.2	60
Smilax glauca	2.5	100	3.8	100	3.9	100	---	---
Leucothoe fontanesiana	0.5	57	3.5	100	1.4	75	3.6	87
Euonymus americanus	1.8	100	2.4	86	2.2	75	2.0	87
Hexastylis heterophylla	0.3	29	2.6	71	3.0	75	2.5	67
Smilax rotundifolia	1.1	57	1.5	71	2.6	100	3.2	100
Parthenocissus quinquefolia	2.6	100	1.8	71	0.9	75	2.4	87
Calycanthus floridus	1.1	29	2.2	57	2.7	75	1.3	40
Viola spp.	1.8	86	1.3	86	1.0	50	3.0	93
Goodyera pubescens	1.6	86	1.8	86	1.7	75	1.6	100
Thelypteris noveboracensis	2.0	100	2.6	86	0.2	25	1.8	80
Arisaema triphyllum ssp. triphyllum	1.8	86	1.4	57	1.4	75	1.9	100
Rhododendron minus	0.5	29	2.1	43	3.0	75	0.6	27
Quercus rubra var. rubra	1.1	71	1.3	71	1.5	50	2.1	93
Prenanthes spp.	1.9	86	1.0	71	0.8	75	1.7	87
Toxicodendron radicans var. radicans	1.0	71	1.3	43	1.0	50	1.8	80
Pyrularia pubera	0.8	43	1.6	57	0.5	75	2.0	80
Liriodendron tulipifera var. tulipifera	1.9	86	1.6	57	0.4	75	0.7	67
Quercus montana	0.9	29	1.0	29	2.0	75	0.6	47
Rubus spp.	1.6	100	1.3	71	0.5	50	0.8	60
Carya glabra	1.7	100	1.3	86	1.2	100	---	---
Nyssa sylvatica	1.4	71	0.8	43	1.5	100	0.4	40

Mesic hemlock/rhododendron, 2 of 2

	ES (7)		MS (7)		LS (4)		LLS (15)	
Species	IV	Constancy	IV	Constancy	IV	Constancy	IV	Constancy
Galax urceolata	1.0	57	0.7	29	1.5	100	0.8	47
Quercus alba	1.4	71	1.2	100	0.3	50	1.1	60
Arundinaria appalachiana	0.6	57	0.7	29	1.8	75	0.7	53
Magnolia fraseri	0.6	57	0.5	71	2.0	100	0.6	53
Tiarella cordifolia	0.1	14	0.7	43	0.7	25	1.8	80
Carex spp.	0.6	43	0.2	29	0.6	50	1.9	93
Halesia tetraptera var. tetraptera	0.7	43	1.1	57	0.5	50	0.8	67
Medeola virginiana	0.6	29	1.0	57	0.4	50	1.2	73
Maianthemum racemosum ssp. racemosum	0.7	71	0.2	29	1.1	75	1.2	80
Decumaria barbara	0.9	57	1.2	43	0.9	25	---	---
Phegopteris hexagonoptera	0.5	43	0.5	43	0.7	50	1.3	67
Fagus grandifolia var. caroliniana	0.7	57	0.5	57	0.9	75	0.7	73
Oxydendrum arboreum	1.0	71	1.3	71	0.1	25	0.4	60
Dioscorea villosa	0.9	71	0.3	43	0.8	75	0.8	73
Viola hastata	1.3	71	0.8	43	0.6	50	---	---
Bignonia capreolata	1.0	71	1.0	71	0.7	75	---	---
Hydrangea radiata	1.0	86	0.3	43	0.5	50	0.9	60
Ilex opaca var. opaca	0.2	43	1.1	57	0.7	50	0.6	47
Polygonatum biflorum	0.7	71	0.4	43	0.6	50	0.8	80
Pinus strobus	0.7	71	0.8	57	0.6	50	0.4	47
Chimaphila maculata	0.4	71	0.2	29	1.2	100	0.7	80
Symplocos tinctoria	0.9	86	1.0	57	0.5	75	0.1	7
Hamamelis virginiana var. virginiana	0.5	29	0.6	57	0.8	100	0.5	47
Dichanthelium spp.	0.9	86	0.5	43	0.2	25	0.7	60
Erigeron pulchellus var. pulchellus	1.2	57	0.1	14	---	---	1.0	67
Trillium spp.	0.1	14	0.3	29	0.6	25	1.2	80
Phryma leptostachya var. leptostachya	1.2	100	0.4	43	0.5	50	---	---
Quercus coccinea	0.6	43	0.5	29	0.5	50	0.4	27

Appendix C: Average importance value (IV) and constancy for woody stem species in each ecosystem type. Values are given for each age-class, and each class is represented by its abbreviated code (ES: 5-25 years, MS: 26-50 years, MLS: 51-70 years, and LS: > 70 years). Number of plots for each age-class are listed in parentheses following the abbreviated code. Only prevalent species are listed. Prevalence was determined by ranking species by the sum of IV across all age-classes, and selecting those species with a total IV of greater than 2 for display.

Xeric oak/blueberry								
		ES (4)		**MS (3)**		**LS (4)**		**LLS (14)**
Species	IV	Constancy	IV	Constancy	IV	Constancy	IV	Constancy
Acer rubrum var. rubrum	18.6	100	20.7	100	26.5	100	21.8	100
Nyssa sylvatica	22.3	100	19.3	100	15.1	100	14.4	100
Quercus coccinea	10.4	100	14.9	100	17.3	100	10.6	79
Oxydendrum arboreum	8.7	100	12.0	100	12.1	100	10.2	100
Quercus alba	3.9	100	11.2	100	1.8	50	9.7	93
Liriodendron tulipifera var. tulipifera	12.7	100	2.7	67	4.4	75	3.3	71
Quercus montana	3.8	75	1.1	33	5.5	100	8.2	79
Quercus velutina	3.5	75	4.7	100	1.6	50	6.6	71
Cornus florida	4.1	100	4.8	100	2.6	75	3.5	79
Carya glabra	1.2	100	4.3	100	1.0	75	---	---
Pinus strobus	3.7	75	0.4	67	0.6	50	1.2	50
Pinus echinata	---	---	0.5	33	4.1	75	0.7	14
Carya [group]	---	---	---	---	---	---	5.4	100
Robinia pseudoacacia	2.2	100	---	---	0.3	50	1.2	50
Carya pallida	1.0	50	0.9	33	1.7	100	---	---
Pinus rigida	0.5	25	0.3	33	0.7	25	0.9	21
Pinus virginiana	0.1	25	1.8	33	---	---	0.4	21
Magnolia fraseri	0.7	75	---	---	0.7	25	0.6	50

Xeric chestnut oak/mountain laurel								
		ES (3)		**MS (4)**		**LS (3)**		**LLS (7)**
Species	IV	Constancy	IV	Constancy	IV	Constancy	IV	Constancy
Quercus montana	12.9	100	26.0	100	38.0	100	33.5	100
Acer rubrum var. rubrum	41.8	100	14.7	100	26.3	100	23.1	100
Nyssa sylvatica	11.0	100	17.6	100	10.5	100	4.9	100
Oxydendrum arboreum	8.1	100	7.6	75	10.2	100	9.5	100
Quercus coccinea	3.2	100	11.1	100	3.9	33	1.4	43
Robinia pseudoacacia	4.5	67	3.0	75	---	---	3.2	86
Tsuga canadensis	2.1	100	0.7	50	1.1	67	5.7	71
Cornus florida	1.0	100	2.0	50	1.1	100	4.8	100
Liriodendron tulipifera var. tulipifera	1.3	100	1.1	50	3.5	67	2.5	71
Quercus velutina	0.5	67	2.8	75	2.5	67	2.4	57
Carya [group]	---	---	---	---	---	---	6.0	86
Pinus strobus	5.1	33	0.2	25	---	---	---	---
Hamamelis virginiana var. virginiana	4.0	67	---	---	0.3	33	0.2	29
Carya pallida	---	---	4.0	50	0.4	33	---	---
Quercus alba	0.0	33	4.0	75	0.4	33	---	---
Halesia tetraptera var. tetraptera	1.3	67	0.6	50	0.3	33	0.7	14
Pinus virginiana	0.2	67	1.9	50	---	---	---	---

Submesic oak/mixed flora								
	ES (7)		**MS (3)**		**LS (3)**		**LLS (9)**	
Species	IV	Constancy	IV	Constancy	IV	Constancy	IV	Constancy
Acer rubrum var. rubrum	23.0	100	25.7	100	23.0	100	17.8	100
Liriodendron tulipifera var. tulipifera	24.8	100	4.4	100	11.9	100	10.3	100
Quercus alba	2.9	100	12.0	100	18.7	100	13.3	89
Oxydendrum arboreum	5.2	86	9.9	100	2.6	67	6.3	100
Quercus montana	0.8	14	1.6	67	9.1	67	8.0	67
Tsuga canadensis	2.2	43	4.0	33	7.9	100	4.4	89
Nyssa sylvatica	4.7	100	6.3	100	3.7	67	2.7	89
Cornus florida	5.7	100	1.5	100	3.7	67	4.1	100
Halesia tetraptera var. tetraptera	4.6	14	5.3	33	1.4	67	3.7	67
Magnolia fraseri	0.7	43	1.4	67	7.8	100	4.1	100
Pinus strobus	6.8	57	2.8	67	---	---	1.4	56
Liquidambar styraciflua	2.9	57	6.1	100	---	---	0.6	22
Carya [group]	---	---	---	---	---	---	8.7	100
Quercus velutina	1.2	86	1.6	67	---	---	4.2	56
Robinia pseudoacacia	1.8	71	1.8	67	1.7	67	1.2	44
Carya glabra	0.4	86	5.2	100	0.8	33	---	---
Quercus rubra var. rubra	0.4	29	---	---	2.6	33	2.7	33
Quercus coccinea	1.5	71	2.0	33	0.7	33	0.8	11
Betula lenta var. lenta	3.1	57	0.5	33	0.4	33	0.9	44
Fagus grandifolia var. caroliniana	0.4	29	0.5	67	1.9	33	1.8	44
Carya alba	1.7	71	2.7	100	---	---	---	---
Sassafras albidum	2.1	57	0.4	33	---	---	---	---
Hamamelis virginiana var. virginiana	---	---	0.7	33	1.2	33	0.4	33

Mesic hardwoods/bloodroot								
	ES (2)		**MS (4)**		**LS (5)**		**LLS (3)**	
Species	IV	Constancy	IV	Constancy	IV	Constancy	IV	Constancy
Liriodendron tulipifera var. tulipifera	36.5	100	34.3	100	24.5	100	34.6	100
Acer rubrum var. rubrum	23.3	100	16.6	100	10.9	100	16.2	100
Halesia tetraptera var. tetraptera	3.4	50	5.1	75	10.1	100	9.8	100
Tsuga canadensis	0.7	50	6.4	75	11.3	60	6.1	67
Carya alba	1.6	100	10.0	100	5.8	60	---	---
Cornus florida	3.5	100	1.2	25	4.6	60	4.5	67
Quercus rubra var. rubra	0.3	50	2.3	75	9.0	80	0.1	33
Nyssa sylvatica	6.9	100	0.8	50	1.2	80	0.3	33
Robinia pseudoacacia	3.7	100	0.3	25	1.2	80	3.2	33
Carya [group]	---	---	---	---	---	---	8.0	100
Betula lenta var. lenta	0.6	50	3.4	100	2.1	60	1.7	100
Tilia americana var. heterophylla	---	---	---	---	1.7	60	6.1	67
Quercus alba	1.3	50	4.7	75	1.5	40	---	---
Carya glabra	2.0	100	1.7	75	3.6	60	---	---
Magnolia fraseri	0.5	50	3.8	100	0.7	80	1.4	100
Hamamelis virginiana var. virginiana	---	---	0.9	50	1.9	20	2.2	33
Fraxinus pennsylvanica	1.1	50	0.8	25	2.6	60	---	---
Liquidambar styraciflua	1.8	50	2.2	50	0.1	20	---	---
Fagus grandifolia var. caroliniana	---	---	---	---	0.4	40	3.4	33
Quercus velutina	3.4	100	0.1	25	0.1	20	---	---
Oxydendrum arboreum	2.0	100	0.3	50	1.0	80	0.2	33
Prunus serotina var. serotina	1.2	50	1.3	50	0.7	20	---	---
Ilex opaca var. opaca	0.3	50	0.2	25	1.6	60	0.7	33
Carya cordiformis	---	---	0.6	25	1.6	40	---	---

Mesic hemlock/rhododendron								
		ES (7)		**MS (7)**		**LS (4)**		**LLS (15)**
Species	IV	Constancy	IV	Constancy	IV	Constancy	IV	Constancy
Tsuga canadensis	8.3	100	26.1	100	45.6	100	34.2	100
Liriodendron tulipifera var. tulipifera	27.6	100	13.8	100	7.1	75	11.1	100
Acer rubrum var. rubrum	14.6	100	12.3	100	9.5	100	10.8	100
Betula lenta var. lenta	2.2	57	9.7	100	2.5	75	5.8	93
Oxydendrum arboreum	5.9	100	5.7	100	4.8	75	2.3	80
Quercus alba	4.4	57	3.9	71	4.9	75	4.4	60
Pinus strobus	3.3	43	3.4	57	6.0	75	4.4	47
Quercus montana	2.8	43	4.1	43	5.3	50	2.4	40
Liquidambar styraciflua	3.9	43	7.6	57	---	---	1.2	33
Fagus grandifolia var. caroliniana	2.5	86	1.6	71	1.0	75	4.4	80
Cornus florida	4.7	100	1.6	71	0.2	50	1.4	60
Nyssa sylvatica	4.4	71	0.5	57	1.1	50	1.1	47
Magnolia fraseri	0.1	14	1.5	29	3.2	75	1.5	67
Carya alba	3.9	86	0.1	14	2.1	50	---	---
Carya [group]	---	---	---	---	---	---	5.4	87
Quercus rubra var. rubra	0.3	43	1.8	57	0.7	25	1.6	53
Tilia americana var. heterophylla	---	---	0.0	14	0.8	25	3.1	60
Robinia pseudoacacia	1.8	43	0.5	29	0.1	25	1.1	33
Hamamelis virginiana var. virginiana	1.0	29	1.3	57	0.3	75	0.9	40
Carya glabra	0.6	43	0.8	57	1.7	100	---	---

Appendix D: Plot Metadata.

PLOT_ID	DATE	X-AXIS BEARING	ECOSYTEM TYPE	SERAL STAGE	LAT_WGS84	LONG_WGS84	ACCURACY (m)	ELEVATION (m)	GENERAL LOCATION
Plot1	5/15/2003	264	XCO	ES	35.04608333	-82.81621667	10	585	Eastatoe Creek
Plot2	5/17/2003	172	MHR	ES	35.0053	-82.81456667	10	387	Smith Creek
Plot3	5/19/2003	38	SOM	ES	35.02451667	-82.7669	10	719	Emery Creek
Plot4	5/23/2003	213	MHR	MS	35.04231667	-82.7575	50	773	Emery Creek
Plot5	6/2/2003	95	XOB	ES	35.03123333	-82.76446667	10	779	Emery Creek
Plot6	6/22/2003	134	MHR	ES	35.05638333	-82.8298	10	762	Flatrock Mountain Creek
Plot7	6/25/2003	195	XOB	LS	35.03863333	-82.95593333	10	595	Mill Creek
Plot8	7/1/2003	304	XOB	LS	35.01851667	-82.98338333	10	469	Thompson River
Plot9	7/3/2003	180	XOB	ES	35.05093333	-82.81886667	10	539	Side-of-Mountain Creek
Plot10	7/6/2003	90	SOM	MS	35.01355	-82.88988333	10	680	Bully Branch
Plot11	7/8/2003	129	XOB	ES	35.01525	-82.76821667	10	639	Willis Creek
Plot12	7/9/2003	55	MHR	LS	35.01	-82.76283333	10	435	Emery Creek
Plot13	7/14/2003	186	MHR	ES	35.02181667	-82.8606	10	608	Cane Creek
Plot14	7/15/2003	276	SOM	ES	35.03666667	-82.8368	10	696	Side-of-Mountain Creek
Plot15	7/21/2003	163	XCO	MS	35.0238	-82.86088333	10	672	Cane Creek
Plot16	7/23/2003	89	XCO	ES	35.02483333	-82.86006667	10	659	Laurel Creek
Plot17	7/24/2003	192	SOM	MS	34.99866667	-82.86588333	10	466	Kinney Creek
Plot18	7/29/2003	128	SOM	ES	35.01761667	-82.75585	10	548	Emery Creek
Plot19	7/30/2003	192	MHB	ES	35.02556667	-82.76443333	10	662	Emery Creek
Plot20	8/5/2003	28	SOM	ES	35.04591667	-82.82248333	10	499	Side-of-Mountain Creek
Plot21	8/6/2003	38	XOB	ES	35.04843333	-82.83283333	10	647	Side-of-Mountain Creek
Plot22	8/6/2003	327	XCO	LS	35.06323333	-82.83723333	10	893	Laurel Fork Creek HW
Plot23	8/9/2003	334	SOM	ES	34.9763	-82.89828333	10	280	Cane Creek
Plot24	8/11/2003	352	SOM	ES	34.99818333	-82.8838	10	390	Cane Creek
Plot25	8/12/2003	211	SOM	ES	35.03842	-82.76157	10	816	Emery Creek
Plot26	8/13/2003	29	MHB	MS	35.00411	-82.88156	10	417	Cane Creek
Plot27	8/15/2003	168	SOM	MS	35.00021	-82.88784	10	428	Cane Creek
Plot28	8/17/2003	182	XOB	MS	35.03171	-82.95847	10	601	Mill Creek
Plot29	8/17/2003	58	XOB	MS	34.99797	-82.96159	10	600	Whitewater River
Plot30	8/20/2003	122	MHR	MS	35.04644	-82.8362	10	590	Side-of-Mountain Creek
Plot31	8/24/2003	138	MHB	LS	35.06801	-82.81893	10	593	Eastatoe Creek
Plot32	9/7/2003	51	XCO	MS	35.01385	-82.74226	10	492	Rachael Creek
Plot33	9/11/2003	127	XCO	MS	35.00018	-82.80089	10	476	Oolenoy Creek
Plot34	9/15/2003	94	MHR	ES	35.03796	-82.80293	10	603	Reedy Cove Creek
Plot35	9/22/2003	114	XOB	LS	35.06051	-82.77143	10	1005	South Saluda River
Plot36	9/24/2003	316	MHB	MS	35.06277	-82.79874	10	727	Abner Creek
Plot37	9/27/2003	96	MHR	MS	34.98959	-82.88379	10	324	Cane Creek
Plot38	9/29/2003	134	MHR	MS	35.01726	-82.73603	10	452	Rachael Creek
Plot39	10/10/2003	230	MHB	LS	35.03725	-82.85909	10	478	Laurel Fork Creek
Plot40	10/15/2003	2	SOM	LS	35.06355	-82.81641	10	579	Eastatoe Creek
Plot41	5/3/2004	40	MHR	LS	35.00233333	-82.89619444	10	557	Bully Branch
Plot42	5/10/2004	188	MHR	MS	34.9837	-82.8985	50	289	Cane Creek
Plot43	5/17/2004	274	XCO	LS	34.98402778	-82.89686111	10	320	Cane Creek
Plot44	5/20/2004	100	MHB	MS	35.03944444	-82.85452778	10	494	Laurel Fork Creek
Plot45	5/25/2004	272	XOB	MS	35.02425	-82.844	10	663	Laurel Branch
Plot46	6/1/2004	54	MHB	MS	35.03266667	-82.76652778	10	723	Reedy Cove Creek
Plot47	6/3/2004	263	MHB	LS	35.06525	-82.79072222	10	908	Abner Creek
Plot48	6/7/2004	228	XCO	ES	35.06397222	-82.79780556	10	729	Abner Creek
Plot49	6/8/2004	101	MHR	ES	35.04344444	-82.81377778	10	542	Eastatoe Creek
Plot50	6/10/2004	48	MHB	LS	35.07566667	-82.82388889	10	836	Eastatoe Creek
Plot51	6/16/2004	148	MHB	ES	35.00497222	-82.78291667	10	442	Eastatoe Creek
Plot52	6/18/2004	31	XOB	LS	34.99486111	-82.92891667	10	390	Bootleg Mountain Creek
Plot53	6/21/2004	138	MHR	LS	34.99902778	-82.95166667	10	356	Musterground Creek
Plot54	6/23/2004	225	MHR	ES	34.99336111	-82.87786111	10	342	Mill Creek
Plot55	6/23/2004	154	XCO	LS	34.99705556	-82.87519444	10	427	Mill Creek
Plot56	6/28/2004	294	MHR	LS	34.96063889	-82.85533333	10	278	Eastatoe Creek
Plot57	7/6/2004	278	MHR	MS	35.03208333	-82.88494444	10	403	Laurel Fork Creek
Plot58	7/12/2004	30	MHR	ES	34.99091667	-82.89944444	10	312	Bully Branch
Plot59	7/20/2004	50	XCO	MS	35.024	-82.77322222	10	840	Reedy Cove Creek
Plot60	7/28/2004	178	MHR	MS	35.02230556	-82.75758333	10	558	Emery Creek
Plot61	8/2/2004	256	MHB	LS	35.02391667	-83.00422222	10	583	Whitewater River
Plot62	10/15/2004	334	SOM	LS	35	-82.8	10000		JG
Plot63	10/16/2004	138	SOM	LS	35	-82.8	10000		JG

Appendix E: Ecological species groups of Jocassee Gorges, S.C as described from Abella and Shelburne (2004).

Woody Stems	
Species Group	Species
Liriodendron tulipifera	*Liriodendron tulipifera*
	Halesia tetraptera
	Quercus rubra
Oxydendrum arboreum	*Oxydendrum arboreum*
	Cornus florida
	Acer rubrum
Quercus alba	*Quercus alba*
	Carya alba/glabra
	Magnolia fraseri
Quercus coccinea	*Quercus coccinea*
	Quercus velutina
	Nyssa sylvatica
Quercus montana	*Quercus montana*
Tsuga canadensis	*Tsuga canadensis*
	Betula lenta
	Fagus grandifolia
	Pinus strobus
	Tilia americana

Ground Flora	
Species Group	Species
Adiantum pedatum	*Adiantum pedatum*
	Actaea pachypoda
	Botrypus virginianus
	Aralia racemosa
	Sanicula canadensis
Arundinaria appalachiana	*Arundinaria appalachiana*
	Quercus coccinea/velutina
	Chimaphila maculata
	Nyssa sylvatica
	Oxydendrum arboreum
Kalmia latifolia	*Kalmia latifolia*
	Quercus montana
	Magnolia fraseri
	Gaylussacia ursina
	Chamaelirium luteum
	Galax urceolata
	Rhododendron minus
Polystichum acrostichoides	*Polystichum acrostichoides*
	Euonymus americanus
	Parthenocissus quinquefolia
	Hydrangea radiata
Rhododendron maximum	*Rhododendron maximum*
	Leucothoe fontanesiana
	Mitchella repens
	Hexastylis heterophylla
	Tsuga canadensis
Sanguinaria canadensis	*Sanguinaria canadensis*
	Caulophyllum thalictroides
	Panax quinquefolius

Ground Flora, cont.	
Species Group	Species
Smilax rotundifolia	*Smilax rotundifolia*
	Acer rubrum
	Carya alba/glabra
	Magnolia fraseri
Thelypteris noveboracensis	*Thelypteris noveboracensis*
	Halesia tetraptera
	Toxicodendron radicans
	Polygonatum biflorum
Tiarella cordifolia	*Tiarella cordifolia*
	Phegopteris hexagonoptera
	Medeola virginiana
	Arisaema triphyllum
Vaccinium pallidum	*Vaccinium pallidum*
	Sassafras albidum
	Euphorbia corollata
	Piptochaetium avenaceum
Vitis rotundifolia	*Vitis rotundifolia*
	Goodyera pubescens
	Pyrularia pubera

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