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RESOURCE QUALITY AND RECRUITMENT OF TREE SPECIES IN

PLANTATION FORESTS OF SOUTHWESTERN MICHIGAN

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RESOURCE QUALITY AND RECRUITMENT OF TREE SPECIES IN PLANTATION FORESTS OF SOUTHWESTERN MICHIGAN

By

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ABSTRACT

RESOURCE QUALITY AND RECRUITMENT OF TREE SPECIES IN PLANTATION FORESTS OF SOUTHWESTERN MICHIGAN

By

Diane Harlow Burbank

Patterns of tree recruitment, soil moisture, potential N mineralization, and light availability were examined for twelve plantations and three oak-hickory forests on similar upland soils in southwestern Michigan. Levels of all resources varied significantly across stands. Stands dominated by hardwoods were highest in soil resources, while red pine and Douglas-fir stands were lowest. Percent light was lowest beneath white pine stands and highest under red pine and scots pine stands. Principal components analysis produced a stand ordination reflecting a contrast between soil resources and light. The most abundant seedling and sapling species were red maple and black cherry, while oaks and several mesic-site species were sparsely represented. Red maple and black cherry showed no relationship to stand type or resource gradients, and were not dispersal-limited. These two species, by exhibiting wide tolerances for resources and aggressive colonization and dispersal, are likely to dominate those plantations allowed to senesce undisturbed.

To my Dad, Richard A. Harlow Jr., who planted the seed, to my family Cynthia, Chip, and David, who nurtured the sapling, and to my husband Mike, who provided the stability and love for the tree to bear fruit, I am eternally in your debt.

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INTRODUCTION

Plantation forests are common feature of the landscape in the Northeast and Lake States Region of the United States. Many of these forests were established 50-60 years ago in an effort to reclaim and restore worn-out agricultural land and clearcut natural hardwood forests. Foresters and other concerned individuals involved in these early restoration efforts often had as their primary concern the stabilization of soils on these degraded landscapes, as well as the potential wood products that could be extracted in the future from these plantations. However, it was the rare individual who thought beyond the 50-year conifer rotation, and wondered about the nature of the contribution these conifers would make to nutrient cycling, succession, and other ecosystem processes occuring on these sites. The effect of conifers on these landscapes is becoming more important now, as rotation age is approached and these stands are either harvested or allowed to senesce and succeed. This study was initiated to explore the effect of these conifers on succession within an oak-hickory landscape in southwestern Michigan. A review of other studies of succession is appropriate to aid in understanding these patterns of vegetation and resource development over time.

Studies of Succession

Over the last 100 years, patterns of succession have been examined in detail for a wide array of herbaceous and woody ecosystems (cf. Cowles 1899;

Clements 1916; Watt 1947; Holt 1972; Forcier 1975; Bormann and Likens 1979; Petranka and McPherson 1979; Woods 1979; West et al. 1981; Werner and Harbeck 1982; Lorimer 1983; Whitney 1986; Host et al. 1987; Tilman 1988; Halpern 1989). In response to this large body of descriptive and empirical research, a concomitant body of literature on successional theory has evolved (cf. Clements 1916; Gleason 1926; Egler 1954; Drury and Nisbet 1973; Horn 1974; Connell and Slatyer 1977; Fox 1977; Bazzaz 1979; Grime 1979; Peet and Christensen 1980; West et al. 1981; Finegan 1984; Tilman 1985; Huston and Smith 1987). This literature, in an attempt to reduce the enormous variability in patterns of succession observed to a few universal tenets, has tended to generate controversy as well as concepts.

However, four general factors which appear to influence plant community dynamics and thereby succession can be discerned from this literature. These are: (1) availability of space and limiting resources, over which plants often compete (Toumey and Keinholz 1931; Grime 1977; Tilman 1985; Zak et al. 1986), (2) climate and physical site characteristics (Barnes et al. 1982; Pregitzer and Barnes 1984; Host et al. 1987), (3) disturbance (Heinselman 1973; Sprugel 1976; Whitney 1986), and (4) predation by insects, pathogens, and other herbivores (McNaughton 1983; Bryant and Chapin 1986). Rarely do these factors operate in a vacuum, and often they vary in importance at different temporal and spatial scales (O'Neill et al. 1986). The thread that ties these factors to patterns of plant response in a successional system is the autecology of individual species (Gleason 1926; Egler 1954; Holt 1972; Forcier 1975; Grime 1977; Bazzaz 1979; Woods 1979; Huston and Smith 1987).

The following review demonstrates the importance of these variables in community development, and the need for their quantification when interpreting patterns of species establishment and recruitment.

Availability of Limiting Resources

Availability and quality of essential resources, and their modification by competing plants, has been suggested as the predominant mechanism operating in succession (Tilman 1985, 1988). In most forest ecosystems, these resources generally include nitrogen, water, and light (Spurr and Barnes 1980). Historically, competition for light or shade tolerance has been seen as a dominant force driving patterns of successional change in forests (Heyer 1852, as cited in Toumey and Kienholz 1931). In 1931, Toumey and Kienholz demonstrated the importance of below-ground competition for soil resources in canopy-understory interactions. Mitchell and Chandler (1939) demonstrated that several deciduous species in the northeastern United States had different tolerances for soil nitrogen levels. However, while species react to differences in resource availability, they also can alter the resource quality of a site.

It is widely recognized that litter quality can influence nutrient availability (Swift et al. 1979; Gosz 1981; Staaf and Berg 1981; Bryant and Chapin 1986; Blair et al. 1990), and that variation exists among species in general and along successional and site quality gradients for litter quality (Robertson and Vitousek 1981; Perala and Alban 1982; Vitousek et al. 1982; Pastor et al. 1984; Zak et al. 1986; Perry et al. 1987; Bryant and Chapin 1986; Montagnini et al. 1989). It has been hypothesized that litter quality and nutrient availability, both of which respond to and bring about species replacements, are keys to understanding the dynamics of secondary succession (Pastor et al. 1984; Thorne and Hamburg 1985; Bryant and Chapin 1986; Tilman 1988).

Tilman (1982, 1985, 1984, 1988), looking at early successional old field communities and, more recently, forest systems, combined competition for light and nitrogen with individual species requirements for these resources into an hypothesis of community dynamics in secondary succession. Tilman's "resource-ratio hypothesis" suggests that temporal changes in the ratio of light and soil nitrogen control the composition and direction of plant community change. Competition for these resources is seen as a selective force on species characteristics, which determines their distribution along a resource-ratio gradient consisting of an inverse relationship between light and nitrogen. However, this hypothesis does not explicitly involve other potentially important factors such as soil moisture levels or disturbance regime. The assumption appears to be that plant responses to nitrogen and light operate at a more fundamental level than responses to other factors ie. factors such as moisture and disturbance ultimately influence light and nitrogen levels, and therefore their effect upon plant community dynamics is seen indirectly through their effect upon these two fundamental resources (Tilman 1988).

An interesting aspect of Tilman's most recent work (1988) is his recognition of the role of transient dynamics in secondary succession, especially on nutrient-rich sites and in forest communities. Transient dynamics is a phenomenon by which plants that are not competitive dominants for a site's equilibrial resource ratio become community dominants nonetheless. Variation in resource availability and species' colonizing abilities have been suggested to strongly influence transient dynamics (Tilman 1988).

Availability of and competition for soil moisture limits the distribution of many plant species (Spurr and Barnes 1980). In addition, moisture is limiting to the microbial biomass present in the soil, which releases nutrients for plant uptake through decomposition. Because of this, nutrient availability is sometimes used as an index of moisture availability (Tilman 1988). As moisture also has a direct physiological effect on tree growth and seedling establishment, a characterization of moisture regime in addition to nutrient regime should be undertaken in any succession study.

Climate and Site

Research has demonstrated the influence of variation in climate, topography and physical site characteristics on successional development (Clements 1916; Daubenmire 1966; Whittaker 1975; Host et al. 1987). The contrasting concepts of discrete communities separated by ecotones (Daubenmire 1966), and continuous distributions of species along environmental gradients (Whittaker 1975), both make use of climate and topography in understanding species replacements and succession. The German Baden-Württemberg model for ecological site classification, and the subsequent Ecological Classification System developed in the United States, make direct use of these variables in the first levels of their respective hierarchies (Barnes et al. 1982; Pregitzer and Barnes 1984). The two models then break broader environmental levels into site units representing the interactions between vegetation, soil and landform. These systems have become increasingly useful, both as a practical management tool for site quality determination and as a conceptual framework for investigating interrelationships among the biological and physical variables influencing community dynamics (Zak et al. 1986; Host et al. 1987, 1988; Padley 1989).

Disturbance

Disturbance has been recognized for its contribution to the maintenance of diversity and vegetative mosaics, and for its influence on successional pathways within forest ecosystems (Heinselman 1973; Pickett and White 1985; Whitney 1986; Boerner et al. 1988; Halpern 1988, 1989). Disturbance in this context ranges from naturally occurring events such as individual treefalls and catastrophic perturbations such as fires, hurricanes, and ice storms, to human-related disturbance such as plantation forests, logging, and forest conversion to agriculture followed by land abandonment and old-field succession back to forest. Gap formation as a result of smaller disturbances, such as small tree falls, has been implicated as a primary factor in secondary succession of older forests (Runkle 1982; Canham 1984, 1989, 1990; Connell 1989). The intensity, frequency, and degree of heterogeneity of large disturbances may also have considerable effect on the direction of community development in forest systems (Heinselman 1973; Sprugel 1976; Runkle 1982; Whitney 1986; Halpern 1988, 1989). Anthropogenic disturbances tend to set forest succession back to stages in which plants ranging from field annuals to pioneer forest species dominate large areas. Regardless of its form, disturbance also interacts with nitrogen mineralization and nitrification through changes in litter quality, soil mixing, and erosion (Bormann and Likens 1979; Vitousek and Matson 1985; Perry et al. 1987), leading eventually to changes in species composition.

Herbivory

Although widely acknowledged as a potential factor influencing forest succession, herbivory has been often neglected in successional studies (Connell and Slatyer 1977; Bryant and Chapin 1986). Plant chemical defenses for herbivory, which decrease the palatability of live foliage to consumers, also tend to decrease the rate at which plant litter is decomposed by soil-based consumers (McNaughton 1983; Bryant and Chapin 1986). This in turn reduces nutrient availability. In fact, Bryant and Chapin (1986) have hypothesized that in boreal forests, mammalian browsing of the palatable tissues of deciduous saplings can lead to their replacement by the less palatable conifers, a typical successional pathway in these forests. Insectivorous leaf feeders such as gypsy moth (*Lymantria dispar*) and spruce budworm (*Choristoneura fumiferana*) are well known for the tree mortality they can cause through successive defoliations. This mortality can play an important role in community dynamics, and may provide an opportunity for changes in species composition. Seed predation by insects, birds, and mammals is another often observed but infrequently quantified phenomenon that could have large impacts upon successional pathways (Fenner 1985).

Autecology

The importance of the autecology of individual plant species in community dynamics and succession is obvious. Life history characteristics such as longevity, age to first reproduction, seed production and dispersal characteristics, as well as physiological tolerance of various stresses, have all been used to explain variation in species composition and success, both spatially and temporally (Gleason 1926; Egler 1954; Curtis 1959; Forcier 1975; Harper, 1977; Bazzaz 1979; McDonnell and Stiles 1983; Huston and Smith 1987). Despite its importance, the explicit incorporation of autecological characteristics in models of succession has only recently become popular (Connell and Slatyer 1977; Grime 1977; Tilman 1982, 1984, 1988; Huston and Smith 1987).

Two such models have been proposed. Grime's (1977) population model hypothesizes that three primary plant strategies exist based upon site conditions (stress tolerators), resource levels (competitors) and disturbance levels (ruderals). Huston and Smith (1987) take an individualistic approach and "envision a continuum of plant strategies resulting in a different hierarchy of relative adaptation to each different set of conditions" (p. 170). These models, in contrast to Tilman's competition model, emphasize that site conditions and disturbance, in addition to competition for resources, interact to produce conditions eliciting different plant strategies. Weldon and Slauson (1986) maintain that any stressful factor, such as abiotic stress or disturbance, has the potential to be as important as competition in directing individual success and ultimately community composition and structure.

Succession in Plantation Forests

In the northeastern United States, the bulk of succession research has focused on old field systems and naturally regenerating primary and secondary forest systems. The majority of this work has examined deciduous forests of New England (Tubbs 1969; Forcier 1975; Bormann and Likens 1979; Woods 1979; Woods and Whittaker 1981; Hibbs 1983), and the Lake States (McIntosh 1957; Peet and Loucks 1977; Lorimer 1983; McCune and Cottam

1985). These investigations have involved examination and manipulation of primary and older second-growth forest communities, and have shown interesting community dynamics involving different combinations of biological, physical and stochastic variables in space and time. Such ecological concepts as reciprocal species replacements and climax or equilibrial states of existence as they relate to forest ecosystems have been explored within these communities.

However, considerably less is known about succession in plantation forests (but see Grisez 1968; Carmean et al. 1976; Artigas and Boerner 1989). In the 1930's, the Civilian Conservation Corps (CCC) was employed to reforest abandoned agricultural land and cut-over forestland throughout the Northeast and Midwest. Often the planted forests resulting from these efforts consisted of conifers, exotic or native, growing outside their natural ranges on what at one time were sites dominated by hardwoods. Many of the hardwood sites on which they have been planted were previously degraded in some way, especially through intensive agriculture or clearcutting that often resulted in the loss of topsoil through erosion. In addition to the CCC, land-grant universities and conservation-minded individuals also established plantations, especially conifers, for economic, aesthetic, and research purposes.

In establishing these plantations, careful consideration was often given to the moisture demands of particular tree species in order to match site and species and thereby maximize success (Walt Lemmien, personal communication). In other instances, species availability in nurseries was the primary consideration (Artigas and Boerner 1989). Soil conditions at these disturbed and depleted sites were often harsh and required repeated replanting. In addition, tree seedlings in these plantations often competed with vigorous weedy herbs, grasses, and hardwood saplings for growing space and resources. During the early years of these plantations, removal of woody competition was often a regular occurrence (Walt Lemmien, personal communication). Once the conifers had gained an advantage , however, the plantations were often left unmanaged, or thinned once or twice. After the introduction of chemical fertilizers and herbicides in the 1940's, more drastic and intensive methods were used to control competition.

The success of these early attempts at forest restoration can be measured in the 50-60 year old forests scattered throughout the Northeast and Lake States. Although many of these forest patches are still under active, often intensive management, many plantations have been abandoned from management and are succeeding naturally.

In one study of 37 plantations of diverse coniferous composition ranging in age from 36-64 years in northwestern Pennsylvania, Grisez (1968) found volunteer seedlings and saplings in all plantations, especially under cover of Scots pine (*Pinus sylvestris*). Volunteer species included black cherry (*Prunus serotina*), red maple (*Acer rubrum*), white ash (*Fraxinus americana*) and oaks (*Quercus* spp.) in order of frequency of occurrence. However, the focus of his research was on growth of the conifers and not on that of the volunteers.

Several plantation studies have looked at and demonstrated how soil properties change with different plantation types. Byrnes and Kardos (1963) demonstrated that water infiltration into upper soil horizons was higher for hardwood forests as compared to red pine (*Pinus resinosa*) plantations, and higher under red pine than in old fields. Challinor (1968) found that soil beneath different species of conifers varied both in litter quantity and in nutrient levels in the upper 5 cm of soil. Perry et al. (1987) documented that nitrogen cycling varied between stands of pure conifers and those mixed with hardwoods. They suggested that a mixed system is more complex than simply adding the effects of individual species involved. Only the study by Carmean et al. (1976) looked at how changes in soil properties due to differences in woody cover affected subsequent growth by hardwoods. In this study, however, the plantation overstory was removed and the hardwoods were planted, making it difficult to generalize about long term changes in natural succession within plantations.

A study recently completed by Artigas and Boerner (1989) analyzed the abundance of seedlings and saplings under replicated plantations of red pine, white pine (*Pinus strobus*), and Virginia pine (*Pinus virginiana*) to determine if successional pathways varied between plantation types. They found that differences in pH levels, litter depth, and stem density over all stands were associated with different suites of sapling/seedling species. They also found differences between plantation types in structural diversity that were associated with increased density of saplings/seedlings. Although ten environmental and five mensurative variables were used to analyze the sapling/seedling data, a notable exception was any measure of nitrogen.

There are several reasons why an investigation into the patterns of successional development in plantation communities would be worthwhile.

It is widely accepted that a mor type of humus development is typical beneath conifer plantations due to the high C:N ratio of coniferous foliage (Spurr and Barnes 1980). In addition, as mentioned above, species differ widely in the resistance of their foliage to decay, and thereby in the efficiency with which nutrients immobilized in the litter they produce can be released for use (Kucera 1959; Perala and Alban 1982; Zak et al. 1986). As Perry et al. (1987) suggest, different combinations of hardwoods and conifers could alter nitrogen dynamics on similar sites. Site quality, simply put, is influenced by the type of species planted. In addition, species vary in the amount of light extinguished through their crowns; plantations of varied composition may offer a natural gradient in light available beneath the dominant canopy. Given that species differ in requirements for essential resources, it would not be unreasonable to suggest that invading species would respond differently to these changes in resource availability. Patterns of succession may therefore vary depending upon the dominant overstory species, as has been found in natural communities. Alternatively, site quality in plantations may vary, regardless of overstory canopy, due to the level of soil degradation before plantation establishment, soil physical characteristics which are difficult to survey accurately, and the cover or crop before planting.

As the study by Artigas and Boerner (1990) appears to be the only one to explicitly investigate patterns of abundance and dominance of volunteer species in plantations, it is difficult to characterize the variability in these patterns, or how the overstory may be modifying environmental conditions to produce these patterns. Investigation in this area could help to determine the appropriate species for planting, depending upon management objectives. Research undertaken within the geographical area of this study provides evidence that red pine, planted on a site previously occupied by hardwoods followed by agricultural crops, exerts a negative feedback on the system via low litter quality (Palik and Pregitzer, unpublished manuscript). It is unclear how this lowering of site quality will affect the establishment and recruitment of hardwoods naturally dispersed into this red pine stand or others like it. Negative feedback is not desirable if the management goal is restoration of productive ecosystems similar to those native to a particular region. Reforestation efforts to avert global warming need to be framed in the context of long-term effects upon the ecosystem as a whole, not just short-term benefits to one part. Certain conifers could conceivably act as nurse crops to hardwoods (Grisez, 1968), providing a short rotation forest product while leaving an established hardwood stand perhaps similar to the original vegetation. A clearer understanding of community development in plantations is needed in order to anticipate, with some degree of certainty, the effect of plantation composition on establishment and recruitment of trees beneath these canopies.

OBJECTIVE AND HYPOTHESES

The general objective of this study is to characterize patterns of variation in tree establishment and recruitment within plantation forests, and to relate these patterns to gradients in light, nitrogen and moisture, and to topographic variation, disturbance history, and distance to potential seed sources. This study does not quantitatively address herbivory due to the time and labor intensive nature of the methods that would be involved, and the preliminary nature of the investigation. Its potential importance is, however, acknowledged. It should be noted also that although I chose to look at nitrogen levels, this does not diminish the potential importance of other nutrients for tree growth. However, nitrogen is an important nutrient in many northeastern forest systems because its supply is more limited than that of other essential nutrients (Spurr and Barnes 1980). In addition, because its input in available form into the forest system is predominantly through decomposition of litter by the microbial biomass, it tends to be more indicative of changes in fertility brought about by overstory composition than other nutrients which are derived from mineral soil.

Nitrogen availability in this study was measured as potential N mineralization. Powers (1980) and others have demonstrated that potential mineralized soil N correlates well with tree growth and yield in conifer stands, and is an effective index of soil N availability. Nitrification levels were not addressed in this study. Several researchers have demonstrated that the nitrification process is not an important contributor of available nitrogen in oak or coniferous forests, and on dry sites in general (Gosz 1981; Aber and Melillo 1982; Vitousek et al. 1982; Zak et al. 1986). However, there is also evidence for considerable variability in nitrification across stands of differing composition and soil depths (Federer 1983). In addition, there is evidence to suggest that nitrification may be important where basswood (*Tilia americana*) or tulip tree (*Liriodendron tulipifera*) are present in the overstory and contribute their nutrient-rich and easily decomposed litter to the system (Pastor et al. 1984; Zak et al. 1986). An investigation into variation in both nitrogen mineralization and nitrification rates among plantation types would be an interesting extension of this study.

The hypotheses to be tested in this study are: (1) levels of light, soil nitrogen and soil moisture form a gradient across different plantation types established on soils of similar origin and physical characteristics, (2) patterns of individual tree species establishment and recruitment vary across different plantation types, and (3) there are associations between resource levels and species establishment and recruitment across plantation types.

A test of these hypotheses will involve (1) determining levels of light, soil nitrogen and soil moisture within each of several different plantation types, (2) plotting resources against plantation types to determine if a gradient exists for each resource, (3) ordination of plantations based upon resources to determine if a gradient exists involving a linear combination of these variables, (4) determining patterns of dominance of individual tree species as seedlings (establishment) and saplings (recruitment) in the understory of different plantation types, (5) using bivariate plots to associate species dominance patterns with individual resources, and (6) comparing plantation ordinations with species dominance patterns to associate establishment and recruitment with a composite of resources. In addition, data collected on site characteristics, disturbance history, and distance to potential seed sources will be used to aid in interpreting the species dominance patterns found.

METHODS

Study Area

The areas chosen for this study are located within the Kellogg Biological Station (KBS), Hickory Corner's, Michigan, and the W. K. Kellogg Experimental Forest (Kellogg Forest), Augusta, Michigan. Both areas are found in Ross Township, Kalamazoo County in southwestern Michigan (Figure 1). These areas are administered by Michigan State University and were acquired as abandoned agricultural land in the early 1930's. The land-use history of these areas up to the beginning of the 1930's was fairly typical of that which occurred throughout much of southwestern Michigan (Whitney 1987). Presently, KBS is a mixture of cultivated and abandoned fields, and old woodlots, while Kellogg Forest consists of a matrix of plantations of varied composition on abandoned agricultural land. The extensive documentation of land use history collected for these two sites by forest and farm managers, and incorporated as an integral part of this research, allows for a case history approach to this study. As a direct focus on succession within plantation communities is rare, this approach seemed to be the appropriate first step. These areas offer interesting contrasts in management techniques for the revegetation of abandoned farmland, as well as fertile ground for comparative analyses of canopy-understory interactions and succession over a wide array of well-documented land uses.

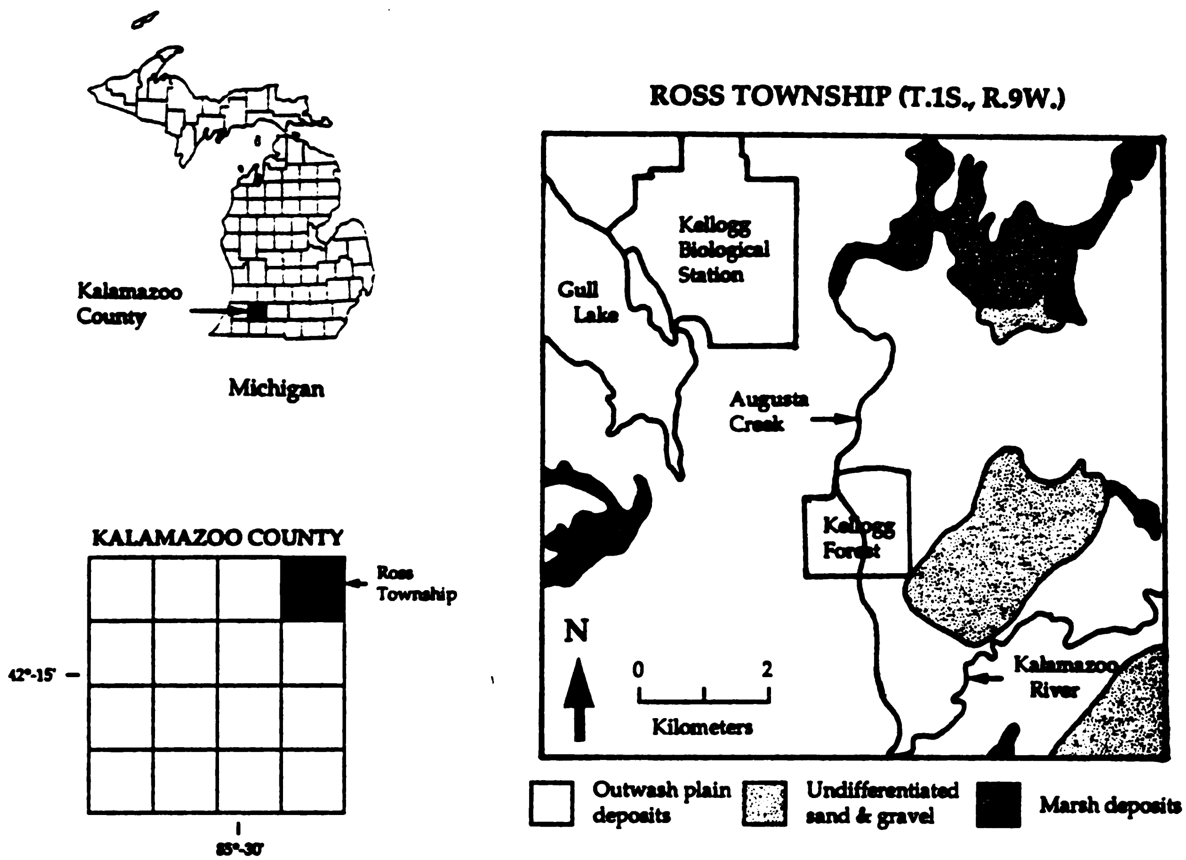


Figure 1. Location of and landforms associated with the study areas of Kellogg Forest and Kellogg Biological Station, Ross Township, Kalamazoo County, Michigan.

The general landscape of Ross Township is characterized by a matrix of agricultural lands and woodlots situated on rolling to hilly terrain, the steeper slopes occurring in the Kellogg Forest. Upland soils tend to be sandy, and are represented primarily by Oshtemo sandy loam on hills (coarse-loamy, mixed, mesic Typic Hapludalf), and Ockley loam and sandy loam (fine-loamy, mixed, mesic Typic Hapludalf) at lower elevations and flatter slopes. Secondary soils include Fox sandy loam (fine-loamy, mixed, mesic Typic Hapludalf), Hillsdale sandy loam (coarse-loamy, mixed, mesic Typic Hapludalf), and Spinks loamy sand (sandy, mixed, mesic Psammentic Hapludalf) (Table 1). These soils are generally deep, well-drained, with moderate to rapid permeability. Kellogg Forest appears to be more xeric in nature than forested areas of KBS.

Monaghan (1984) has described the glacial geology in detail of Kalamazoo County, and a series of maps for this county describe its surficial and bedrock geology (Monaghan and Larson, 1982). The two study areas in general occupy glacial outwash composed of medium to coarse sand and

Table 1. Type characteristics of several soils found in the W. K. Kellogg Forest and Kellogg Biological Station, southwestern Michigan (Austin & Konwinski 1979).

	Characteristic			
	Subgroup	Texture	Drainage [1/]	Depth of Solum (cm)
Soil Type				
Oshtemo	Typic Hapludalf	sandy loam	WD	102-190
Ockley	Typic Hapludalf	sandy loam to loam	WD	102-183
Spinks	Psammentic Hapludalf	loamy sand	WD	91-152
Fox	Typic Hapludalf	sandy loam	WD	61-102
Hillsdale	Typic Hapludalf	sandy loam	WD	102-203

[1/] WD, well-drained.

gravel. Soils of KBS and the western half of the Kellogg Forest were formed in outwash deposits of the Galesburg-Vicksburg outwash plain. Soils of the eastern half of the Kellogg Forest were formed in outwash deposited by Augusta Creek, which formed an incised valley train within the Galesburg-Vicksburg outwash plain. These deposits are on the northwestern edge of larger masses of undifferentiated sand and till associated with the Tekonsha Moraine.

The present natural vegetation of Kellogg Forest woodlots is dominated by black, white and to some extent red oak (*Quercus velutina, Q. alba, Q. rubra*), and pignut and shagbark hickories (*Carya glabra, C. ovata*), with black cherry, red maple, sassafras (*Sassafras albidum*) and flowering dogwood (*Cornus florida*) in the understory. The natural forest vegetation at KBS is more mesic in nature, and consists of one woodlot, Long Woods, that is dominated by red oak, sugar maple (*Acer saccharum*) and pignut hickory. The understory is represented by black cherry, sassafras, flowering dogwood, and sugar maple. The average age of the dominant natural vegetation of Kellogg Forest appears to be 124 years (C. Ramm, personal communication). Long Woods is at least 50 years old with an extensive area of larger trees of at least 100 years of age. In addition, there are several remnant seed trees that remained uncut during farming practices and occurred in the middle of fields or along fence rows in both of these areas. These seed trees were mapped at Kellogg Forest in an intensive vegetation survey conducted in 1940. Many of these trees are still present in the landscape today and are producing seed.

Historical Records

Under the auspices of the General Land Office (GLO) survey program, all townships in Michigan, including Ross Township, were surveyed by the federal government prior to settlement. In the early to mid-1800's, surveyors systematically recorded the nature of the vegetation and landscape as they traversed the state, providing a detailed picture of the presettlement vegetation in the nineteenth century. These notes have seen increasing use as they offer a quantitative, though systematic, sample of the vegetation every 800 m along both range and township lines in the state.

Several researchers have investigated the reliability of these surveys in providing a reconstruction of presettlement vegetation (Buordo 1956; Curtis 1959; Whitney 1986). Bias in selection of witness trees (towards moderate-sized, long-lived trees), and fictitious data have been found to be potential problems, although these appear to be of limited extent in Michigan (Buordo 1956; Whitney 1986).

An initial investigation of the GLO survey notes (located at the Real Estate Division, Michigan Department of Natural Resources, East Lansing, Michigan) for Kellogg Forest and KBS was undertaken to provide a description of the presettlement vegetation. The survey of the interior of Ross Township (T 1 S, R 9 W) was conducted between 1825-1826. Generally, the two nearest trees in different quadrants at each quarter section corner were blazed as witness trees, and their species, diameter, and distance to corner recorded. In addition, soil, topographic, and general vegetation descriptions were recorded for each section line, and disturbances such as burned areas or windthrow were noted as surveyors crossed through them.

For the purposes of this study, all witness trees at section and quarter section corners that fell within or on KBS and Kellogg Forest boundaries were transcribed from the survey notes. Average diameter, relative basal area, relative density, and relative frequency were then calculated for each species. Section line descriptions of soils, topography, and vegetation were also noted to develop a picture of the presettlement landscape.

Records for changes in land use and disturbance regimes in this area since the GLO survey were located in the literature, as well as in the diaries, surveys, and notes recorded by forest managers at Kellogg Forest.

Stand Selection

Upland plantation and natural communities, representing combinations of various cover types and topographic positions, were chosen to quantify and compare patterns of tree seedling and sapling importance and site variation. Stands selected were at least 0.5 ha in size, 45 m wide, and 50 years old, with minimal to no man-made disturbance over the past 25-50 years. These criteria were established to ensure at least the potential presence of tree seedlings and saplings and to avoid edge effects. Out of 71 compartments and subcompartments of natural and planted vegetation available at Kellogg Forest, 56 could be classified as upland communities. Within these 56 compartments, 14 stand types met the stand selection criteria and were chosen for sampling. Most rejections were due either to age or size.

Of the 14 stands selected, 12 consisted of plantations composed of various single and multiple species combinations (Table 2). Plantation types included two white pine plantations, two red pine plantations, two Scots pine plantations, one European larch (*Larix decidua*) plantation, one Douglas-fir (*Pseudotsuga menziesii*) plantation, one plantation mix of white and Scots pine, one plantation mix of white and red pine, one plantation mix of white pine, red oak and basswood, and one plantation of tulip tree. Within 7 of the 12 plantations, thinning plots had been established within the past 50 years. Where these plot locations were known (in 4 out of 7 occasions), they were avoided for sampling. It was often necessary to locate sampling plots within the established thinning control plots, which were randomly distributed within the stand and undisturbed. This was due to an inadequate buffer of otherwise undisturbed vegetation within these thinned stands. In the remaining 3 stands with unknown thinning plot locations, potential plot locations where recent removal of trees was evident were rejected.

Table 2. Stand types surveyed in the W. K. Kellogg Forest and Kellogg Biological Station, southwestern Michigan.

NATURAL	PLANTED HARDWOOD	HARDWOOD-CONIFER MIX	CONIFER MIX	CONIFER MONOCULTURE
Oak-hickory (3)	Tulip tree	White pine-red oak-basswood	Red pine-white pine	Red pine (2)
			Scots pine-white pine	Scots pine (2)
				White pine (2)
				European larch
				Douglas-fir

The variation in replication of plantation types is reflective of the distribution of these types in the area. Red, white and Scots pine were frequently planted species throughout much of the Northeast, and Kellogg Forest is no exception. Therefore, there were more stands of these types in which to sample. The mixed species plantations, as well as those of European larch, Douglas-fir, and tulip tree, were infrequent plantation types in this area. Therefore only one representative stand of each was found to meet the size area and disturbance criteria required.

Included among the 14 stand types are two naturally established oak-hickory woodlots to serve as representatives of the natural vegetation native to this area (Table 2). An additional oak-hickory woodlot at KBS, known as Long Woods, also met selection criteria and was chosen for sampling, bringing the total number of stands sampled to 15. These woodlots are generally even-aged, and have been subjected to a variety of man-made disturbances, including silvicultural operations, livestock grazing and firewood cutting (personal communication, KBS and Kellogg Forest staff). The last grazing in these woodlots occurred before 1965, and one woodlot has been preserved since 1956 as a natural area. Areas within these woodlots undergoing current silvicultural treatments were avoided for sampling; for the most part control plots of undisturbed forest in the woodlots have been maintained for at least 25 years, and offered a large enough area in which to sample.

Field Sampling

Within each of the 15 stands chosen, three plots were randomly located in which to sample overstory tree dominance, seedling and sapling composition and importance, soil mineralizable nitrogen, soil moisture, light, and topographic variables. Distance to potential seed sources was measured in relation to these plots as well. Exact locations of these plots and the stands in which they are found are presented in the Appendix.

Site

Three topographic measures were recorded for each plot. Quantitative measures of topography consisted of percent slope and aspect by 45° class. A description of topographic position was also included (eg. middle slope, high plateau) to aid in interpretation of the data. Soil series were determined using both a map produced in an intensive soil survey of Kellogg Forest in 1966, and the Soil Survey of Kalamazoo County (1979).

Vegetation

Within each stand, three .01 ha circular plots (radius=5.64 m) were permanently established (Figure 2). These sample plots were randomly located by using a random number table and a dot sheet laid over a map of each stand. Within each plot, species, diameter at breast height (dbh, 1.37 m) by 2.5 cm classes (eg. 8.6-10.0 cm), and height (meters) were recorded for each individual. Three classes of individuals were defined based upon vertical stratification within stands: overstory, saplings, and seedlings. For the purposes of this study, dominance in the seedling class represents species success at establishment, while dominance in the sapling class represents species recruitment success. All individuals with a dbh of at least 8.6 cm were classified as overstory trees. Tree saplings were defined as individuals with the capacity to become overstory dominants having a dbh of 1.3-8.6 cm. Tree seedlings, defined as having a dbh of less than 1.3 cm, were sampled by using

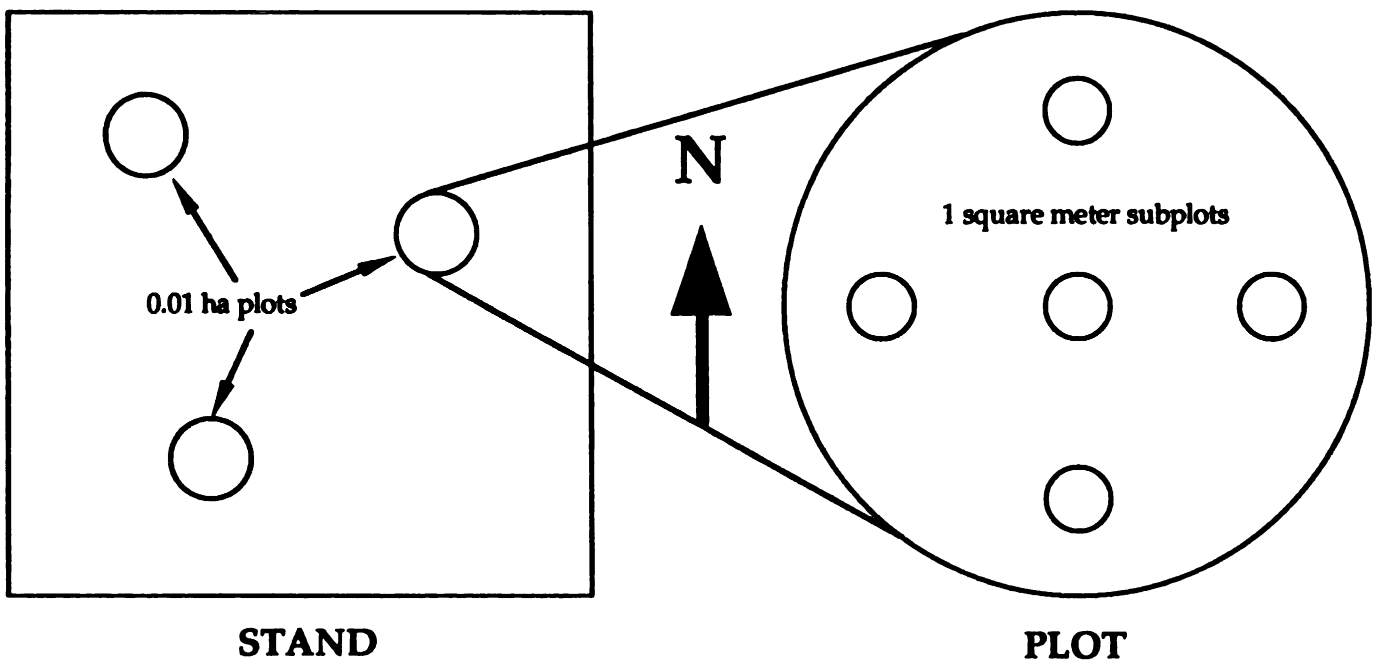


Figure 2. Field sampling design used in the planted and natural stands surveyed at the W. K. Kellogg Forest and Kellogg Biological Station, southwestern Michigan.

five 1-m^2 circular subplots (radius=.56 m). One subplot was placed at plot center, while the other four were located 3 m from plot center in each cardinal direction (Figure 2). Species, basal diameter and heights of tree seedlings within each subplot were recorded. In addition, species, presence and number of small trees, shrubs and ground flora characteristic of forest understories were recorded.

Light

Within each seedling subplot, percent light was determined at three levels below the canopy: ground level (LT0), at 2.5 m above the ground (LT25), and at 5.0 m above the ground (LT5). The understory layer was generally, though not always, less than 5.0 m in height. This allowed light intercepted by overstory, sapling, and seedling crowns to be differentiated. A Decagon sunfleck ceptometer was used for these measures. It has the capacity to make 80 simultaneous readings of incoming photosynthetically active radiation (PAR, 400-700 nm) at one sample point, and produce and store the average photon flux density ($\mu e \cdot cm^{-2} \cdot s^{-1}$) and time at each point. The utility and reliability of this instrument was tested by Pierce and Running (1988), and found superior to techniques that use a single photodiode moved quickly from point to point.

Sampling was completed during five cloudless days in a seven day period in August 1989. An average of three stands per day across the range of overstory types was measured for light intensity between 10:00 AM and 2:00 PM local solar time. Eight samples were taken within each subplot and at each height by extending the ceptometer out from the subplot center, rotating in a 360°circle, and stopping for a measure every 45°. The 2.5 m and 5.0 m measurements were made using a telescoping pole. Subplot averages were stored in the ceptometer's microcomputer along with the time each measurement was taken. A measure of full sunlight was also taken before and after sampling in each stand. From this information, full sunlight was estimated for each time recorded with a measure of understory PAR. Percent of full sunlight was then calculated for each light measurement taken at each height.

Soil

Soil samples were collected randomly from within each of the five subplots and composited for each .01 ha plot. Soil samples for measuring potential N mineralization and pH were obtained by removing 100 cm^2 x 5 cm deep soil cores, starting below the O1 horizon, or loose litter (L) layer. Shallow sampling is used to avoid "priming effects" as described by Salonius (1978), Thorne and Hamburg (1985) and Zak et al (1986). A priming effect can be defined as an acceleration of microbial activity stimulated by the introduction of less decomposed and more readily available organic matter into deeper soil horizons through mixing of a deep soil sample (Salonius, 1978). This can lead to an overestimation of net mineralizable N. Samples were placed undisturbed in polyethylene bags and placed in a cooler on ice until they could be refrigerated at 2°C. Laboratory analysis was initiated within 48 hours of sample collection.

Soil samples for moisture determinations were collected randomly within each subplot using a 1.5 cm diameter soil probe inserted to a 20 cm depth, again starting below the O1 horizon. All samples were removed between 10:00 AM and 4:00 PM during one day in July of 1989. A composite for each plot was obtained by combining subplot samples. Samples were then stored in polyethyelene bags and kept on ice in a cooler until they could be refrigerated. Soils were prepared and analyses begun within 48 hours of sampling.

Although there are obvious problems with using one measure in time to characterize a moisture regime for a forested stand, one can still compare stand values and get an impression of relative moisture holding capacity. It was presumed that the relatively dry climatic conditions which preceded this sampling would accentuate any stand differences in moisture holding capacity.

Distance to Potential Seed Source

As indicated earlier, the vast majority of Kellogg Forest had been cleared of trees for agriculture in the early to mid 1800's. However, older seed-producing trees were not infrequent in these early farmlands. Large individuals were often left in the center of pasture and fields to provide shade for farmhands and grazing livestock. Trees and shrubs were established and maintained along fencerows, which were a common feature in the landscape. In addition, the 2 large woodlots in the area, while providing lumber and firewood, also functioned as a repository for seeds of the native forest vegetation.

Potential seed sources for each sapling species found within the plantations and woodlots were located using a combination of aerial photographs taken in 1938, and maps produced during an intensive vegetation survey of the Kellogg Forest study area in 1940. All potential seed sources were visible using both sources of information, providing mutual verification of seed source location. In addition, the two information sources were complementary, in that the photographs provided an indication of tree size and therefore an inference of age, while the maps provided the species designations. Only those sapling species capable of becoming overstory dominants, and those species mentioned in the GLO survey notes for this area, were examined in this aspect of the study. Distance to the nearest potential seed source was measured from each plot center to the nearest edge of the seed source crown. Composition in 1930 of the Kellogg Forest woodlots was determined from early stand records, and the nearest woodlot edge was used as the nearest seed source when there were no closer individuals to be found. Plots in the oak-hickory woodlots were not examined for distance to seed source because most, if not all, sources of seed for sapling species present are located within the woodlots.

Laboratory Analysis

Potential Net Mineralizable Nitrogen

Potential net mineralizable nitrogen (NH_4^+-N) was determined using anaerobic soil incubation (Waring and Bremner, 1964, Powers, 1980; Keeney, 1982; Perry et al., 1987). This method was chosen over that of aerobic or *in situ* incubations due to its relative simplicity and because determinations of nitrification potentials were not within the realm of this study (Vitousek et al., 1982). The technique, developed by Waring and Bremner (1964), has met with mixed reviews as an index of actual N mineralization rates and nitrogen availability (Powers 1980; Keeney 1982; Myrold 1987; Padley 1989). However, Myrold (1987) suggests that this technique measures N mineralized from the microbial biomass and that microbial biomass N may represent a pool of readily available N for plant uptake. Padley (1989), in a review of techniques for measuring potential N mineralization, concludes that a measure of microbial biomass N would be an appropriate index of overall site potential.

In preparation for analysis, the field moist soil sample for each plot was thoroughly mixed and sieved, excluding material >2 mm but rubbing through fine roots. From the remaining plot sample material, six 10 g subsamples were removed for analysis of potential mineralizable nitrogen. Two subsamples were oven-dried to constant mass at 110°C for 24 hours in order to provide replication of the field moist to dry soil ratio needed for N-mineralization calculations. Another two subsamples were extracted using 40 ml of 2*M* KCl to measure initial levels of ammonium (Myrold 1987). The soil-KCl solution was shaken mechanically for 15 minutes, after which it was centrifuged for 5 minutes at approximately 5000 RPM (Perry et al. 1987). After settling, two 1 ml samples of the supernatant were pipetted into plastic technicon cups, capped, and stored refrigerated until analysis. The last two subsamples were placed into two plastic centrifuge tubes, and 20 ml of deionized water was added to each. The tubes were sealed with paraffin to ensure anaerobic conditions (Padley 1989), stoppered, and placed in an oven with a constant temperature of 40°C for 7 days. At the end of incubation, the samples were extracted with 20 ml of 4*M* KCl as outlined above and refrigerated. Initial and incubated deionized water assays were included as controls.

All soil samples were analyzed colorimetrically for NH_4^+-N using a Technicon Autoanalyzer II. Solution concentrations were determined based upon peak height, and then converted to ammonium concentrations. Potential mineralizable nitrogen is determined by the difference between the initial concentration of NH_4^+-N and the incubated concentration. As bulk density was not determined, all mineralization values are expressed in µg/g.

pH

Soil pH was determined using the method outlined by McLean (1982), involving a 1:1 soil-distilled water mixture and measurement by glass electrodes on a standardized pH meter. Two 10 g subsamples per plot were removed from the sieved samples used in the nitrogen assays for this purpose.

Soil Moisture

Gravimetric moisture determinations were made on the soil sample composites taken from 0-20 cm depth. The sample for each plot was thoroughly mixed, after which a 100g subsample was removed for analysis. The subsample was then oven-dried to constant mass at 110°C for 24 hours. The difference between dry and fresh weights divided by dry weight gives the proportion of moisture available within that range of depth at that one point in time (Robertson and Vitousek 1981).

Data Analysis

Overstory and sapling basal area per hectare, by species, was calculated for each plot and averaged for each of the 15 stands. Seedling dominance was characterized as numbers per hectare and averaged by species at the plot and stand levels. Potential mineralized N (MN), percent moisture (PM), percent light at each height (LT0, LT25, LT5), and pH were averaged for each stand.

Aspect was converted to a more ecologically meaningful value using the Beers et al. (1966) transformation. Means of slope (SLP) and aspect (ASP) were then calculated at the stand level.

There are several statistical hurdles that this study was unable to clear. These included adequate replication of stands, adequate sample size, and normality of the vegetation data. However, replication of plots within stands is sufficient to explore associations apparent in the data when the inference space is not larger than that over which the plots were distributed (Hurlbert 1984). In this study, inferences are restricted to Kellogg Forest and Kellogg Biological Station. The lack of suitable stands as replicates in the near vicinity prevents broader generalizations.

Resource levels and pH were analyzed at the stand level using analysis of variance; in this data, the "treatment" implies the stand classification, and is appropriate for assessing whether or not levels of these variables differ from stand to stand (Steel and Torrie 1980). In order to stabilize variance, soil moisture and light variables were transformed for this analysis using the Box-Cox family of transformations (Box et al. 1978). Fisher's protected LSD for unplanned comparisons was used to compare means (Steel and Torrie 1980; Feldman and Gagnon 1986). Univariate plots of resource levels and pH across stands, and bivariate plots of resources in relation to each other, were constructed to look for gradients and correlations of these variables. Spearman's coefficients of rank correlation were then determined for the untransformed variables. However, product-moment correlation coefficients were used in principal components analysis as it is a distribution-free method.

Principal components analyses (PCA) were run on resource and site data to reduce the dimensionality of these variables and to present a two-dimensional image of how stands are distributed in relation to linear composites of these variables. Biplots showing the position, in two-dimensional space, of the scaled eigenvectors for site variables and PC scores for stands were constructed to aid in interpretation. The correlation matrix was used in PCA because the variables were measured in different scales. Although this scaling procedure is somewhat arbitrary and does not solve scaling problems, it seems appropriate in this case because research has supported the relatively equal importance of these variables (Chatfield and Collins 1980). Two sets of site data were used in PCA: one set including the resource variables mineralizable nitrogen, percent moisture, and percent light at three heights, and another set consisting of the data just mentioned as well as pH, slope and aspect. More rigorous multivariate techniques, such as canonical correlation analysis, could not be applied because assumptions of multivariate normality, adequate sample size and equal covariance matrices would be violated (Morrison 1990).

Plots of sapling and seedling species distributions across stands and in relation to individual resources were constructed by ranking stands from low to high levels of a resource variable and then comparing the distributions. These distributions were based upon the dominance values for individual species: basal area/ha for saplings and number of stems/ha for seedlings. Relative dominance of saplings and seedlings were also compared to the PCA results using a graphical method devised by Curtis and McIntosh (1951). This provided a visual representation of species relationships to the linear composite of resources for both seedling and sapling classes.

Measures of central tendency were obtained for distances of potential seed sources to plot centers for the plantations. Plot distances were then compared with sapling species densities for those species native and common to the region in presettlement times. Due to various problems with the sapling density data, such as generally low frequencies and densities, unstable variances, and non-normal distributions, relationships between dispersal distances and sapling densities were analyzed nonparametrically. Distance data were divided into four classes, and then compared with presence data for each sapling species in order to detect trends or patterns relative to potential dispersal distance. The distributions of plot sapling densities across these distance classes, for each sapling species, were also examined. Chi-square goodness-of-fit analyses, by species, were performed using two distance classes: 0-100 m and >100 m. Pooling of classes was necessary in order to attain expected values of > 1.0, a necessity for this test (Box et al. 1978) although considered low by others (Sokal and Rohlf 1981). A uniform distribution of plots having a given species present across these two classes was tested, as other more meaningful distributions tended to produce expected values of < 1.0 for most species.

RESULTS

Presettlement Vegetation

Kenoyer (1929, 1934, 1940) has described the presettlement vegetation of Kalamazoo County using the survey notes of southwestern Michigan, He found this vegetation to be representative of six major associations: beech-maple (*Fagus grandifolia-Acer* spp.); oak-hickory (*Quercus* spp.-*Carya* spp.); swamp forests; oak-pine (*Quercus* spp.-*Pinus* spp.); bur oak (*Quercus macrocarpa*); and prairie. Beech-maple and oak-hickory types were the most prevalent in Kalamazoo County between 1826-1830. In addition, Kenoyer (1929) noted the presence of oak barrens or savannas scattered throughout the oak-hickory and bur oak types.

In the presettlement survey notes of the Kellogg Forest and KBS areas, the species of highest relative density was white oak at 75-80% (Table 3a,b). "Yellow" or chinkapin oak (*Quercus muehlenbergii*) and bur oak were also constituents in both areas. Elm (*Ulmus* spp.) and hophornbeam (*Ostrya virginiana*) were less frequent. Swamp forest vegetation was represented by tamarack (*Larix laricina*) and black ash (*Fraxinus nigra*).

The section line descriptions add insight into the general landscape and vegetation of both areas. The land was generally described as rolling or hilly, with "second rate" soil. Vegetation was often described simply as oak,

Table 3a. Kellogg Forest Presettlement Vegetation-1826.
T1S, R9W--Sections 21,22,27,28; 21 corners.

Bearing and Line Trees	Number of Individuals	Relative Density	Number of Points w/ Species	Frequency	Relative Frequency
Quercus alba	45	80%	19	90%	73%
Quercus velutina	3	5%	1	5%	4%
Quercus muehlenbergii	1	2%	1	5%	4%
Larix laricina	2	4%	1	5%	4%
Ostrya virginiana	2	4%	2	10%	8%
Ulmus spp.	2	4%	1	5%	4%
Fraxinus nigra	1	2%	1	5%	4%
TOTALS	56	100%		124%	100%

Table 3b. Kellogg Biological Station Presettlement Vegetation-1826
T1S, R9W--Sections 5,6,7,8, &1/2 of 4 & 9; 17 corners.

Bearing and Line Trees	Number of Individuals	Relative Density	Number of Points w/ Species	Frequency	Relative Frequency
Quercus alba	39	75%	15	88%	60%
Quercus muehlenbergii	5	10%	4	24%	16%
Quercus velutina	5	10%	3	18%	12%
Ulmus spp.	1	2%	1	6%	4%
Fagus grandifolia	1	2%	1	6%	4%
Acer saccharum	1	2%	1	6%	4%
TOTALS	52	100%		147%	100%

although more often bur, white and black oak were differentiated. The section lines in the eastern third of KBS were described as thinly timbered, suggesting an oak savanna. A comparison of the distance to corner and diameter, by species, between lines described as thinly timbered and those described as oak showed an almost two-fold increase in both variables for the thinly timbered lines, supporting the hypothesis of an oak savanna (Table 4).

Post Settlement Records

Kalamazoo County was first settled in the 1830's, and most of the area was immediately converted to farmland (Kenoyer 1929). The land was productive initially, and was used especially for corn at the turn of the century with the advent of the cereal business (Wright and Rudolph 1982). Woodlots were generally high-graded for lumber and firewood, as well as grazed by cattle and other livestock (Whitney 1987; W. Lemmien, personal communication). By the early 1900's, much of the land had eroded badly and farms were abandoned (Wright and Rudolph 1982). Between 1928-1931, W. K. Kellogg, who resided in the Battle Creek area, donated to Michigan State College parcels of worn out farmland which would become the Kellogg Biological Station (421 ha; 1928-1930) and the Kellogg Reforestation Tract (114 ha; 1931). Kellogg's goal in donating this land was to have it returned to productive status through reforestation and conservative farming practices (Wright and Rudolph 1982).

Between 1932-1940, most of the original Reforestation Tract was planted to trees, predominantly red, white and Scots pines (Wright and Rudolph 1982). However, as species was secondary to the reforestation mission, any species available was often planted, creating a remarkably

Table 4. Presettlement mean distances and diameters for species chosen as bearing trees, classified by line description, Kellogg Biological Station, southwestern Michigan.

	Lines described as "Thinly timbered"				
Species	No. Trees	Mean Distance To Post	Std. dev.	Mean Diameter	Std. dev.
		*links**		*inches †*	
Quercus alba	11.0	121.7	106.8	19.5	9.3
Quercus muehlenbergii	2.0	154.5	135.1	19.0	1.4
Quercus velutina	3.0	46.7	25.6	23.0	11.4
Other	0.0	0.0	0.0	0.0	0.0
All Species Present	16.0	111.8	100.3	20.1	8.8

	Lines described generally as "Oak"				
Species	No. Trees	Mean Distance To Post	Std. dev.	Mean Diameter	Std. dev.
		*links**		*inches †*	
Quercus alba	16.0	58.8	34.2	11.8	3.9
Quercus muehlenbergii	3.0	20.3	4.9	16.7	6.4
Quercus velutina	0.0	0.0	0.0	0.0	0.0
Other	3.0	40.0	24.1	8.7	1.5
All Species Present	22.0	60.0	33.1	12.0	4.4

	All Lines				
Species	No. Trees	Mean Distance To Post	Std. dev.	Mean Diameter	Std. dev.
		*links**		*inches †*	
Quercus alba	27.0	84.4	77.8	14.9	7.5
Quercus muehlenbergii	5.0	74.0	99.9	17.6	4.8
Quercus velutina	3.0	46.7	25.6	23.0	11.4
Other	3.0	40.0	24.1	8.7	1.5
All Species	38.0	76.6	75.0	15.4	7.6

* 1 link=0.2012 meter

† 1 inch=2.54 cm

diverse group of plantations. In most cases species were planted in what at that time appeared to be their most ecologically suitable environments (W. Lemmien, personal communication).

Research and demonstration were also missions for the new forest. R. H. Westveld and Merle Dieters were the first managers of the Reforestation Tract, and were responsible for the establishment of most of the stands surveyed in this study. Initial inventories, compartment descriptions, and planting records were recorded in detail by these two men. Walter Lemmien, who began his 41 year tenure as forest manager in 1941, also kept meticulous and detailed records of plantings and research carried out on the forest. This degree of documentation is very unusual to find, and provides a reliable account of disturbance and silvicultural manipulations operating over that span of time. In addition, an engaging history of Kellogg Forest can be found in a report by Wright and Rudolph (1982).

Kellogg Biological Station was donated to Michigan State College for the original purpose of demonstrating conservative farming practices. Consequently, much of the area is in active fields. However, an ecological reserve has recently been set aside, enabling the detailed study of old-field succession. This reserve includes fields that have been abandoned for as many as 40 years, as well as the woodlot, Long Woods, investigated in this study.

Natural Disturbance and Herbivory

Diaries and notes of each forest manager contain several references to natural disturbance at the forest. In 1931, severe defoliation in the woodlot oaks by June beetle (*Phyllophaga* spp.) was noted by the comment, "This insect has been particularly serious during the past two years...and this two year defoliation combined with the drought during the last few seasons on this upland area has caused the death of a considerable number of large oaks". In 1933, *Xenotemna pallorana* (Tortricidae) was introduced via nursery stock to the forest and was causing serious damage to the planted conifers by 1939. In 1938, the pine sawfly (*Neodiprion* spp.) and European pine shoot moth (*Rhyacionia buoliana*) were also causing damage, leading to the control of these insects by insecticides in 1939. In the 1950's, an increase in the size of the deer herd, although welcome, led to severe overbrowsing in the forest. Since 1960, hunting has been allowed to control the population, although evidence of browsing is still frequent today. A hard winter in 1976 and serious ice storm in 1982 caused extensive damage to plantation canopies, from which it appears several areas are still recovering. Although hard winters and ice storms obviously occurred between 1931 and 1976, they apparently were not as noteworthy as these.

Stand Descriptions and Histories

The following series of descriptions provides, when available, a history of disturbance and changes in composition for each stand. Histories were found in the notes and diaries of the forest managers, especially those of Walt Lemmien, and from personal communications with present and past forest staff. The section starts with the natural oak-hickory stands, and progresses through the remaining hardwood and mixed stands to the conifer plantations. In addition, Table 5 provides a summary of overstory, soil, and topographic characteristics found in these stands.

Table 5. Overstory, soil, and topographic characteristics of 15 planted and natural stands in the W. K. Kellogg Forest and Kellogg Biological Station, southwestern Michigan. All overstory values, except age, are means with standard errors in parentheses; n=3 for all stands. Dashes indicate basal areas of 0.

	STAND														
	DGF	EUL	LIR	OH1	OH2	OH3	POB	RP1	RP2	RXW	SP1	SP2	SXW	WP1	WP2
Overstory															
Age (yr)	50	52	50	124	>100	>50	54-57	52	51-53	54-57	51	50	54-58	54-56	52
Height (m)	15.9 (0.5)	18.3 (0.6)	28.2 (3.9)	19.5 (1.7)	20.3 (2.0)	20.3 (2.3)	25.8 (3.9)	21.1 (0.7)	20.0 (1.3)	24.1 (1.0)	23.1 (1.1)	19.3 (1.0)	25.1 (0.1)	25.9 (2.2)	23.4 (0.3)
Density (stems/ha)	1033 (353)	1233 (120)	500 (100)	633 (67)	433 (120)	500 (58)	400 (115)	800 (231)	1167 (203)	700 (115)	333 (88)	833 (120)	300 (58)	333 (67)	567 (88)
Total basal area (sq m/ha)	33.0 (9.7)	42.7 (1.54)	37.7 (7.5)	61.8 (15.7)	26.9 (14.7)	54.5 (27.4)	41.2 (9.3)	40.4 (8.1)	53.7 (6.1)	49.4 (7.1)	24.3 (3.6)	32.2 (3.1)	25.8 (5.1)	41.6 (8.0)	50.7 (2.5)
Species basal area (sq m/ha)															
Quercus rubra	-	-	-	18.4 (18.4)	4.0 (2.5)	38.7 (34.5)	6.0 (3.1)	-	-	-	-	-	-	-	-
Quercus alba	-	-	-	3.3 (3.3)	16.6 (16.6)	5.7 (5.7)	-	-	-	-	-	-	-	-	-
Quercus velutina	-	-	-	29.7 (2.8)	-	-	-	-	-	-	-	-	-	-	-
Acer rubrum	-	-	-	8.4 (6.9)	1.5 (0.3)	2.4 (1.5)	-	-	-	-	-	-	-	-	-
Carya glabra	-	-	-	2.0 (2.0)	-	7.7 (3.8)	-	-	-	-	-	-	-	-	-
Prunus serotina	-	-	-	-	4.4 (3.5)	-	-	-	-	-	-	-	-	-	-
Ulmus americana	-	-	-	-	0.4 (0.4)	-	-	-	-	-	-	-	-	-	-
Liriodendron tulipifera	-	-	37.7 (7.5)	-	-	-	-	-	-	-	-	-	-	-	-
Tilia americana	-	-	-	-	-	-	4.8 (2.8)	-	-	-	-	-	-	-	-
Pinus strobus	-	-	-	-	-	-	30.4 (10.3)	-	-	14.4 (10.1)	-	-	7.7 (5.0)	41.0 (7.5)	50.7 (2.5)
Pinus sylvestris	-	-	-	-	-	-	-	-	-	-	24.3 (3.6)	32.2 (3.1)	18.1 (5.5)	0.6 (0.6)	-
Pinus resinosa	-	-	-	-	-	-	-	40.4 (8.1)	53.7 (6.1)	35.0 (6.7)	-	-	-	-	-
Larix decidua	-	42.7 (1.5)	-	-	-	-	-	-	-	-	-	-	-	-	-
Pseudotsuga menziesii	33.0 (9.7)	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Soil type 1/	Os	Oc	Oc	Sp, Oc, Os	Os, Fx	Fx	Oc	Os	Os	Os, Hi	Os	Os	Oc	Os	Oc
Topographic characteristics															
Elevation (m)	277	256-262	259-262	274-290	262-274	274-283	253-259	259-265	274-286	271-286	274-280	262-271	256-262	262-265	277-280
Position 2/	us	ls	lp, ls	us, hp	lp, ls	lp, ls, ms	lp, ls	ls, ms	ls, us, hp	ls, ms, us	ms, us, hp	ls, ms	lp	ls, ms	hp
Slope (%)	8-13	4	2-5	3-15	0-5	0-6	2-12	6-7	3-23	4-10	0-16	11-17	2-3	10-13	0-2
Aspect	SW	SW, W	W	S, NW	E, SE	NE, W	W	SW, W	W, NW	SW, W	E, SE	SE, SW	NW	N, E, SE	S

1/ Os, Oshtemo; Oc, Ockley; Sp, Spinks; Fx, Fox; Hi, Hillsdale.

2/ lp, low plateau; hp, high plateau; ls, low slope; ms, midslope; us, upperslope.

Oak-Hickory 1 (OH1)

This stand, located in Compartment 10 of the forest, has had a long history of use. Covering 18 ha, this woodlot has provided firewood, lumber, and research material for at least the last 60 years. In 1931, an area of approximately 11 ha in the western two-thirds of Compartment 10 was covered with mature trees. The remainder of this stand was dominated by sapling and pole-size trees as a result of clearcutting undertaken within the previous 20-30 years. An inventory taken in 1931 noted the dominant presence of red, black and white oaks, and hickory in the woodlot. Black cherry and red (soft) maple were also noted as occasional dominants, while aspen (*Populus* spp.), sassafras, white ash, sugar maple, and dogwood were noted as common components of the understory and disturbed areas. Some cutting in the mature timber was done in 1931, primarily to remove dead and defective trees, and "inferior" species such as sassafras, aspen, and dogwood; red maple was removed when it interfered with the growth of oak.

In 1954, a hardwood regeneration study was initiated in the mature forest which involved several silvicultural manipulations conducted every five years until 1987. Four 0.4 ha rectangular control plots of undisturbed vegetation were also established at this time for the duration of the study. In 1987, an oak regeneration study was initiated overlaying the layout of the original study. This study involved removal of overstory trees except in the control plots, effectively shrinking the area of undisturbed, mature forest available for sampling to 1.6 ha spread over four patches.

The three plots for my study were randomly located in the control areas of the oak regeneration study, one plot per area. As can be seen in Table 5, there is variability in soil series and topography that was unavoidable due to location of the control areas. It is also clear from Table 5 that species composition and dominance in Compartment 10 have not changed substantially over the past 60 years.

Oak-Hickory 2 (OH2)

This stand, located in Compartment 22B, is a small 2.5 ha woodlot that has been relatively undisturbed since 1954. Purchased in 1939, a cruise of the woodlot in 1942 found it dominated by red, black and white oaks, shagbark hickory, red maple, and black cherry. All of these species were well represented in the larger diameter classes (> 30 cm dbh). Surprisingly, the largest volume tallied was for black cherry, followed by red maple and then the oaks and hickory. Slippery elm (*Ulmus rubra*) was also represented in the woodlot. This area has seen limited tree removal, primarily dead trees, and was set aside as a natural area in 1954.

The stand composition today is similar to what it was in 1939 (Table 5). It does appear that canopy gaps are more frequent now; one plot had a basal area of only 5 sq m/ha due to the presence of a recently dead black oak 76 cm in dbh that dominated the plot. Unlike OH1, witch hazel (*Hamamelis virginiana*) and maple-leaf viburnum (*Viburnum acerifolium*) are common in the understory. The oaks, mostly black and white, are often quite large, and vertical stratification is becoming less defined in this stand. OH2 is located in a more mesic part of Kellogg Forest than OH1, and appears to be somewhat sheltered as well (Table 5). Higher site quality is also indicated by the average canopy height of 33 m, which is much greater than that of OH1 (Table 5).

Long Woods (OH3)

This 10 ha stand, located at KBS, has a less well documented history than the other oak-hickory stands. It is known that grazing of livestock had been allowed in the woodlot up to the early 1960's, and that there was occasional cutting of trees for firewood and building supplies. Aerial photos for 1938 also indicate that the eastern half of the woodlot had recently been clearcut, while the western half appeared relatively contiguous. Indications of grazing, such as the abundance of barberry (*Berberis thunbergii*) and Japanese rose (*Rosa multiflora*), are prevalent in the northern half of the original forested portion of the woodlot.

The composition of this woodlot is predominantly oak-hickory, although stand characteristics varied considerably from plot to plot (Table 5). Plot 1 was located in a mesic area in the southern portion of the woodlot, and was dominated exclusively by very large red oaks having an average canopy height of 32 m and dbh > 50 cm. Plot 2 was located farther north, and had indications of previous grazing from the thorny ground flora. Here, pignut hickory and white oak were more common, and the average canopy height was shorter than Plot 1 at 26 m. Plot 3 was located to the east in the younger forest, where canopy height was even shorter at 20 m, and canopy dominants included smaller pignut hickory, red oak, and red maple.

Tulip Tree (LIR)

This 0.8 ha plantation was established in 1939, and has a linear configuration, barely making the width criteria for stand selection. Located in Compartment 22C, it is adjacent to OH2, and resides in the same mesic sheltered location as that stand (Table 5). Ground cover at the time of establishment included mixed grass, dewberry (*Rubus flagellaris*), and Canada thistle (*Cirsium arvense*). Disturbance in this plantation has been intermittent, consisting of selection thinnings in 1969 and 1971. Although this appears to violate disturbance criteria, disturbance to the stand appeared minimal, and there were plenty of seedlings and saplings of all sizes present. Average canopy height at 32 m is substantial for a 50 year old plantation, although not unusual for tulip tree on a mesic site (Table 5).

White Pine-Red Oak-Basswood (POB)

Located in Compartment 13C, this 1.7 ha plantation is perhaps the most interesting because of the unusual species mix planted. This stand was established between 1932-1935 with an 8 x 8 foot spacing (2.4 m) of species planted in alternate rows. For three years prior to planting, the site had been in hay; previous to this the area had been in cultivation for many years. Ground flora at the time of establishment consisted of a heavy cover of Canada thistle, timothy (*Phleum pratense*), and other grasses. By the 1940 vegetation survey, Queen Anne's Lace (*Daucus carota*) had gained considerable dominance. The survey also noted the occurrence of maple, hickory, and elm seed trees within the stand boundaries. This stand has been undisturbed since establishment.

Topographically, the stand occupies a generally west-facing, middle to low slope (Table 5). In all but one plot, each species planted was represented. However, white pine appears to be larger in diameter and height than the other components of the overstory, especially towards the lower part of the slope (Table 5). The low to flat slope portion of the stand also has an extensive ground cover of Virginia creeper (*Parthenocissus quinquefolia*) with an abrupt edge to the east as the slope steepens.

Scots Pine-White Pine (SXW)

This 2.8 ha plantation in Compartment 4A occupies a very gentle northwest slope (Table 5), close to Augusta Creek. The northwestern half of the stand closest to the creek grows on a Sleeth soil, which belongs to a different taxonomic family, and was therefore avoided in sampling. The stand was established between 1931-1935 using an 8 x 8 foot spacing for white pine and a 6 x 6 foot spacing for Scots pine. The last crop grown on the site was wheat (*Triticum aestivum*) in 1929. The area was seeded to timothy and clover (*Trifolium* spp.) immediately after the wheat harvest, with the last cut for hay in 1931. Prior to planting, the sod cover was approximately 40%. The 1940 vegetation survey showed a ground cover of clover, grass, and daisy fleabane (*Erigeron annuus*), as well as seed trees of oak, hickory, cherry, elm, basswood, and sugar maple within or on the edges of the stand.

In 1948, a thinning and pruning study was initiated that lasted until 1951 when the last cut was made. In 1958, a survey of the stand indicated advanced reproduction of red and sugar maple, black cherry, white ash, basswood, elm, and oak. Recommendations were to allow for a natural conversion to hardwoods. Therefore, in 1962, a selection thinning was performed in this stand to remove poor individuals of all species, leaving vigorous pine and hardwoods. In addition, open areas were planted to tulip tree to provide a future seed source, although none were observed while sampling. The plots studied in this research indicate that white pine, although infrequent in the overstory, is quite vigorous, and has grown to considerable height (Table 5). The Scots pine is present in larger numbers, and also has grown quite tall, combining with white pine for an average stand height of 25.1 m.

Red Pine-White Pine (RXW)

This 3.8 ha stand, comprising all of Compartment 7, occupies a steep, irregularly broken west slope (Table 5), with severe erosion from the 1930's still evident in places. The plantation was established between 1933-1935 using an 8 x 8 foot spacing. Although the area was in pasture before being planted, ground cover was described as sparse, consisting of mostly sorrel (*Rumex acetosella*) and june grass (*Poa pratensis*) with patches of goldenrod (*Solidago* spp.) (Rudolph and Lemmien 1955). By 1940, the ground cover hadn't changed much except for the appearance of poverty grass (*Danthonia spicata*). A wide fencerow of aspen, sassafras, and oak was noted along the eastern stand edge.

After a selection thinning in 1956, an ongoing thinning study was initiated in which permanent plots, including control plots, were established. The study was stratified by three slope positions, with two controls in each stratum. This allowed for the random location of my study plots within these controls, although it also necessitated spreading the plots out across a slope gradient. The slope gradient also reflects a gradient in size and species dominance, with the steep upper slope and midslope having smaller sizes and red pine dominant, while the lower slope has larger white pine dominant. The mean stand basal area does appear to reflect the greater relative success of red pine on this site as compared to white pine, although the mean stand height is likely biased upwards by the much taller white pine on the lowslope (Table 5). In 1964, a reproduction survey noted the overwhelming abundance of white pine seedlings (average of 102 per milacre plot), while a few individuals of black cherry, sugar maple, sassafras, red maple, and oak were also counted.

Red Pine 1 (RP1)

This 5.1 ha plantation in Compartment 8A, established in 1937 using a 6 x 6 foot spacing, occupies a rolling but gentle southwestern facing slope which continues on to Augusta Creek (Table 5). The 1940 survey shows mixed grasses and poverty grass as dominant, but interspersed with patches of 7-finger (*Potentilla recta*), goldenrod, and sandbur (*Cenchrus* spp.). Hawthornes (*Crataegus* spp.) and hazelnut (*Corylus* spp.) were noted in the area, as well as a large oak at the northern edge of the stand surrounded by a wide circle of oak reproduction. In 1960, a thinning study was initiated throughout most of the stand, although some areas were left undisturbed in addition to controls. Plots for this study were located in these unthinned areas.

Red Pine 2 (RP2)

Established between 1936-1938, this 3.4 ha plantation in Compartment 9 consists of red pine with a 6 x 6 foot spacing, occupying the northwest, west, and south faces of a southwest-oriented ridge (Table 5). Erosional gullies from the 1930's are still evident, and the stand has a very xeric appearance. The ground cover at the time of establishment and in 1940 consisted of a sparse covering of mixed grass with scattered patches of 7-finger. The only occurrence of juniper (*Juniperus* spp.) noted in the 1940 vegetation survey was in this plantation. In addition, several black cherries, and an occasional hickory and oak seed tree were found within stand boundaries.

The thinning study initiated in 1960 for RP1 also involved this plantation. However, most of the plots occurred on the lower slopes of this stand, leaving a relatively steep but large area of unthinned pine on the upper slopes. There is also a low, somewhat protected area in the northern third of the plantation having a northeast-southwest orientation. Within this gully one can find scattered about several large black cherries, presumed to be natural, and a few large tulip trees, the origin of which is uncertain but probably planted from stock. Two of the plots for this study are located in the pine on the upper slopes, one at the top of the slope and another on the steep midslope; the third is on a low slope, near but not in the gully, randomly placed in a control plot. There is a decrease in red pine basal area as one moves downslope, with a corresponding slight increase in canopy height (Table 5). Again, as in the RXW stand, choosing plots perpendicular to the slope gradient was necessitated by the lack of enough undisturbed plantation at any one topographic position.

European Larch (EUL)

This plantation, located in Compartment 9, was established in 1937 at the foot of the ridge which extends into RP2, and is generally flat in slope and narrow in width (Table 5). Approximately 1 ha in size, the area was planted with European larch at a 7 x 8 foot spacing, in north-south oriented rows. Ground cover at the time of establishment consisted of mixed grasses, with scattered patches of dewberry, goldenrod, and poverty grass, and two hawthornes. In 1966, thinning plots were established within the plantation. The control plots for the thinning study provided a relatively undisturbed location for my plots. Larch basal area is relatively uniform in the stand, as is height (Table 5). However, common buckthorn (*Rhamnus cathartica*) is especially prevalent in the sapling size classes in this stand, with an average of 2000 stems/ha.

Douglas-Fir (DGF)

This 1.1 ha plantation was established in 1939 at a dense spacing, and is located in the center of Compartment 22A. This irregularly shaped stand occupies the southwest face of a slight ridge, and has a relatively gentle slope (Table 5). The dominant ground cover of this area in 1940 was poverty grass, with patches of 7-finger and blue joint grass (*Calamagrostis canadensis*). On the western edge of the plantation was a small patch of undisturbed vegetation consisting mostly of oaks, black cherry, hickory and red maple. This plantation has not been disturbed since planting. Although relatively uniform in diameter and height (Table 5), there is some mortality of Douglas-fir presumably due to competition. This has allowed patches of sunlight into the stand, although the dead trees remain standing with many of their fine branches intact.

Scots Pine 2 (SP2)

To the south and east of DGF, this 1.2 ha plantation in Compartment 22A was established in 1939 around the brow of the southeast-oriented ridge that extends through DGF. The southeastern slopes are relatively steep, as compared to the southwestern slopes (Table 5). Dominant ground cover in this area during planting was poverty grass, with patches of sandbur, sumac (*Rhus* spp.), and dewberry. Although a selection thinning was noted to have taken place in 1973, I could find no clear indication of the location in records or in the field; the understory was also quite vigorous and well distributed over diameter classes. Plot 2 in this stand was unusual in that several of the Scots pine occurring there had damaged or dying crowns, and light penetration to the understory was considerable. It is likely that this damage was caused by the 1982 ice storm.

Scots Pine 1 (SP1)

The remaining three stands occur in the portion of Kellogg Forest west of Augusta Road. This region of the forest is a little different from the eastern part, in that it consists of an extensive plateau surrounded by steep, often irregular slopes. Several steep erosional gullies from the 1930's add to this irregularity. SP1 covers approximately 0.8 ha in Compartment 21, and was established in 1938 at a 6 x 8 foot spacing. Slopes in this plantation vary from flat to steep, while aspects vary from north to southeast (Table 5). The 1940 survey shows 7-finger as the dominant ground cover, and a fencerow along the western edge consisting of hawthorne, cherry, and sassafras. A mature hickory and white oak were nearby as potential seed sources. A selection thinning took place in the western and southern portions of the plantation in 1980, and these areas were avoided for sampling. This plantation had the lowest mean basal area of all stands, although it appeared quite uniform in distribution (Table 5).

White Pine 1 (WP1)

This 2.8 ha plantation was established between 1933-1935 at an 8 x 8 foot spacing in Compartment 18. The site includes a lower flat and slope with a generally east and northeast exposure (Table 5). The steeper portions of this slope were described in 1933 as having lost much of the surface soil through erosion, and having patchy grass cover. The lower slope and flat were described as relatively fertile with a uniformly dense June grass sod. By 1940, the herbaceous vegetation was dominated by timothy, poverty grass, and blue grass, with patches of dewberry and 7-finger. Cherry, sassafras, hawthorne, and dogwood were noted along the fencerows surrounding the area. A portion of the eastern edge of the plantation was removed when Augusta Road was widened. Otherwise, disturbance to this stand has been minimal. White pines in the study plots are relatively uniform in size with a moderate basal area (Table 5); slopes are also similar among plots.

White Pine 2 (WP2)

This stand sits on top of the plateau described earlier for this portion of the forest. Established in 1937 in Compartment 20A, this 0.5 ha plantation has a 6 x 8 foot spacing of white pine with virtually no slope or aspect (Table 5). The ground cover during planting was June grass and timothy. By 1940, the entire plateau was described uniformly as mixed grasses with goldenrod and yarrow (*Achillea millefolium*). A selection thinning was done in 1975, although there was no indication of cutting in the areas where the plots were located. Although basal area for this stand is the fourth largest, canopy height is less than that of the other stands with white pine as a dominant (Table 5).

Resource/pH Gradients and Correlations

Gradients in pH, moisture, mineralizable nitrogen, and light in each stand are given in Figure 3. Results of ANOVA and multiple comparison tests are also displayed. Moisture and light data were transformed in order to stabilize their variances, and statistical tests were then performed on these data. Multiple comparisons of means for each variable showed significant differences for soil-based resources and light levels. Ranges for each variable were generally substantial: soil moisture ranged from 6.8 to 21.5%; mineralizable nitrogen ranged from 42.9 to 123.8 μg/g; and light ranged from 0.4 to 6.9% at 0 meters, 0.6 to 17.1% at 2.5 meters, and 1.9 to 22.5% at 5 meters. A more subtle gradient in pH from 4.8 to 6.7 was also detected. There are several patterns worth noting in Figure 3. Stands OH1, OH2, OH3, and LIR grouped consistently at the high end of the N, moisture, and pH gradients. RP1 and RP2 grouped together towards the low end of the pH and moisture gradients, while DGF and EUL grouped close together at the low end of the moisture and N gradients. SP1 and SP2, alternatively, grouped together in the middle of the pH and N gradients. The remaining conifer stands did not appear to show a consistent pattern in relation to these soil variables.

Along the light gradient, there were also consistencies among stands across the range of heights at which light was measured. However, there was considerable variability among plots for this resource (Figure 3 D,E,F). One clear pattern is that WP1 and WP2, along with SXW, always group very close together at the low end of the gradient. This is not surprising given the relatively deep crowns and large heights of the white pine in these stands. The hardwood stands were variable in their position along the gradient,

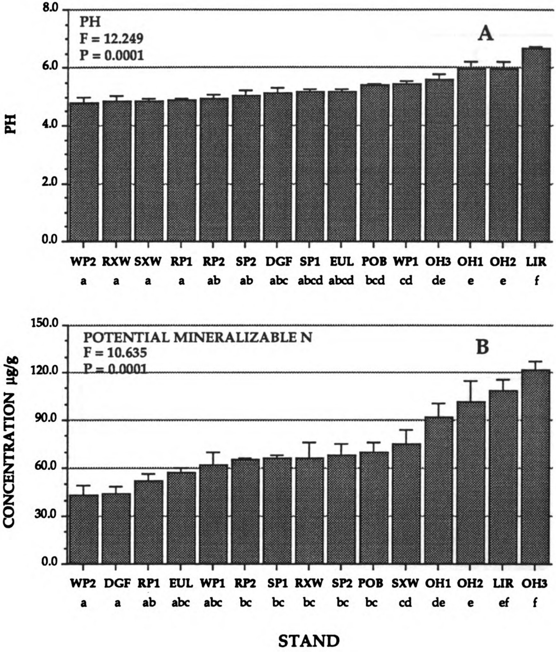
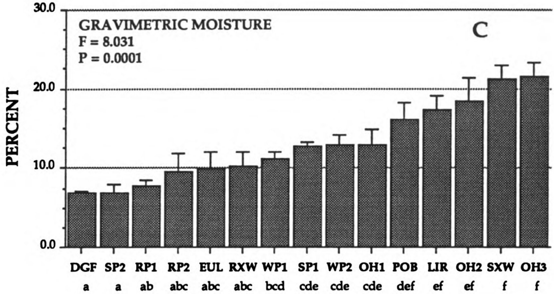


Figure 3. Levels of pH and resources for 15 stands in the W.K. Kellogg Forest and Kellogg Biological Station, southwestern Michigan. Columns represent the mean of three plots with standard error bars of 1 unit above the mean. Stands associated with the same letter are not significantly different (alpha=0.05). For figures C-F, ANOVA results are based upon data transformed in order to stabilize variance.



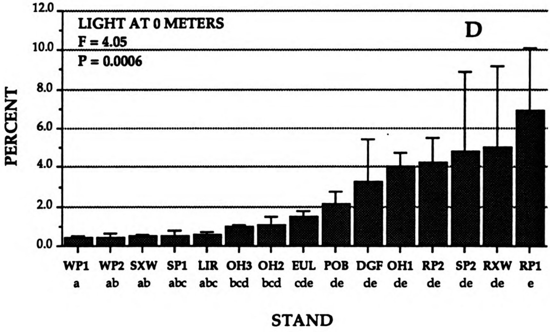


Figure 3 (cont'd.).

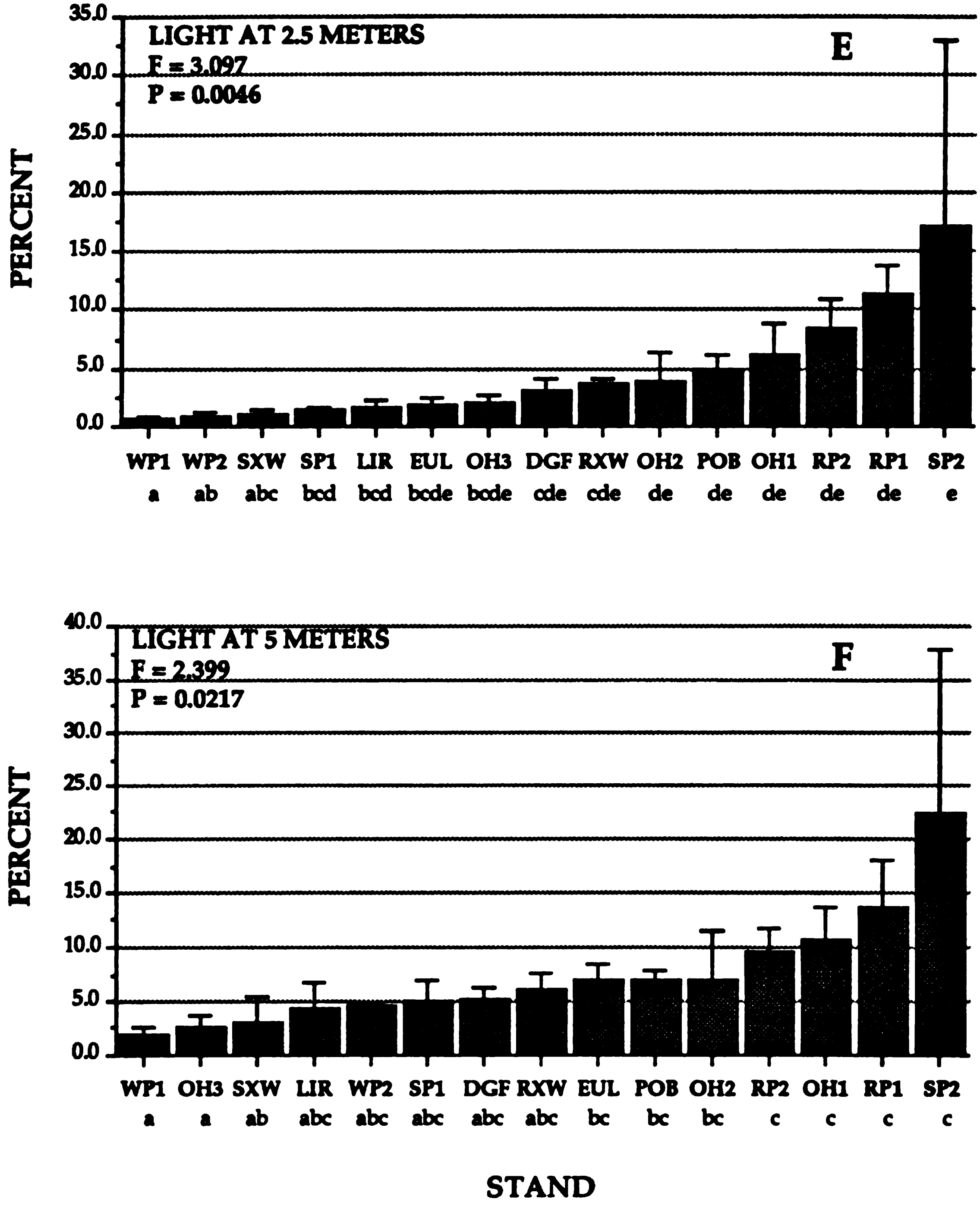


Figure 3 (cont'd.).

although OH3 and LIR always had the least light available of the hardwood group. RP1, RP2, and SP2 tended to group together near the high end of the light gradient. SP2 is a special case, as mentioned earlier, due to one plot with considerable crown damage which allowed for an increase in light penetration. If this plot had been removed from consideration, the two Scots pine stands would then group together at a lower point along the light gradient.

Spearman's rank correlation analyses were run and bivariate plots created using the 15 possible resource-pH pairs (Figure 4). The high positive correlations of light measured at various heights are not unexpected. What is apparent from the plots involving light is the existence of one strong outlier at the high end of the light spectrum. One stand, SP2, was mentioned earlier as having one plot with very high light levels at 2.5 and 5.0 meters. This stand is important because it provides a means of assessing other variables under high light conditions, which could be important for successional dynamics in plantation forests. Increases in mineralizable nitrogen were significantly correlated with increases in both soil moisture and pH, while decreases in soil moisture were significantly correlated with increases in light at 0 meters; pH was found to be unassociated with both soil moisture and light (Figure 4). The plots of moisture against light at three heights also suggest a curvilinear relationship between these two resources.

PCA of Site Variables

Although it is the level of essential resources to which plants will respond, it is often the case that other site variables, such as slope, aspect, and pH, are significantly correlated with resources. An increase in slope will

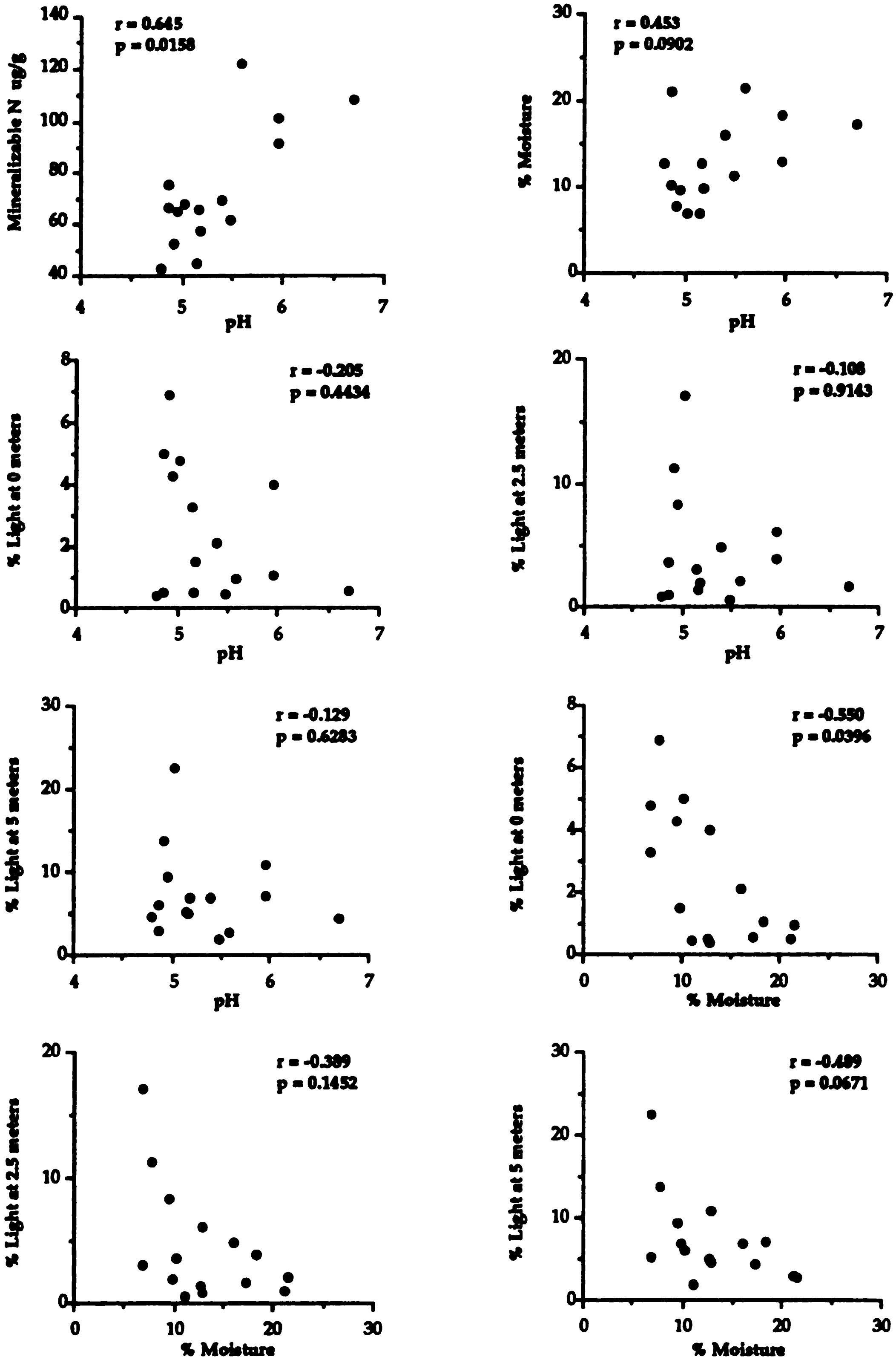


Figure 4. Bivariate plots and Spearman's coefficient of rank correlation of resource variables and pH for 15 stands at the W.K. Kellogg Forest and Kellogg Biological Station, southwestern Michigan.

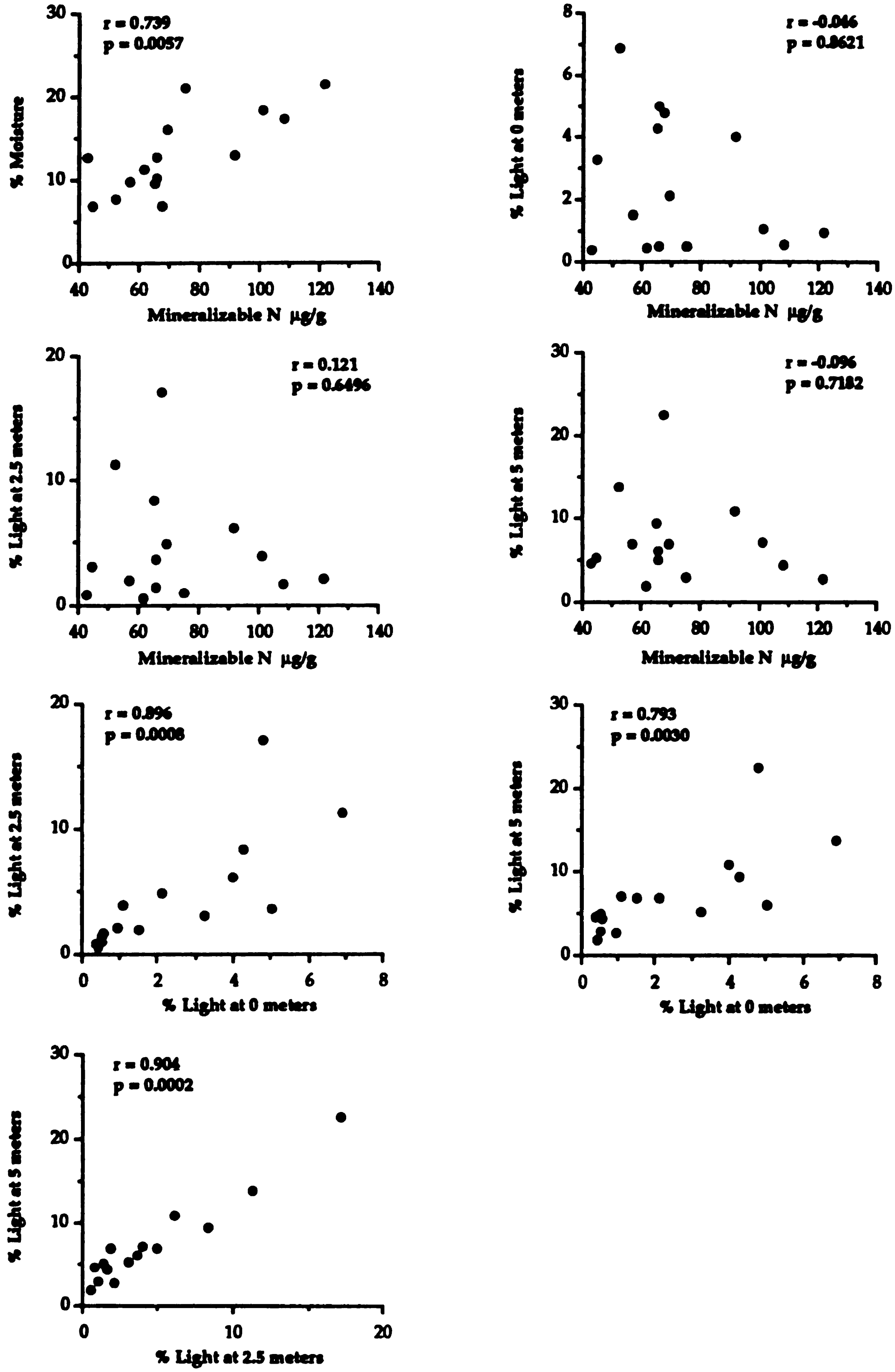


Figure 4 (cont'd).

sometimes increase drainage and lead to less moisture availability, while southwestern aspects expose sites to higher light levels for longer periods of time, often resulting in lower moisture. In addition, pH may also influence microbial activity, which in turn affects nitrogen availability; this relationship is supported by the significance of the previous correlation of pH with mineralizable nitrogen. Therefore, principal components analyses (PCA) of two data sets, one with resource variables, and one with resources as well as slope, aspect, and pH, were run to determine if the addition of these other site variables would help in understanding the ordination of stands with respect to resources.

PCA of Resources

A PCA was run using the product-moment correlation matrix for soil moisture, mineralizable nitrogen, and light (Table 6). The correlation coefficients are based on the untransformed data because PCA does not require multivariate normality. The PCA indicates that 90% of the variability present in the data set can be attributed to the first two PC's (Table 7). Using Joliffe's (1986) suggestion, I have ignored the PC's with eigenvalues < 0.7,

Table 6. Correlation matrix used in PCA for the untransformed resource variables mineralizable nitrogen, soil moisture, and light.

	Variable			
Variable	Nitrogen	Moisture	Light at 0 m	Light at 2.5 m
Moisture	0.738			
Light at 0 m	-0.289	-0.650		
Light at 2.5 m	-0.127	-0.514	0.777	
Light at 5 m	-0.169	-0.546	0.716	0.966

Table 7. Eigenvalues, their proportion of explained variance, and their associated eigenvectors for PCA of resource correlation matrix.

Variable	Component (Eigenvector) 1	2	3	4	5
Moisture	-0.4558	0.4302	-0.0700	0.7693	0.1031
Nitrogen	-0.2727	0.7458	0.2485	-0.5546	-0.0104
Light at 0 m	0.4588	0.1156	0.8056	0.2746	0.1618
Light at 2.5 m	0.4912	0.3719	-0.2570	0.1571	-0.7278
Light at 5 m	0.4907	0.3271	-0.4672	-0.0230	0.6583
Eigenvalue	3.2794	1.2439	0.3046	0.1477	0.0244
% of variance	0.6559	0.2488	0.0609	0.0295	0.0049

which leaves the first two PC's for this analysis. The first PC accounted for greater than 65% of the variability in the data set, and appears to represent a contrast between soil moisture and light. The eigenvectors for light at each height level were almost identical in the first PC, suggesting that either an average across levels or any one height level would be a sufficient characterization of this resource. Percent moisture was assigned a larger eigenvector than mineralizable N for the first PC, indicative of its greater importance in that side of the contrast. The second PC accounted for an additional 25% of the variability, and emphasized the importance of mineralizable nitrogen, as evidenced by the large eigenvector for this variable (Table 7). This PC could be interpreted as a weighted average across all resources with heavy weight given to mineralizable nitrogen.

A biplot of the first two PC's, based on stand scores and scaled resource coefficients, provides a visual representation of stand relationships to resources (Figure 5). Those stands with high soil moisture and low light

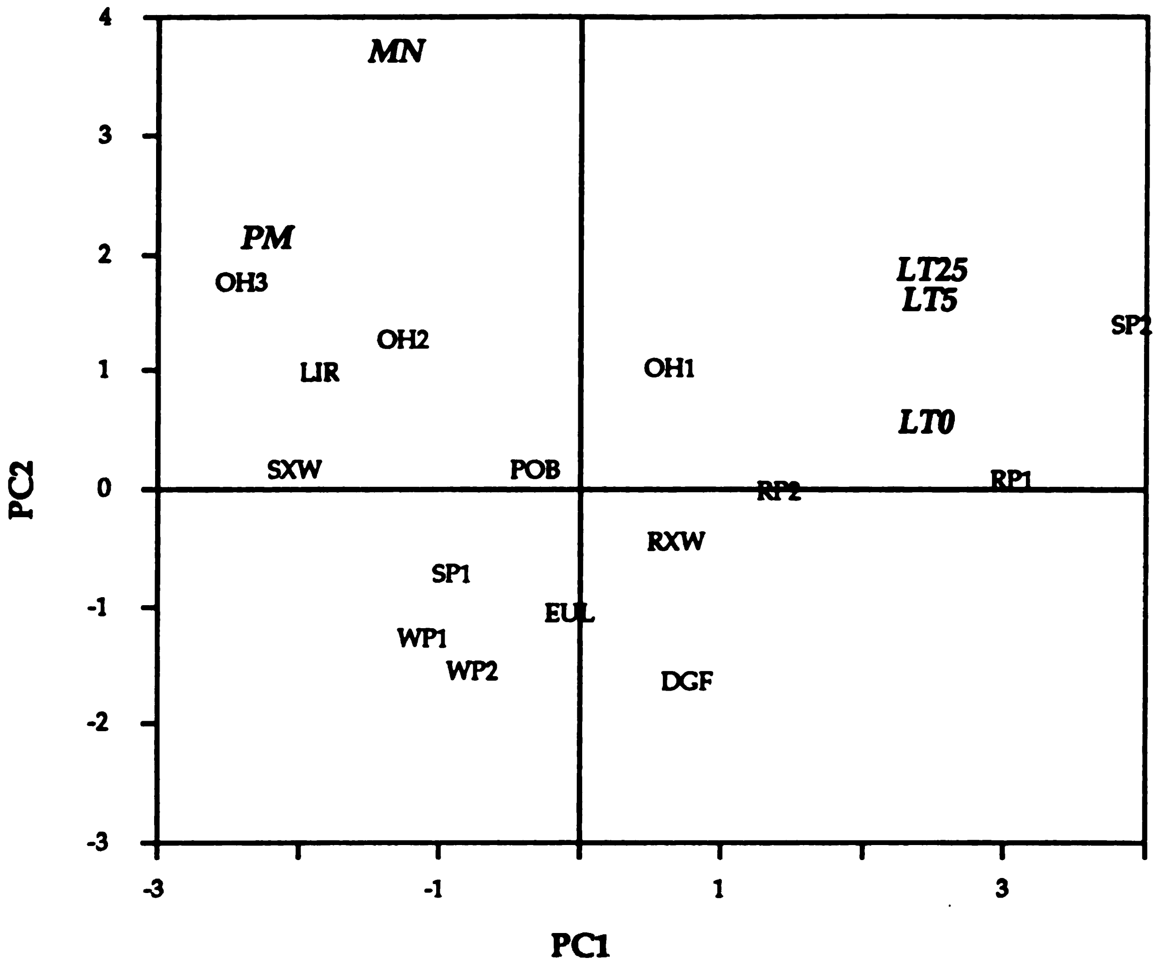


Figure 5. The relationship between the distribution of stands and the first and second principal components for resource variables. Scaled eigenvectors for each variable are also plotted: PM, percent moisture; MN, mineralizable nitrogen; LT0, light at 0 meters; LT25, light at 2.5 meters; LT5, light at 5 meters.

group to the left side of the plot, while those with high light and low soil moisture fall to the right. The second axis further separates the stands based primarily upon an average resource gradient dominated by nitrogen. Those stands with high mineralizable nitrogen (or high light in the cases of RP1 and RP2) gather in the upper half of the plot, while those stands with low levels of mineralizable nitrogen and other resources are found in the lower half of the plot.

Stands did not tend to form distinct clusters in this biplot; rather, they were distributed somewhat evenly across both axes. However, three general groups of stands can be discerned. The first consists of the Scots pine stand SP2, and the two red pine stands RP1 and RP2, all with generally high light levels and low soil resource levels (Figure 5). The second group consists of all the hardwood stands (OH1, OH2, OH3, and LIR), as well as the mixed hardwood-conifer stand POB and the mixed conifer stand SXW. These have in common generally low to moderate light levels and high soil resource levels. The third group includes the mixed conifer stand RXW, the larch stand EUL, the Scots pine stand SP1, the Douglas-fir stand DGF, and the two white pine stands WP1 and WP2. These stands can be classified as having generally low levels of all resources. This ordination of stands suggests that by planting hardwoods, hardwood-conifer mixtures, or a combination of different conifers, soil fertility has been enhanced more so than by planting any one conifer species alone.

PCA of Resources, pH, and Topographic Variables

Principal components analysis was also run on resource and other site data together using the product-moment correlation matrix (Table 8). Spearman's rank correlations of the new variable combinations were performed and, not unexpectedly, significant correlations were found between soil moisture and slope (Spearman's r = -0.654, p = 0.0144), soil moisture and aspect (Spearman's r = 0.563, p = 0.0350), and between light at 0 meters and aspect (Spearman's r = -0.688, p = 0.0101). The Beers aspect transformation used on the aspect data allocates the highest values to NE aspects, where growing conditions tend to be more favorable, while SW aspects have the lowest values.

In this PCA, the first three components have eigenvalues > 0.7 and together account for 85% of the variability in the data set (Table 9). Again,

Table 8. Correlation matrix used in PCA for the untransformed resource variables and pH, aspect, and slope.

	Variable						
Variable	pH	Nitrogen	Moisture	Light at 0m	Light at 2.5m	Light at 5m	Aspect
Nitrogen	0.757						
Moisture	0.455	0.738					
Light at 0 m	-0.345	-0.289	-0.650				
Light at 2.5 m	-0.232	-0.127	-0.514	0.777			
Light at 5 m	-0.208	-0.169	-0.549	0.716	0.966		
Aspect	0.240	0.440	0.550	-0.641	-0.322	-0.333	
Slope	-0.180	-0.307	-0.684	0.532	0.551	0.513	-0.123

Table 9. Eigenvalues, their proportion of explained variance, and their associated eigenvectors for PCA of resource and site correlation matrix.

Variable	Component (Eigenvector)							
	1	2	3	4	5	6	7	8
pH	-0.2516	0.4977	-0.1948	0.5959	-0.3589	-0.1555	0.3779	-0.0124
Moisture	-0.4228	0.1846	-0.1019	0.3784	0.2813	0.5158	0.5048	0.1828
Nitrogen	-0.2924	0.5888	-0.1038	0.0299	0.3538	-0.0306	-0.6545	-0.0419
Light at 0 m	0.4192	0.1694	-0.2598	0.0394	-0.1440	0.1328	0.1553	-0.7229
Light at 2.5 m	0.3884	0.3994	0.0467	0.3199	0.5763	-0.5008	0.3313	0.1839
Light at 5 m	0.3853	0.3759	0.0358	0.2978	-0.4459	0.0992	-0.1122	0.6317
Aspect	-0.2960	0.1459	0.7593	0.2392	-0.0207	-0.4789	0.1635	0.0276
Slope	0.3310	0.1440	0.5416	-0.5010	0.3389	0.4485	0.0293	0.0919
Eigenvalue	4.3088	1.6208	0.9055	0.6831	0.3028	0.1101	0.0498	0.0191
% of variance	0.5386	0.2026	0.1132	0.0854	0.0378	0.0138	0.0062	0.0024

using Joliffe's (1986) suggestion, I will only consider these three components in discussion. The first two PC's explain a majority (74%) of the variation in the data set. The first PC, accounting for 54% of the variation, represents a contrast between soil resources, primarily moisture, and light, as in the previous PCA. However, added to the soil resource side of the contrast are pH and aspect, while slope was added to the light side of the contrast. The second PC again appears to represent a composite or average of all variables, and accounts for an additional 20% of the variation in the data (Table 9). This PC is dominated by both mineralizable nitrogen and pH. The smaller loadings received by the topographic variables in the first two PC's seem to indicate that these variables do not contribute much more to the interpretation of stand distribution than do resources, at least for these components. The third PC is dominated by aspect and to a lesser degree slope, and explains another 11% of the variance (Table 9). This component represents the primary contribution of adding topographic variables to the resource data set, as it is the only one in which these variables are dominant.

The addition of pH and topographic variables did lead to the formation of loose clusters of stands in a plot of PC1 against PC2 (Figure 6), as opposed to the more even distribution of stands in the resource biplot (Figure 5). Along the first axis, the stand ordination remained virtually unchanged from that of the first analysis. However, the second axis contributed two changes to the ordination. The mixed conifer stand SXW was drawn from the hardwood group to a position in the lower half of the plot with the bulk of the conifer stands having low levels of soil resources. The distinction in this case is the low pH of SXW as compared to that of the hardwoods, despite its higher levels of mineralizable nitrogen. The second change is a more subtle shift of WP2 away from the conifer group and further down the PC2 axis. This change is also indicative of the stand's lower pH, and therefore its low fertility in comparison to the other stands. The three general groupings of stands mentioned earlier remain in the same relative positions as in the previous PCA biplot, and can be defined similarly as stands with low light and high soil resources, stands with high light and low soil resources, or stands with low levels of all resources. In this case soil resources include pH.

The biplot of PC1 and PC3 distinguishes WP1 and SP1 as a small cluster, as well as SP2 and LIR as a cluster about the plot center (Figure 7). WP1 and SP1 are stands with relatively steep slopes, but with the northeasterly aspects more favorable for plant growth, a condition not distinguished in the plot of the first two components. LIR is separated from the oak-hickory stands, presumably due to its association with a southwest aspect along the second axis. The biplot of PC2 and PC3 also emphasizes the distinctness of WP1 and SP1 as a group, and LIR (Figure 8). The three oak-

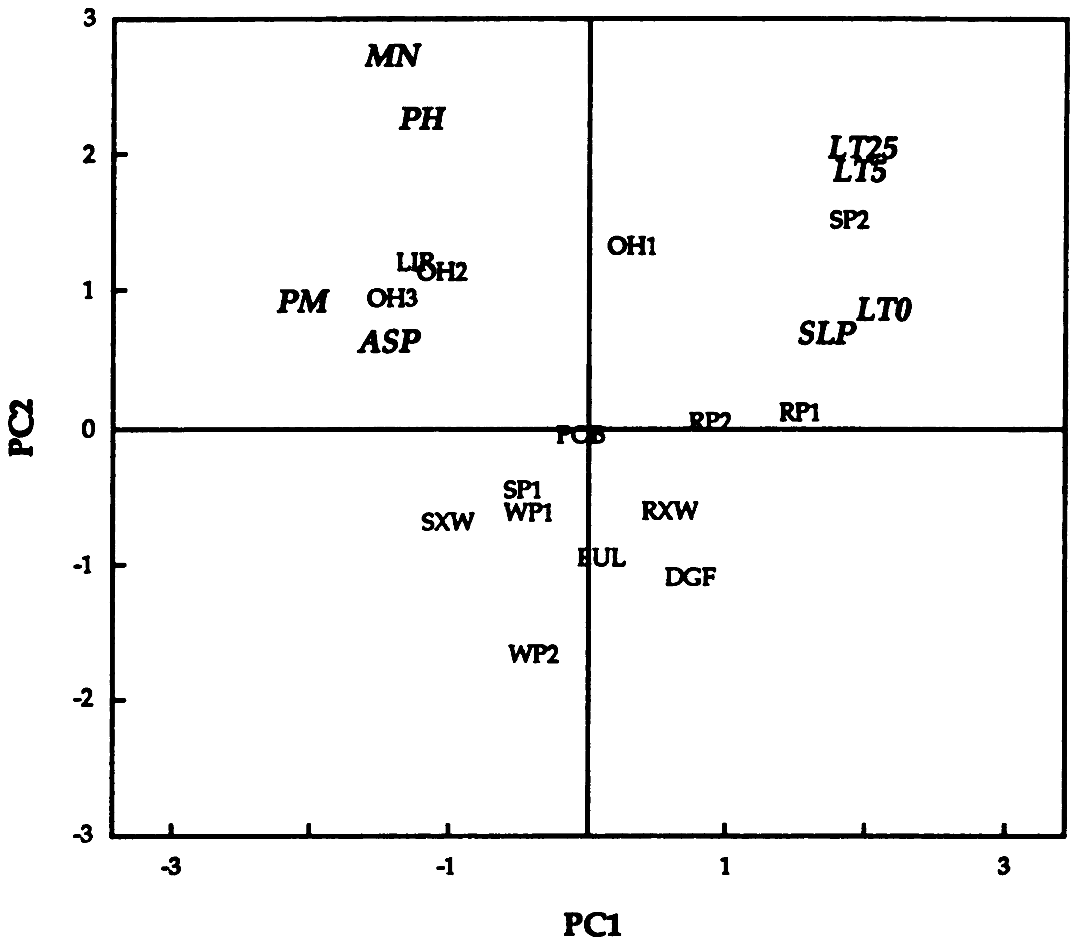


Figure 6. The relationship between the distribution of stands and the first and second principal components for resource and site variables. Scaled eigenvectors for each variable are also plotted: labels as defined in Figure 5, with the addition of PH, ASP, aspect; SLP, slope.

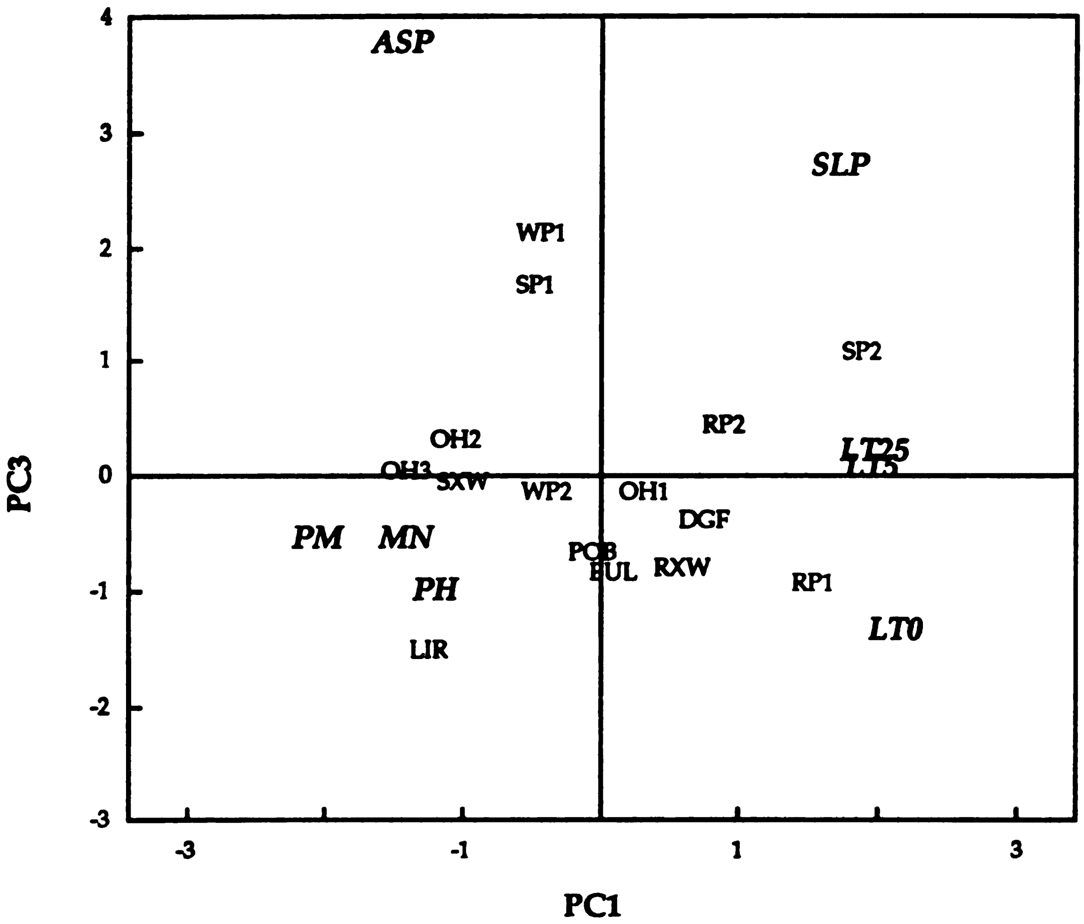


Figure 7. The relationship between the distribution of stands and the first and third principal components for resource and site variables. Scaled eigenvectors for each variable are also plotted: labels as defined in Figure 6.

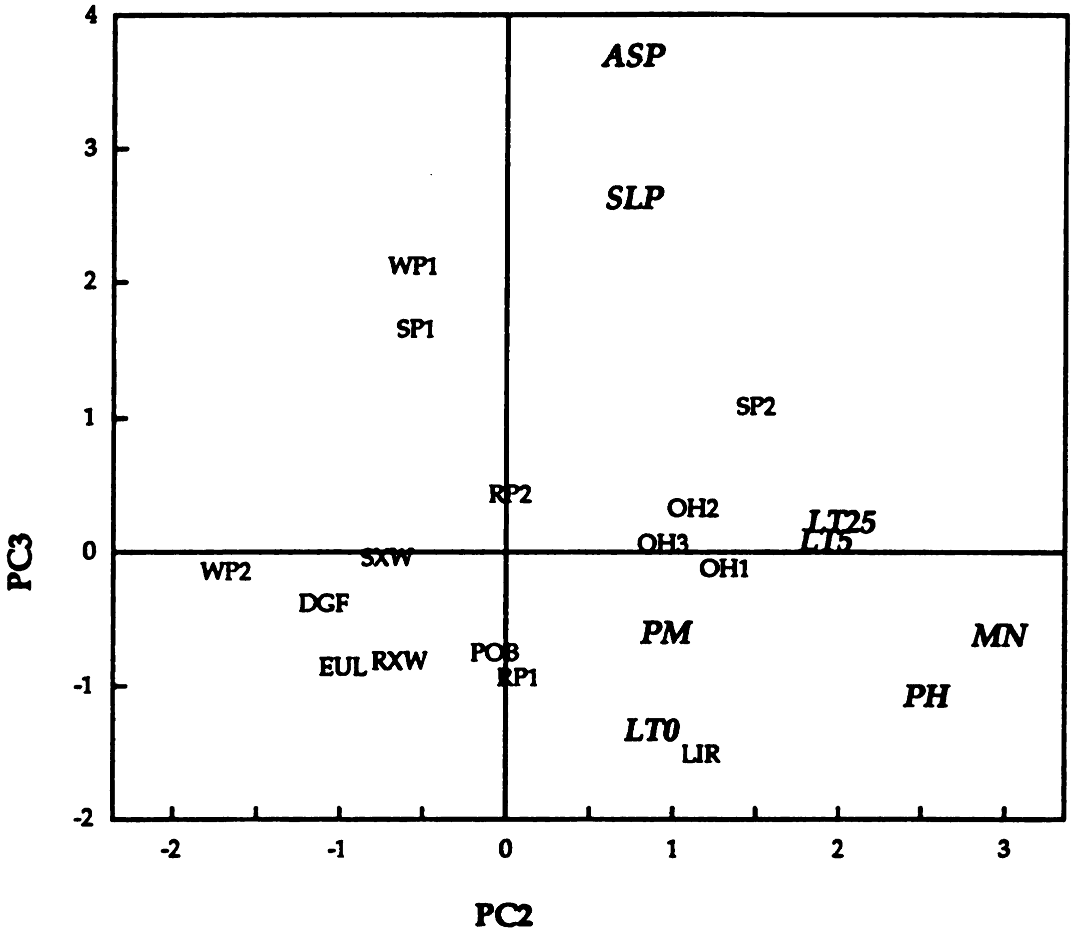


Figure 8. The relationship between the distribution of stands and the second and third principal components for resource and site variables. Scaled eigenvectors for each variable are also plotted: labels as defined in Figure 6.

hickory stands form a tight cluster in this plot, not having done so in the previous two. Here, as in previous biplots, their positions tend to suggest moderately favorable growing conditions in most respects.

Graphically the PCA biplots that include other site variables in addition to resources did not contribute significantly to an understanding of the stand ordination, ie. they do not dramatically change the interpretation of stand associations based on the PCA using resources alone. Relationships between site characteristics and resources that were apparent in the correlation analyses of these variables: aspect and pH with soil resources, and slope with light, were reinforced in these biplots. This suggests that in some cases the physical heterogeneity of this landscape may interact with overstory composition to influence resource levels and thereby the ordination of these stands. It appears, then, that measures of actual resource levels best characterize the ordination of these plantation and natural forests. For this reason, in ensuing sections that use these data to explore different questions, the resource data set without the other site variables will be employed.

To summarize, it appears that three groups of stands can be discerned from the PCA ordination: one group with low to moderate light and high soil resource levels (OH1, OH2, OH3, LIR, POB, SXW), a second group with high light and low to moderate soil resource levels (SP2, RP1, RP2), and a third group with generally low levels of all resources (RXW, SP1, EUL, WP1, WP2, DGF). It is also interesting to note that POB, a hardwood-conifer mix plantation, consistently occupied the middle of all ordinations depicted in the PCA biplots.

Species-Resource Relationships

This section describes the relationship between species and resource distributions across stands. Saplings and seedlings will be analyzed separately. In some cases, species with potential to reach the overstory occurred with low constancy and frequency, and were subsequently dropped from the analysis. Exceptions to this were cases where occurrence appeared to be directly related to levels of a particular resource.

Saplings and Resources

There are clear differences among stands in numbers and basal area of sapling species (Table 10). The high light SP2 stand has the largest number of species, with 10 out of 19 present. Stands with a Scots pine component (SP1, SP2, SXW), as well as WP1, also have the largest total sapling basal area of all stands. The stand DGF has only 2 of the 19 species present, with the large aspen basal area here due to one large individual (Table 10); the plots were representative of this plantation, as it appeared quite barren of advanced regeneration of woody plants. Basal areas of all species are fairly low in general, often representing only one individual of a species in a stand. Most often, large basal areas represent high numbers of small stems, rather than a few larger individuals; this was especially true for red maple.

Red maple, black cherry, and to some extent white ash, American elm, and sassafras are quite ubiquitous throughout the area. In fact, red maple and black cherry dominate the sapling stratum in 11 out of 15 stands (Table 10). Of these two species, red maple appears to be the primary dominant in terms of basal area. There do not appear to be any recognizable relationships between

Table 10. Sapling dominance (mean square meters of basal area per hectare) for 15 stands in the W. K. Kellogg Forest and Kellogg Biological Station, southwestern Michigan.

	STAND														
Species	DGF	EUL	LIR	OH1	OH2	OH3	POB	RP1	RP2	RXW	SP1	SP2	SXW	WP1	WP2
Acer negundo	-	0.017	-	-	-	-	-	-	-	-	-	-	0.422	-	0.221
Acer rubrum	-	0.625	1.167	0.321	0.085	0.152	0.339	0.680	0.085	-	4.199	1.608	1.977	1.777	0.068
Acer saccharum	-	-	0.135	-	0.017	-	-	0.017	-	-	-	-	0.575	-	-
Carya cordiformis	-	-	0.017	-	0.017	-	-	-	-	-	-	-	-	-	-
Carya glabra	0.017	-	-	-	0.017	-	-	-	-	0.017	0.085	0.034	-	0.017	-
Celtis occidentalis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.034
Fagus grandifolia	-	-	-	-	-	-	0.017	-	-	-	-	0.677	-	-	-
Fraxinus americana	-	0.660	-	-	-	0.287	-	0.102	0.068	0.017	0.135	-	0.220	0.119	0.017
Liriodendron tulipifera	-	-	0.389	-	-	-	-	-	-	-	-	-	-	-	0.017
Pinus strobus	-	-	-	-	-	-	-	-	-	-	-	0.017	-	-	-
Populus grandidentata	2.196	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Prunus avium	-	-	-	-	-	0.017	-	-	0.017	-	0.017	0.220	-	0.068	-
Prunus serotina	-	0.305	1.200	0.017	0.068	0.458	0.017	0.085	0.625	0.034	2.415	0.457	0.271	0.254	-
Quercus rubra	-	-	-	-	-	0.220	-	0.017	-	-	0.220	-	-	0.068	-
Quercus velutina	-	-	-	-	-	-	-	0.017	-	-	-	0.442	-	-	-
Sassafras albidum	-	-	-	0.085	-	0.068	-	0.017	-	0.017	0.034	0.034	0.085	-	0.713
Tilia americana	-	-	-	0.068	-	-	0.068	-	-	-	-	0.017	-	0.051	-
Ulmus americana	-	0.034	0.679	0.152	0.322	-	0.321	0.017	-	-	0.017	0.017	0.457	1.081	-
Ulmus rubra	-	-	-	-	0.085	0.186	-	-	-	-	-	-	-	-	-
Total basal area	2.213	1.641	3.587	0.642	0.610	1.388	0.762	0.952	0.795	0.085	7.123	3.522	4.006	3.434	1.070

stand type and species basal area, except for an increase in the basal area of red maple in association with Scots pine.

Of the 19 species present in the stands, 11 were chosen to study the relationship between patterns of sapling dominance and resource levels. Box elder, sassafras, and sweet cherry were not considered because they are unlikely to become important members of future stands. In addition, none of these species is present in enough numbers (except sassafras in WP2) to be a potential competitor at this time in these stands (Table 10). Bitternut hickory, hackberry, beech, aspen, and white pine, although all potential overstory dominants, occurred with such low frequency and/or constancy in these plots that they were also not considered (Table 10). However, there are some interesting notes to make on these five species. Bitternut hickory and hackberry occur as saplings only in close proximity to seed sources, which are quite infrequent and localized in these stands (personal observation). Alternatively, white pine occurred as a sapling only once in all stands surveyed, although this species makes up a large proportion of the overstory basal area in many of these stands. This individual was found in the one high light plot of SP2. The high basal area of beech in SP2 and aspen in DGF were due to one individual of each species, and there appeared to be no relationship between their locations and those of potential seed sources.

To determine if there were associations between patterns of sapling dominance and resource levels, stands were first ranked, from low to high levels, for soil moisture, mineralizable nitrogen and an average of light at 2.5 and 5 meters. This light measure is more biologically meaningful in this study because sapling height is generally below 5 meters; the saplings are more likely to respond to light at these levels and not at the ground. This average is also supported by the similar loadings both light levels received in the PCA's. Once stands were ranked for each resource level, basal area/ha by species was graphed against each resource gradient (Figures 9-11).

Red maple, black cherry, and to a lesser extent white ash and American elm occurred relatively evenly over a wide range of moisture and nitrogen levels (Figures 9-10). American elm did appear to associate with somewhat higher levels of these variables. In terms of light levels, all four species except white ash showed a marginal shift in distribution towards lower light levels (Figure 11). An explanation for the relationship of red maple and black cherry with low light is that these species are creating, rather than responding to, low light levels. This reasoning would primarily apply to the stand SP1, where heights averaged 4.7 meters for red maple and 7.3 meters for black cherry. The height of these saplings would have influenced the light meter readings at all levels measured.

Four of the seven remaining sapling species exhibited distinct trends in dominance associated with individual resources. Sugar maple, tulip tree, and slippery elm exhibited larger basal areas at high moisture and high mineralizable N ends of each gradient (Figures 9-10). Black oak, in contrast, had its highest basal area at the low end of the soil moisture gradient and in the middle of the mineralizable nitrogen gradient. Along the light gradient, these two groups of species had complementary distributions, with sugar maple, tulip tree and slippery elm grouping with low light, and black oak with high light (Figure 11).

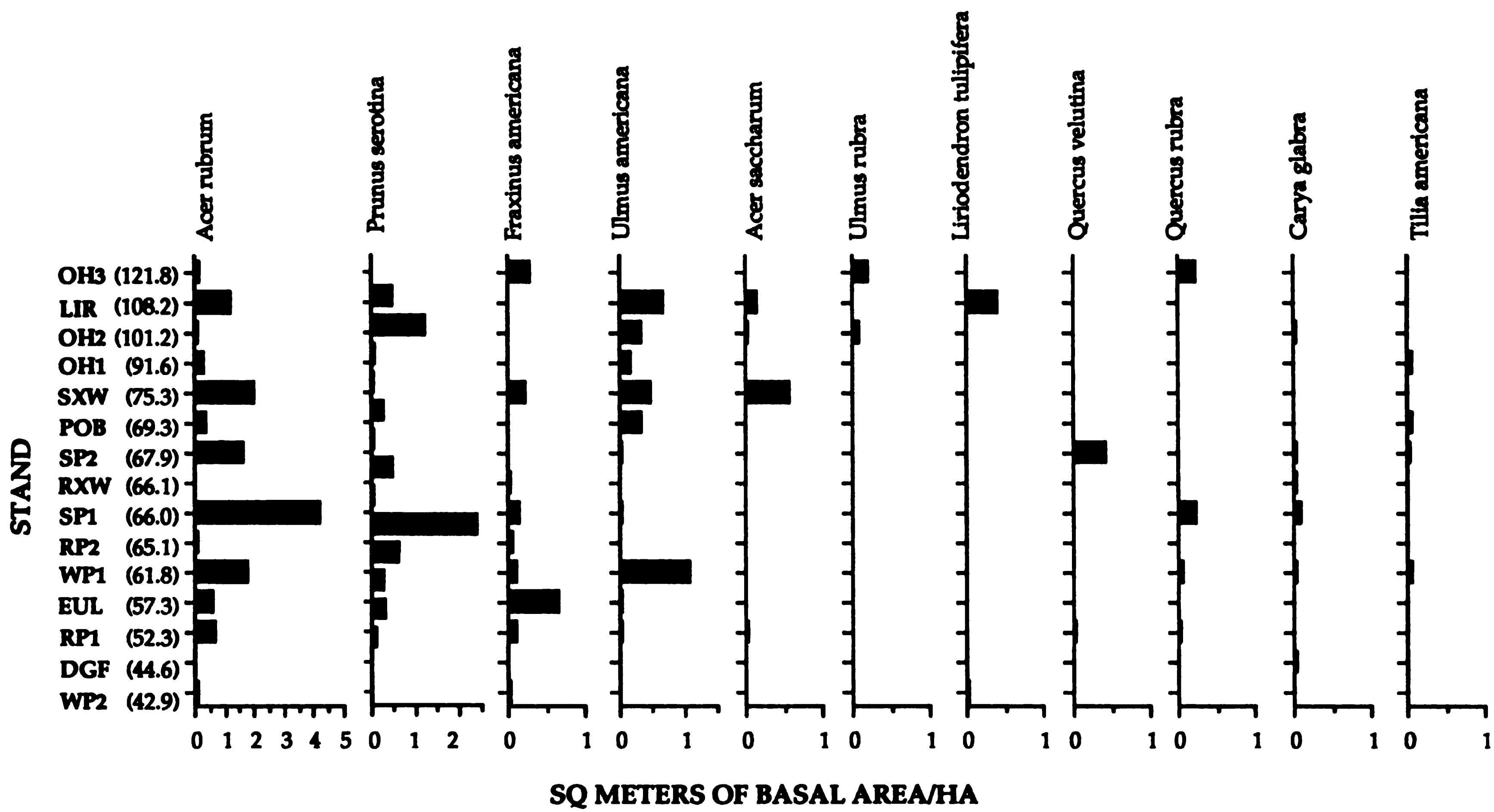


Figure 9. Sapling basal area in square meters/ha for 15 stands in the W.K. Kellogg Forest and Kellogg Biological Station, southwestern Michigan. Stands are ranked from low to high values for mineralizable nitrogen (µg/g).

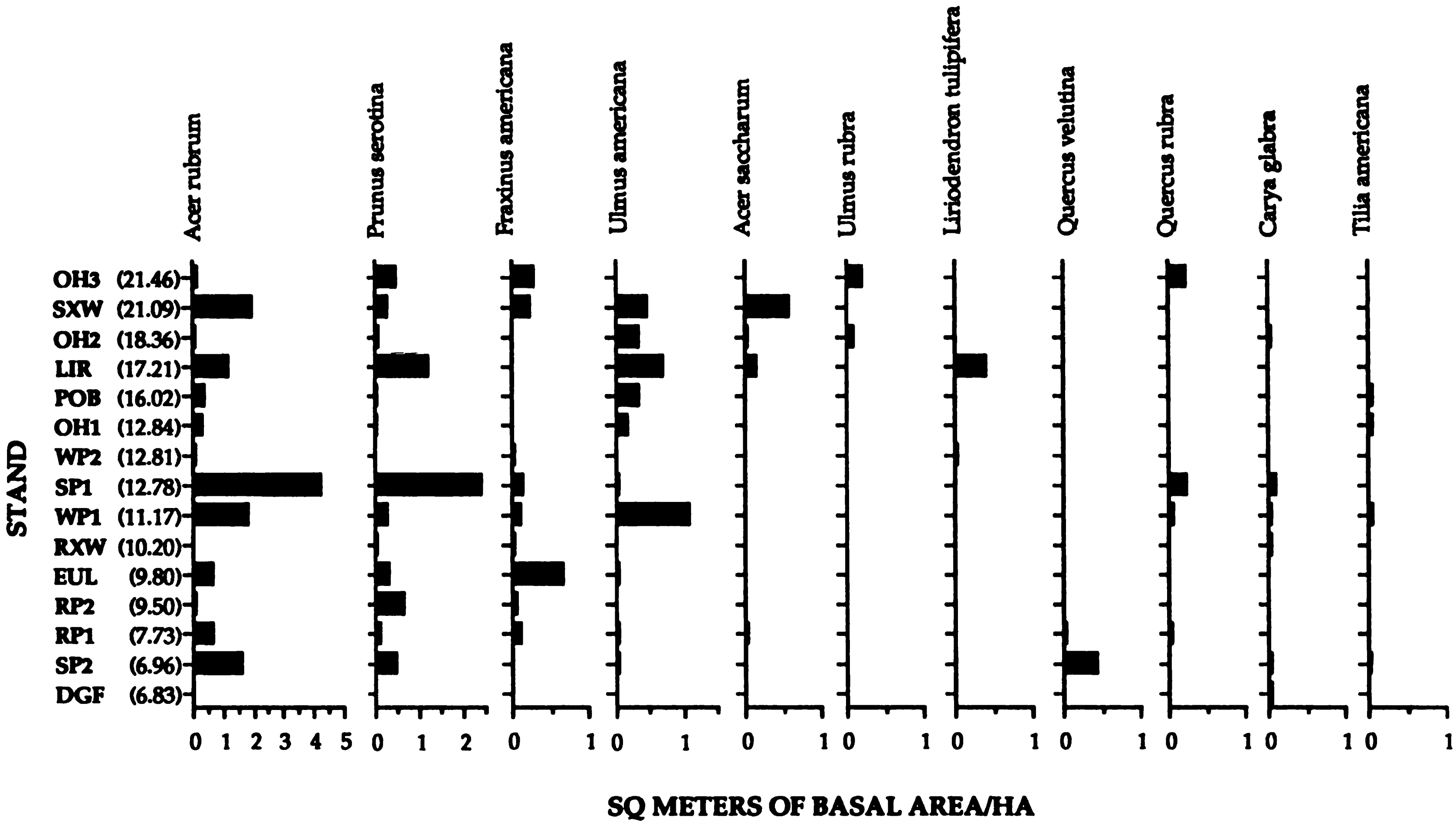


Figure 10. Sapling basal area in square meters/ha for 15 stands in the W. K. Kellogg Forest and Kellogg Biological Station, southwestern Michigan. Stands are ranked from low to high values for soil moisture (%).

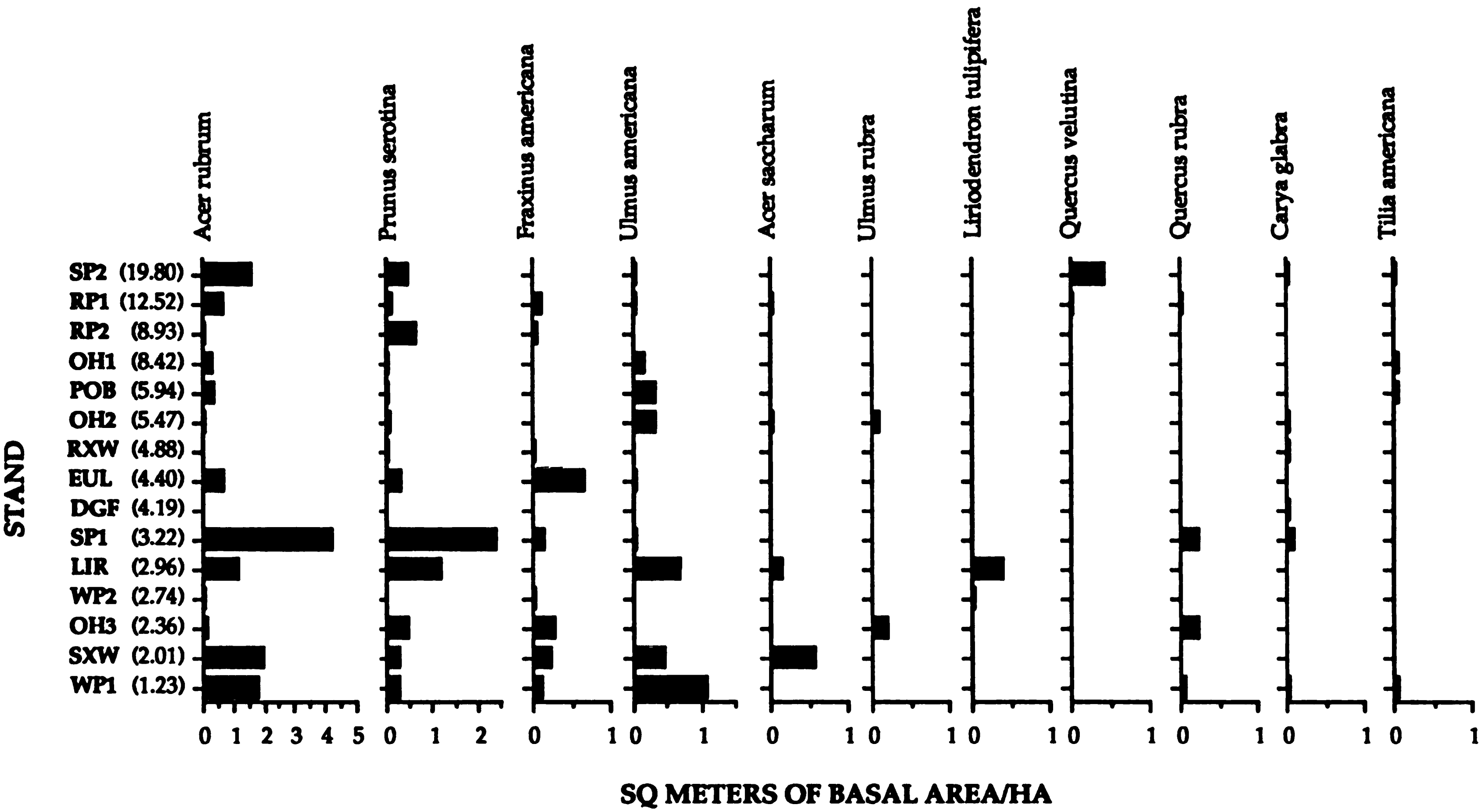


Figure 11. Sapling basal area in square meters/ha for 15 stands in the W. K. Kellogg Forest and Kellogg Biological Station, southwestern Michigan. Stands are ranked from low to high values for light averaged over 2.5 m and 5 m heights (%).

Pignut hickory, with a distribution as wide as those of red maple and black cherry, had small dominances associated with the stands in which it was found, making the interpretation of its relationship to resources difficult (Figures 9-11). Both red oak and basswood occurred in only four stands, and their distributions were also difficult to characterize in relation to resources. Basswood tended to be evenly distributed across the middle of both soil resource gradients, while red oak, though also spread widely, tended towards the higher end of these gradients (Figures 9-10). Along the light gradient, however, the distributions of the two species were not parallel: red oak occurred at lower light levels and basswood at higher light levels (Figure 11).

In order to compare relationships between species and stands along the composite gradient generated by the PCA of resources, relative sapling basal areas on a stand basis were determined, and then stands were classified by species on a 0-5 scale of 20% relative basal area increments. These stand classes were then plotted in place of the stands on the PCA biplot (Figure 5) for each species (Figure 12). One will recall that three groupings of stands were depicted in this biplot: stands with low resource levels in the lower half; stands with high light and low to moderate soil resource levels to the upper right; and stands with low to moderate light and high soil resource levels to the upper left.

For the four most common species, red maple, black cherry, white ash, and American elm, there were again no strong trends towards association with any of the three groups of stands (Figure 12). Red maple and white ash appear to associate more with stands having generally low levels of all resources, while American elm exhibits larger relative basal areas in stands

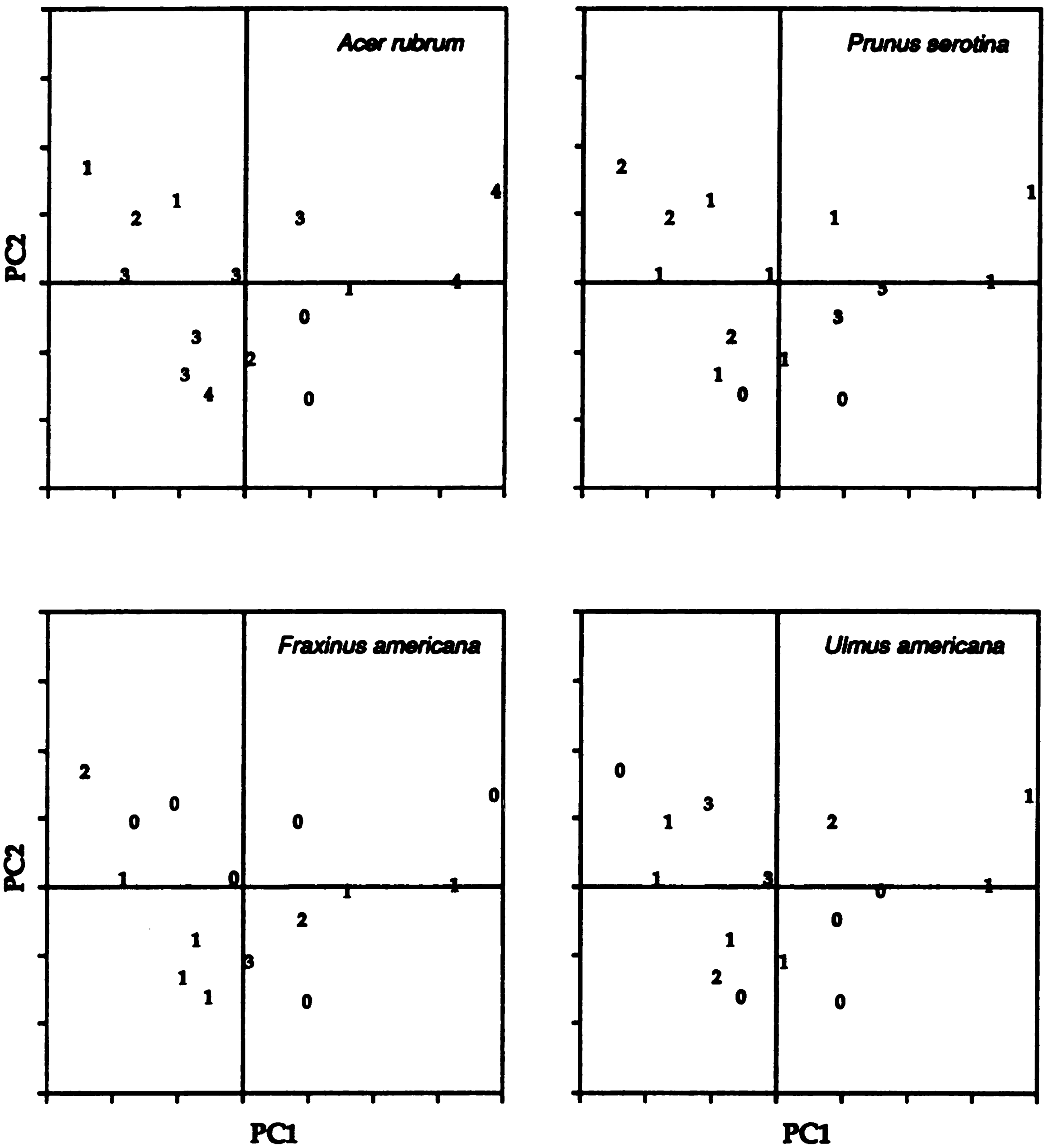


Figure 12. Distribution of 11 sapling species, relative to the first and second principal component axes for resources. Values indicate species importance on a 0-5 scale using divisions of 20% relative basal area: 0, 0%; 1, 1-20%; 2, 21-40%; 3, 41-60%; 4, 61-80%; 5, 81-100%.

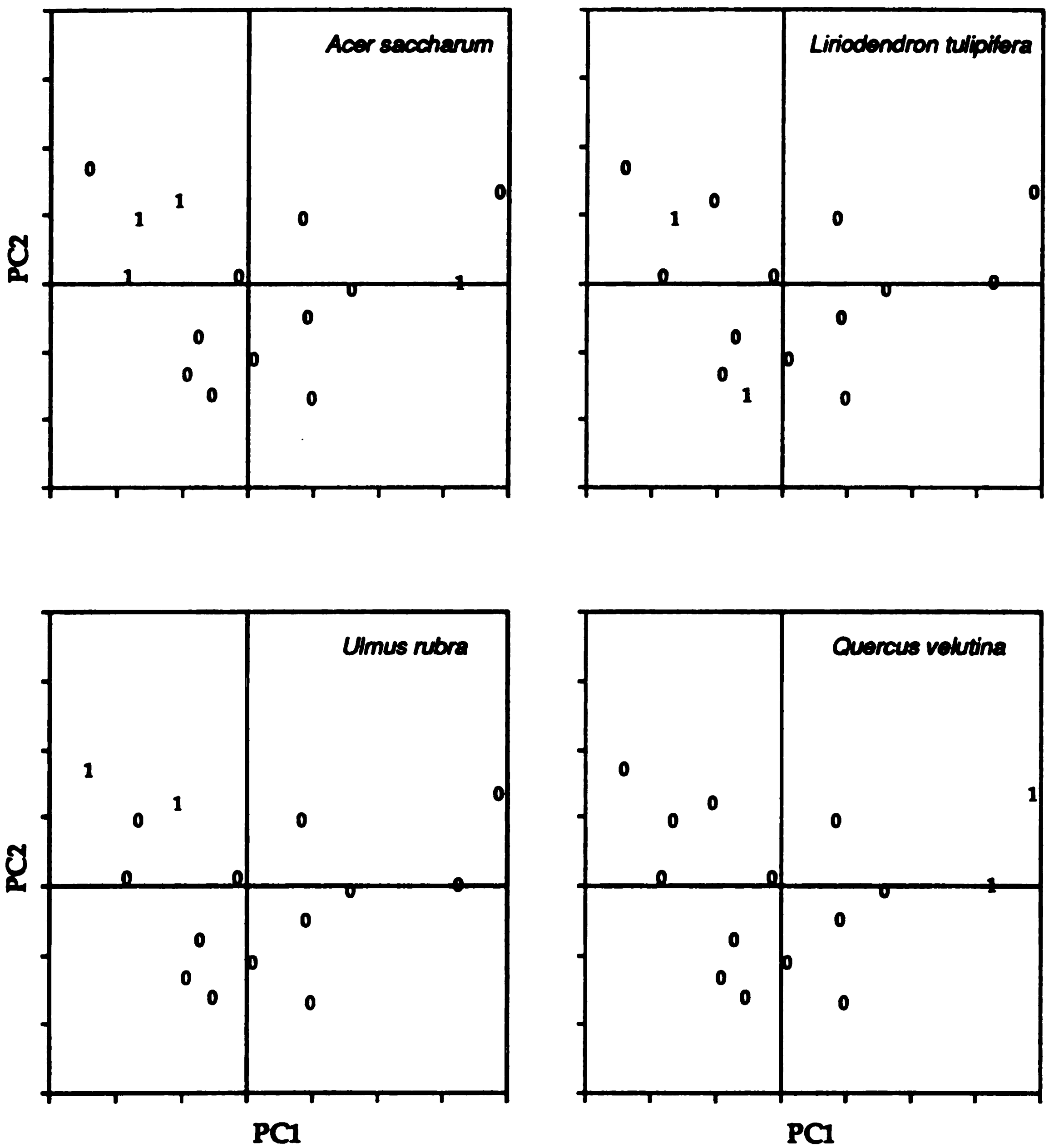


Figure 12. (cont'd.).

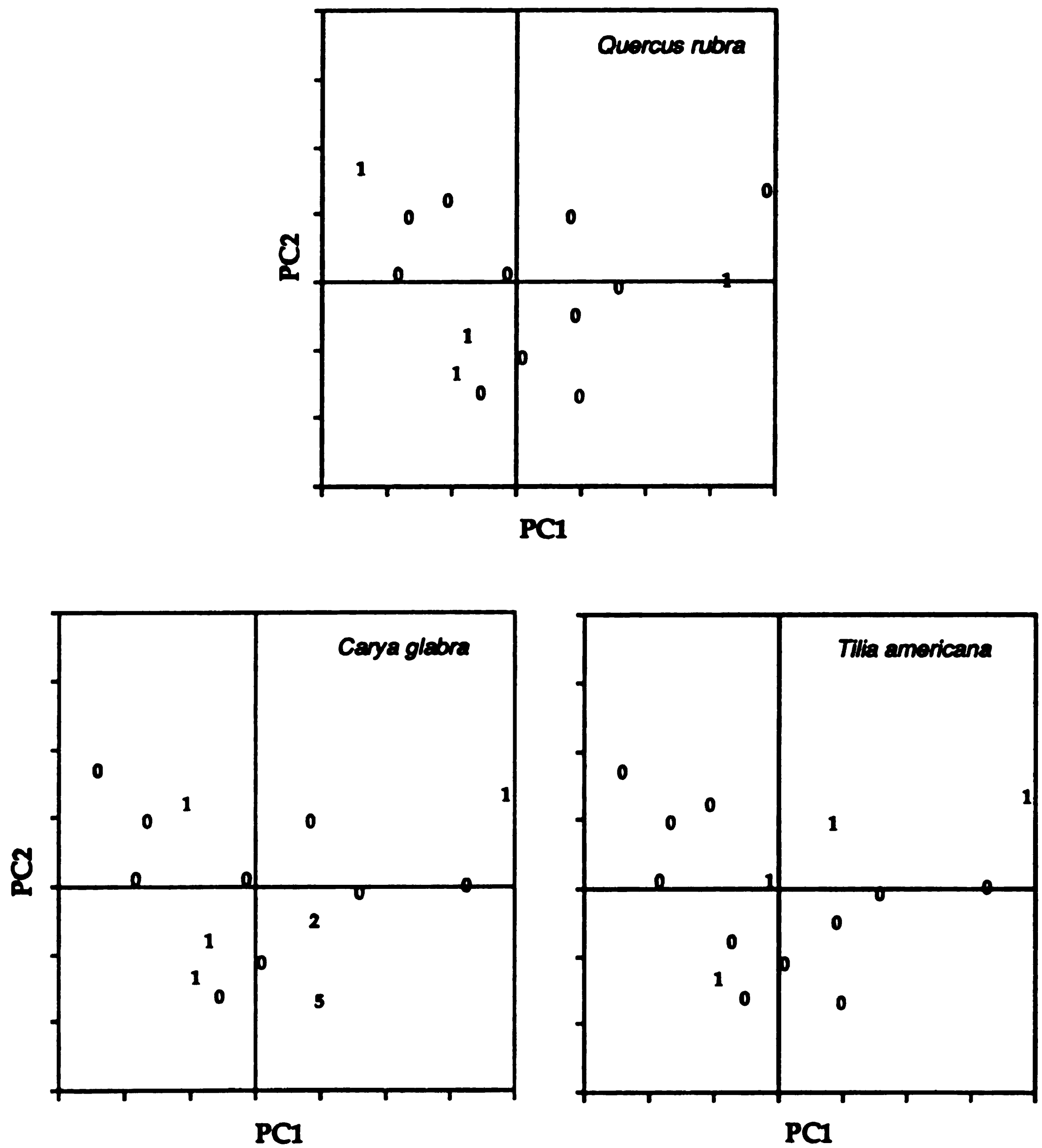


Figure 12. (cont'd.).

with lower light and higher soil resource levels. Black cherry shows a slight association with stands having more moderate to high levels of all resources (the upper half of the plot). The trends described earlier that were obvious for sugar maple, tulip tree, slippery elm, and black oak, are equally obvious with this biplot; ie. black oak is associated with stands having high light and low soil resource levels, with the complimentary association for the other species (Figure 12). The association of pignut hickory with stands having lower levels of all resources is more apparent in Figure 12, although it also is found in the other two groups of stands. Red oak and basswood occur with low relative basal area in each of the three groups making interpretation of their distribution in relation to resources again difficult.

Seedlings and Resources

For seedlings, there appear to be no distinguishable patterns of species recruitment associated with a particular stand type, as in the sapling stratum (Table 11). As before, red maple and black cherry are dominant members of the understory tree community in almost all stands, natural and planted. In the seedling stratum, black cherry is the primary dominant and occurs in every stand, while red maple shows reduced constancy. This situation is the reverse of that found in the sapling stratum (Table 10). Species richness however, does vary across stand types (Table 11). The oak-hickory stands have limited seedling species richness when compared to all other stands except EUL, SP1, and SXW. It is interesting to note that stands with relatively low sapling species richness, especially DGF, RP2, and RXW (Table 10), increase in numbers of species in the seedling stratum (Table 11). The stands EUL, SP1, and SXW show a marked decrease in species richness from the sapling stratum to the seedling stratum. A possible explanation for this

Table 11. Seedling dominance (mean number of stems per hectare) for 15 stands in the W. K. Kellogg Forest and Kellogg Biological Station, southwestern Michigan.

	STAND														
Species	DGF	EUL	LIR	OH1	OH2	OH3	POB	RP1	RP2	RXW	SP1	SP2	SXW	WP1	WP2
Acer negundo	-	-	667	-	-	-	-	-	-	667	-	-	-	-	-
Acer rubrum	17333	-	-	667	-	-	9333	26667	2000	11333	8000	-	-	2667	-
Acer saccharum	-	-	-	-	-	-	-	-	-	667	-	-	-	667	-
Amelanchier spp.	-	-	-	667	-	-	-	-	-	-	-	-	-	-	-
Carya glabra	-	-	-	-	-	-	-	-	667	667	-	-	-	-	-
Carya ovata	-	-	2000	-	-	-	-	-	-	-	-	-	667	667	-
Celtis occidentalis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	667
Fraxinus americana	-	-	-	-	-	18667	-	4000	1333	667	-	1333	-	667	-
Liriodendron tulipifera	667	-	7333	-	-	-	-	-	-	-	-	-	-	-	-
Pinus strobus	-	-	-	-	-	-	-	1333	-	20667	-	667	-	-	667
Populus tremuloides	-	-	667	-	-	-	-	-	-	-	-	-	-	-	-
Prunus avium	-	-	-	-	-	-	-	-	667	-	-	-	-	667	-
Prunus serotina	1333	667	12667	4667	1333	8667	4667	5333	2000	1333	2667	13333	4667	8667	2000
Pseudotsuga menziesii	2000	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Quercus alba	-	-	-	-	-	-	-	667	-	-	-	667	-	-	-
Quercus rubra	-	-	-	-	-	-	667	-	1333	667	-	-	-	667	-
Quercus velutina	-	-	-	-	-	-	-	-	-	2000	-	667	-	-	-
Robinia pseudoacacia	667	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sassafras albidum	2667	-	-	4000	-	-	-	-	8667	4000	4667	-	-	3333	4000
Tilia americana	-	-	-	-	-	-	1333	-	667	-	-	-	-	-	-
Ulmus americana	-	-	3333	-	-	-	667	-	-	-	-	-	-	667	-
Ulmus rubra	-	-	667	-	667	-	-	-	-	-	-	-	-	-	-
Total density	24667	667	27334	10001	2000	27334	16667	38000	17334	42668	15334	16667	5334	18669	7334

phenomenon is that succession had been delayed in stands with higher seedling diversity, either by earlier thinnings and hardwood removal, or harsher site conditions. The lack of seedling diversity in stands with high sapling diversity may be due to increased competition.

Of 22 species present as seedlings, only ten were chosen to compare with stands across resources. Four species, box elder, serviceberry, sweet cherry, and sassafras were not considered for the same reasons as stated for the sapling analysis. Of these four, sassafras has the potential to be a competitive threat because of its often large numbers (Table 11), although it will never become a member of the overstory. There were also eight species that, due to low constancy (eg. ≤ 2 individuals across 45 subplots), were not included in this part of the analysis: sugar maple, pignut hickory, hackberry, aspen, Douglas-fir, white oak, black locust, and slippery elm. Two new species were, however, added to the ranks of potential recruits. These were white pine and shagbark hickory, both of which were not present in the sapling stratum. It is interesting to note that hackberry seedlings occurred only in WP2, the only stand close to the lone hackberry seed source, and that Douglas-fir seedlings only appeared in the Douglas-fir stand (Table. 11).

The seedling data was depicted in the same graphical manner as the sapling data in order to look at possible patterns in species responses to resources in these stands (Figures 13-15). However, the light level used in this case was light at ground level, which is the most biologically meaningful measure of light for the seedlings.

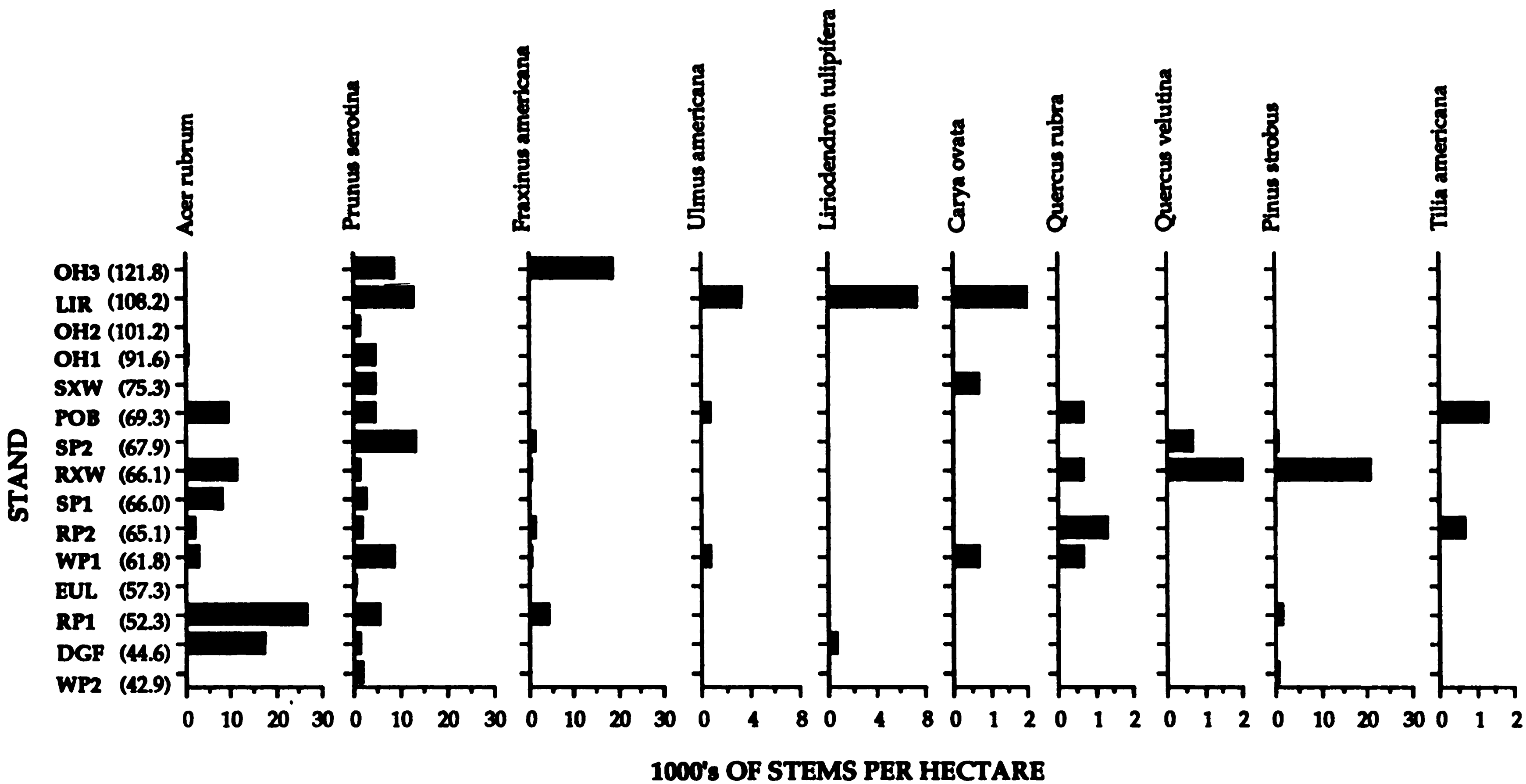


Figure 13. Seedling numbers/ha, in 1000's, for 15 stands in the W. K. Kellogg Forest and Kellogg Biological Station, southwestern Michigan. Stands are ranked from low to high values of mineralizable nitrogen (μg/g).

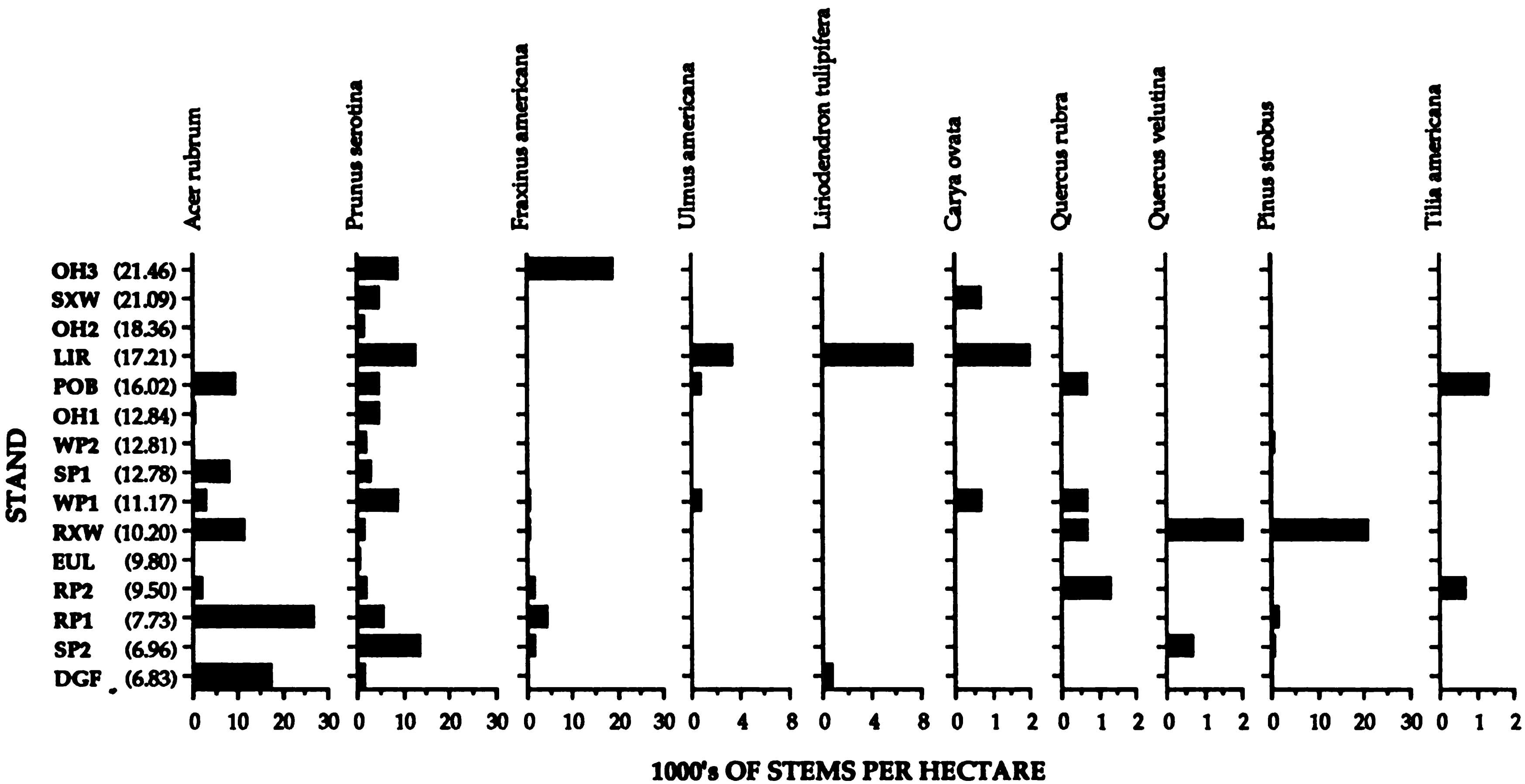


Figure 14. Seedling numbers/ha, in 1000's, for 15 stands in the W. K. Kellogg Forest and Kellogg Biological Station, southwestern Michigan. Stands are ranked from low to high values of soil moisture (%).

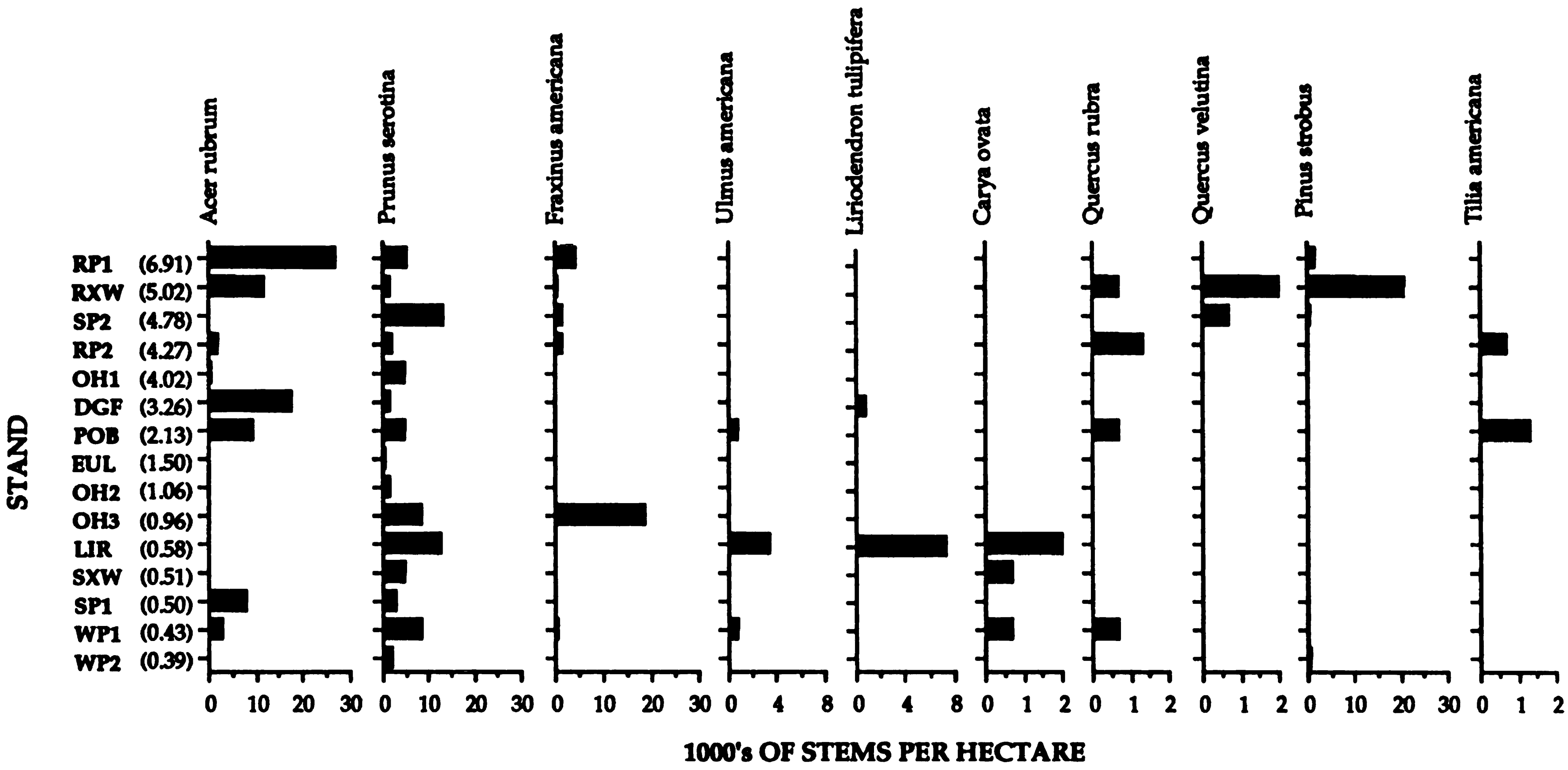


Figure 15. Seedling numbers/ha, in 1000's, for 15 stands in the W. K. Kellogg Forest and Kellogg Biological Station, southwestern Michigan. Stands are ranked from low to high values of light at 0 meters (%).

Seedling species more or less mirrored the distributions of their sapling counterparts relative to individual resources (Figure 13-15). For example, black cherry had a uniform, wide distribution across the range of resource levels as both a seedling and sapling. In fact, the seedling distribution of this species in relation to light was wider than it was for saplings (Figures 15). Red maple as a seedling also had a similar dominance pattern as a sapling, although there was a bias in seedling dominance towards lower moisture and nitrogen, and higher light levels (Figures 13-15). White ash seedlings occurred over the range of resource levels, with peaks in dominance towards the high ends of the soil gradients and low end of the light gradient (Figures 13-15). Basswood was again associated with the middle of all gradients. White pine was clearly associated with high light, and with moderate levels of moisture and nitrogen. Seedling distributions of shagbark hickory, tulip tree, and elm coincided at high levels of soil resources and lower levels of light (Figures 13-15). Among the oaks, red oak seedlings had a broader distribution than black oak seedlings, while both were more abundant when associated with moderate levels of soil resources and higher levels of light (Figures 13-15).

Figures 16 shows the distribution of each seedling species, by relative density class, relative to the composite resource gradients of the PCA for resources in Figure 5. Again, the arrangement of seedling dominances across this biplot tend to support and/or amplify the seedling relationships in evidence with the individual resources. Black cherry and white ash seedling densities appear to be spread somewhat evenly across the three groups of stands depicted earlier for this plot, while the higher red maple seedling densities tend to be found in stands with low to moderate light and soil

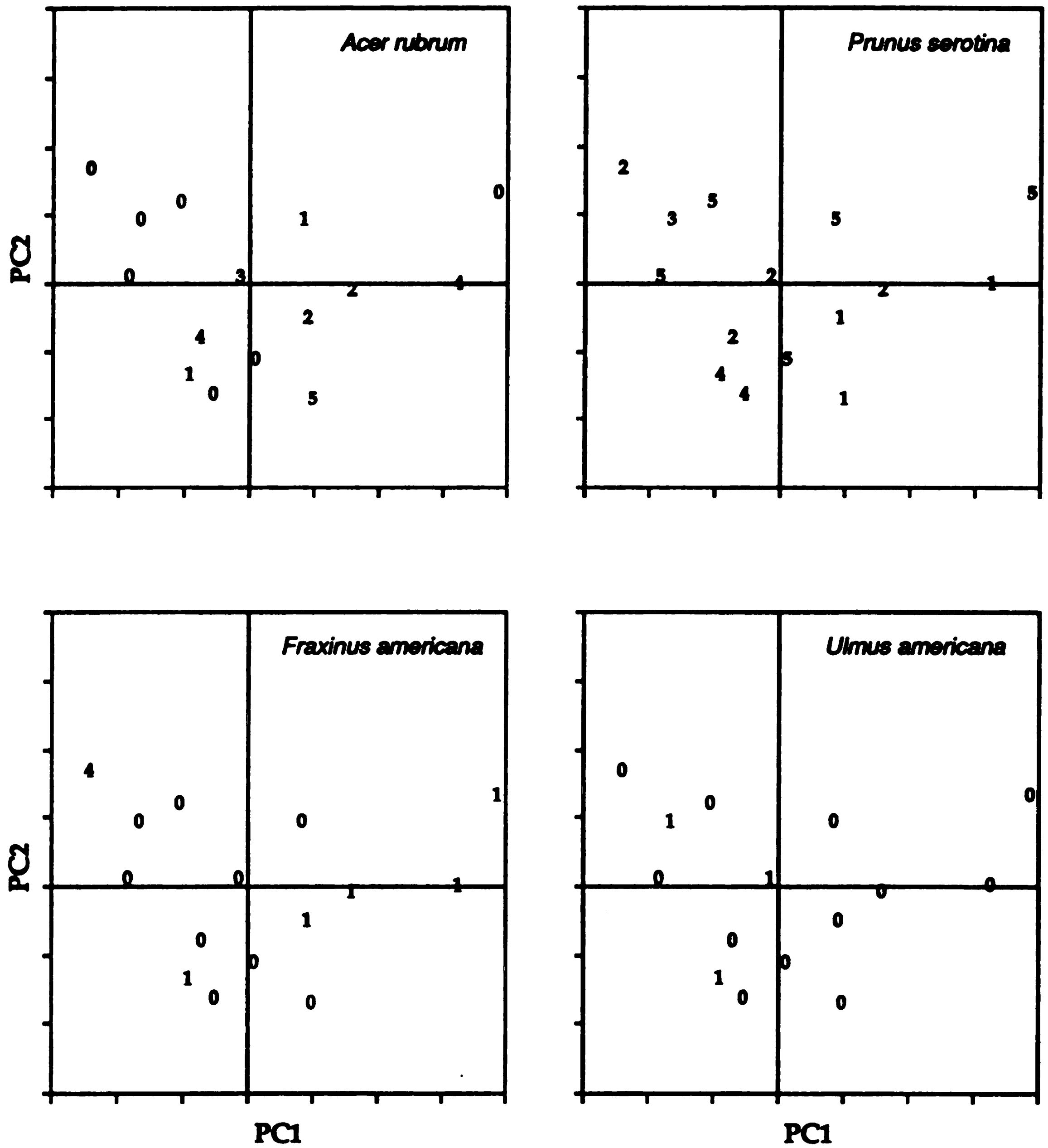


Figure 16. Distribution of 10 seedling species, relative to the first and second principal component axes for resources. Values indicate species importance on a 0-5 scale using divisions of 20% relative density: 0, 0%; 1, 1-20%; 2, 21-40%; 3, 41-60%; 4, 61-80%; 5, 81-100%.

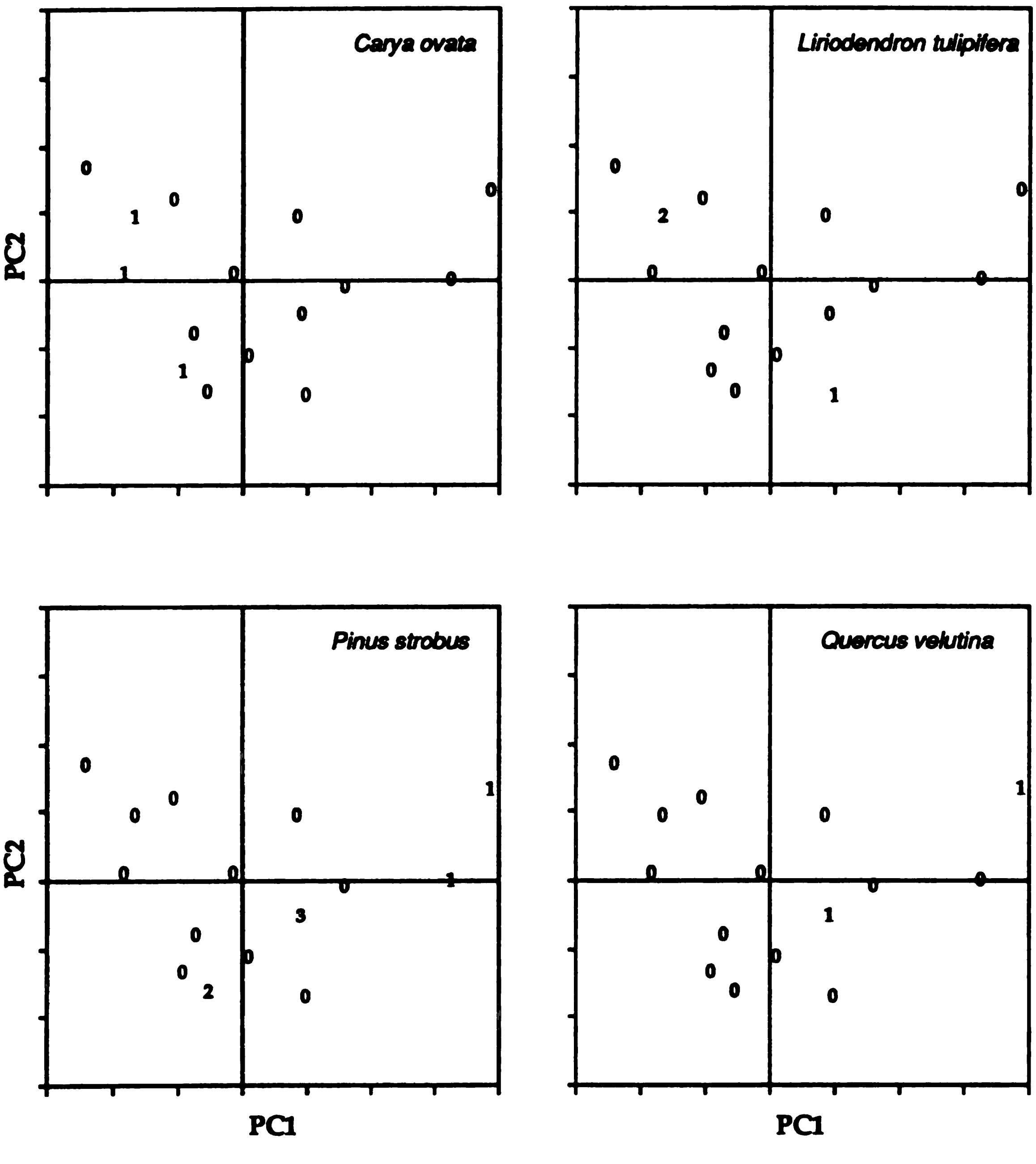
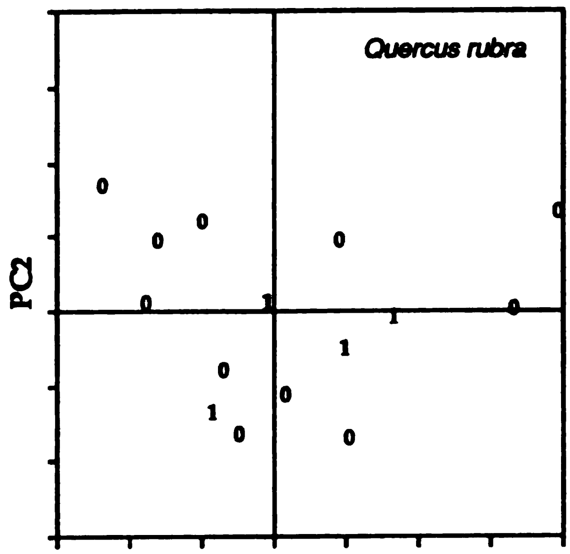


Figure 16. (cont'd.).



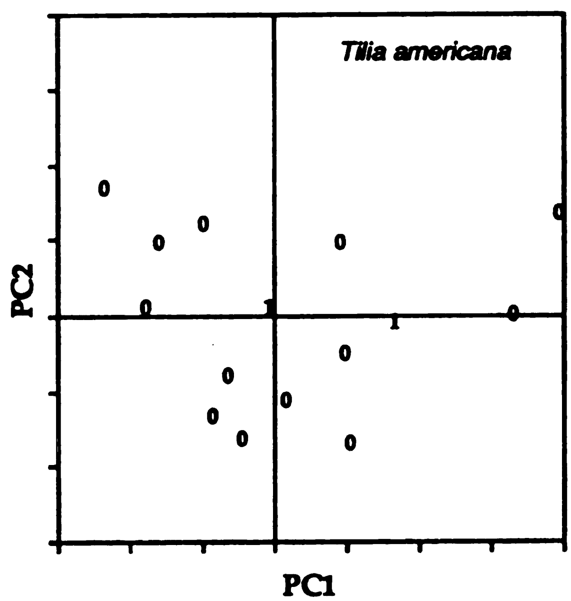


Figure 16. (cont'd.).

resource levels (Figure 16). American elm seedlings appear to favor lower light levels and higher soil resource levels, although the association is not as well defined as that for elm saplings. Shagbark hickory mirrored the individual resource results, being clearly associated with stands having higher soil resources and low light. Both the oak and white pine associations found in the individual resource charts were also maintained in this biplot (Figure 16).

To summarize, red maple and black cherry are the most common species of the understory in both seedling and sapling strata, not only having high constancy, but also dominating each stratum. However, these species showed no definitive associations with resource levels. Red maple tended to dominate the sapling layer in more stands than black cherry, while cherry dominated the seedling layer in more stands than red maple. American elm was also a dominant member of the sapling community in three stands, and white ash was common to both sapling and seedling strata, although it rarely dominated either. There appears to be little recruitment in all stands of the dominant, naturally occurring tree species in this landscape ie. the oaks and hickories; they are present, but in very low numbers. Although there are no apparent patterns of sapling and seedling recruitment in relation to stand type, certain patterns did emerge for some species in relation to the resource levels found at these stands. Saplings and seedlings of the elms, tulip tree, sugar maple, and shagbark hickory tended to have higher dominances in association with stands having higher soil resource levels and lower light levels. White pine and black oak dominances in the understory were clearly associated with low to moderate soil resource levels and high light levels. However, most of the strong associations concerned species with relatively low dominance or frequency. Although this may be an important indication of recruitment limitation, the high variability associated with low sample size allows little more than speculation.

Species-Seed Source Relationships

To further explore patterns in the distribution of understory species in the 12 plantations studied, distances to the nearest original seed sources of species present in each stand were determined at the plot level. The goal was to see if the distributional patterns of understory tree species could be attributed to dispersal limitation, as indicated by seed source distance. Distances were measured from potential seed source to each of the 36 plots (3 per stand), rather than to stands, as the smaller scale is more meaningful in relating individual species dominances to a distance. Numbers of stems were used instead of basal area because, intuitively, this measure is more a reflection of dispersal success and survival, while basal area reflects survival and growth after dispersal has occurred. In addition, only the sapling data is presented here. The relationship of seed source to seedlings is confounded by the fact that the seed rain to the plot that produced those seedlings could have come from a combination of original and later sources; only distance data on original sources was gathered. This problem may also be present with saplings, although minimized somewhat by looking at the older regeneration in these plantations.

There were several problems with this part of the study that need to be discussed. First, for the elms, cherries and hickories, only the generic names "elm", "cherry", and "hickory" were referred to on the maps, although sweet and black cherry, slippery and American elm, and shagbark and pignut hickory were all present in the area. Because sweet cherry was an introduced species, and because it and slippery elm and shagbark hickory were not abundant in the landscape of 1930-1940, I assumed that the species represented by these generic names were American elm, black cherry, and pignut hickory. I believe this to be a fair assumption, although certainly not without violation.

The second and more serious problem involves the maples and oaks. In many cases, species on the maps were defined, but in several cases, only the generic names "oak" and "maple" again were used. Unlike the cherry, elm and hickory situation, white, red, and black oak were all important trees in the landscape, as were red and sugar maple. So in cases, for example, where the generic "oak" seed source was closer to a plot than a "red oak" seed source, a subjective decision was made as to whether the "oak" was more likely to have been a red oak or some other species. This decision was aided by field observations in some cases, although not all seed sources were traced in the field. Generally, unless the distance seemed quite unreasonable, the specific source was used for distance. In some instances, however, the difference in distance to plot between the generic and specific seed sources determined whether the plot was quite close or quite far from the source; differences were >200 m in a few cases.

A third problem was encountered when species of trees found in the overstories of both natural and planted stands were investigated. Of special concern was red oak, as this species was a dominant in the plantation POB, and obviously has been of seed-bearing age for at least the past 20 years. This has allowed plenty of time for its offspring to reach sapling size. So in this case, distance to the nearest seed source, either planted or natural, was used.

There are a wide range of distances that seeds of various species have to traverse in order to reach the plots (Table 12). Closest sources ranged from 5 m away for several species to 34 m away for sugar maple and white ash. Farthest distances varied substantially, ranging from 122 m for black cherry to 849 m for sugar maple. Mean distances from nearest potential seed source, by species, ranged from 33.34 m for black cherry to 301.31 m for sugar maple (Table 12). Given the ranges in Table 12 for the wind-disseminated species (the maples, ash, and elm), there is potential for dispersal limitation, although long distance dispersal is an infrequent but important event. For animal-dispersed species such as hickory, the oaks, and black cherry, dispersal limitation may be present, but less likely a function of these distances than of the interspersion and juxtaposition of old fields, young plantations, woodlots, and corridors dominating this landscape; none of the ranges in distance from potential seed source to these species appears unreasonable for an animal to traverse (Table 12). Black cherry is noteworthy because it was so prevalent along fencerows at the time of plantation establishment; consequently no saplings were found farther than 122 meters from a potential seed source.

For each species, the 36 plots examined were classified into four seed source distance categories (0-50 m, 51-100 m, 101-200 m, and > 200 m). Distance classes were chosen as such based upon seed dispersal literature for forests, which indicates that the bulk of seed produced by wind-disseminated species falls within 50 m of the source (Johnson et al. 1981), although dispersal to within 100 to 200 m is somewhat easily achieved (Green 1980). Proportions

Table 12. Distance (m) from plot center to potential seed sources for sapling species found frequently in plots in the W. K. Kellogg Forest, southwestern Michigan.

		Species							
Stand	Plot	Red oak	Black oak	Cherry	Elm	White ash	Red maple	Sugar maple	Hickory
DGF	1	30	30	30	91	325	30	189	148
	2	34	34	34	56	317	34	204	125
	3	37	37	37	44	317	37	222	114
EUL	1	88	136	84	73	136	136	136	6
	2	101	139	72	49	139	139	139	50
	3	113	154	88	66	149	149	154	53
LIR	1	62	5	62	98	256	62	358	62
	2	117	56	43	43	312	43	385	117
	3	98	98	5	11	352	15	407	154
POB	1	15	277	91	91	277	47	73	69
	2	15	239	88	56	291	5	46	32
	3	20	235	34	44	338	67	108	55
RP1	1	20	291	27	119	152	117	139	128
	2	82	226	85	111	149	149	178	216
	3	52	276	105	58	103	103	125	152
RP2	1	34	34	5	73	34	34	34	34
	2	76	81	18	20	81	81	81	15
	3	82	82	6	79	82	82	82	50
RXW	1	174	174	88	180	174	174	174	174
	2	87	87	46	224	87	87	87	87
	3	128	128	122	226	128	128	128	128
SP1	1	72	155	5	53	76	67	846	49
	2	125	125	5	72	40	5	815	27
	3	165	168	6	21	70	52	849	58
SP2	1	105	94	59	61	331	59	340	114
	2	72	72	72	90	343	70	317	122
	3	84	84	70	70	370	84	350	151
SXW	1	88	172	43	62	210	27	87	64
	2	53	137	35	96	186	5	122	37
	3	69	157	53	90	166	5	102	40
WP1	1	152	396	14	5	175	175	526	126
	2	140	355	5	69	166	198	459	58
	3	218	392	26	160	244	302	425	104
WP2	1	122	122	5	149	120	122	748	122
	2	148	148	30	180	133	148	719	148
	3	175	175	55	198	130	175	693	155
Mean distance		90.36	154.75	45.92	88.56	193.31	89.25	301.31	92.89
SD		50.75	100.17	33.34	57.08	101.10	66.84	251.47	52.01

of those plots in each class having saplings present were then determined (Figure 17). Given the literature just mentioned on the subject, one would expect a decreasing proportion of plots to be occupied as distance increases. However, the only wind-disseminated species appearing to support this trend is American elm (Figure 17). Of the other wind-disseminated species, red maple occurs in a high proportion of the plots within each class, while sugar maple does not. For both of these species, long distance dispersal beyond 200 m does occur, suggesting that these species are not limited by seed dispersal. However, 10 of the 17 plots in the 200+ m class for sugar maple were farther than 400 m from a potential seed source (Table 12), and no saplings of this species were found in these plots. This suggests upper limits to long-distance dispersal for sugar maple. As sugar maple was the only species for which plot distances from seed sources occurred above 400 m, upper limits cannot be suggested for the other species examined. In addition, the low proportion of plots occupied by this species overall suggests that other factors besides dispersal distance are limiting sugar maple. White ash shows a strikingly high level of occurrence (73%) in the 15 plots within the 101-200 m class, but does not occur at all in the 14 plots beyond 200 m (Figure 17). This pattern suggests dispersal limitation beyond 200 m for this species, but also indicates that within 0-200 m of the nearest potential source, other factors are involved in limiting this species' occurrence.

Of the animal-dispersed species, only black cherry showed high levels of occurrence, and only within the 0-100 m range (Figure 17). As only 2 plots occurred beyond 100 m, it is impossible to draw conclusions about long-distance dispersal. It is clear, however, that at least for these plantations, black cherry has little need for long distance dispersal, with 94% of the plots

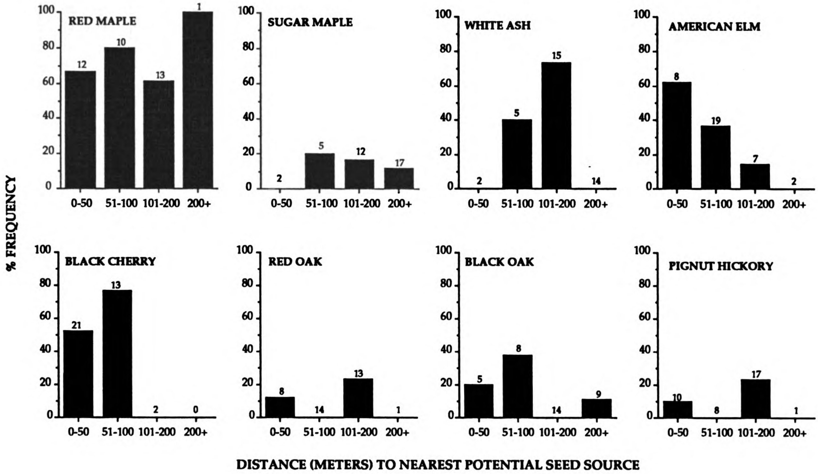


Figure 17. Percent frequency of plots occupied by each sapling species, classified by distance from nearest potential seed source, for 36 plots in 12 plantations of the W. K. Kellogg Forest, southwestern Michigan. Numbers above bars refer to the total number of plots within each distance class.

sampled falling within 100 m of a potential source. As most potential cherry seed sources were found in hedgerows of the 1940 landscape, it is interesting to note that a higher proportion of saplings occurred in the 51-101 m class, rather than in the 0-50 m class. This may be related to perch selection by birds disseminating these fruits, with more attractive perches occurring farther than 50 m from the hedgerows (McDonnell and Stiles 1983). The oaks and hickory are present in low proportions of the plots in each class, and therefore distinct patterns do not emerge for these species (Figure 17). As the farthest distance class was undersampled for red oak and hickory, one cannot speculate about long-distance dispersal limitation. Only one plot farther than 200 m from a black oak seed source was found to harbor a black oak sapling; the remaining 8 plots were farther than 230 m from a source, suggesting the possibility of long-distance dispersal limitation for this species. However, dispersal limitation for the oaks and hickory may have more to do with animal vector ranges, and less to do with absolute distance to a particular seed source. The low proportion of plots in each class occupied by these species also suggests that other factors are more limiting towards their success.

Table 13 shows the results of the chi-square goodness-of-fit analysis, for each species, across two distance classes pooled from the previous four classes. Black cherry was not included as it occurred in only one of the two classes. A uniform distribution was used to test the goodness-of-fit of the species distributions. Only the distributions of white ash and American elm across distance classes are significantly different from a uniform distribution, while the distributions of the other species could not be distinguished from such a theoretical distribution (Table 13). There could be two explanations for this. These species, except for white ash and elm, could in fact have equal

Table 13. One-way chi-square goodness-of-fit analyses, for each species, comparing the distribution, across distance classes, of plots with saplings present with a theoretically uniform distribution of the same plots.

		SPECIES						
DISTANCE CLASS	VALUE TYPE	Red maple	Sugar maple	White ash	American elm	Red oak	Black oak	Pignut hickory
0-100 m	Observed	16.0	1.0	2.0	12.0	1.0	4.0	1.0
	Expected	12.5	2.5	6.5	6.5	2.0	2.5	2.5
>100 m	Observed	9.0	4.0	11.0	1.0	3.0	1.0	4.0
	Expected	12.5	2.5	6.5	6.5	2.0	2.5	2.5
$\chi 2$		1.96	1.80	6.23*	9.31**	1.00	1.80	1.80

* Values >3.83 are significant at alpha=0.05 for 1 df.
**Values >6.62 are significant at alpha=0.01 for 1 df.

probabilities of occuring in either distance class. This may be due to the fact that over the past 40 years, inequities in site quality or herbivory among plots have eliminated the saplings in such a way as to produce these distributions. This may be more likely for red maple, for which there were enough plots in which it was present to produce statistically reliable expected values. Alternatively, it could be argued that this test was not powerful enough to detect deviations from a uniform distribution due to the low frequencies of plots in which these species were found, leading to low (<5.0) expected values. This is most likely the case for sugar maple, the oaks, and hickory, although site conditions and herbivory could still be important factors limiting the success of these species.

Since expected values for white ash and American elm were above 5.0, there is some confidence in the results for these species. The opposing trends of these two species, in terms of presence relative to distance, found in Figure 17 are further emphasized here (Table 13). Although the non-uniform distribution of American elm is supported by the literature for wind-dispersed species (Green 1980; Johnson et al. 1981), that of white ash is not. A likely explanation for the unusual distribution of white ash appears to be that most saplings occurring in the 7 plots within the 0-100 m class may have been eliminated by adverse site conditions for this species, or by herbivory.

To determine if trends in species distributions relative to distance changed when distances were compared with species densities, frequency plots similar to those in Figure 17 were constructed (Figure 18). In this figure, numbers above bars refer to the absolute number of stems counted in each class for each species. Although changes in magnitude for each class changed somewhat from those in Figure 17, the patterns were maintained for all distributions except that of red maple (Figure 18). For red maple, 98% of the saplings counted were found within 200 m of a potential seed source. However, only one plot, occupied by 4 saplings, was found further than 200 m from a source. This suggests that, although red maple does not appear to be dispersal limited in these plantations, its lack of dominance in this plot may be due to the greatly reduced numbers of seeds likely to reach it. Adverse site quality in this plot for red maple is unlikely, as the other two plots in this stand (WP1) each had more than 10 individuals in residence.

As far as the other species are concerned, it is clear that the low frequencies of saplings in the >200 m distance class (Figure 18) correspond to the low proportion of plots occurring in that class that are occupied by each species (Figure 17). This data suggests that dispersal distance may be limiting the ability of all species to dominate plots further than 200 m from a seed source, although it does not appear to limit the ability of the seeds of red

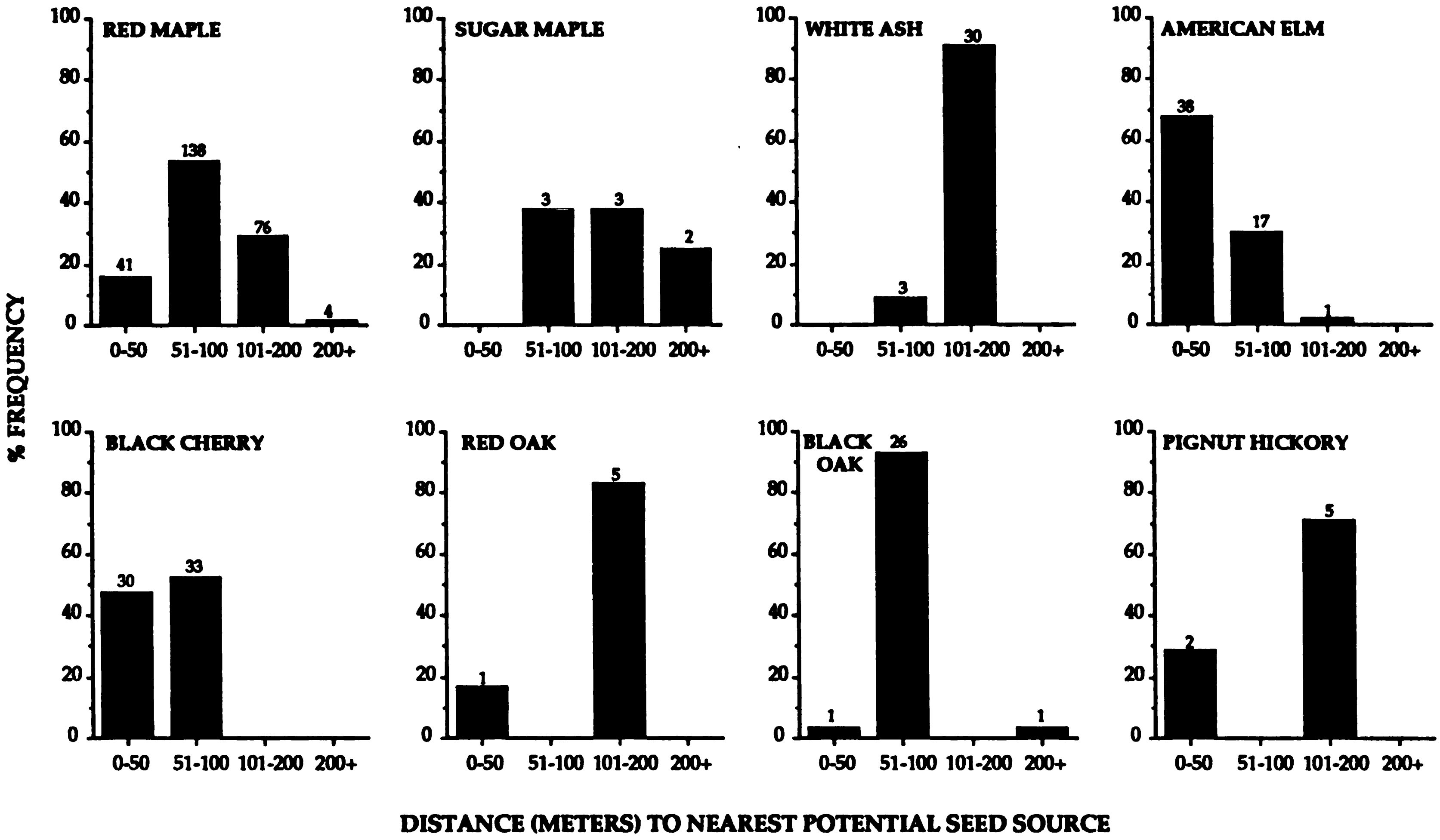


Figure 18. Percent frequency of numbers of each sapling species counted, by distance to potential seed source class, across 36 plots in 12 plantations of the W. K. Kellogg Forest, southwestern Michigan. Numbers above bars refer to the absolute number of saplings counted within each distance class.

maple, sugar maple, and black oak to at least reach these sites and germinate successfully. As only sugar maple seed sources average greater than 200 m from the plots established in these plantations (Table 12), it may be likely that this long-distance dispersal limitation was not important in the development of the understories sampled. For seed source distances between 0-200 m, the distributions and dominances of all species except American elm indicate that dispersal is not limiting to their successful establishment in the plantations surveyed (Figures 17-18). American elm is the only species clearly exhibiting the trend of decreasing presence and dominance with increasing distance from potential seed sources. In the 9 plots occurring beyond 100 m from an elm seed source, only one sapling was found, and this at 111 m (Figure 17). This data strongly suggests the lack of adequate dispersal of American elm seeds over distances greater than 100 m. It should be noted that although this is a distinctive trend, resource quality at these 9 plots could have been harsh enough to preclude the successful establishment of this species, despite its ability to reach these plots.

DISCUSSION

Stands and Resources

Soil resource levels ranged widely across stands examined, and this was especially true for potential mineralizable nitrogen, with threefold differences in rates. Other studies have also shown such wide variation, but generally across much larger geographical regions such as counties or states, and across different soil and forest cover types. Padley (1989) used an almost identical nitrogen mineralization assay as was used in this study, and found a range in mineralized nitrogen concentrations from 26.5 to 150.0 ppm for several different forest ecosystems across northeastern Lower Michigan. Myrold (1987) also found wide variation (18.8-101.0 ppm) in mineralized nitrogen, using anaerobic incubation, for several forest types found across Oregon. Powers (1980), sampling forests across Northern California, and Smith (1981) across Washington, found much lower, but still wide-ranging, values for mineralized nitrogen using anaerobic incubation. These five studies found three- to sixfold variation in rates across broad geographical regions, different soils, and different forest compositions. In contrast, this study found threefold differences across a 114 ha forest and very similar soils, but quite different overstory compositions.

Values for pH in Northeastern forests tend to range from 3.2-5.8 (Vitousek et al. 1982; Zak et al. 1986). In studies by Nadelhoffer et al. (1983), Artigas and Boerner (1989), and Glitzenstein et al. (1990), plantations and natural forests of differing species composition occurring over relatively small areas (325-512 ha) and on similar soils were examined. Values for pH in these three studies were also widespread, with ranges of 4.4-6.3, 3.6-5.0, and 4.0-5.5, respectively. The range in this study, 4.8-6.7, tends to be high, although only one stand (LIR) had a pH > 6.0. The higher trends in pH at the Kellogg Forest, in predominantly conifer stands, may be explained by the forest's relatively recent agricultural past history.

Moisture levels found in this study, although wide-ranging, tended to be low compared to values presented in the literature for Northeastern forests, which may range from 18-37% (Robertson and Vitousek 1981; Pastor et al. 1984; Glitzenstein et al. 1990). Moisture availability at Kellogg Forest and KBS may have been influenced by a short dry spell that had occurred before sampling.

These soil resource data clearly suggest the hypothesis that rates of potential nitrogen mineralization at 0-5 cm, pH at 0-5 cm, and possibly moisture at 0-15 cm, are influenced by the species composition of plantation forests. However, large variation in each of these three variables can occur over relatively small spatial scales, as was found by Robertson et al (1988) in a 0.5 ha old field ecosystem at KBS. Strong spatial dependence was found at 25-30 m scales for mineralizable nitrogen, < 20 m scales for pH, and <10 m scales for moisture. It is unclear how comparable these patterns are to those in a forest system, as little if any research has been undertaken to quantify small scale spatial variability in soil resources for forests (Leonard 1985), although it is well-known to exist (Stone 1975). More extensive sampling in each stand,

and across other stands with similar soils and species compositions, would be necessary to adequately begin to test this hypothesis.

Although light levels in this study also varied substantially and significantly across stands at each height measured, this was not unexpected, given the wide variety in overstory species composition. The ranges found tend to exceed in breadth those found in the literature for fewer stand types. Canham et al. (1990) found a range of 0.5-5.2% global transmission of PAR at 1.5 m height across five temperate and tropical old-growth forest ecosystems, while Artigas and Boerner (1989) found global transmission of PAR under three different pine types in Ohio to range from 13.2-14.6% at ground level. The strong associations of white pine-dominated stands with the lowest light levels, and red pine-dominated stands with generally higher light levels, clearly suggest a species-dependent effect upon this resource.

Correlations of resource and other site variables with each other help to suggest mechanisms for overstory effects on resources. The more important correlations are those between moisture and light, moisture and mineralizable nitrogen, and pH and mineralizable nitrogen. The first two form the basis for the stand ordination using PCA. Secondary relationships that prove useful also include those between moisture, slope, and aspect, and between light and aspect.

Decreases in soil moisture are known to inhibit the activity of both the soil bacteria and fungi that mineralize nitrogen (Griffen 1972; Swift et al. 1979), thus supporting the positive correlation between these two variables found in this study. Therefore, any species-dependent attribute or activity of the overstory that is likely to reduce moisture levels may also decrease nitrogen availability. Of the three groups of stands identified in the PCA ordination, two groups were characterized as having low to moderate levels of the two soil resources. The first group (RP1, RP2, SP2) also has generally high light levels, strongly suggesting that high light can reduce soil moisture through evaporation, thereby limiting both the microbial biomass and nitrogen mineralization. This contention is supported by the strong negative correlation found here between light and moisture. In particular, red pine appears to allow more light to pass through its canopy than other species, although plantation ages and spacings were relatively constant.

However, more moderate levels of mineralizable nitrogen were found in the SP2 stand, the canopy of which was damaged in a 1982 ice storm. The plot most affected by this damage probably had an increase in both litter and light following the storm. More snow was likely to be captured in the new small openings scattered about, leading to increases in available moisture in the following spring. This moisture, combined with high light levels and organic material, and a generally southwest exposure, may have boosted the microbial population at this site and led to high rates of microbial activity and mineralization of nitrogen (Swift et al. 1979). Although moisture levels have since declined, higher soil temperatures are still likely in this high light plot, and may counteract any low moisture effects on the rate at which the microbial populations mineralize nitrogen.

For the second PCA group with low soil moisture and mineralizable nitrogen (DGF, EUL, WP1, WP2, RXW, SP1), the mechanism for reducing soil moisture is less obvious, as these stands are also characterized as having low light levels, although RXW has the highest light levels of the group and tends to be dominated by red pine. These stands, with the exception of DGF, have more available moisture than the previous three high light stands, suggesting that increases in light only exacerbate an already poor situation. The link between low moisture and low mineralization rates in these stands may be related more to past history, erosion, and differences in the underlying physical soil template, than to effects of species on moisture.

Stands having high moisture and mineralizable nitrogen levels (OH1, OH2, OH3, LIR, POB, SXW), were found to have low to moderate light levels, again reflecting the positive correlation between mineralizable nitrogen and soil moisture, and suggesting deep shade as a mechanism for conserving soil moisture. With the exception of OH1 and POB, however, these stands were characterized by low slopes, northeastern aspects, and/or low plateau topographic positions, ie. having topographic characteristics that also tend to conserve moisture (Spurr and Barnes 1980). In fact, the correlation between moisture and topography (negative with slope, positive with transformed aspect) was strong across these stands, as was the negative correlation between transformed aspect and light at the ground. It appears that the effect of different canopies on light penetration is complicated by topographic variation among stands, which can vary moisture regimes independent of stand composition. This can be done directly by altering the physical characteristics of the soil, and indirectly by altering the light regime experienced by the soil. For example, the stands POB and OH1 not only had more moderate slopes, but also more westerly aspects (a low value transformed). These two stands also tended to have moderate light levels and lower moisture values than the other hardwood stands. The differences between these two stands and the others in this group may reflect the moderating influence of topography upon light and moisture holding capacity.

The relationship found between pH and mineralizable nitrogen appears to be less direct. PH is often used as an indicator of soil microbial activity: low pH's tend to inhibit soil bacteria but not soil fungi (Swift et al. 1979). As both groups mineralize nitrogen, the mineralization process appears to be less sensitive to pH than nitrification (Paul and Clark 1989). As microbial mineralization of nitrogen is more likely to be affected by litter quality (eg. C:N ratio, lignin content, phenolics), and poor litter quality is often correlated with low soil pH, the relationship between mineralizable nitrogen and pH may be an indirect measure of the effect of litter quality on mineralization by microbes (Swift et al. 1979). If this is the case, it is the strongest argument for an overstory species-specific effect on soil resources, as litter quality is directly linked to species composition; conifers are considered to have more recalcitrant litter than hardwoods (Swift et al. 1979; Nadelhoffer et al. 1983).

An interesting phenomenon that should be noted here is that, when samples were collected for N mineralization analysis in early July, few stands possessed an O1 layer in their soil profiles. RP1, RP2, DGF, and RXW (which was dominated by red pine) had distinct O1 layers < 2.5 cm in depth, but no O2 layer; SP2 had scattered debris from storm damage, but no distinct O1 layer. The other stands varied from having pockets of litter accumulation to virtually no litter present. Nadelhoffer et al. (1983) found the same situation in 40 year old plantations on Alfisols in Wisconsin. They attributed the lack of an O1 to earthworms fragmenting and incorporating the litter into mineral soil by mid-July, and the lack of an O2 to faunal mixing of the forest floor into mineral soil directly. What this implies is that the mor soil typically associated with coniferous forests has not yet developed in the conifer plantations, and that this may be due to the presence of earthworms in these former agricultural soils. The earthworms' apparent ability, in concert with other soil fauna, to completely break down all but red pine and Douglas-fir litter, suggests a more explicit mechanism for species-mediated effects on site productivity through litter quality. In fact, Nadelhoffer et al. (1983) go on to suggest that red pine litter is of lower quality than either white pine litter or combined white pine-red pine litter, thereby reducing net N mineralization rates to the lowest found in their study.

From this discussion of relationships between resources and species-specific effects on those resources, two general points can be made. First, the strongest relationship which differentiates stands from one another appears to be a contrast between light and soil resources, with <u>both</u> moisture and nitrogen playing important roles. Although similar to Tilman's (1984, 1985, 1988) nitrogen-light resource gradient model, these data suggest a more prominent role for soil moisture in these stands, and do in fact suggest moisture as the driving variable. This makes sense biologically, as both plants and the soil microorganisms that mineralize nitrogen depend upon adequate soil moisture to survive and prosper. The role of species-specific effects on the relationship between moisture and light is uncertain, as it appears to be complicated by topography and other physical site and soil characteristics not measured in this study.

The second point to be made comes as a result of the relationship between pH and mineralizable nitrogen, and the stands SP2 and WP2, which are exceptions to the general moisture-nitrogen relationship: SP2 has very low soil moisture levels and moderate mineralizable nitrogen levels, while WP2 has moderately high moisture levels and very low mineralizable nitrogen. There appears to be an influence of other variables on nitrogen availability, which act independently of soil moisture. It is likely that these variables include soil temperature and litter quantity and quality, none of which were measured in this study. Litter quality is indicated by the strong relationship between mineralizable nitrogen and pH, and in WP2 where pH was the lowest of the stands; soil temperature is implicated in SP2, where light levels are very high, and in WP2, where light levels are very low; litter quality may be implicated in SP2, where debris from ice storm damage is still present. Other studies investigating plantation forests of similar age and varying deciduous and coniferous compositions in the Midwest have also found litter quality and quantity, and soil pH and temperature, to be important variables in sorting stands along a site quality gradient (Nadelhoffer et al. 1983; Artigas and Boerner 1989).

Species Distributions Among Plantations

Among the stands investigated, there did not appear to be any distinguishable pattern of recruitment for any species in relation to stand composition. However, differences among stands for total basal area of saplings per hectare, and total number of seedlings per hectare, were quite large. Of interest especially are the large basal areas associated with WP1 and stands having a Scots pine component, and very small basal areas of saplings but large numbers of seedlings under red pine dominated stands and DGF (excluding the large aspen sapling). The resource data for the high basal area stands suggest a relationship with mineralizable nitrogen, as this is the only resource for which these four stands are not significantly different. In addition, increased structural complexity in Scots pine stands may increase bird dispersal of seeds (Smith 1975; Artigas and Boerner 1989), although the mixed species stands, which tend also to be structurally diverse, show only a slight trend towards higher densities for seedlings, but not saplings. In the plantation study conducted by Artigas and Boerner (1989), they found higher densities of seedlings and saplings under Virginia pine (*Pinus virginiana*), as compared to white or red pine, which they did attribute to higher structural complexity; Virginia pine is similar to Scots pine, as grown in the Northeast, in having relatively short needles with two per fascicle, generally short stature and scrubby form, and high susceptibility to ice, snow, and wind damage to the crown.

There are two possible explanations for the differences in sapling and seedling biomass in DGF and the red pine dominated stands. First, the low sapling and high seedling values could indicate that site conditions have improved enough to allow seedlings to germinate and survive. Alternatively, conditions may still be harsh enough that most of these seedlings will die before reaching the sapling stage, and that this type of mortality has been ongoing. This latter hypothesis is suggested for DGF, where seedlings appeared to be in their first or second year with no indications of survival beyond this age (personal observation). In the red pine stands, the presence of older seedlings was variable by plot, and tended to occur where plots were topographically sheltered from moisture loss, suggesting improving site conditions there.

Red maple and black cherry are the dominant members of the understory community in almost all stands, natural and planted. However, dominance of red maple is greatest as a sapling and declines as a seedling, while black cherry exhibits the opposite trend. A reasonable explanation for this appears to be an initial floristics model (*sensu* Egler 1954) whereby an increase in mortality of black cherry seedlings, relative to red maple of the same age, occurs because shade tolerance of black cherry tends to decline with age; light levels at 0 and 2.5 meters (the seedling stratum) tend to fall below 5% in these stands, which can inhibit the growth of black cherry (Fowells 1965; Auclair and Cottam 1971). The difference between an average potential dispersal distance for black cherry of 46 m, compared to 89 m for red maple, may also contribute to the dominance of black cherry as a seedling.

In addition to overall dominance, red maple and black cherry appear to follow no particular pattern in relation to resource levels, and do not appear to be limited by seed dispersal. The dominance of these two species in the understory is consistent with the literature for both hardwood invasion of plantations, and successional dynamics in oak forests of the Northeast. In 36-64 year-old plantations in Northwestern Pennsylvania, Grisez (1968) found that black cherry seedlings and saplings occurred in 76% of their plots, and red maple in 65% of plots. Artigas and Boerner (1989) found a predominance of red maple saplings and seedlings across their pine plantations in South-central Ohio. Lorimer (1984) found red maple saplings dominating the sapling layer in permanent plots established on four upland oak sites in New York and Massachusetts. Auclair and Cottam (1971) found black cherry seedlings and saplings to average 50% and attain 100% dominance in oak forests of Southern Wisconsin.

The autecologies of red maple and black cherry, relative to other hardwoods, appear to ensure the success of these species in invading plantation forests, given adequate dispersal distances and numbers of seed sources. Both species have excellent colonizing abilities: red maple is wind-dispersed while black cherry has plentiful bird dispersal (Fowells 1965; Smith 1975). Neither species needs much light for germination, and both respond vigorously to release from shade, although black cherry has a more limited window for this release response (Fowells 1965; Smith 1975; Lorimer 1984). In addition, both species are flexible in their requirements for moisture, although red maple has a wider range of conditions over which it will successfully germinate (Fowells 1965).

In addition to red maple and black cherry, white ash and American elm are also important members of the sapling community, and with the former two species comprise the bulk of the sapling biomass. American elm drops out of the group in the seedling stratum. Wind-dissemination of seeds of these two species may also provide them with an advantage over other species in these stands, as it does for red maple. American elm and white ash show slightly increased dominances in stands having high moisture and nitrogen availability, although their presence still ranges broadly across all resource gradients. In addition, dispersal distances appear to be a very important factor for success of American elm, as measured in this study, and may also be for white ash, which has the most peculiar relationship to dispersal distance of the species examined. The largest numbers and basal area of white ash were found within 150 m of a seed source, but on a site (EUL) with somewhat lower soil fertility. Many of the ash in this plantation were spindly, and there was considerable mortality. It may be that there was enough moisture available for establishment, but not enough to maintain good growth and that this dominance is short-lived.

Secondary mesic site species, including slippery elm, tulip tree, shagbark hickory, and sugar maple, showed distinct associations as saplings or seedlings with the mesic, fertile, shady ends of the resource gradients. Three of these species are wind-disseminated, but potential seed sources tended to be few and scattered, localized, or great distances from plots. This suggests both resource and dispersal limitation for these species. Basswood and red oak, also considered mesic species, did not consistently associate with the fertile portion of the stand ordination with resources, and both ranged somewhat widely across resource levels. Dispersal for both species occurs primarily by animals. Therefore it appears likely that red oak and basswood may be more limited by the vagaries of animal behavior and microsite variation rather than by general resource levels in these stands.

Secondary dry-mesic to xeric site species, including white pine and black oak, also demonstrated affinities for the appropriate dry, sunny, and more or less fertile portions of the stand ordination. Black oak was only prevalent in SP2, where it was within an easy 72 m from the nearest potential seed source. The one plot in SP2 with high available light conditions has seen an explosion of black oak regeneration. What is unclear about this phenomenon is whether the black oak seeds had already established and germinated before the disturbance and were simply responding to the increase in light, or if seedling germination and establishment occurred *de novo* after light levels were increased. Determining the ages of the reproduction would provide an answer to this question. Although black oak is characterized as moderately tolerant, it has the lowest tolerance of shade of the oaks in this area, and, as with many oaks, can respond quite vigorously to disturbance. The addition to this situation of a southwest exposure for the plot, and the relatively high frequency of good seed years as compared to other oaks, appears to have given a boost to the successful establishment of black oak on this particular site.

The case of white pine is also interesting because, although it was heavily planted in the forest, and its seeds are wind-dispersed, it was only prevalent in RXW, and only as a seedling. The moderately high light conditions in this stand at ground level are a general requirement for successful germination and establishment of white pine, although Fowells (1965) states that dry mineral soil or thick pine litter do not provide favorable seed beds for this species. This suggests that the plots in which white pine was prevalent at this site may not have had as dense a pine litter layer as other red pine stands in the area. White pine's absence from SP2 may be explained either by competition or by a dry mineral soil seed bed.

Pignut hickory, although also considered a dry-mesic species, appeared to show no correspondence to resource levels, and did not appear to be dispersal limited. This hickory tended towards low frequency and constancy among stands, although it was found in 6 of 15 stands and ranged widely over the full range of resource levels available. Pignut hickory is also intermediate in tolerance, and can exist on sites of varied fertility. It's range in site tolerance and lack of exact requirements for light seem to suggest that success of pignut hickory in these stands depends upon the behavior of the animal vectors that disperse its seed, and the frequency of mast years.

Long-term Community Development

Speculating into the future concerning the development of the hardwood understory of these stands, it appears that black cherry and red maple may become the most important members of the overstory as the plantations senesce. Both species can disseminate propagules over long distances, and are common in fencerows, as members of the natural forest community, and as old field "standards". Their lack of exacting site requirements and their fast growth makes them superior colonizers, and perhaps competitors, in these plantations. The continuation of natural disturbance in the form of ice and wind storms is likely to help cherry maintain its presence, as its requirement for light increases with age. These speculations appear to be consistent with hypotheses presented by Lorimer (1984) and Auclair and Cottam (1971). Lorimer (1984) has advanced a red maple dominance hypothesis, suggesting that the invasion of red maple into old-growth oak forests with sparse oak sprouts will continue and lead to a new forest type in the Northeast dominated by red maple, although uncertainties still exist about its lifespan. Auclair and Cottam (1971) suggest that because black cherry and sugar maple tend to favor the mesic, fertile, well-drained sites, black cherry may replace sugar maple in succeeding into these sites in fragmented landscapes with few sugar maple seed sources; they argue that higher degrees of fragmentation in the landscape tend to favor colonization by pioneers.

These results are different than those obtained by Artigas and Boerner (1989) who argue that in their forests, the sapling and seedling species assemblages generally resemble those found in second growth xeric forests of that region, and that if plantations are allowed to senesce, the advanced hardwood regeneration would dominate and quickly blend into the surrounding forest matrix. This present study suggests that the advanced hardwood regeneration present in the understory is dominated by species which are not common in the surrounding oak-hickory matrix, and that initially these new stands may remain distinctly different from the typical oak-hickory forest of this landscape. The rate at which these senescing plantations will blend into the surrounding forested landscape, and the degree to which this type of succession may or may not result in an accelerated conversion of the natural oak-hickory forests to a different hardwood ecosystem is unknown.

Most other species important in the natural oak-hickory communities of the Kellogg Forest and KBS do not appear in dominant roles in the understory. American elm does well in a few places, but its future is far from secure due to Dutch elm disease. White ash is present in a number of stands, but is dominant in only one and is senescing in that stand, either from rigorous self-thinning or poor site conditions. White ash is not a long-lived species as well, so its role in the new developing hardwood forest is not likely to be one of importance. There also does not appear to be an imminent, or even threatening, invasion of more mesic hardwoods into the Kellogg Forest area. However, because sugar maple and beech are already established in the forest as a small stand and a few individuals, respectively, these species may become more important in the distant future.

Dominance, and possibly presence, of oaks and hickories in these stands without some form of disturbance or human intervention (eg. prescribed burning) is unlikely, except perhaps in SP2. These species tend to be at a competitive disadvantage when compared to red maple and black cherry; they are species with heavy seeds, sporadic mast years, often unpredictable animal vectors, widespread predation of seeds and sprouts, and slower growth. The fact that periodic fires no longer occur to eliminate competition and stimulate oak sprouts has further endangered the survival of the oak-hickory ecosystem as it presently exists at the Kellogg Forest and KBS. However, the phenomenon occurring in SP2 does indicate that under certain conditions, black oak has the capacity to establish dominance in the understory of these plantations and successfully, at least in the short-term, coexist with red maple and black cherry.

SUMMARY AND CONCLUSIONS

The general objective of this study was to characterize patterns of variation in tree establishment and recruitment within plantation forests, and to relate these patterns to gradients in light, nitrogen and moisture, and to topographic variation, disturbance history, and distance to potential seed sources. The first hypothesis tested suggested that resource levels varied significantly across plantations and forests of different compositions, but which occurred on similar soils. There does indeed appear to be substantial and significant variation in resource availability among these stands, and some of this appears to be attributable to species-specific effects of the overstory brought about either by changing the light regime received in the understory, or by litter quality and quantity effects. However, it was apparent that the stands sampled were more physically heterogeneous, primarily in topography, than first supposed. This heterogeneity manifested itself both as interactions between topography and stand composition as they affected resource levels, and effects of topography directly on moisture availability.

The second and third hypotheses deal with sapling and seedling species distributions relative to stands and their resource levels. It was found that red maple and black cherry are the predominant recruits in these plantation and natural forests, and that neither species appeared to be limited by either resource levels or dispersal distances. Nor were these species associated in any way with a stand type. These species are aggressive colonizers, have flexible resource tolerances, and have plentiful vectors for seed dispersal, the sources for which are on average within 100 m of any given plot sampled. Secondary sapling and seedling species appear to be limited by a combination of resource availability and dispersal distance, although again there did not appear to be any distinct association with stand type. Scots pine stands appear to offer suitable habitat for the establishment of a number of different species, which possibly is related to an increase in structural diversity in these stands due to susceptibility to crown damage. Stands dominated by Douglas-fir or red pine appear to offer the least hospitable environments for tree establishment, and were also the only stands having a well-defined forest floor layer.

In conclusion, while it does appear that planting different species will have different effects upon the soil resources that tend to limit tree establishment and growth, the types of conifers planted, *per se*, do not appear to influence current successional trends in these forests. Effects of conifers upon resource levels may only slow down the incursions of black cherry and red maple into these stands, but are unlikely to prevent the ultimate success of these two species.

As this is one of only two studies explicitly looking at successional trends in plantation forests, the need for further research is quite clear. More detailed soil sampling to characterize litter quality and quantity, populations of soil microorganisms, soil temperature, nitrification rates, exchangeable cations, soil texture, and small scale spatial heterogeneity in forest soils are needed in order to test hypotheses concerning the mechanisms by which the different plantation species surveyed affect soil resources. Tests for dispersal limitations (seed traps and seed bank analysis) and herbivory limitations to the success of various sapling and seedling tree species are also needed to characterize the roles of these factors in successional development. Competition experiments on sapling/seedling species combinations would be useful for predicting the future success of the sapling species found, and for testing hypotheses concerning early development of these understories. Research focusing on the effects of disturbance, and on various silvicultural manipulations that could be performed to encourage the successful establishment of oak species in these plantation understories, could also be very important, especially in those areas where future forests dominated by oaks are desired.

APPENDIX

APPENDIX

DIRECTIONS TO PLOTS IN THE 15 STANDS SURVEYED

STAND: Tulip tree (LIR)

LOCATION: Compartment 22C, east of Augusta Road, W. K. Kellogg Forest

DIRECTIONS:

- From center line of intersection of main woods road and forest trail, along northern edge of Compartment 22C, proceed South 0° and 208.5 ft to Plot 1.
- From Plot 1, proceed South 26° West and 187 ft to Plot 2.
- From Plot 2, proceed South 47° West and 140 ft to Plot 3.

STAND: Scots pine 2 (SP2)

LOCATION: Compartment 22A, east of Augusta Road, W. K. Kellogg Forest

DIRECTIONS:

- From the northwest corner of a sign titled "Spruce Christmas Tree Demonstration Area", in the northeast corner of the demonstration area, along the southern side of main woods road in Compartment 22A, proceed North 39° East and 184 ft to Plot 3.
- From Plot 3, proceed North 0° and 115 ft to Plot 2.
- From Plot 2, proceed North 90° East and 106.5 ft, then South 0° and 33 ft to Plot 1.

STAND: Oak-hickory 2 (OH2)

LOCATION: Compartment 22B, east of Augusta Road, W. K. Kellogg Forest

DIRECTIONS:

- From center line of intersection of main woods road and forest trail, along northern edge of Compartment 22C, proceed North 40° East and 137 ft to Plot 1.
- From Plot 1, proceed North 40° East and 200 ft, then North 29° East and 60 ft to Plot 2.
- From Plot 2, proceed North 90° West and 251 ft to Plot 3.

STAND: Douglas-fir (DGF)

LOCATION: Compartment 22A, east of Augusta Road, W. K. Kellogg Forest

DIRECTIONS:

- From intersection of main woods road and forest trail bisecting Compartment 22A north to south, proceed North on forest trail to first intersection with another trail bearing East. From center line of this intersection, proceed South 9° East and 86 ft to Plot 1.
- From Plot 1, proceed South 50° East and 63.5 ft to Plot 2.
- From Plot 2, proceed South 31° East and 61 ft to Plot 3.

STAND: Oak-hickory 1 (OH1)

LOCATION: Compartment 10, east of Augusta Road, W. K. Kellogg Forest

DIRECTIONS:

- From southwest corner of sub-compartment 12 of Compartment 10, from a stake painted red north of the trail that passes this corner, proceed North 34° East and 154 ft to Plot 1.
- From southeast corner of sub-compartment 15 of Compartment 10, proceed N 51° West and 59.1 ft to Plot 2.
- From the southeast corner post of the lookout building, located south of the main woods road at the boundary between Compartments 9 and 10, proceed North 41° East and 207 ft to Plot 3.

STAND: Red pine 2 (RP2)

LOCATION: Compartment 9, east of Augusta Road, W. K. Kellogg Forest

DIRECTIONS:

- From the southeast corner post of the lookout building, located south of the main woods road at the boundary between Compartments 9 and 10, proceed South 83° West and 104.3 ft to Plot 1.
- From Plot 1, proceed South 56° West and 187 ft to Plot 2.
- From Plot 2, proceed North 0° and 200 ft, then North 70° West and 34 ft to Plot 3.

STAND: Red pine-White pine (RXW)

LOCATION: Compartment 7, east of Augusta Road, W. K. Kellogg Forest

DIRECTIONS:

- From the northwest corner post of Compartment 7-plot F5, proceed South 58° East and 49 ft to Plot 3.
- From the northwest corner post of Compartment 7-plot D1, proceed South 22° East and 50 ft to Plot 2.
- From the northwest corner post of Compartment 7-plot B4, proceed South 52° East and 28.4 ft to Plot 1.

STAND: Scots pine-White pine (SXW)

LOCATION: Compartment 4A, east of Augusta Road, W. K. Kellogg Forest

DIRECTIONS:

- From the center line of main woods road at intersection at the northwest corner of Compartment 7, proceed North 6° East and 200 ft along northern extension of main woods road. Then continue North 4° East and 123 ft along road. Then turn and proceed North 86° West and 138 ft to Plot 1.
- From Plot 1, proceed North 42° West and 87.5 ft to Plot 3.
- From Plot 1, proceed North 0° and 116 ft to Plot 2.

STAND: Red pine 1 (RP1)

LOCATION: Compartment 8A, east of Augusta Road, W. K. Kellogg Forest

DIRECTIONS:

- From center line of main woods road at intersection with power line (poles) on northern borders of Compartments 8A and 9, proceed on road South 7° East and 200 ft, then South 4° West and 139 ft. Turn and proceed North 85° West and 93 ft to Plot 2.
- From Plot 2, proceed South 70° West and 179 ft to Plot 3.
- From Plot 3, proceed South 70° West and 65 ft, then North 41° West and 131 ft to trail. Turn and proceed North 12° East and 157 ft to Plot 1.

STAND: European larch (EUL)

LOCATION: Compartment 9, east of Augusta Road, W. K. Kellogg Forest

DIRECTIONS:

- From center line of main woods road and forest trail with oak leak emblem and the number "19", along the western border of Compartment 9, proceed South 60° East and 98 ft to Plot 1.
- From Plot 1, proceed North 0° and 180 ft to Plot 2.
- From Plot 2, proceed North 75° West and 56 ft to Plot 3.

STAND: White pine-Red oak-Basswood (WOB)

LOCATION: Compartment 13C, east of Augusta Road, W. K. Kellogg Forest

DIRECTIONS:

- From the southern post of the Kellogg Forest sign at junction of entrance road and main woods road, in the northwest corner of Compartment 13C, proceed South 22° East and 200 ft, then North 58° East and 38 ft to Plot 1.
- From Plot 1, proceed South 56° East and 155 ft to Plot 2.
- From Plot 2, proceed South 64° West and 200 ft, then South 31° West and 24 ft to Plot 3.

STAND: White pine 1 (WP1)

LOCATION: Compartment 18, west of Augusta Road, W. K. Kellogg Forest

DIRECTIONS:

- At gate to entrance to western portion of forest, proceed along forest trail that bears north parallel to Augusta Road (just inside the fenceline) to the first forest trail on the left (bearing west). From center line of the intersection of the two trails, proceed South 81° West and 96 ft to Plot 3.
- From Plot 3, proceed North 2° East and 345 ft to Plot 2.
- From Plot 2, proceed North 44° West and 248.5 ft to Plot 1.

STAND: White pine 2 (WP2)

LOCATION: Compartment 20A, west of Augusta Road, W. K. Kellogg Forest

DIRECTIONS:

- Proceed west along the forest trail bordering the southern edge of Compartment 20A until it intersects a forest trail bearing north at the southwest corner of this compartment (where C. 20A, C. 21, and C. 24I meet). From a 7-inch *Sassafras albidum* at this corner of Compartment 20A, proceed North 25° East and 126 ft to Plot 1.
- From Plot 1, proceed South 71° East and 98.5 ft to Plot 2.
- From Plot 2, proceed North 71° East and 86 ft to Plot 3.

STAND: Scots pine 1 (SP1)

LOCATION: Compartment 21, west of Augusta Road, W. K. Kellogg Forest

DIRECTIONS:

- At the intersection of trails located at the northwest corner of Compartment 20A, proceed along the trail that bears due west, up the hill, until it intersects a trail bearing north-south that divides Compartment 21 from 29. Go to the southwest corner of the stand occupying the northeast quadrant of this intersection (in Compartment 21). Proceed North 43° East and 63 ft to Plot 3.
- From Plot 3, proceed North 10° East and 208 ft to Plot 1.
- From Plot 3, proceed North 44° East and 170 ft to Plot 2.

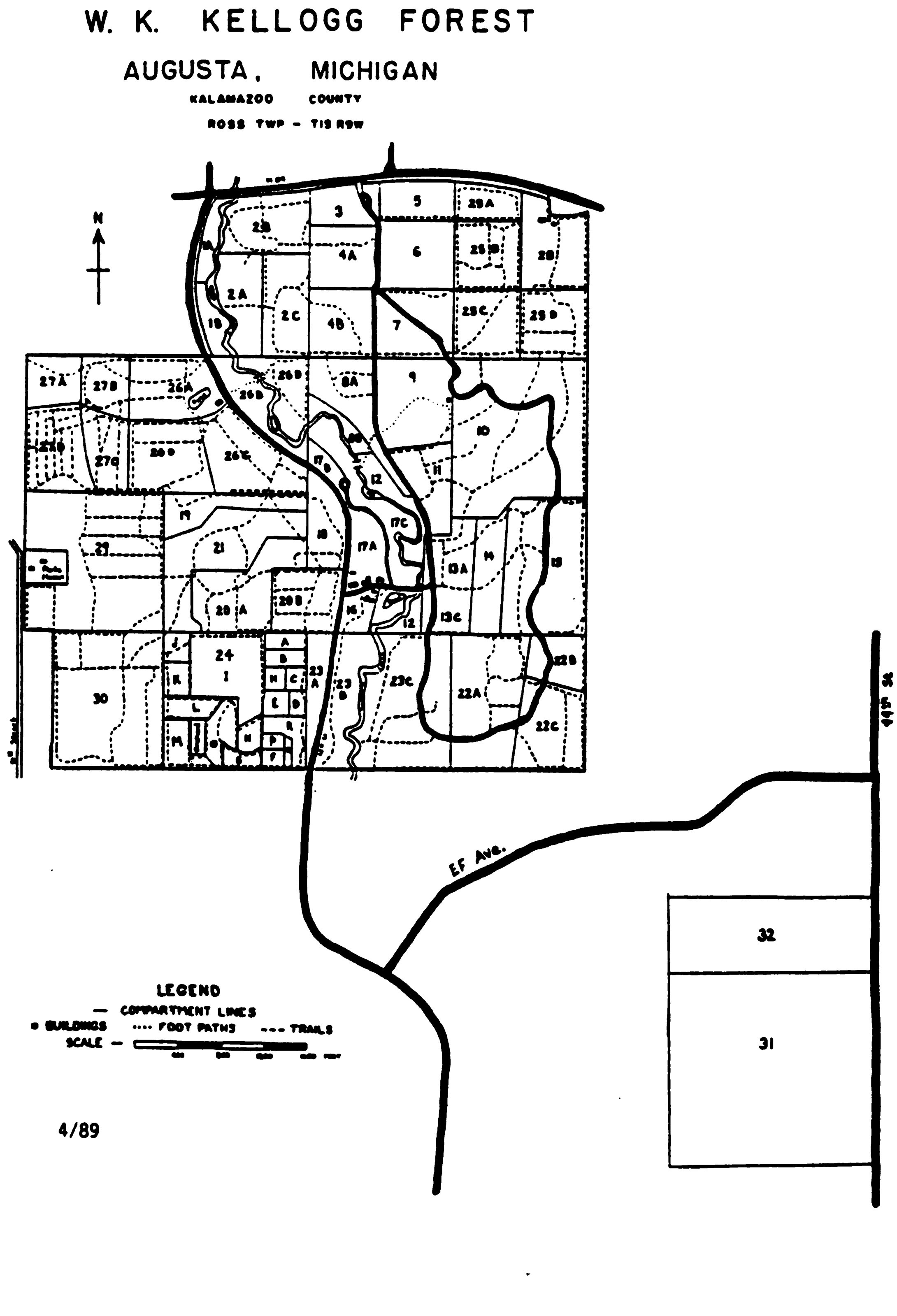
STAND: Long Woods (OH3)

LOCATION: W. K. Kellogg Biological Station

DIRECTIONS:

- Proceed through gate and east along road that borders the southern edge of Cantlon Fields, until the road turns a corner to the south. At this corner, to the south and west is a young stand of *Juglans nigra*. From a *J. nigra* having a circumference of 2.2 ft at the corner of this stand, proceed North 90° East and 288 ft to Plot 1.
- From Plot 1, proceed North 17° East and 87 ft, then North 0° and 400 ft to Plot 2.
- From Plot 2, proceed North 47° East and 50 ft, then North 56° East and 400 ft to Plot 3.

COMPARTMENT MAP OF THE W. K. KELLOGG FOREST



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