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Patterns of oak advance reproduction in mature oak-hickory forests in the ridge and valley physiographic province of Tennessee

Leslie Suzanne Chadwell

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To the Graduate Council:

I am submitting herewith a thesis written by Leslie Suzanne Chadwell entitled "Patterns of oak advance reproduction in mature oak-hickory forests in the ridge and valley physiographic province of Tennessee." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Forestry.

David S. Buckley, Major Professor

We have read this thesis and recommend its acceptance:

Wayne Clatterbuck, Glendon Smalley

Accepted for the Council:
Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

To the Graduate Council:

I am submitting herewith a thesis written by Leslie Suzanne Chadwell entitled "Patterns of Oak Advance Reproduction in Mature Oak-Hickory Forests in the Ridge and Valley Physiographic Province of Tennessee." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Forestry.

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We have read this thesis
and recommend its acceptance:

Wayne K. Clatterbuck

Glendon W. Smalley, Adj. Prof.

Accepted for the Council:

Interim Vice Provost and
Dean of the Graduate School

PATTERNS OF OAK ADVANCE REPRODUCTION IN MATURE OAK-HICKORY FORESTS IN THE RIDGE AND VALLEY PHYSIOGRAPHIC PROVINCE OF TENNESSEE

A Thesis
Presented for the
Master of Science
Degree
The University of Tennessee, Knoxville

Leslie Suzanne Chadwell
August 2001

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ABSTRACT

Most oak (*Quercus*) regeneration research over the past two decades has focused on improving the competitive position and growth performance of established oak reproduction. Less research has been conducted on factors underlying the presence and abundance of oak advance reproduction. Oak reproduction patterns and underlying factors in east Tennessee forests are also poorly documented. The objective of the research was to investigate relationships between the abundance, size, and composition of oak advance reproduction and site factors on six soil associations and three landform positions (ridgetop, northwest slope, and southeast slope) in the Ridge and Valley Province of Tennessee.

Topography within the soil associations sampled ranged from hilly and rolling to steep ridges with rolling valleys. Soils included in this study ranged from moderately high productivity to shallow, acidic soils low in productivity and covered 68% of the land area in the Ridge and Valley Province. Two replicate transects were sampled within each soil association-landform position combination yielding a total sample size of 33 transects (transects within the J52 soil association could not be replicated). Size and abundance data were collected for four classes of oak regeneration; 1) 0 to 25 cm in height, 2) 26-50 cm in height, 3) 51-150 cm in height, and 4) greater than 150 cm in height and less than 8 cm dbh. Site factors investigated were landform position, soil association, slope, overstory and understory competitors, seed source, light regime, basal area, and litter thickness. Regression equations for predicting the abundance of oak reproduction for each size class and species of oak were developed using r^2 variable selection, response surface analysis, and a general linear models procedure.

Eight species of oak were encountered: chestnut oak (*Q. montana*), white oak (*Q. alba*), black oak (*Q. velutina*), northern red oak (*Q. rubra*), southern red oak (*Q. falcata*), scarlet oak (*Q. coccinea*), chinkapin oak (*Q. muehlenbergii*), and post oak (*Q. stellata*). Chinkapin and post oak were only found on one site and, therefore, were not analyzed as individual species. Preliminary analyses suggested that both landform position and soil association were important factors influencing the presence of many of the oak species and size classes. Therefore, models for predicting oak abundance were developed within every landform position – soil association combination for all species of oak and all size classes.

Except for northern red oak, the smaller size class oak seedlings were more abundant on the more productive soils and landform positions. In contrast, the largest size class oak seedlings were more abundant on the less productive soils and landform positions. Conditions for germination and early growth may be best on northwest slopes, but chances for survival to the fourth size class were apparently greater on the drier, less productive southeast slopes. The regeneration patterns for chestnut oak, black oak, and the scarlet-southern red oak group were consistent with current hypotheses that these species perform better on the drier, poorer sites.

Variables such as oak seed source, potentially competing mature canopy trees, potentially competing saplings, and canopy depth were consistently significant throughout all species and size classes of oak. For all oak species, importance value of canopy trees (seed source) was positively related to the abundance of the smaller size classes of oak seedlings. Importance value of competing species was significantly related to the number of larger size class oak seedlings. Dogwood (*Cornus florida*) saplings consistently had a negative relationship with the abundance of oak seedlings of most species. Canopy depth was expected to have a negative relationship with oak abundance because less light would be available with increasing depth. However, this relationship was variable. Only northern red oak had a negative relationship, white and chestnut oak had positive relationships, and black and scarlet oak had no relationship. Land managers can use these relationships between oak regeneration and soil and site condition as guidelines for making decisions on where to concentrate oak regeneration and management efforts (silvicultural treatments) in the Ridge and Valley Province.

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Introduction

Researchers have been studying the continuing decline of oak regeneration in this country for the past two decades. Oaks are considered the most abundant forest type in the US, but forest management techniques used over the past 50 years have tended to favor more shade tolerant or faster growing species (Clark, 1993). Researchers have used multi-factor site and land classifications to analyze oak decline on a regional basis, but little has been done in the way of a more local analysis (Lorimer, 1992). Tennessee forests are 71% oak-hickory forest type, 12% oak-pine forest type, and 4% oak-gum-cypress forest type (Schweitzer, 2000a). Since mixed oak forests cover nearly 85 % of Tennessee, the continuing decline of oak regeneration will cause significant portions of the landscape of the state to change, affecting the oak timber resource and wildlife habitat. Little or no information exists on the severity of the oak regeneration problem in Tennessee. Several factors are thought to contribute to the lack of oak regeneration. A few of these factors are drought, fire suppression, canopy structure, increased consumption of acorns by wildlife, defoliating insects, and various soil properties (Lorimer, 1989; LeBlanc, 1998; Rogers and Johnson, 1998; and Cook et al., 1998).

The impact of drought on oak ecosystems was demonstrated in a study by LeBlanc (1998), where he found that a drought in 1953-54, which decreased the growth and vigor of oaks, might have predisposed oaks to mortality after a drought in 1988. Fire suppression programs were first implemented on public lands during the 1930's. Lorimer (1993) gives a detailed account of the oak regeneration problem. After reviewing past research, he found that the periodic burning of forests reduced the density of the shade-tolerant understory and shrub layer that would hinder the regeneration of oak. The intentional elimination of fire made it more difficult for oaks to remain the dominant canopy species by allowing an understory of fire intolerant, shade tolerant species to form a closed canopy.

Looking at post-harvest oak regeneration from sprouts, Cook et al. (1998) found that a stump age between 50-80 years had very little effect on the number of sprouts for white oak and scarlet oak. However, for a stump age between 80-150 years, they found a substantial decrease in sprout number. The age of the stand at the time of harvest has a considerable effect on the ability of that stand to regenerate a sufficient number of oak seedlings and sprouts to ensure that oaks will recapture the canopy and remain the dominant species.

Due to the increased competition from species such as maple, yellow poplar, and beech, there is concern over whether oaks will remain the dominant species in hardwood forests in the future. McGee (1984) found that on average and productive sites, established oak seedlings in the understory were unable to capture small or large canopy gaps. The slow growth of oak seedlings has been found to occur even under ideal light conditions. Defoliation and browsing damage by deer decreases the abundance and performance of oak regeneration, and can change the structure and composition of the understory (Healy, 1997). Insects can also contribute to the decline of oak regeneration. The gypsy moth can cause dramatic defoliation of oaks across the US, and the oak weevil has been known to infest up to 90% of acorns produced in a year (Gibson, 1982). Soil properties have been found to influence forest composition and growth. Soil texture, litter depth, pH, and soil moisture may not directly lead to regeneration declines, but they do have an effect on the germination, growth and mortality of hardwood species (Meredieu et al., 1996; Meiners et al., 1984).

Past research has indicated two primary hypotheses concerning oak regeneration. First, the amount of oak regeneration should increase with the presence of fewer numbers of potential competitors. Secondly, oak regeneration is more successful on drier, poorer soils, warmer aspects, and upper slope positions where competitors are limited by growing conditions.

Most oak research has focused on different management techniques for releasing advanced reproduction that is already established. Fewer studies have investigated the underlying factors that affect the presence, absence, and abundance of oak advanced reproduction available for subsequent management. This is the first study of this kind to take place in the Ridge and Valley Province. Information on oak reproduction patterns and underlying factors is needed by forest managers to identify sites best suited for oak management. In addition, this information may allow identification of effective methods for enhancing the abundance of oak advanced reproduction prior to application of competition control and release treatments.

Objectives

The overall objective of this study was to determine and model site factors and environmental conditions that contribute to the successful establishment and growth of oak seedlings in selected East Tennessee forest types. To make the transition from regional to local factors leading to successful oak regeneration, the focus was on site characteristics such as soils, light, topography, seedling density (for oaks and competitors), canopy cover, and canopy composition. Hypotheses generated from past research were tested on a local level in the Ridge and Valley Physiographic Province of Eastern Tennessee. Specific questions investigated in this study were: 1) how do the soil associations of the region enhance or inhibit oak regeneration; 2) how does landform position affect the distribution, reproduction, and growth of selected oak species; 3) what type of canopy and stand structure promotes oak regeneration; 4) what potential competing species most influence the establishment and growth of oak seedlings; 5) does percent slope influence species composition on a site; and 6) does litter depth play an important role in the successful establishment of oak seedlings?

Literature Review

Economic Importance of Oak

Red oaks and white oaks are among the hardwoods in highest demand in both the domestic and international forest product market (Araman, 1988). The hardwood forests of the Eastern United States make up approximately 52% of the total commercial forestland in the United States (Clark, 1986). Within these hardwood forests, the oak-hickory forest type is the most valuable and most common, accounting for 44% of the eastern hardwood acreage (Clark, 1986; Probst, 1979). The Appalachian region of the United States (which includes MO, IN, IL, OH, KY, eastern TN, western NC, VA, WV, PA, NJ, NY, MD, and DE) produces over half of the red oak (*Quercus rubra*) sawtimber in the eastern U.S. (Luppold, 1997). In 1985, Araman (1988) compiled resource evaluation reports for the eastern U.S. states to determine the species composition and quality of eastern hardwood sawtimber. He found that 32% of the sawtimber sized trees inventoried were the species in high demand. Of this percentage of sawtimber, 59% were selected oaks. Fifteen percent of the selected species in demand are log grade 1, 24% were log grade 2, and 61 % were log grade 3 and 4. These results indicate that over half of the U.S. hardwood output is made up of lesser quality material.

The forest products industry, especially oak products, is very important to the economic well being of Tennessee. Approximately 55% (14 million acres) of the total land area of Tennessee is forested, with 89% consisting of hardwood forest type (Vissage and Duncan, 1990; Schweitzer, 2000b; Idassi et al, 1998). Eighty percent of the hardwood forest type in Tennessee is of the oak-hickory group (Schweitzer, 2000a).

According to Stratton and Wright (1999), the hardwood output in the eastern region is responsible for 12% of the total roundwood output for the state, with red oak and white oak (*Quercus alba*) representing 50% of the total hardwood output. In 1994, the forest products industry directly employed 69,811 and indirectly employed 162,886 people in the state of Tennessee (Idassi et al., 1998).

Ecological Importance of Oak

Oaks are ecologically important mainly because of their ability to supply food and shelter to a wide array of wildlife species. According to Martin et al. (1951), oaks are a food source for over 96 species of waterfowl, songbirds, fur and game animals, small mammals, and hoofed browsers. In the eastern portion of the United States, oaks contributed 10-25 % of the diet of ruffed grouse (*Bonasa umbellus*), nuthatch (*Sitta* spp.), brown thrasher (*Toxostoma rufum*), thrush (*Catharus* spp.), red-headed (*Melanerpes erythrocephalus*) and red-bellied woodpecker (*M. carolinus*), and fox squirrel (*Sciurus niger*); over 25 % of the diet of wood duck (*Aix sponsa*), wild quail (*Colinus virginianus*), blue jay (*Cyanocitta colliei*), black bear (*Ursus americana*), raccoon (*Procyon lotor*) , gray fox (*Urocyon cinereoargenteus*); and over 50% of the diet of white-tailed deer (*Odocoileus virginianus*). Van Dersal (1940) determined that the various parts of oaks provide 186 animal species with nourishment.

In a study to determine the brood habitat preference for wild turkey (*Meleagris gallopavo*) in West Virginia, Pack et al. (1980) found that 17 out of 19 broods preferred white oak forest type. There seemed to be an avoidance of white pine (*Pinus strobus*), chestnut oak (*Quercus montana*), and Virginia pine (*Pinus virginiana*) forest types.

Overall, none of the turkey broods preferred a conifer forest type. They concluded that this preference might be due to the lack of understory vegetation in some conifer stands and the dense understory vegetation in others. Gill et al. (1975) compared the habitat preferences of white tailed deer, gray squirrels, ruffed grouse, and turkeys in seven different forest types (yellow pine, oak-pine, red oak-scarlet oak, white oak-red oak-hickory, mixed hardwood, and white pine) in West Virginia. Within these forest types, turkeys preferred oak forest types, deer favored oak-pine, and squirrels preferred mixed hardwood.

History of the problem

Foresters began to notice a problem regenerating oak as early as the 1930's. In fact, Kortsian (1927) made reference to oak regeneration problems when looking at the factors that affect the germination and early survival of northern red oak in the mid-1920's. Early observations were centered on noticing that stands previously dominated by oak were returning as stands dominated by more shade tolerant and fast growing species such as maple, yellow-poplar, ash (*Fraxinus* spp.), and black cherry (*Prunus serotina*) (Clark, 1993; Lorimer, 1984, 1993; McGee and Hooper, 1975).

Gammon et al. (1960) reported on the seven-year re-establishment of a mature northern red and white oak dominated forest after a clearcut in 1950. Seven years later, the main canopy was made up of (in order of abundance) white ash (*Fraxinus americana*), sugar maple (*Acer saccharum*), American elm (*Ulmus americana*), black cherry, and red maple (*Acer rubrum*). White oak did not produce a significant amount of seedlings or sprouts for representation in the canopy. Northern red oak seedlings were established, but by the end of seven years of growth, none were present in the largest sapling size class. Also, while the red oak sprouts were the most abundant and fastest growing sprouts in the new regeneration, only 22% of the original sprouts from the second year of growth survived to the seventh year.

To examine the effects of different levels of cutting intensity on early reproduction, Trimble and Hart (1961) selected three site quality classes (excellent, good, and fair) with site index 80, 70, and 60 respectively. Four cutting regimes (clearcut, diameter limit cut, extensive selection cut, and intensive selection cut) were assigned to each site class. Prior to cutting, it was observed that as site index decreased, oak increased in abundance, while sugar maple, yellow-poplar, beech, and red maple dominated the better quality sites. Five years after cutting, oak regeneration was essentially absent from excellent sites, but was reasonably abundant on the low quality sites. Ten years after the cuttings, small and large reproduction was dominated by sugar maple, yellow-poplar, and black locust (*Robinia pseudoacacia*) on all cutting intensities. In general, heavier cuttings seemed to favor intolerant species, such as oak, while the lighter selection cuts favored tolerant species.

In West Virginia, Weitzman and Trimble (1957) found that oak regeneration was more widespread on medium to poor sites. There was a decreasing proportion of oak with increasing site quality. For example, for site index 80 for oak, only 3% of the established regeneration was oak, even though 32% of the original overstory was made up of oaks. They concluded that oaks are able to maintain their dominance on sites with site index of 65 or lower, mainly due to the lack of competition associated with poorer sites as compared to better quality sites.

Once research on adequate oak regeneration began, researchers began to notice that the continual absence of oak in the upper canopy after cutting or disturbance is not necessarily caused by lack of seed production (Kortsian, 1927; Tryon and Carvell, 1958), but more of a seedling establishment problem (Beck, 1993; Johnson, 1979). Carvell and Tryon (1961) examined factors that affect acorn production and establishment. It was determined that differences in the amount of regeneration occurring on two sites were the result of individual site factors affecting the acorn after it had fallen. A difference was also found in establishment success between oak species. White oak acorns were more successful in establishment than red oak, although their abundance decreased with increasing height. Kortsian (1927) discovered that approximately 99% of all acorns produced by one white oak in North Carolina were either destroyed by animals and insects or are were naturally aborted. Less than one percent actually germinated, some of which later died.

By the 1970's, researchers were very aware of the regional oak regeneration problem and many more studies on the problem were initiated (Lorimer, 1993). Sander (1971) found that a relationship exists between the vigor of an oak sprout and the diameter of the sprout. For an oak sprout to successfully compete for the canopy of a new forest, the advance regeneration prior to cutting must be at least 0.5 inches diameter at the ground line.

In a study in the Southern Appalachians, McGee and Hooper (1975) observed that a mixed hardwood stand that was dominated by oaks before a clearcut developed into a stand dominated by (in order of abundance) black locust, yellow-poplar, sweet birch (*Betula lenta*), and red maple. Before the clearcut, there were 1,450 northern red oak seedlings per acre. Ten years later, only 10 northern red oak seedlings were free to grow. Black oak (*Quercus velutina*), chestnut oak, and white oak were also present prior to the clearcut, but they performed no better after ten years. Later Beck and Hooper (1986) completed a follow up study to see if the trends had changed. The four species that dominated the stand ten years earlier continued to dominate the stand, but the species had shifted in dominance. In 1983, yellow-poplar now represented 80% of the stems in the 8-inch diameter class. Black locust and red maple followed with 11% and 5% of the stems in the same diameter class, respectively. The once dominant sweet birch now had most of its stems in the 2 to 4-inch diameter classes. Oaks represented less than 7% of the stems in the larger diameter classes, with northern red oak absent altogether.

Johnson (1976) measured the survival, height, and success of different hardwood species interplanted in a clearcut. Overall, sugar maple, red maple, and white ash continually grew faster than all other planted species on all sites. Even though the red oak seedlings were fairly tall at the time of planting, they exhibited the lowest success rate and the most variation in survivor height of all species planted.

Lorimer (1984) proposed that the succession of oak forests is due to red maple dominance, i.e., the combined effect of a lack of disturbance in oak forests and high shade tolerance has allowed the suppressed red maples in the understory to occupy the canopy after the death of an overstory oak.

Causes and Evidence of Decline

Acorn predation/production

Annual seed crops for oak are very erratic, ranging from zero to 250,000 acorns per acre in any one location, in any one year (Beck, 1993; Lorimer, 1989; Beck and Olson, 1968; Gysel, 1957). Good seed years occur anywhere from every 2 to 10 years (Oak, 1993; Beck, 1977; USDA, 1974; Goodrum et al., 1971). Many factors contribute to erratic acorn production (Beck, 1993). There is still much debate on whether or not flower formation effects the production of seed. Variables such as temperature, relative humidity, precipitation, and wind affect the process of pollination, which will in turn affect the amount of seed produced by an individual. In Louisiana, Goodrum et al. (1971) found that after a late freeze at the time of fruit setting, both white oak and black oak groups showed a definitive decrease in acorn yield. Even though these environmental factors do affect acorn production, the amount of available resources is thought to be the most limiting factor that affects the amount of seed production (Stevenson, 1981). Herbivory, defoliation, and leaf shading affect resource availability by suspending the flow of nutrients from the leaves to the fruits.

Insects have a major impact on oak regeneration success. The most damaging insect is the oak weevil (*Curculio* spp.) (Oak, 1993; Gibson, 1982; Beck and Olson, 1968). Oak weevils, whose larvae consume the meat of the acorn, have been known to infest more than 90% of acorns collections. Not all acorns infested by oak weevil larvae are nonviable, but those that germinate will most likely develop into abnormal, slow growing seedlings (Korstian, 1927).

Gypsy moth larvae prefer oak to any other species group (Gottschalk et al., 1989). In New England, Campbell and Sloan (1977) found that gypsy moth caused 48% of the mortality occurred in the oaks and only 9% and 6% of white pine and red maple, respectively. In an overview of the impacts of the gypsy moth on the oak resources, Gottschalk et al.(1989) states that as the percent of oak within a forest increases, the defoliation and mortality caused by the gypsy moth increases. Defoliation by the gypsy moth makes oaks susceptible to secondary pest and pathogen invasions (predominantly *Armillaria* spp. and *Agrilus bilineatus*). The first response of oak after defoliation is to refoliate. This utilizes stored reserves and further weakens the tree. Once secondary organisms invade, tree mortality is inevitable.

The "acorn moth" (*Valentinia glandulella*) is a secondary insect pest, or a scavenger, of acorns (Gibson, 1982; Galford, 1986). The larvae infest sprouting acorns and feed on the nutmeat of the acorn, but the larvae are only occasionally detrimental to the acorn. Galford (1986) found that *V. landulella* only reduced nutrient availability for seedling establishment. Interestingly, he found high infestation rates by nitidulids of previously *V. glandulella* infested acorns. Nitidulids then killed the germinating seedling by consuming the remaining nutmeat.

Acorn consumption by wildlife (mostly deer and rodents) is a limiting factor in many areas. In the Southern Appalachians the average acorn production was 289 lbs/ac per year, of which 65% were sound (Beck, 1977). Within a 12 year period, acorn production varied considerably, with 500 lbs/ac produced for 4 out of 12 years, 75-220 lbs/ac for 5 years, and less than 30 lbs/ac for 3 years. Acorn production less than 200 lbs/ac is usually completely consumed by wildlife (Johnson et al., 1989).

Acorns are the most important food source for white-tailed deer in the southern Appalachians during the fall and winter months (Johnson et al., 1995). During this period, 20-50% of their diet consisted of acorns, which varied depending on the size of the annual acorn crop (Johnson et al., 1995). In Pennsylvania, Marquis et al. (1976) found that insects, rodents, and white-tailed deer greatly impacted the amount of oak regeneration occurring on two sites. The inadequate amount of oak regeneration was caused not only by lower acorn production, but also by a higher incidence of rodent and insect predation. The two insects with the greatest effect on oak regeneration in their study were the oak weevil and a moth (*Melissopus latiferreanus*). The average germination rate was less than 10 percent on these sites.

Although acorns are a preferred food source for many wildlife and insect species, there have been a number of studies that have found that insect infestation, wildlife predation, and erratic acorn production do not fully explain the occurrence of regeneration failures (Lorimer, 1989). Factors that affect the amount of acorn production are age, bole diameter, and crown size and position (Beck, 1993; Goodrum et al., 1971). Many oak species do not begin producing seed until 20 to 25 years of age (USDA, 1974). In the upper coastal plain of Louisiana and east Texas, Goodrum, et al. (1971) found that there was a significant increase in acorn production for trees older than 40 years. A positive linear relationship was found between stem size and mast production. For all oak species studied, there was not only an increase in acorn yield as tree diameter increased, but also a larger percentage of trees produced acorns. Oaks in closed canopy stands produced fewer acorns than trees in more open stands. Oaks with large crown widths and/or in dominant crown positions enhanced acorn yields (Beck, 1993; Goodrum et al., 1971; Burns and Christisen, 1954). Seventy-five percent or more of the trees in the co-dominant and dominant crown classes produced acorns, while only 38% of trees in the intermediate and 9% of the trees in the suppressed classes produced acorns (Drake, 1991).

Seedling Predation

Deer tend to consume the tender, new stem growth of seedlings during spring and summer (Johnson et al., 1995). The timing of this browsing causes slower growth and poorer form for surviving seedlings. In the southern Appalachians over 50% of white-tailed deer diet consisted of leaves and stems during the spring. Oaks are among the most commonly browsed species, along with red maple, *Smilax* spp., sourwood (*Oxydendrum arboreum*), and yellow-poplar (Johnson et al., 1995). The combination of intensive deer browsing, insect and disease damage, drought, and increased competition can greatly increase the occurrence of regeneration failure (Trumbull et al., 1989).

Pennsylvania forests support a high deer population and most of the research on deer browsing effects on forests has been focused in that area (Lorimer, 1993; Marquis and Brenneman, 1981). The Allegheny hardwood forests have experienced severe browsing from deer over the years that effects regeneration establishment three ways: 1) due to preferential browsing by deer, there is insufficient stocking of commercial tree species; 2) seedling establishment takes longer, which delays a financial return on the stand; and 3) the new regeneration will consist of lesser-valued species.

Selective browsing changes the structure and composition of the understory (Horsley and Marquis, 1983; Strole and Anderson, 1992; Trumball et al., 1989). A study on white-tailed deer in central Illinois determined that deer favored white oak seedlings, while sugar maple was a less preferred species. In central Massachusetts, stands with higher deer densities had fewer seedlings per hectare, fewer tall seedlings, and lower species richness (Healy, 1997). More specifically, in the stands with higher deer densities, there was an absence of oak seedlings in the 100 + cm height class, and only 2 out of 8 stands contained oak seedlings in the 30-99 cm height class. The area, which had been heavily forested for some time, had begun to take on characteristics typical of a savanna.

Tilghman (1989) found that blackberry cover in thinned stands on the Allegheny Plateau was greatly reduced when deer densities were high, while the less preferred fern species were higher. The presence of a dense fern layer decreased the survival and growth rates of seedlings (Horsley and Marquis, 1983). Deer prefer to browse woody stems over grazing grasses and forbs (Trumball et al., 1989). An increased herbaceous layer out competes oak seedlings for available light and nitrogen, decreases seedling growth or completely displaces seedlings.

Fire

Historically, fire has been very important to the development of oak forests (Abrams, 1992; DeVivo, 1991; Van Lear and Watt, 1993; Crow, 1988; Lorimer, 1985). The use of fire across the eastern United States has been documented by European explorers as far back as pre-settlement times (DeVivo, 1991; Lorimer, 1993). Native Americans used fire to create grasslands favored by preferred wildlife, to clear land for agriculture, to protect villages from wildfire, to flush wildlife, and to attain desired vegetation (DeVivo, 1991). During the post-settlement era (1750-1930) fire was heavily used in agriculture (Lorimer, 1993). Fire was used to remove forest vegetation for farmland and grazing. The frequent use of fire by Indians and early settlers may have secured oak as the dominant forest cover type (Abrams, 1992).

In the Great Smoky Mountains, Harrod and White (1999) investigated why shade tolerant species were replacing the oak and pine forests. They determined that the 10 to15- year fire rotation typical of the 19th and early 20th century limited the recruitment of fire sensitive, shade tolerant species. These frequent fires favored oaks and pine because they created an open canopy and a thin litter layer that permitted rapid growth. The decrease in fire frequency created a denser canopy and allowed shade tolerant species, like white pine and red maple, to survive.

Oaks are adapted to fire due to their thick bark that protects the stem from fire damage, rot resistant wood that protects the stem from decay after scarring, and rootstocks that will repeatedly resprout after fire. Seedbeds created by fire also enhance acorn germination. Other competing species are less adapted to fire. Barnes and Van Lear (1998) found that the rootstock densities for oaks were continually larger in the burned treatments than in the unburned treatments, with 8,000 per acre and 2,500 per acre respectively. Larger rootstocks and larger root-shoot ratios allow oaks to resprout after being top-killed by fire, while competing species are killed. The presence of fire in a stand will reduce the litter layer, which is not only preferred by squirrels and blue jays for acorn burial, but also facilitates emergence of freshly germinated seedlings (Van Lear and Watt, 1993). The repeated consumption of the forest floor reduces the moisture content of the soil, thereby xerifying the site and enhancing oak establishment (Barnes and Van Lear, 1998). When compared to competitors, oaks are better adapted to drier sites. Oaks are adapted to drought conditions because of their deep root system, xeromorphic leaves, low water potential threshold for stomatal closure, and their ability to adjust osmotically (Abrams, 1990). Oak replacement tends to be slower and the occurrence of later successional species is less frequent on the more xeric sites (Abrams, 1992).

Fire suppression programs were implemented in the 1930's by the Federal and State Forestry agencies. Since implementation, these programs have lead to the continual decline of oak presence in future stands (Lorimer, 1993; Abrams, 1992; Van Lear and Waldrop, 1989). As a result, fire intolerant species (such as maple, beech, yellow-poplar, and blackgum) established themselves and are now of a size that they are no longer sensitive to fire (Van Lear, 1991). Another effect of decreasing fire frequency is canopy closure that results in more mesic, shady conditions that allow the growth of shade tolerant species (Crow, 1988). Their establishment in the understory makes it harder for oak seedlings to maintain dominance in the canopy after a disturbance.

Since it was realized that fire is beneficial to oak, researchers have been studying the effects of fire frequency, intensity, and timing on establishment and competition removal. After forty years of burning mixed pine-hardwood stands in the lower South Carolina coastal plain, hardwood sprouts were highly affected by season and frequency of burn (Waldrop and Lloyd, 1991). The annual summer burn was the only burning regime that eliminated hardwood sprouts, while the periodic winter and summer, and annual winter burns allowed enough time for sprouts to replenish carbohydrate reserves to resist mortality. In a similar study, annual winter burns reduced the growth vigor of hardwood sprouts and might lead to the eventual elimination of hardwood regeneration (White et al., 1991).

Comparing the impact of seasonal fires on oak regeneration, Brose and Van Lear (1998) found that a single spring fire reduced the mid-story and understory the same degree as three winter burns. The two most important competitors of oak were yellow-poplar and dogwood, which were significantly reduced by the presence of fire. In the spring burn, 83% of the oak seedlings were not damaged, while 33 and 56% of the yellow-poplar and dogwood seedlings showed no damage, respectively. In the winter burns, 70% of the oaks showed no damage, while only 8 and 16%, respectively, of the yellow-poplar and dogwood seedlings showed no damage. Brose et al. (1999) studied the effects of prescribed fire on oak regeneration in post-harvest conditions on productive upland sites in the Piedmont region of Virginia. After a shelterwood cut, pre-burn vegetation conditions showed that yellow-poplar was more abundant, faster growing, and taller than oak seedlings. After burning, oak regeneration density was three times greater than in the control plots. There was a greater amount of oak regeneration in the high-intensity spring burn and the low-to-medium summer burn than in other burn treatments. Evidently, oak was in a more competitive position after all burn treatments.

Competition

Oaks are generally considered to be intolerant or intermediate in tolerance of shade (Abrams, 1992; Burns and Honkala, 1990). A slow growth rate is typical of oak seedlings grown under heavily shaded conditions (Lorimer et al., 1994). The total absence of light causes the death of the apical meristem, although the axial buds are still able to develop, resulting in stunted, bushy growth. Shade also leads to small, poorly developed leaves, which affects the potential rate of photosynthesis that could occur (Axelsson et al., 1979). When compared to shade tolerant species, oaks have a higher light compensation point for photosynthesis, i.e., they require higher light intensities, longer periods of light, and/or a better quality of light (Loach, 1967; Woods and Turner, 1971; Teskey and Shrestha, 1985). Light intensities near the forest floor of hardwood stands are often below the compensation point for oaks due to the dense main canopy or the continuous mid-canopy (Hodges and Gardiner, 1993). Understory vegetation has been found to negatively impact the survival of oak seedlings, possibly more so than the main canopy (Lorimer et al., 1994; Beck, 1970; Sander, 1972). The removal of tall understory lead to an oak seedling survival rate of more than 70%, while undisturbed sites had less than 7% of the planted oak seedlings survive (Lorimer et al., 1994). Oak seedlings present on sites with understory removal showed an increase in height growth, whereas undisturbed sites had oak seedling heights that decreased or stayed the same.

Oaks are poor competitors on good sites due to slow initial growth, as well as shade intolerance. Slow juvenile growth is caused by a conservative growth strategy where oak seedlings divert photosynthetic resources to root system development prior to shoot growth (Immel et al., 1978; Crow, 1988; Dickson, 1991; Lorimer, 1993). Stem growth and biomass accumulation for cherrybark oak (*Quercus pagoda*) were greatest under moderate light conditions, while the largest root-shoot ratio was associated with the seedling grown in full sunlight and lowest under moderate sunlight (Gardiner and Hodges, 1998). The growth strategy that allows oaks to dominate xeric sites results in their inability to rapidly respond to release on good sites (Hodges and Gardiner, 1993;

Gardiner and Hodges, 1998). Seedlings that establish below closed canopies generally do not respond when released due to physiological and morphological characteristics (Hodges and Gardiner, 1993). Canopy gaps are quickly dominated by shade tolerant species in the understory that can acclimate more rapidly and more efficiently to newly available space and nutrients. Oaks tend to be inflexible in open environments, i.e., they do not respond fast enough to release to compete with shade tolerant species. Budbreak and leaf development was earlier for oaks grown under shaded conditions (McGee, 1975, 1986). Earlier budbreak and leaf expansion exposes the seedlings to frost damage, which will delay stem growth when the canopy is removed.

Tolerance Differences Between Species

White oak and chestnut oak are categorized as being of intermediate shade tolerance (Burns and Honkala, 1990). However, they are more tolerant of shaded conditions than northern red oak, black oak, and scarlet oak (*Q. coccinea*). Ashton and Berlyn (1994) conducted a study comparing the physiology of black oak, northern red oak, and scarlet oak in different light qualities. All three species exhibited increased stomatal conductivity with increasing amounts of photon photosynthetic flux (PPF). Black oak increased stomatal conductivity the most, followed by scarlet oak, then northern red oak. Black oak was the most light demanding and the most drought tolerant, while northern red oak was the most shade tolerant and least drought resistant. Overall, black oak had the highest level of plasticity and northern red oak the least, suggesting that black oak had the best ability to adapt to changing environments.

II. Methods

Stand Types and Study Region

All stands had oak as the dominant canopy species and had not been significantly disturbed (natural or human) within the last 50 years. All stands were sampled between June and early September of 1999. Mature mixed oak/hardwood stands were sampled within five counties of the Ridge and Valley Physiographic Region of Tennessee, also known as The Great Valley of East Tennessee (Figure 1). The Ridge and Valley is one of nine general soil areas in Tennessee and constitutes 18 percent of the total land area in Tennessee (Springer and Elder, 1980). The region is characterized by its folded rock formations oriented in a northeast-southwest direction, comprising nearly five million acres of land.

There are seven soil provinces within the region, each further divided into soil associations (Table 1). Three soil provinces were not sampled because either the land was mostly in agriculture or of limited extent. There were a total of eight different soil associations within the four soil provinces sampled. Two of the eight soil associations were not sampled due to soils such as calcareous shales and calcareous sandstones that were not characteristic of the other soils in the region. Therefore, six different soil associations were sampled within the four soil provinces included in this study. The research focused on soil associations that had a reasonable amount of forest acreage and also had a good probability of supporting stands that met the criteria above. The different soil associations in the Ridge and Valley region, as well as characteristics of the soils are summarized below (Tables 1 and 2).

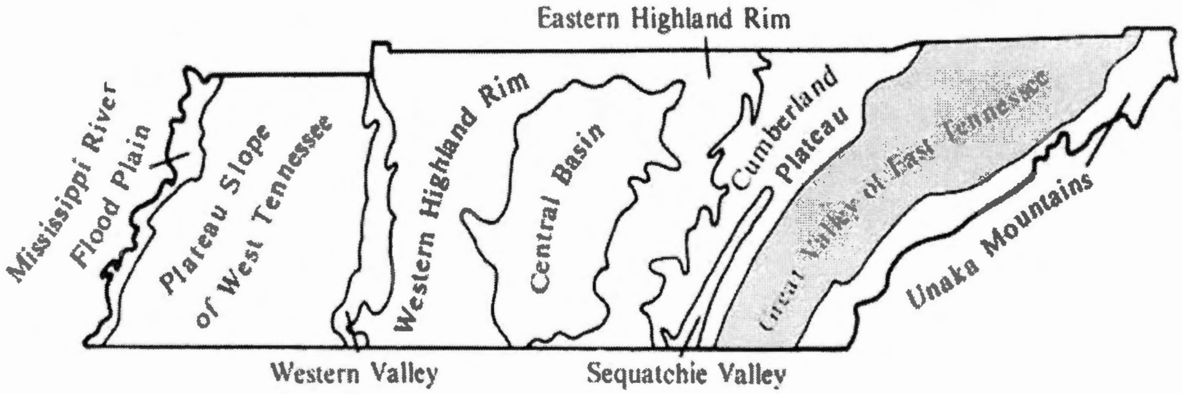


Figure 1. Map of Tennessee delineating the nine different Physiographic regions. The shaded area denotes the Ridge and Valley region of Tennessee, in which this study took place. *Source: E.T Luther(1977).*

Table 1. Area covered by each soil association in the Ridge and Valley Physiographic Province. Adapted from Springer and Elder, 1980.

Symbol	Soil Association	Acreage	Percent Area*
J11	Fullerton – Dewey	782,900	16.4 **
J12	Fullerton – Bodine	510,000	10.7
J21	Dunmore – Dewey	767,200	16.1
J31	Decatur – Dewey – Waynesboro	314,300	6.6
J32	Waynesboro – Etowah – Sequatchie – Allen	207,200	4.3
J33	Waynesboro – Allen – Sequatchie - Statler	48,600	1.0
J34	Holston – Monongahela	117,100	2.5
J41	Dandridge – Needmore - Whitesburg	437,200	9.2
J51	Talbott – Rock Outcrop – Etowah	205,700	4.3
J52	Litz – Sequoia – Talbott	212,900	4.5
J53	Talbott – Sequoia – Dandridge	42,800	0.9
J61	Wallen – Talbott – Montevallo	767,600	16.1
J62	Ramsey – Wallen – Jefferson	160,000	3.3
J71	Tellico - Alcoa	202,900	4.2

* percentage of area covered by soil association in the Ridge and Valley Region
** shaded regions denote soils sampled in this study

Table 2. Comparison of the soil associations in the Ridge and Valley Physiographic Province sampled in this study. Adapted from Springer and Elder, 1980.

Soil Symbol	Parent Material	Landscape	Soil Productivity	Annual Precip. (in)	Temp. (°C)*
J11	Dolomitic Limestone	Hilly and rolling	Mod. High	53	1 | 57
J12	Dolomitic Limestone	Hilly	Strongly acid; low fertility	54	17 | 58
J21	Dolomitic Limestone	Rolling and hilly	Mod.	42	16 | 57
J51	Clayey Limestone	Undulating to hilly	Mod.	55	19 | 59
J52	Shale	Undulating and rolling	Mod.; lots of coarse fragments	55	19 | 59
J61	Sandstone, Shale, & Dolomitic Limestone	Steep ridges and rolling valleys	Low; shallow soil	53	20 | 61

* first number is mean temperature in January, sencond number is mean July temperature.

Soil Associations

J11: Fullerton-Dewey

The Fullerton-Dewey soil association covers 782,900 acres of land, or 16%, in the Ridge and Valley Province (Springer and Elder, 1980). The main soils are clayey, kaolinitic Paleudults, formed from dolomitic limestone. They are well-drained, strongly acidic and highly leached. The 30-year mean temperature (hereafter referred to as the normal temperature) varies from 1°C in January to 57°C in July. Fullerton- Dewey soils are loamy soils with moderately high productivity (USDA, 1969). The landscape is generally hilly and rolling, with a few areas of choppy hills and steep ridges (Springer and Elder, 1980). The average annual precipitation is 53 inches as measured at the nearest weather station (Owenby and Ezell, 1992). Upland oaks, yellow-poplar, and shortleaf pine are common species adapted to these soils (USDA, 1969). This soil association was sampled in Union County on the Chuck Swan State Forest and Wildlife Management Area.

J12: Fullerton-Bodine

The Fullerton-Bodine soil association comprises 11% of the soil in the Ridge and Valley, covering a total of 510,000 acres (Springer and Elder, 1980). The main soils are clayey, kaolinitic and loamy skeletal, siliceous Paleudults. Fullerton-Bodine soils are cherty silt loams derived from dolomitic limestone. They are generally well drained, strongly to very strongly acidic, low on natural fertility, and highly leached. At the Oak Ridge weather station, the normal temperature ranges from 17.2°C in January to 58°C in July with an annual normal precipitation of 53.8 inches (Owenby and Ezell, 1992). The landscape consists of highly dissected rounded hills with moderately steep and steep hills with slopes between 15 and 45% (Springer and Elder, 1980). One-third of the land within this association is in hardwood forests. This association was sampled in Anderson County on Chestnut Ridge within the boundaries of the University of Tennessee Arboretum in Oak Ridge, TN.

J21: Dunmore-Dewey

The Dunmore-Dewey association makes up 16% of the soils in the Ridge and Valley, totaling 767,200 acres in area (Springer and Elder, 1980). The main soils are clayey, kaolinitic Paleudults. These deep and well-drained soils with reddish clayey subsoils are derived from dolomitic limestone. Dunmore-Dewey soils are moderately productive silty clay loams that can be very rocky and highly eroded, depending on the slope (USDA, 1969). The landscape is typically low, rounded hills with frequent limestone sinks and depressions. This soil association was sampled on Miller Knob and Howard Ridge in Washington County, northwest of Jonesboro, TN. At the Greenville Experiment Station, in nearby Greene County, the normal temperatures are 16.3°C in January to 57.4°C in July with annual rainfall of 42 inches (Owenby and Ezell, 1992).

J51: Talbott-Rock outcrop-Etowah

The Talbott-Rock outcrop-Etowah association covers 4% of the land area in the Ridge and Valley or a total of 205,700 acres. The main soils are fine, mixed Hapludalfs; loamy Paleudults; and some Lithic Rendolls. These soils are deep to shallow and well drained derived from clayey limestone. The landscape consists of wide undulating to hilly valleys with steep, high ridges, with very little level land (Springer and Elder, 1980). The mixed hardwood forests remain on the rocky areas. The Talbott-Rock outcrop-Etowah soil association was sampled on White Oak Mountain in Bradley County, northeast of Chattanooga, TN. In nearby Cleveland, the normal temperature ranges from 18.7°C in January to 58.8°C in July with 54.65 inches of annual rainfall (Owenby and Ezell, 1992).

J52: Litz-Sequioa-Talbott

The Litz-Sequoia-Talbott association comprises 5% of the total land area in the Ridge and Valley, extending over 212,900 acres (Springer and Elder, 1980). This soil association was derived from shale with a few areas of limestone. The main soils are loamy-skeletal, mixed Dystrochrepts; clayey, mixed Hapludults; and fine, mixed Hapludalfs (Springer and Elder, 1980). The soils are strongly acid, with low to moderate available water capacity. The soils are moderately productive silty clay loams with large amounts of course fragments (USDA, 1969). The rocky soils are best suited for pines (USDA, 1969). The landscape for this sub-association is generally undulating and rolling. This soil association was also sampled along No Pone Valley in Bradley County and has the same temperature and moisture regime as the Talbott-Rock outcrop-Etowah association.

J61: Wallen-Talbott-Montevallo

The Wallen-Talbott-Montevallo association covers 767,600 acres, or 16% of the Ridge and Valley region (Springer and Elder, 1980). These soils were derived from sandstone, shale and dolomitic limestone. The main soils are loamy-skeletal Dystrochrepts; fine, mixed Hapludalfs; and clayey and loamy Hapludults. The shaly silt loams found in this soil association are less productive than the other soils because of the limited soil depth (USDA, 1969). The landscape consists of long, rolling valleys with high, linear wooded ridges. This soil association was sampled on Pine Ridge in Anderson County on the University of Tennessee Arboretum in Oak Ridge, TN. The normal temperature ranges from 17.2°C in January to 58°C in July with an annual normal precipitation of 53.8 inches (Owenby and Ezell, 1992).

Measurements

In each stand, a 60 m long by 5 m wide belt transect was laid out parallel to the contour (Figure 2). Two replicates of three transects were used to sample each soil association. For each replicate, one transect was assigned to a southeast mid-slope position, one was assigned to a northwest mid-slope position, and the remaining transect was assigned to the ridge top. The southeast or northwest-facing aspects coincide with the dominant orientation of the ridges in the Ridge and Valley Physiographic region. Two types of measurements were taken along each transect, site factor measurements and oak measurements. Measurements of site factors included percent ground cover, canopy profile, litter depth, litter composition, basal area, percent full photosynthetically active radiation (PAR), and percent canopy cover. All site factor measurements were recorded at three central points located at 10m, 30m, and 50m down the center of the transect, except for percent full PAR and canopy cover percent (Figure 2). Percent full PAR and canopy cover percent were recorded every 10m along the center of the transect. Data for

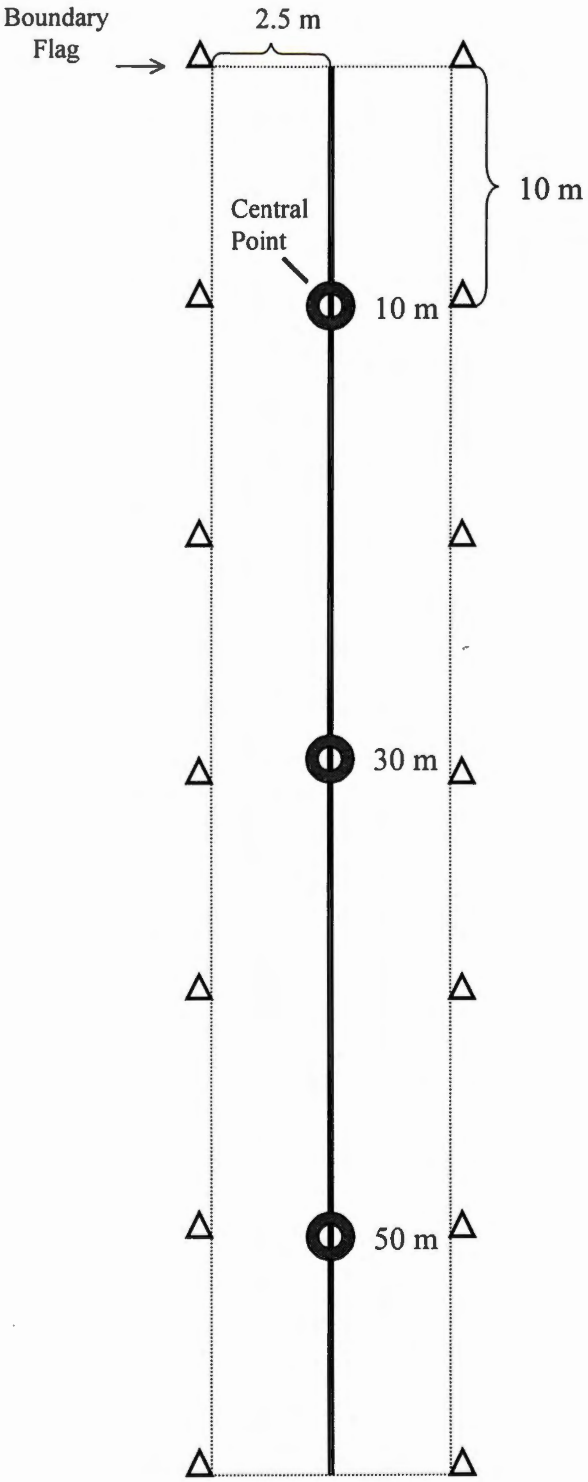


Figure 2. Transect design used for site factor measurements.

each measurement were averaged over the three plots, or five plots, to get one data point for each factor and transect.

Percent groundcover was measured by placing a m^2 quadrat frame over each central point (Figure 2) and recording all vegetation under 1 meter in height by species. The number of 10x10 cm areas covered by each species were estimated withing the frame. The count of the number of 10x10 cm areas covered by each species was then converted to percent cover, with one 10x10 cm area corresponding to 1% coverage. The canopy profile was determined by placing a height pole at each central point, extending the pole, and recording the heights of limbs, crown tops, and crown bases of all trees directly over the central point. The canopy profile was separated into two sections; upper canopy and mid- canopy. Upper canopy was defined as any canopy above 13 meters, while the middle canopy was defined as foliage between 4 and 13 meters above the ground. Litter depth was measured to the nearest centimeter at each central point. Litter composition was determined by recording the species of leaf litter within the m^2 quadrat. Basal area of the stand was determined with the use of a 10 BAF prism over each central point. The species and diameter at breast height for all 'in' trees were recorded. From the basal area measurement, importance values were calculated for each species on each transect using the method described in Krebs (1985). The importance value for species x is equal to the sum of the following equations:

$$\text{(a) Relative density} = \frac{\text{number of individuals of species } x}{\text{total number of all species}} \times 100$$

$$\text{(b) Relative frequency} = \frac{\text{frequency of species } x}{\text{sum of frequency values of all species}} \times 100$$

(c) Relative dominance = $\frac{\text{basal area of species } x}{\text{total basal area of all species}} \times 100$

Percent full PAR and percent canopy cover were measured every 10 m along the center of the belt transect. PAR consists of all wavelengths of light that are used in photosynthesis. PAR was measured using an AccuPAR ceptometer (Decagon; Pullman, WA) held one meter above the center points along the transect. Below canopy PAR was measured in eight compass directions and an average was recorded. A comparison of the total amount of sunlight that could be received to the amount actually received was made by taking three PAR measurements in the open prior to use under the canopy. The ratio of below canopy PAR to PAR in the open was used to calculate percent full PAR. Percent canopy cover was calculated using a CI-110 Digital Plant Canopy Imager, which measured the fraction of sky that was visible from beneath the canopy (CID, Inc.; Vancouver, WA). The Plant Canopy Imager was held one meter above the central point while facing north.

Oak reproduction was sampled along the entire area of the belt transect. The three plots used for these measurements extended 5m on both sides of the central transect line. Thus, three 5 x 20m subplots were created (Figure 3). Species and size class were tallied for all oak seedlings and saplings within each subplot. Oak seedlings were defined as any stem less than 1.5 m in height, while saplings were any stems greater than 1.5 m in height, but less than 8 cm in diameter. Oak seedlings and saplings were further seperated into four size classes: 1) 0-25 cm tall; 2) 26-50 cm tall; 3) 51-150 cm tall; and

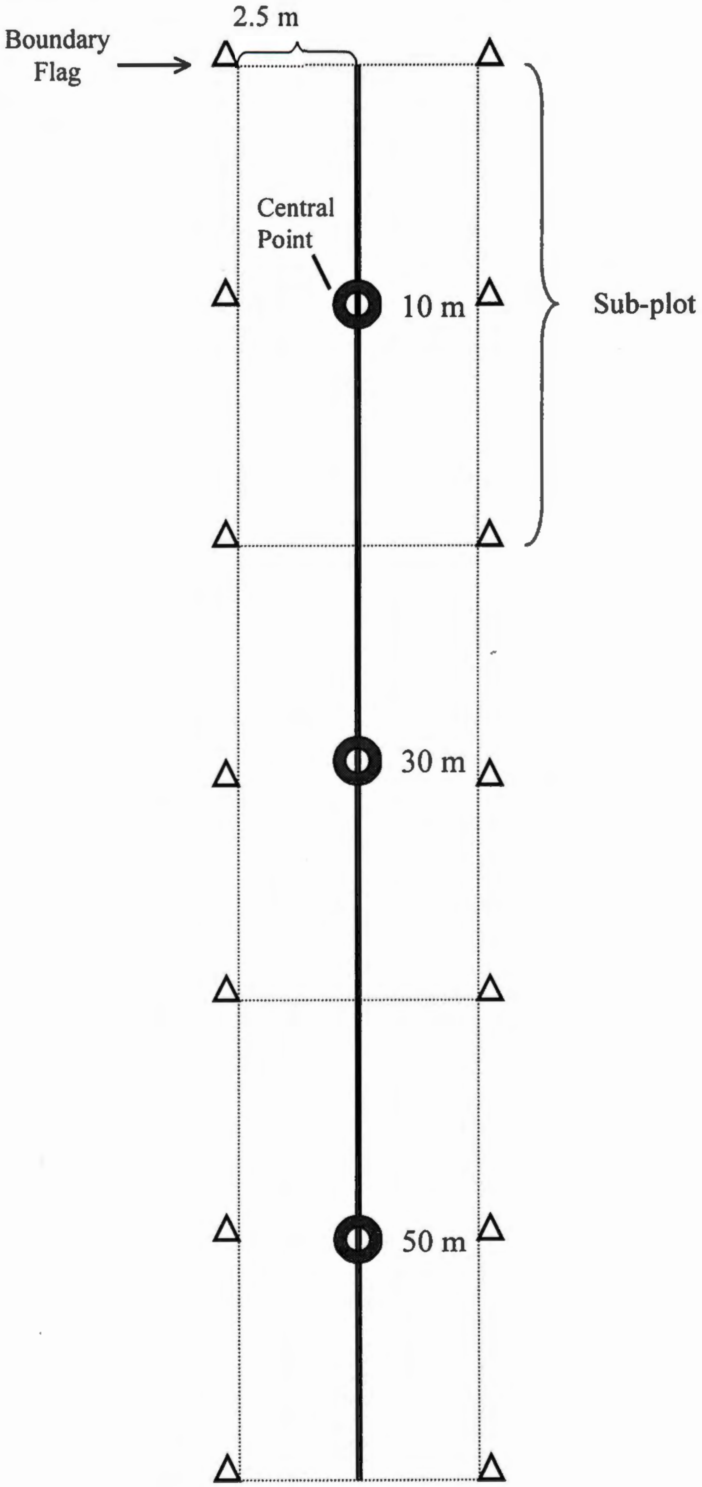


Figure 3. Transect design used for oak measurements.

4) greater than 150 cm tall, but less than 8cm dbh. For each oak seedling or sapling, origin (independent or sprout) and presence of browsing were also recorded. All competing species in the fourth size class within each 5m x 20m plot area were also recorded by species.

Data Analysis

Regeneration data were averaged over each transect and analyzed using Response Surface and General Linear Model (GLM) analysis (SAS Institute, 1999). Prior to Response Surface analysis, important variables were selected through R^2 Variable Selection (SAS Institute, 1999). Landform position and soil association were class variables and were not appropriate for variable selection or Response Surface analysis. Therefore, GLM was used. Preliminary analysis indicated that the class variables were important across all species and size classes. Thus, analyses were run within landform position-soil association combinations. R^2 Variable selection was conducted at the 90% confidence level, while Response Surface and GLM were conducted at the 95% confidence level. Separate models were created for each oak species due to differences in their habitat requirements, as well as for each size class of oak due to changing requirements at different life stages.

III. Results

R^2 variable selection indicated percent groundcover, litter depth, litter composition, and various potential competitors in the 4th size class were not significantly related to the amount of oak regeneration that occurred on the site ($P>.05$). Percent slope ranged from 0 to 58 % and was significant only in the all oak species and size classes combined and black oak models. Soil association was a significant variable ($P<.05$) in at least one size class for all oak species. Consequently, soil association was included in all the prediction equations for oak regeneration. Similarly, landform position was found to be significant for white oak, chestnut oak, and black oak and was also included in all equations.

Eight species of oak were encountered (white oak, chestnut oak, black oak, northern red oak, scarlet oak, southern red oak, post oak, and chinkapin oak). Post oak and chinkapin oak were removed from individual species analysis because of low abundance and spotty distribution, but were included in the total oak analysis. Scarlet and southern red oaks have similar habitat requirements and were represented in low numbers. Thus, they were analyzed in a combined group. Chestnut oak was the most abundant oak species throughout the region (Table 3). The scarlet/southern red oak group was the least abundant species group, without any saplings occurring in the largest size class. Oak abundance was greatest on the NW-facing slopes and least on the SE-facing slopes (Table 4).

Table 3. Total number of oak seedlings counted in each size class by species.

Species	**Size Class***				**Total**	**Percent**
	1st	**2nd**	**3rd**	**4th**		
Black Oak	1034	197	49	23	1303	10.7
N. Red Oak	806	220	65	17	1108	9.1
Chestnut Oak	6742	425	69	10	7246	59.3
White Oak	1675	318	49	11	2053	16.8
Scarlet & S. Red Oak	458	50	2	0	510	4.2
Total	10715	1212	237	65	12220	100

* 1st size class = 0-25 cm; 2nd size class = 26-50cm; 3rd size class = 51-150cm; 4th size class = >15cm in height, but <8cm dbh

Table 4: Total number of oak seedlings tallied by species and landform position.

Species	**NW**	**RT**	**SE**
Black Oak	271	739	293
N. Red Oak	614	242	252
Chestnut Oak	2950	2365	1931
White Oak	1144	191	718
Scarlet & S. Red Oak	334	100	76
Total	5313	3637	3270

NW = northwest-facing, midslope position
RT = ridgetop
SE = southeast-facing, midslope position

All Species and All Size Classes

A total of 12,220 oak seedlings were tallied over the 33 sample sites. The smallest size class comprised 88% of the total number of oak seedlings, while the tallest size class comprised only 0.5% of the total. Oak seedlings of all oak species and size classes were most common on the J51/ NW landform position-soil association combination and least abundant on the J51/ RT combination (Figure 4). The smallest size class seedlings were most abundant on the NW/ J51 combination and least abundant on the J51/ RT combination (Figure 5). On average, the total number of 2nd size class oak seedlings was most abundant on the J21/ NW combination and least abundant on the J51/ RT landform position/soil association combination (Figure 6). Third size class seedlings were most abundant on the J52/ SE combination and least abundant on the J11/ RT combination (Figure 7). The J52/ SE combination contained the highest average number of oak seedlings in the tallest size class, while no 4th size class seedlings were tallied on the J11/ SE, RT, NW; J12 / NW; J51/ NW; or J61/ SE, RT combinations (Figure 8).

Estimated regression equations for all species and size classes of oak regeneration combined are located in Table 5. The equations show that the amount of oak regeneration for all species and size classes decreased with an increasing number of hickory saplings. As shown in Figures 9A and 9B, the positive relationships between total amount of oak and average mid-canopy depth and chestnut oak importance value were weak.

Table 6 contains the significant model variables for the total number of oak seedlings of all species and size classes. Chestnut oak importance value was an important variable in the 1st and 2nd size classes, but not for the larger size classes. The relationship between 1st size class oak seedlings and chestnut oak importance value was slightly

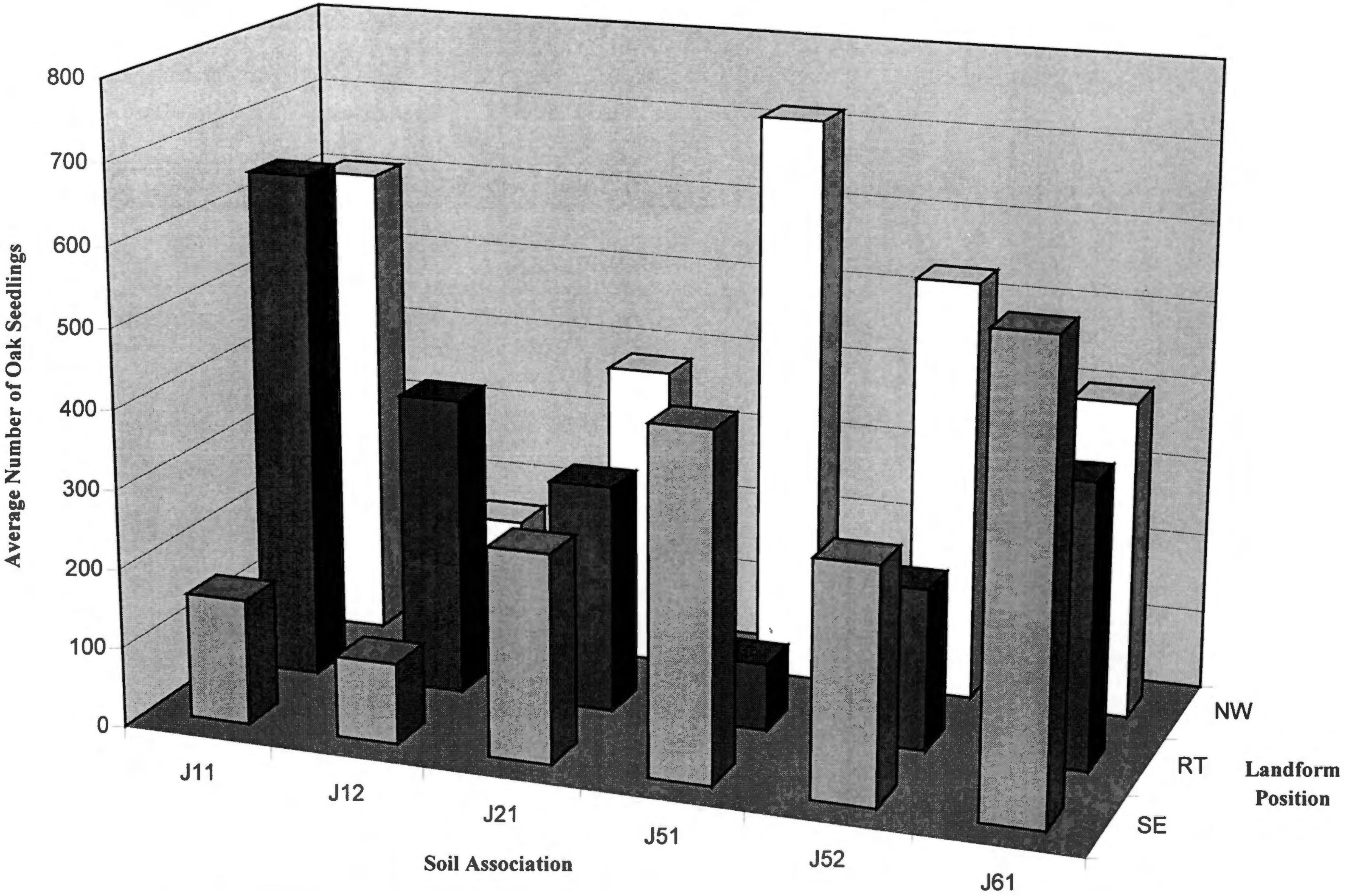


Figure 4. Number of oak seedlings (all species and size classes combined) by landform position and soil association combination.

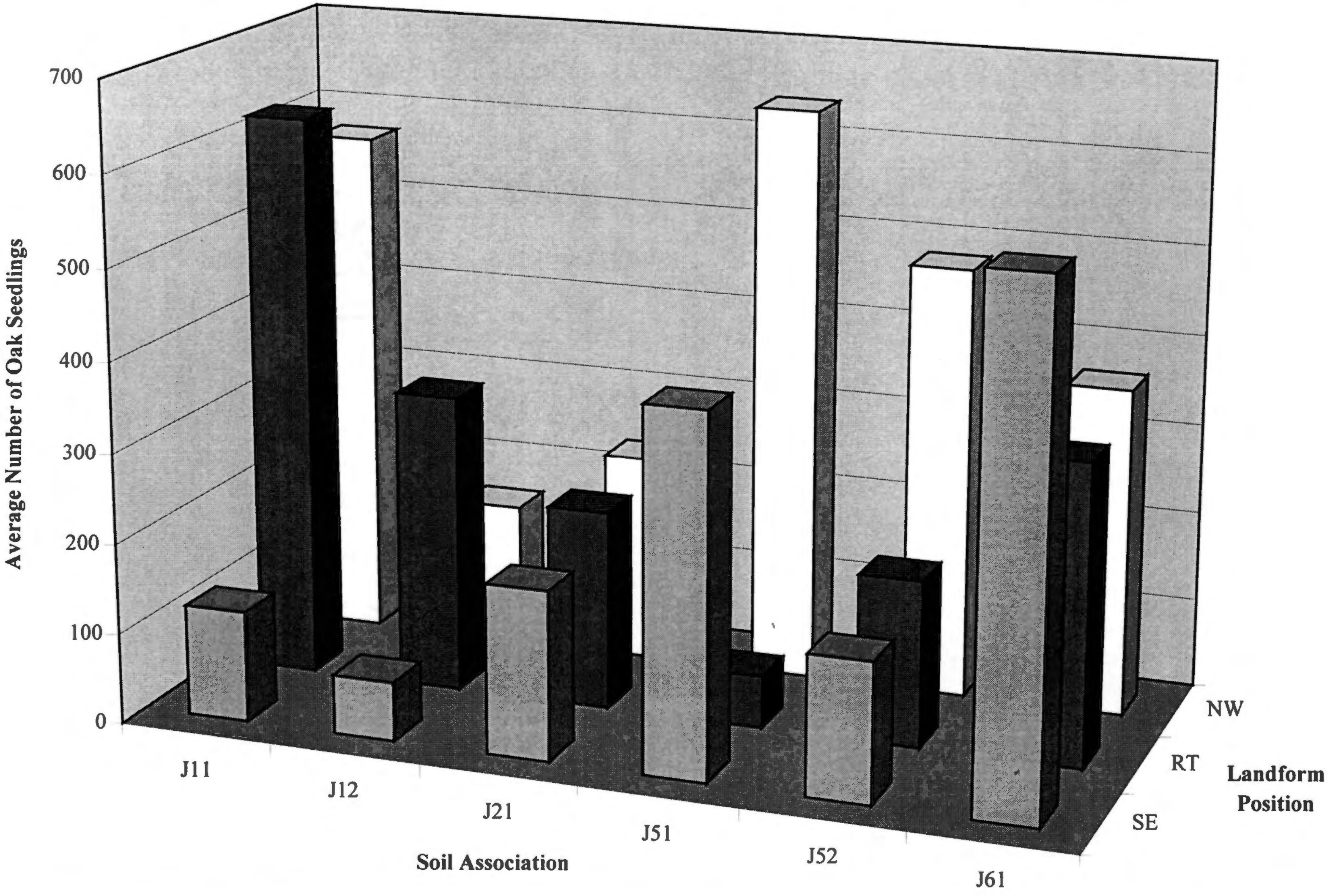


Figure 5. Number of oak seedlings (all species combined in the 1st size class) by landform position and soil association combination

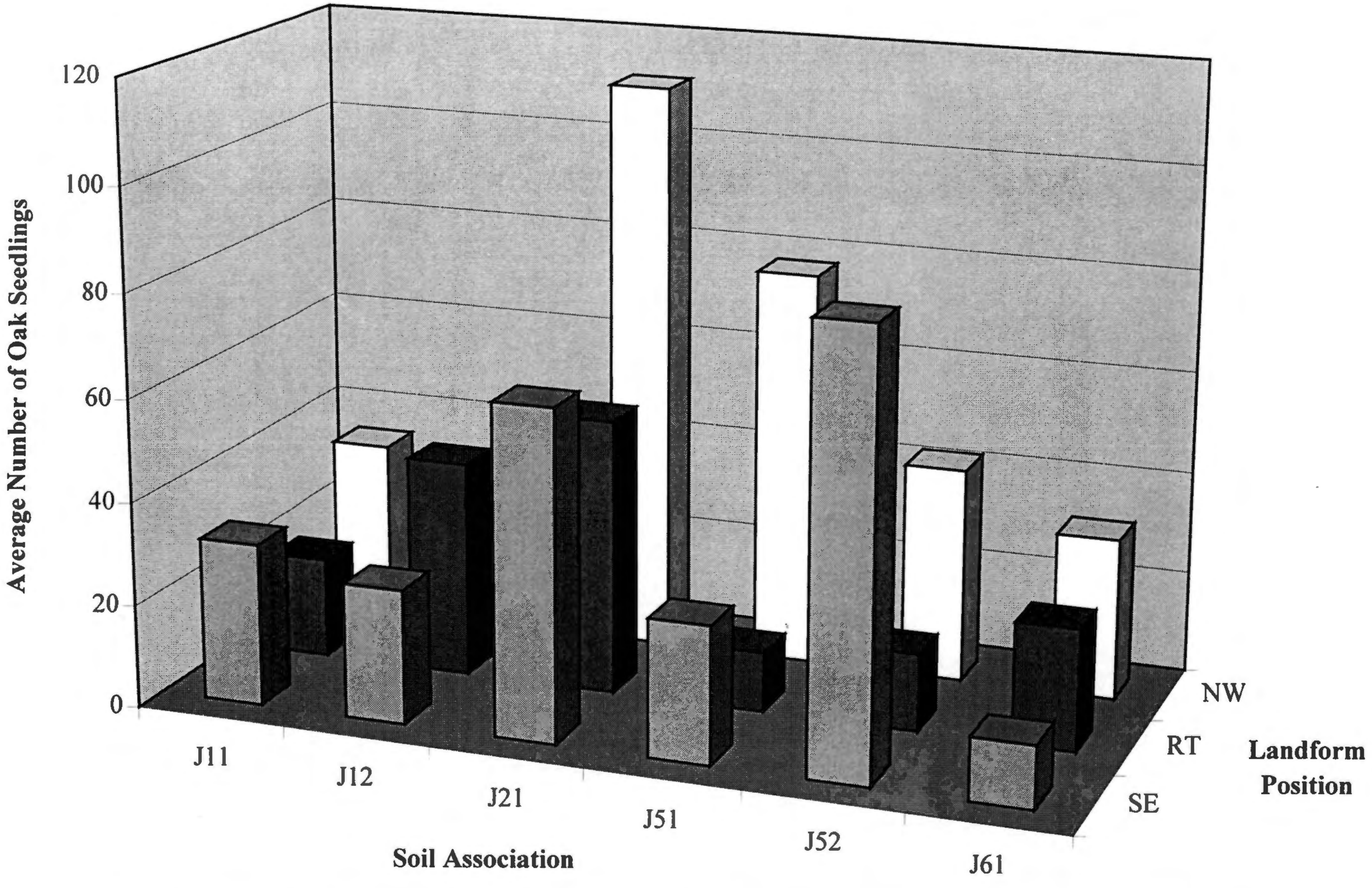


Figure 6. Number of oak seedlings (all species combined in the 2nd size class) by landform position and soil association combination.

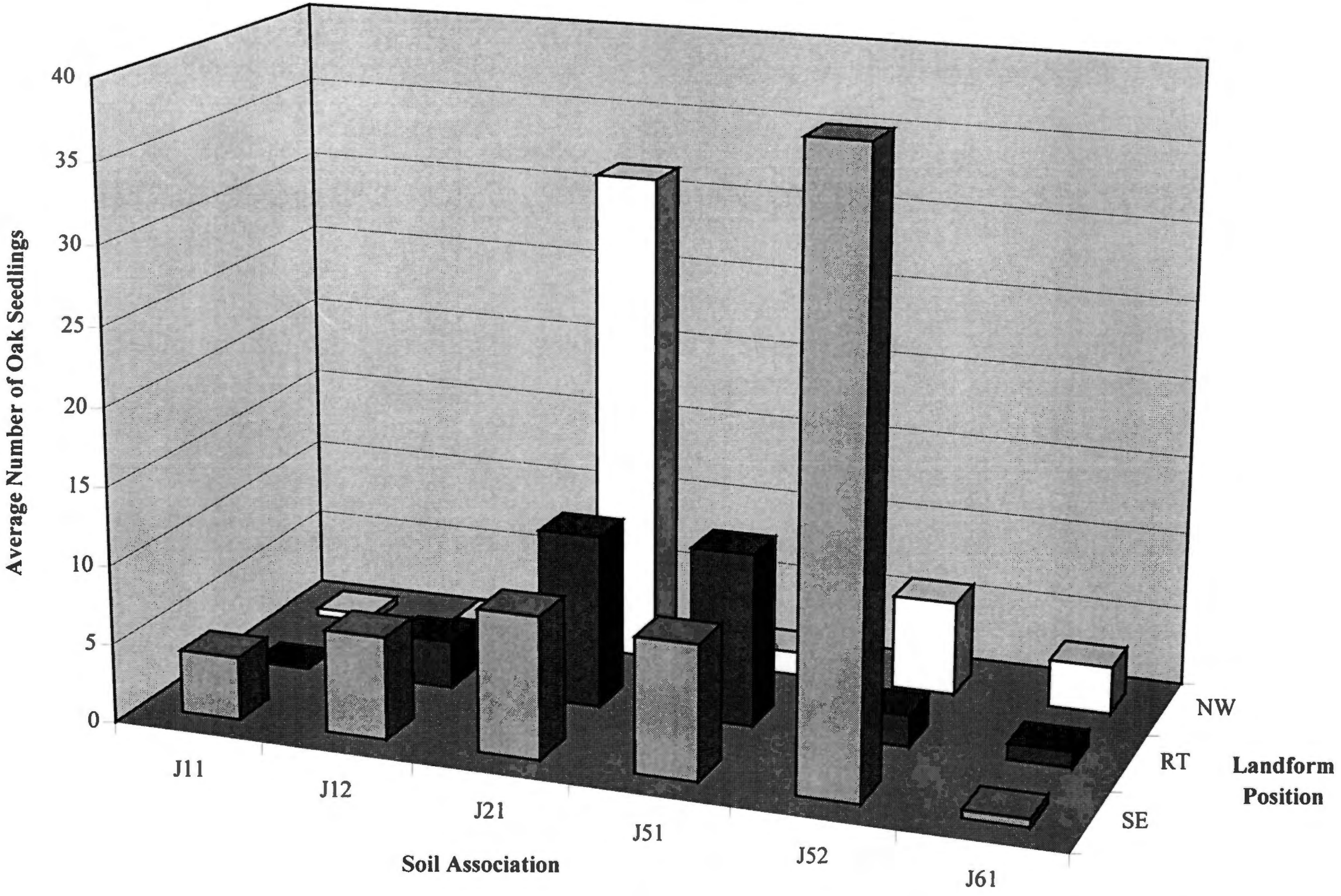


Figure 7. Number of oak seedlings (all species combined in the 3rd size class) by landform position and soil associaiton combination.

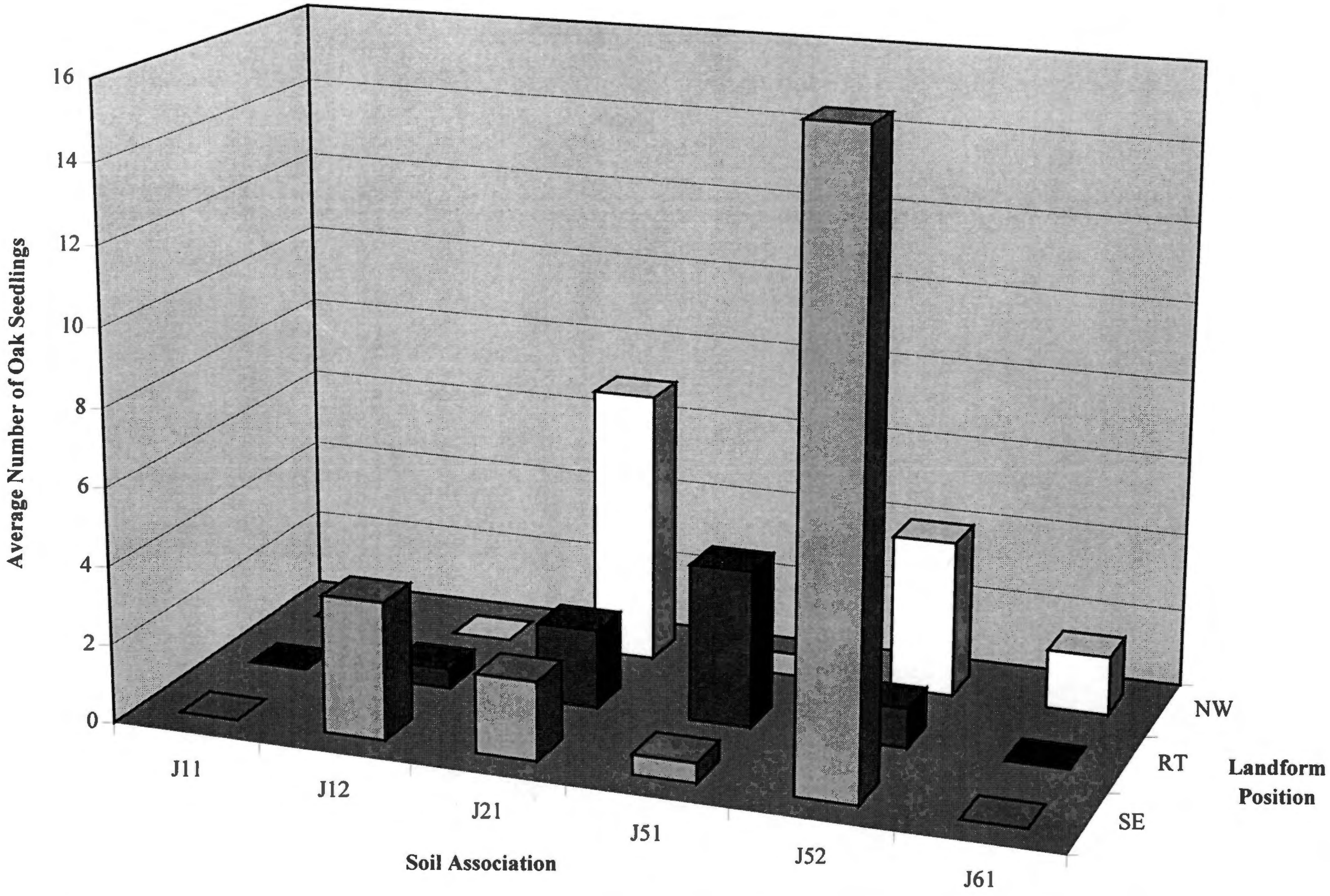


Figure 8. Number of oak seedlings (all species combined in the 4th size class) by landform position and soil association combination.

Table 5: Equations for all species and size classes of oak regeneration combined, by landform position/ soil association combination. R-square was 54.2% (P<.0297) for these equations.

Landform Position / Soil Association	Equation
NW / J11	313.87 – (33.37) hick + (72.87) midcan + (1.42) coiv
RT / J11	296.67 – (33.37) hick + (72.87) midcan + (1.42) coiv
SE / J11	173.34 – (33.37) hick + (72.87) midcan + (1.42) coiv
NW / J12	33.58 – (33.37) hick + (72.87) midcan + (1.42) coiv
RT / J12	16.38 – (33.37) hick + (72.87) midcan + (1.42) coiv
SE / J12	-106.95 – (33.37) hick + (72.87) midcan + (1.42) coiv
NW / J21	174.80 – (33.37) hick + (72.87) midcan + (1.42) coiv
RT / J21	157.60 – (33.37) hick + (72.87) midcan + (1.42) coiv
SE / J21	34.27 – (33.37) hick + (72.87) midcan + (1.42) coiv
NW / J51	375.41 – (33.37) hick + (72.87) midcan + (1.42) coiv
RT / J51	358.21 – (33.37) hick + (72.87) midcan + (1.42) coiv
SE / J51	234.88 – (33.37) hick + (72.87) midcan + (1.42) coiv
NW / J52	377.19 – (33.37) hick + (72.87) midcan + (1.42) coiv
RT / J52	359.99 – (33.37) hick + (72.87) midcan + (1.42) coiv
SE / J52	236.66 – (33.37) hick + (72.87) midcan + (1.42) coiv
NW / J61	110.10 – (33.37) hick + (72.87) midcan + (1.42) coiv
RT / J61	92.90 – (33.37) hick + (72.87) midcan + (1.42) coiv
SE / J61	-30.34 – (33.37) hick + (72.87) midcan + (1.42) coiv

- NW, SE, RT = northwest, southeast facing aspects at midslope positions, or ridge top position
- J11, J12, J21, J51, J52, J61 = soil associations
- hick = total number of hickory in the 4th size class
- midcan = average mid-canopy depth (m)
- coiv = chestnut oak importance value

Table 6. Significant model variables for all species of oak regeneration combined.

Y-variable	Model	R-square	P-value
Total	LFPos Soil Hick Midcan Coiv	54.2%	.0297
1st Size Class	LFPos Soil Rbud Coiv	41.3%	.1226
2nd Size Class	LFPos Soil Woiv Coiv Dogw	53.5%	.0331
3rd Size Class	LFPos Soil Slope Hickiv Dogw	70%	.0007
4th Size Class	LFPos Soil Slope Hickiv Midcan	79.4%	<.0001

- LFPos = landform position
- Soil = soil association
- Hick = total number of hickory saplings in 4th size class
- Midcan = average mid-canopy depth (m)
- Coiv = chestnut oak importance value
- Rbud = total number of redbud saplings in 4th size class
- Dogw = total number of dogwood saplings in 4th size class
- Woiv = white oak importance value
- Slope = average percent slope
- Hickiv = hickory importance value

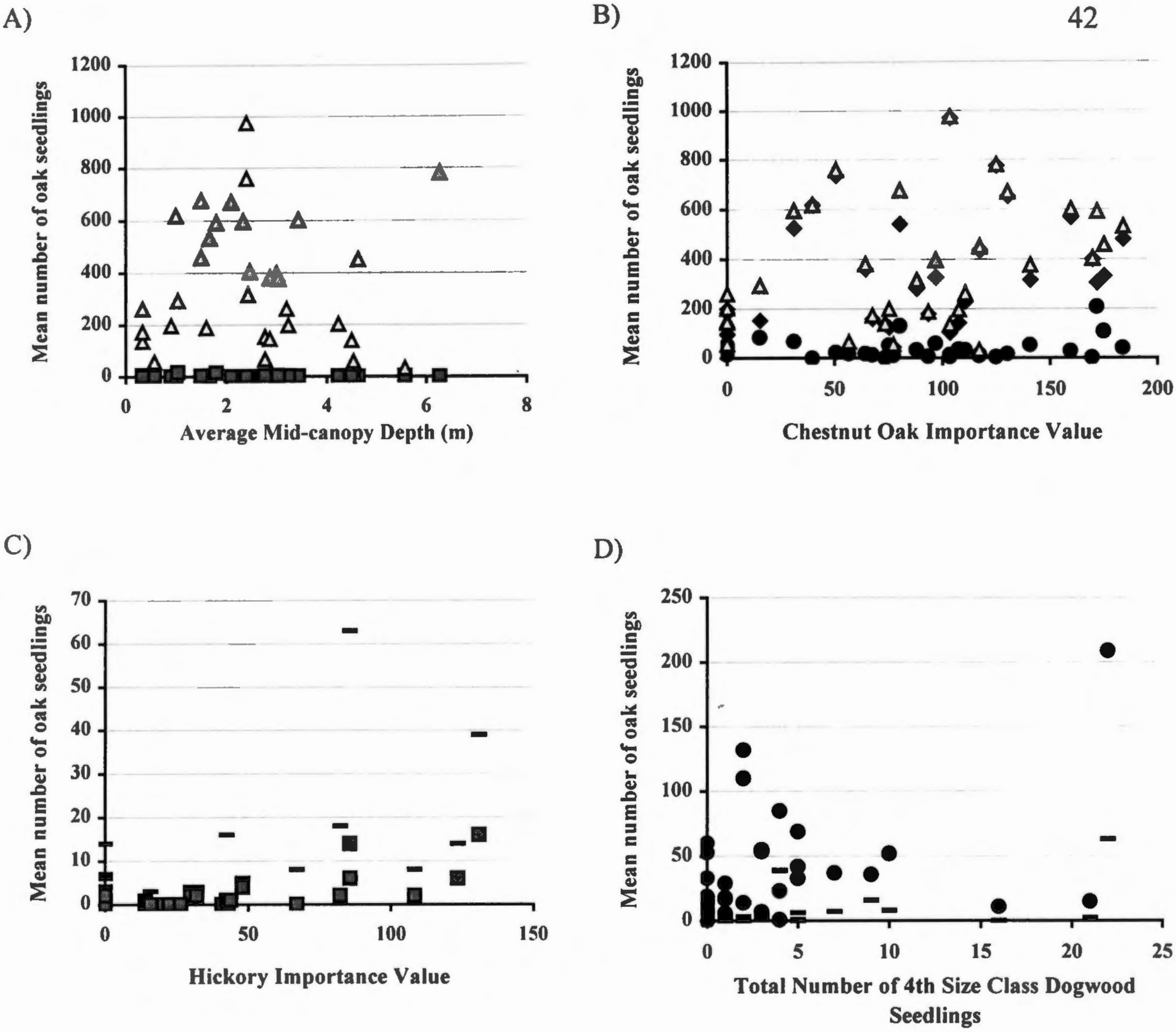


Figure 9. Relationships between the mean number of oak seedlings of all species and (A) average mid-canopy depth, (B) chestnut oak importance value, (C) hickory importance value, and (D) number of 4th size class dogwood seedlings.

◆ 1st Size Class	■ 4th Size Class
● 2nd Size Class	△ All Size Classes
▬ 3rd Size Class	

positive, while the strength of the relationship between 2nd size class oak seedlings and chestnut oak importance value was unclear (Figure 9B). Hickory importance value was an important variable in the 3rd and 4th size class models, with a slightly positive relationship with the number of oak seedlings (Figure 9C). The total number of dogwood saplings in the 4th size class had a negative relationship with the number of 2nd and 3rd size class oak seedlings (Figure 9D). Although statistical analysis showed a relationship between average mid-canopy depth and the number of 4th size class oak seedlings, the strength of the relationship was unclear (Figure 9A).

White Oak

A total of 2,053 white oak seedlings were tallied over all of the sample sites. Eighty-two percent of the total number of white oak seedlings was in the 1st size class, while only 0.5% was in the 4th size class. On average, white oak seedlings of all size classes were most abundant on the NW landform position and J21 soil association combination and least abundant on the SE/ J21 combination (Figure 10). First size class seedlings were greatest in number on the NW/ J21 combination and least in number on the SE/ J21 combination (Figure 11). On average, 2nd size class white oak seedlings were most abundant on the RT/ J51 landform position/soil association combination (Figure 12). Second size class seedlings were typically absent from the NW/ J11 and SE/ J21 combinations. On average, 3rd size class white oak seedlings were most abundant on the SE/ J52 landform position/soil association combination, while none were tallied on the J11 soil association and SE/ J21, NW/ J51, and RT/ J52 combinations (Figure 13). The

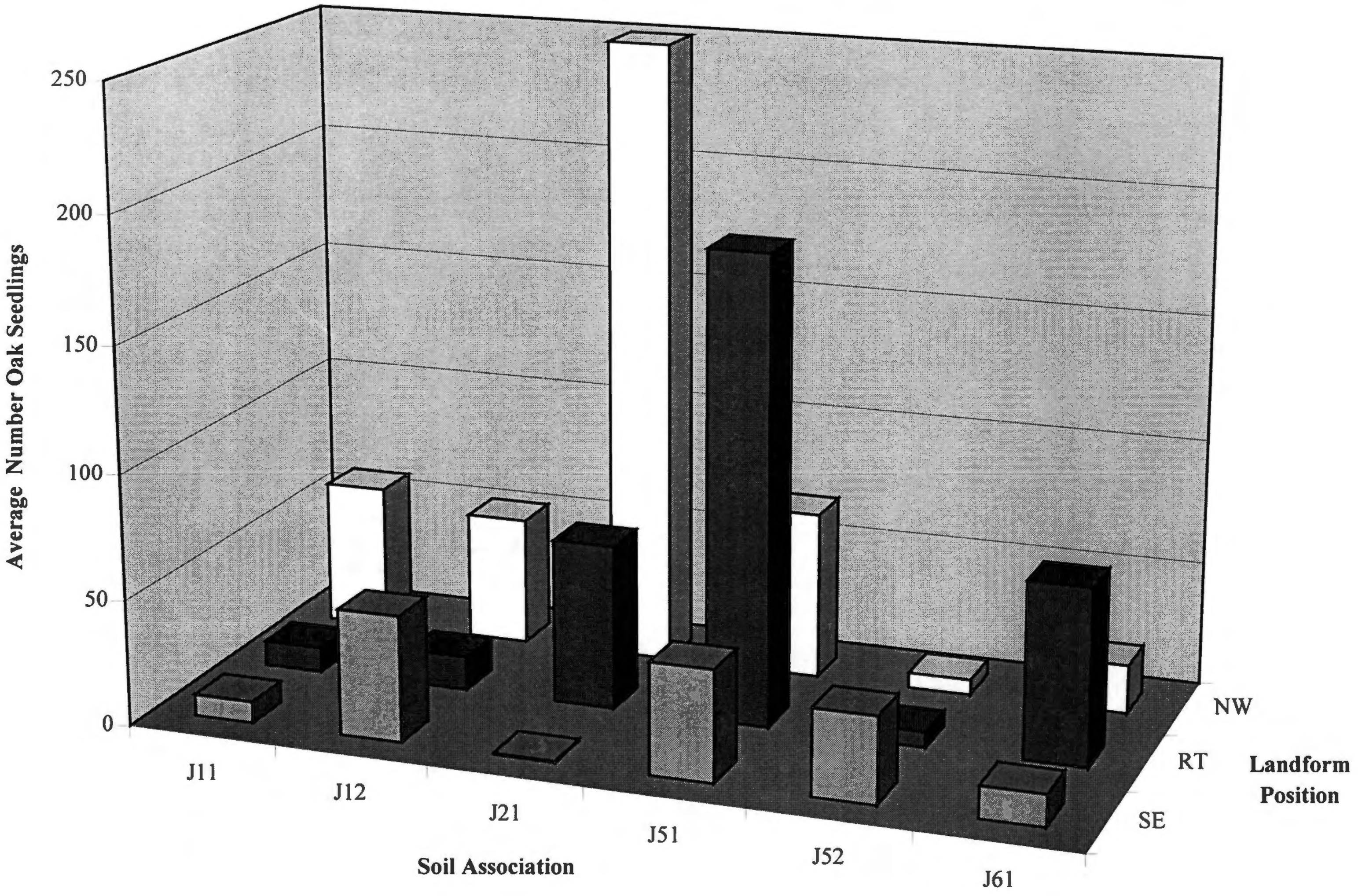


Figure 10. Number of white oak seedlings (all size classes combined) by landform position and soil association combination.

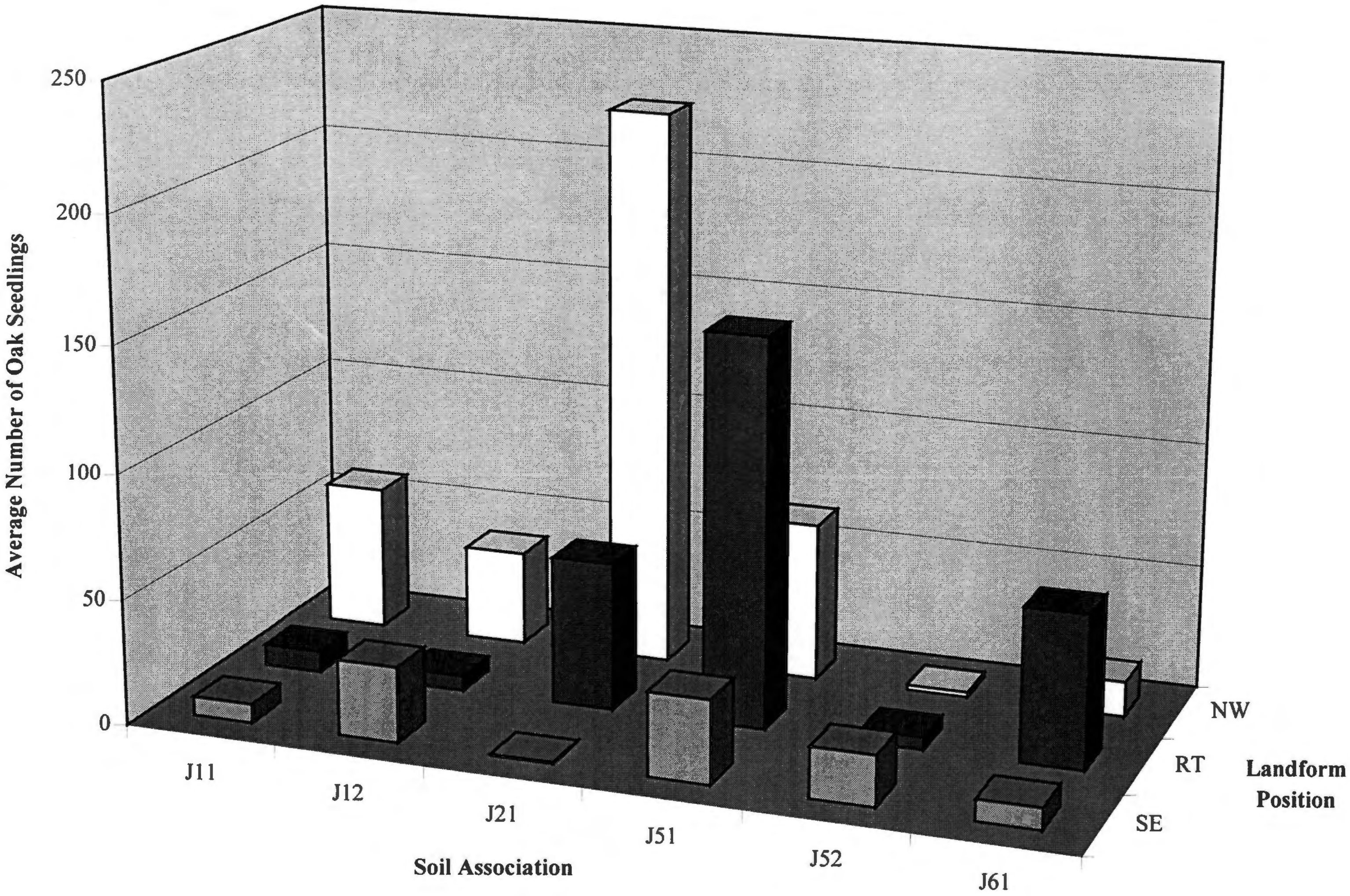


Figure 11. Number of white oak seedlings in the 1st size class by landform position and soil association combination.

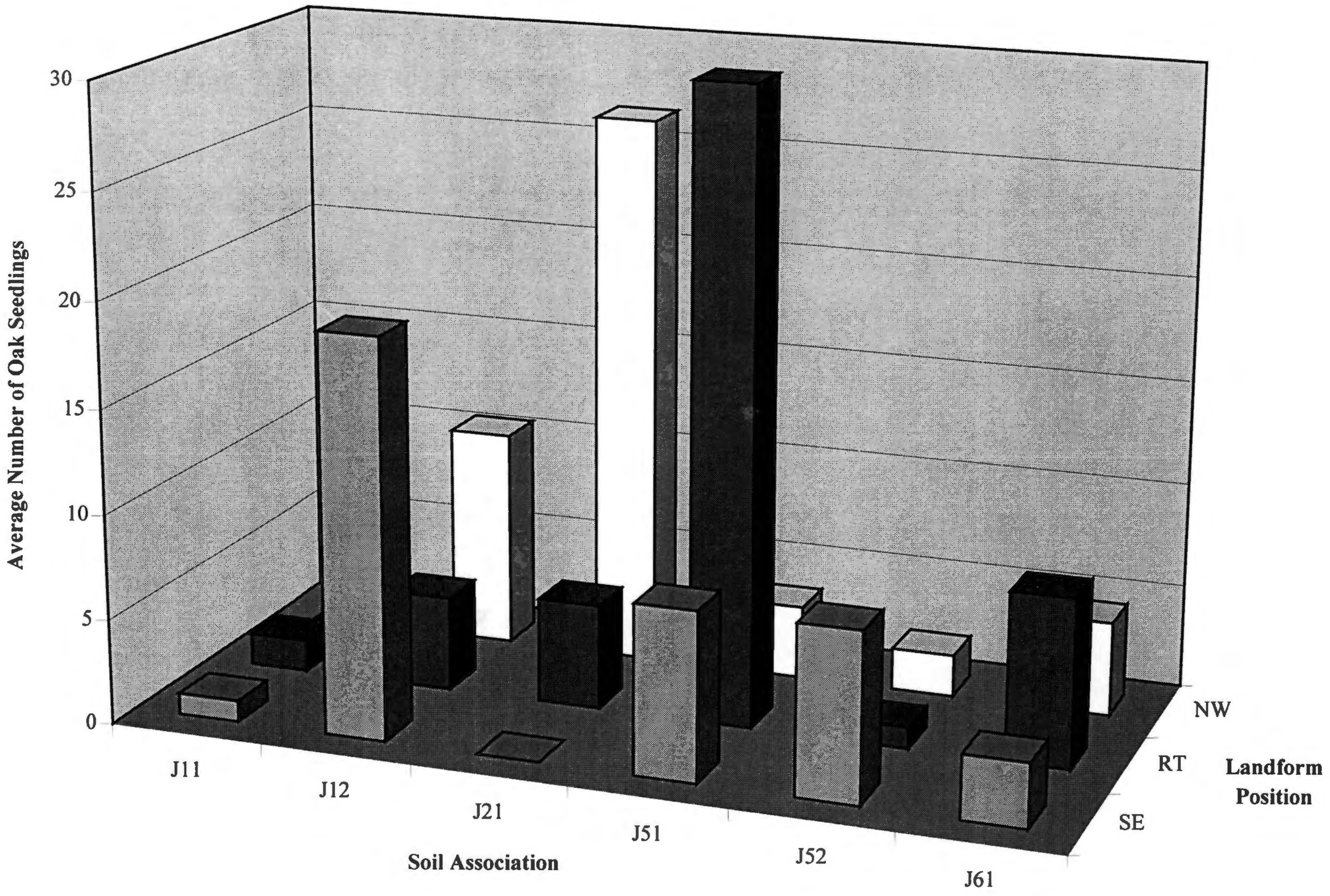


Figure 12. Number of white oak seedlings in the 2nd size class by landform position and soil association

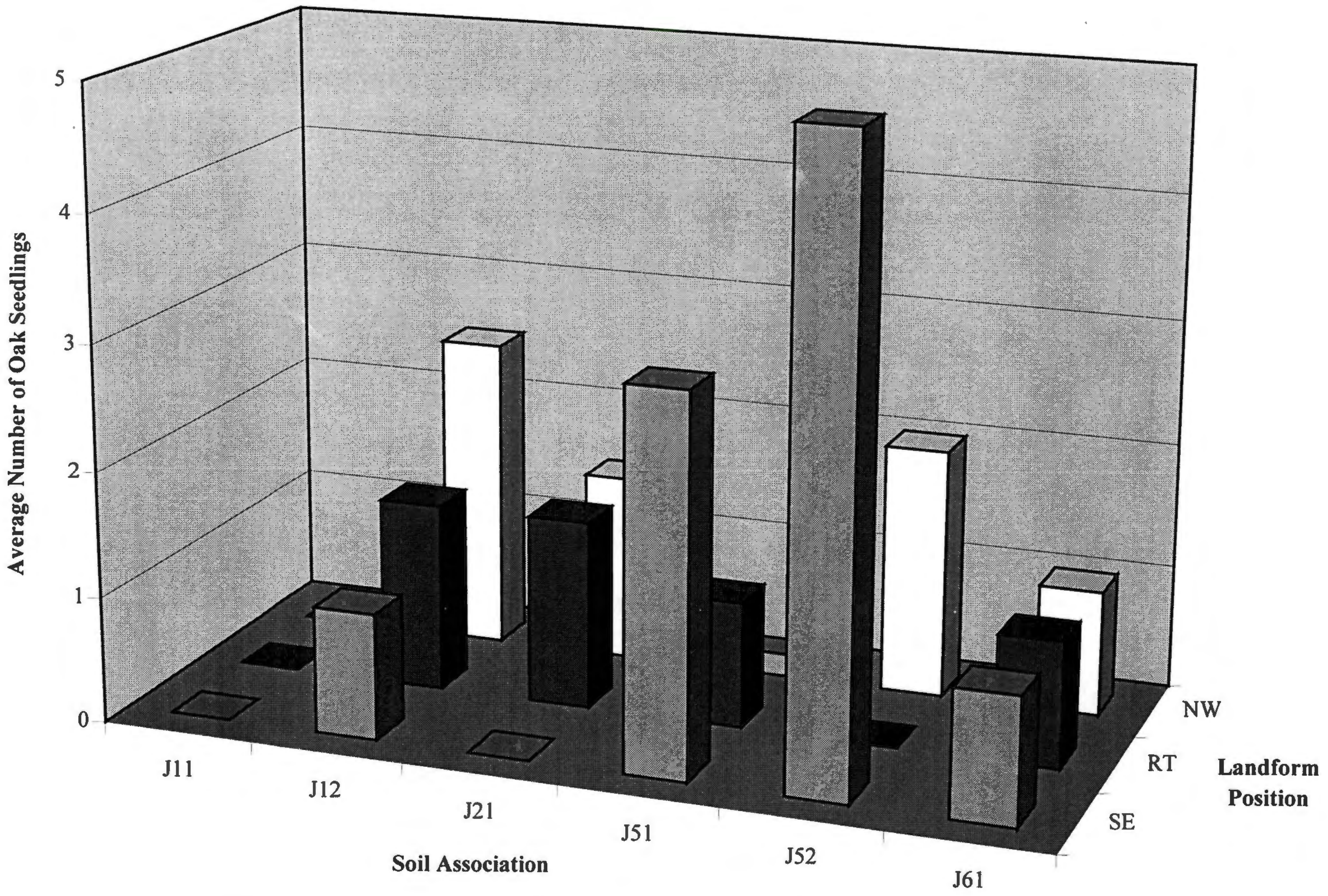


Figure 13. Number of whte oak seedlings in the 3rd size class by landform position and soil association combination.

RT/ J12 combination contained the highest average number of 4th size class white oak seedlings (Figure 14). Estimated regression equations for total white oak regeneration are shown in Table 7. The equations show that as white oak importance value, average canopy depth, and American beech importance value increase, the number of white oak seedlings increase (R-square = 86.9%; P=<.0001). Based on the equations, there appears to be a common trend across the soil associations where the number of white oaks would decrease as the landform positions changed from NW to SE to RT.

Canopy measurements were consistently important as a model variable for white oak regeneration (Table 8). Average canopy depth had a weak positive effect on the number of 1st size class and total white oak seedlings, while the exact relationship with the 4th size class seedlings was unclear (Figure 15A). The presence of blackgum in the sapling size class also had a slightly positive relationship with white oak seedlings in the 2nd, 3rd, and 4th size classes (Figure 15B). The importance value for mature white oaks has a significantly positive relationship with the white oak seedlings in the 1st size classes, while its relationship with the 2nd size class of white oak seedlings is only slightly positive (Figure 15C). The importance value of hickory is significant in the larger size classes with a slightly positive relationship with the 3rd and 4th size class white oak seedlings, while the importance value of beech has a strong positive relationship with the 1st size class (Figures 15D and 15E).

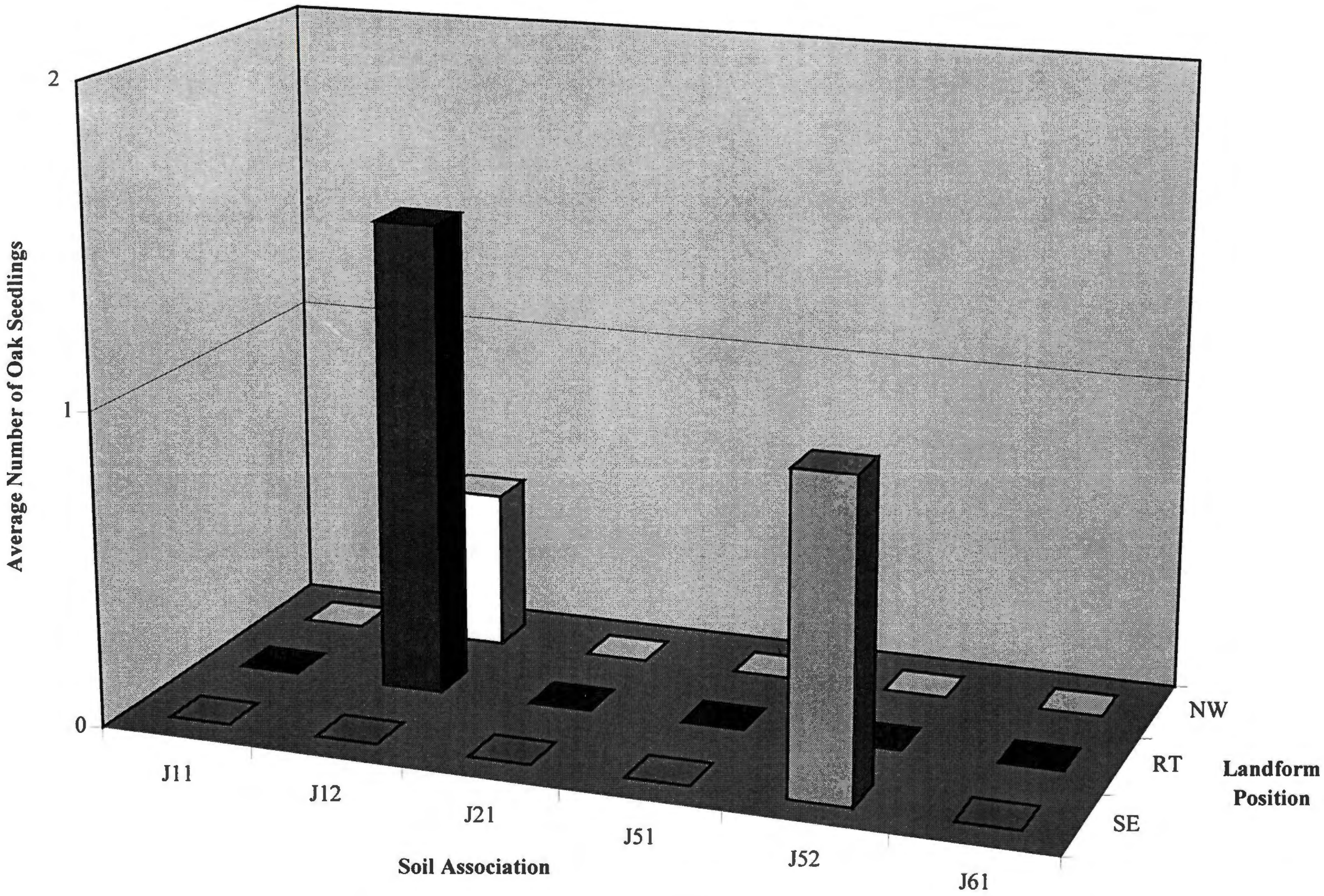


Figure 14. Number of 4th size class white oak seedlings by landform position and soil association combinations.

Table 7. Equations for all size classes of white oak regeneration combined, by landform position/ soil association. The R-square was 86.9% (P<.0001) for this group of equations.

Landform Position / Soil Association	Equation
NW / J11	-38.82 + (2.72) woiv + (5.27) Candep + (5.49) Bchiv
RT / J11	-55.18 + (2.72) woiv + (5.27) Candep + (5.49) Bchiv
SE / J11	-51.66 + (2.72) woiv + (5.27) Candep + (5.49) Bchiv
NW / J12	-75.01 + (2.72) woiv + (5.27) Candep + (5.49) Bchiv
RT / J12	-91.34+ (2.72) woiv + (5.27) Candep + (5.49) Bchiv
SE / J12	-87.82 + (2.72) woiv + (5.27) Candep + (5.49) Bchiv
NW / J21	-66.53 + (2.72) woiv + (5.27) Candep + (5.49) Bchiv
RT / J21	-82.86 + (2.72) woiv + (5.27) Candep + (5.49) Bchiv
SE / J21	- 79.34+ (2.72) woiv + (5.27) Candep + (5.49) Bchiv
NW / J51	-45.34 + (2.72) woiv + (5.27) Candep + (5.49) Bchiv
RT / J51	-61.67 + (2.72) woiv + (5.27) Candep + (5.49) Bchiv
SE / J51	-58.15 + (2.72) woiv + (5.27) Candep + (5.49) Bchiv
NW / J52	-5.51 + (2.72) woiv + (5.27) Candep + (5.49) Bchiv
RT / J52	-21.84 + (2.72) woiv + (5.27) Candep + (5.49) Bchiv
SE / J52	-18.32 + (2.72) woiv + (5.27) Candep + (5.49) Bchiv
NW / J61	-57.96 + (2.72) woiv + (5.27) Candep + (5.49) Bchiv
RT / J61	-74.29 + (2.72) woiv + (5.27) Candep + (5.49) Bchiv
SE / J61	-70.77 + (2.72) woiv + (5.27) Candep + (5.49) Bchiv

- NW, SE, RT = northwest, southeast facing aspects at midslope positions, and ridge top position
- J11, J12, J21, J51, J52, J61 = soil associations
- Woiv = white oak importance value
- Candep = average canopy depth (m)
- Bchiv = American beech importance value

Table 8. Significant model variables for white oak regeneration, all size classes.

y-variable	Model Variables	R-square	P-value
Total	LFPos Soil Woiv Candep Bchiv	86.9%	<.0001
1st size Class	LFPos Soil Woiv Bchiv Candep	88.5%	<.0001
2nd Size Class	LFPos Soil Woiv Blgm Uprcan	76.5%	<.0001
3rd Size Class	LFPos Soil Hickiv Blgm Midcan	84.3%	<.0001
4th Size Class	LFPos Soil Candep Blgm Hickiv	84.9%	<.0001

- LFPos = Landform position (ridge top, NW aspect at midslope, and SE aspect at midslope)
- Soil = soil association
- Woiv = white oak importance value
- Candep = average canopy depth (m)
- Bchiv = American beech importance value
- Blgm = total number of blackgum saplings in 4th size class
- Uprcan = average upper canopy depth (m)
- Hickiv = hickory importance value
- Midcan = average mid-canopy depth (m)

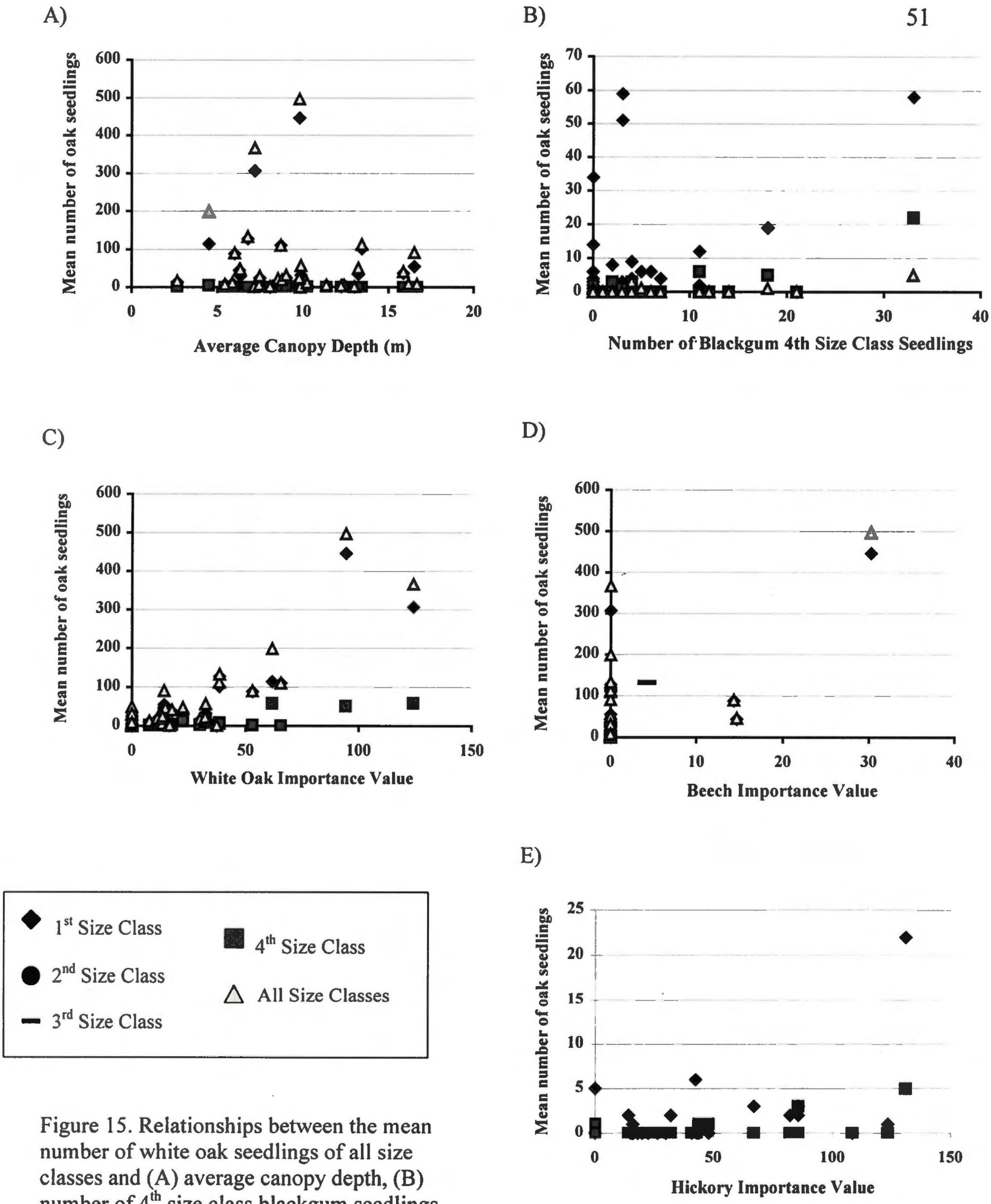


Figure 15. Relationships between the mean number of white oak seedlings of all size classes and (A) average canopy depth, (B) number of 4th size class blackgum seedlings, (C) white oak importance value, (D) beech importance value, and (E) hickory importance value.

Chestnut Oak

A total of 7,246 chestnut oak seedlings were tallied over all of the sample sites. The 1st size class comprised 93% of the total number of chestnut oak seedlings, while the 4th size class comprised only 0.14% of the total. On average, chestnut oak seedlings were most abundant on the RT landform position and J11 soil association combination, and least abundant on the NW/ J52 and RT/ J52 landform position and soil association combinations (Figure 16). First size class seedlings were greatest in number on the RT/ J11 combination and least in number on the NW/ J52 combination (Figure 17). The RT/ J61 combination contained the highest average number of 2nd size class chestnut oak seedlings, while the least were tallied on the NW/ J12 and RT/ J52 landform position/soil association combinations (Figure 18). On average, 3rd size class seedlings were most abundant on the RT/ J61 combination (Figure 19). The RT/ J61 combination contained the highest average number of white oak seedlings in the 4th size class (Figure 20).

Estimated regression equations for total chestnut oak regeneration are located in Table 9. The equations suggest that as chestnut oak importance value, average canopy depth, and number of blackgum saplings increase, the number of chestnut oak seedlings also increase. There is also a negative relationship between total chestnut oak regeneration and average PAR and number of sassafras saplings in the 4th size class (R-square = 69.9%; P=.0041). The intercepts of the regression equation decrease as the site changes from NW to RT to SE.

Potential competitors in the 4th size class appear to have a significant relationship with the amount of chestnut oak in all size classes (Table 10). Figures 21A-C illustrate the strength of the relationships between the number of chestnut oak seedlings and

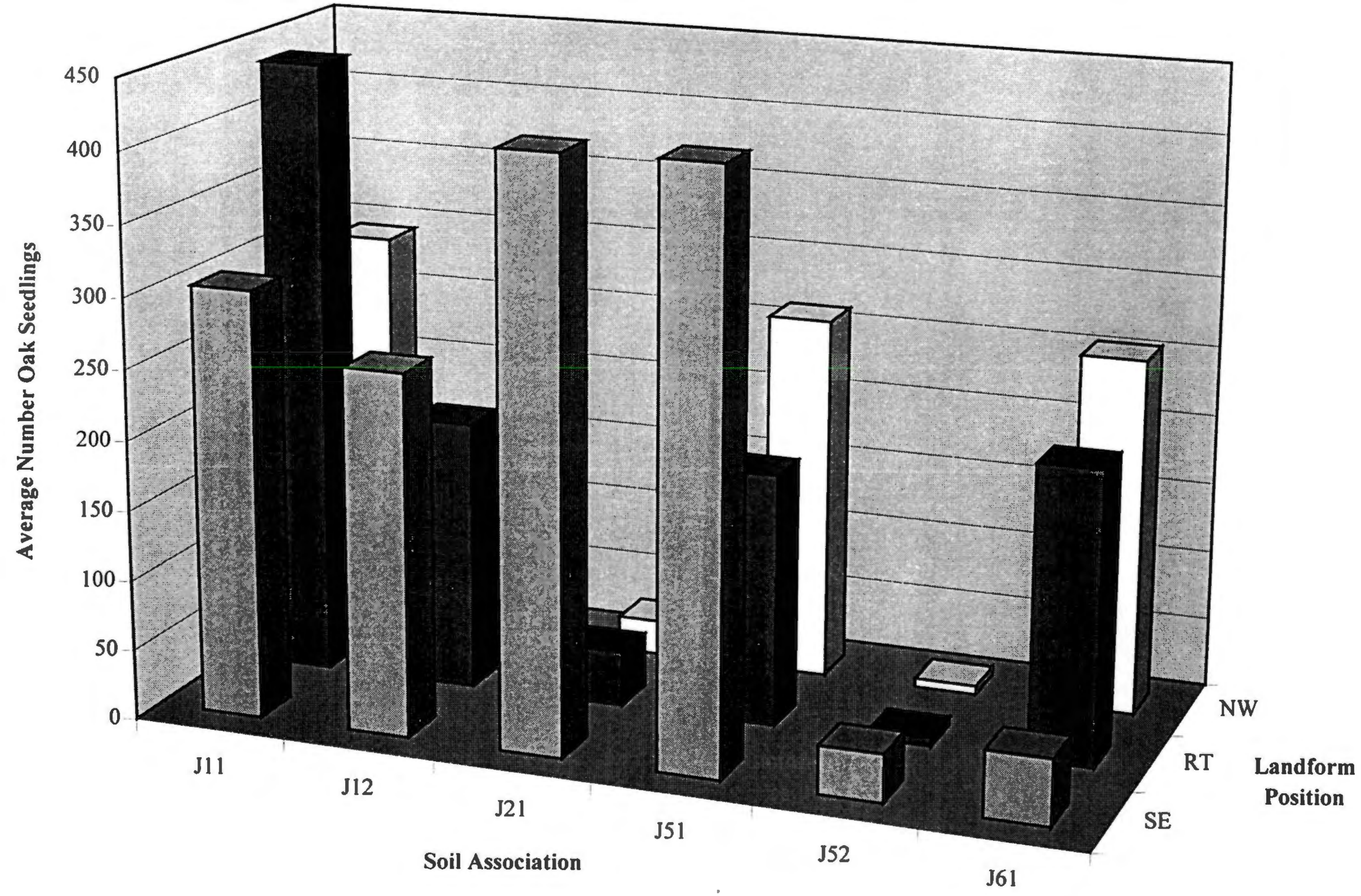


Figure 16. Number of chestnut oak seedlings (all size classes combined) by landform position and soil association combination.

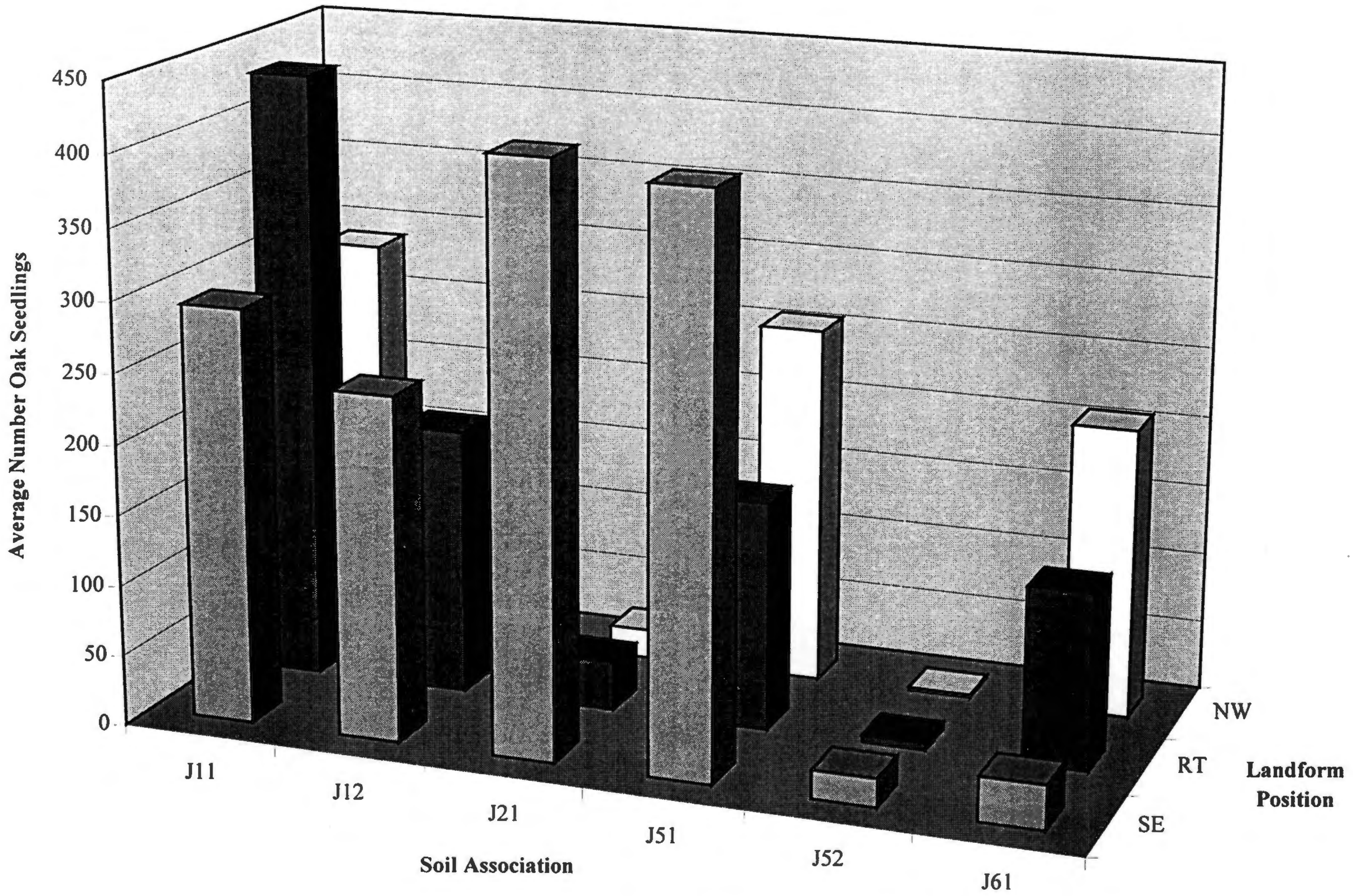


Figure 17. Number of 1st size class chestnut oak seedlings by landform position and soil association combination.

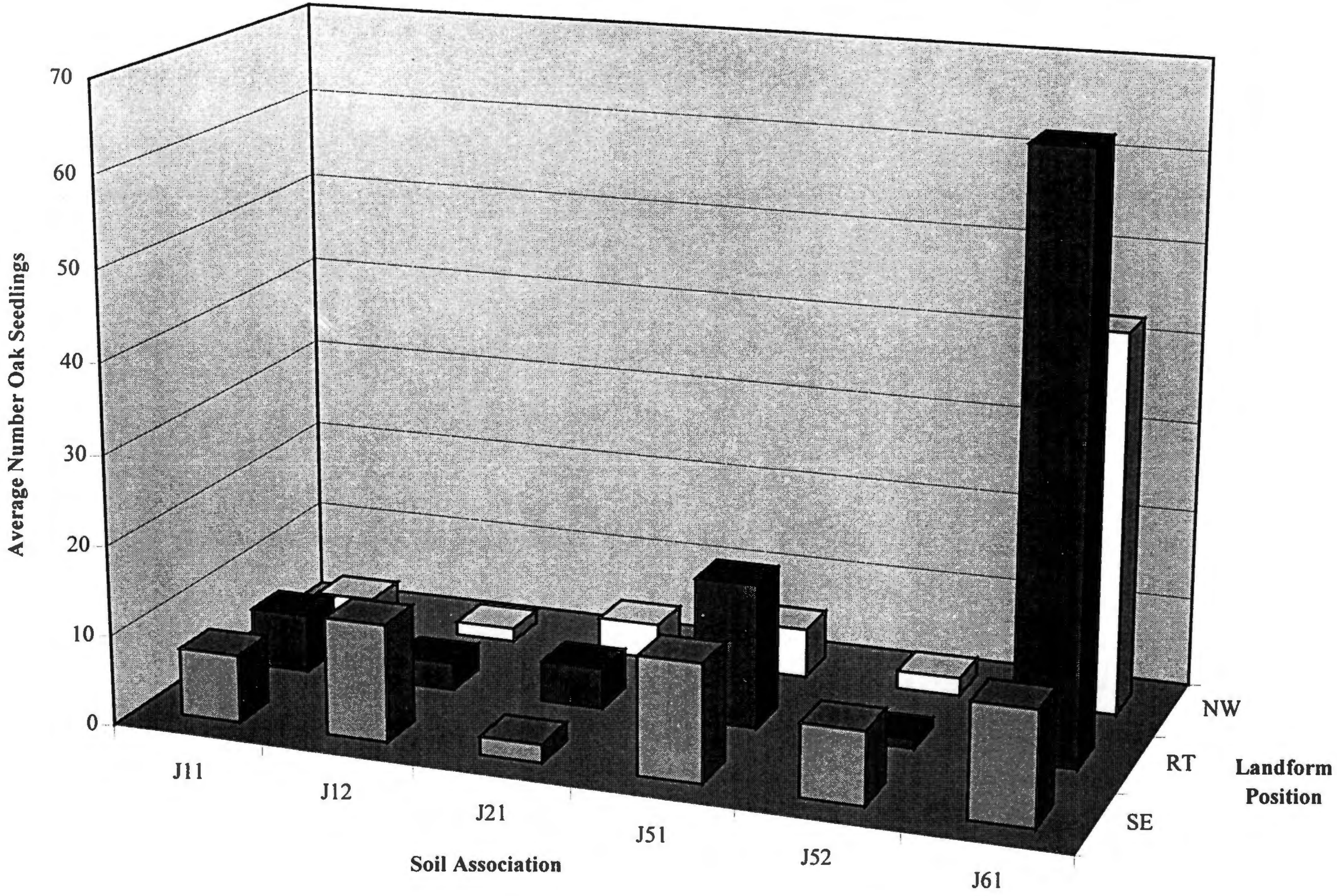


Figure 18. Number of 2nd size class chestnut oak seedlings by landform position and soil association combination.

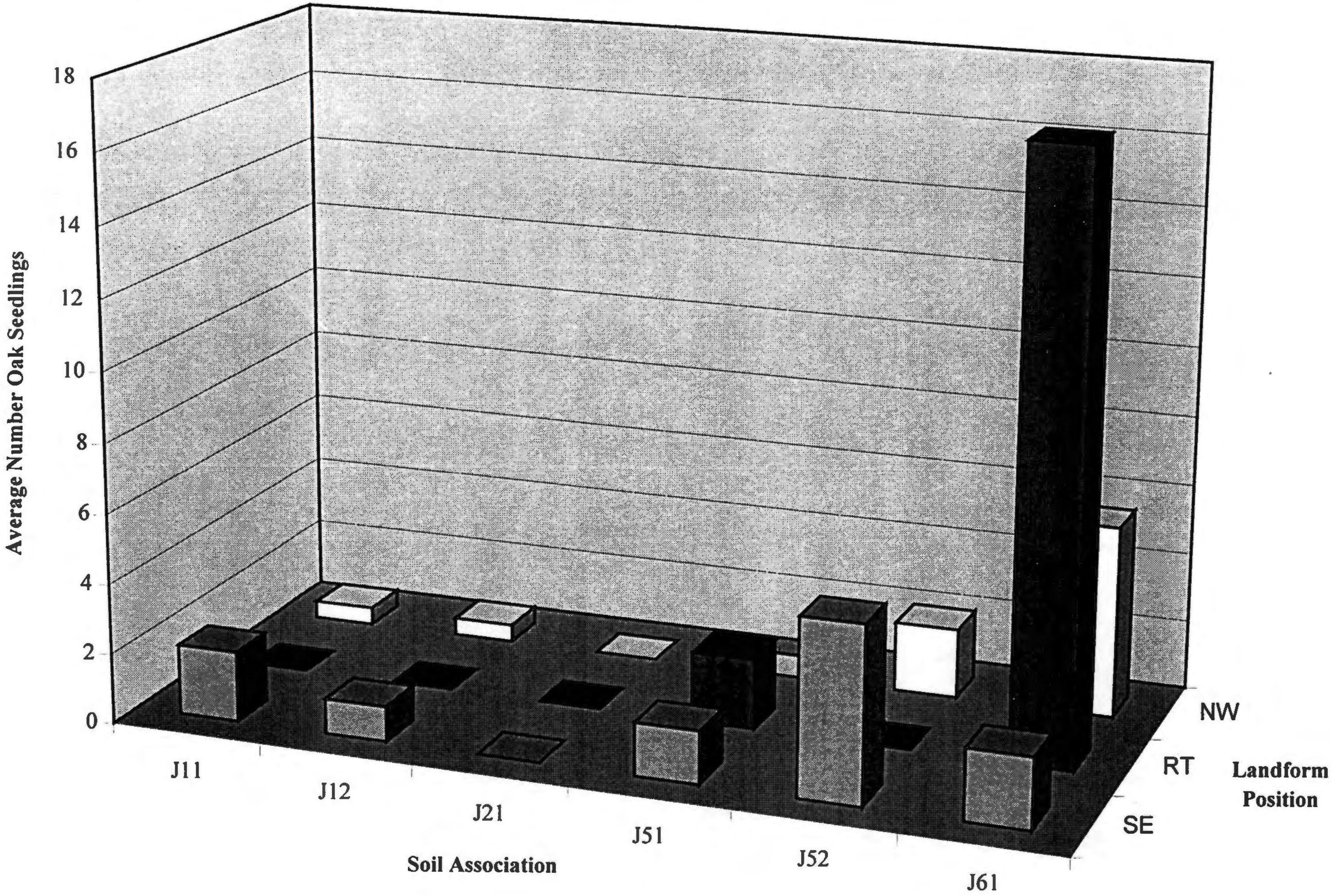


Figure 19. Number of 3rd size class chestnut oak seedlings by landform position and soil association combination.

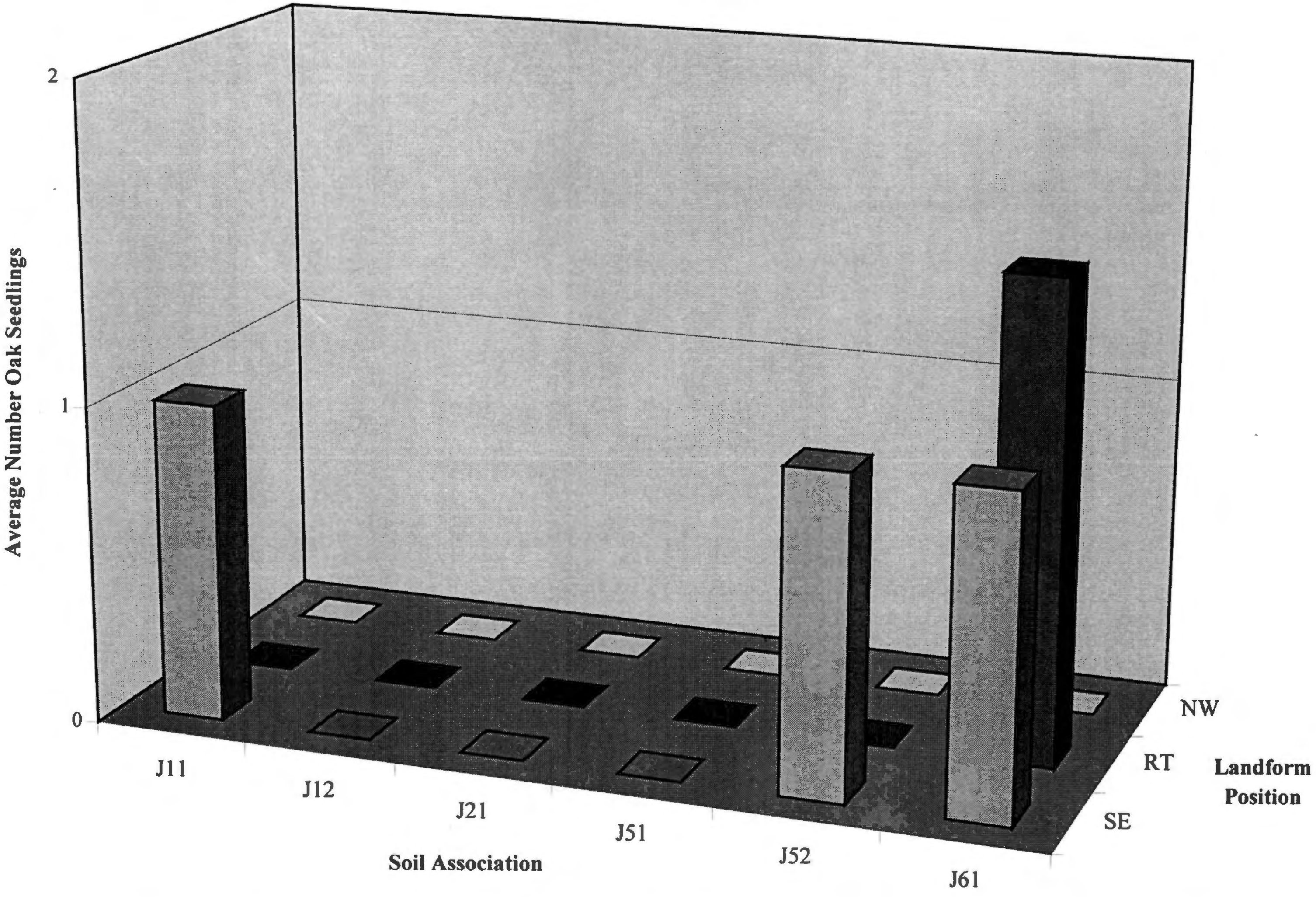


Figure 20. Number of 4th size class chestnut oak seedlings by landform position and soil association combination.

Table 9. Equations for all size classes of chestnut oak regeneration combined, by landform position/ soil association. R-square was 69.6% (P=.0041) for these equations.

Landform Position / Soil Association	Equation
NW / J11	-295.59 + (3.05) coiv + (34.44) candep - (701.78) par + (16.61) blgm - (41.21) sass
RT / J11	-388.24 + (3.05) coiv + (34.44) candep - (701.78) par + (16.61) blgm - (41.21) sass
SE / J11	-398.07 + (3.05) coiv + (34.44) candep - (701.78) par + (16.61) blgm - (41.21) sass
NW / J12	-324.81 + (3.05) coiv + (34.44) candep - (701.78) par + (16.61) blgm - (41.21) sass
RT / J12	-417.47 + (3.05) coiv + (34.44) candep - (701.78) par + (16.61) blgm - (41.21) sass
SE / J12	-427.29 + (3.05) coiv + (34.44) candep - (701.78) par + (16.61) blgm - (41.21) sass
NW / J21	-448.57 + (3.05) coiv + (34.44) candep - (701.78) par + (16.61) blgm - (41.21) sass
RT / J21	-541.23 + (3.05) coiv + (34.44) candep - (701.78) par + (16.61) blgm - (41.21) sass
SE / J21	-551.05 + (3.05) coiv + (34.44) candep - (701.78) par + (16.61) blgm - (41.21) sass
NW / J51	-266.35 + (3.05) coiv + (34.44) candep - (701.78) par + (16.61) blgm - (41.21) sass
RT / J51	-359.01 + (3.05) coiv + (34.44) candep - (701.78) par + (16.61) blgm - (41.21) sass
SE / J51	-368.83 + (3.05) coiv + (34.44) candep - (701.78) par + (16.61) blgm - (41.21) sass
NW / J52	-308.22 + (3.05) coiv + (34.44) candep - (701.78) par + (16.61) blgm - (41.21) sass
RT / J52	-400.88 + (3.05) coiv + (34.44) candep - (701.78) par + (16.61) blgm - (41.21) sass
SE / J52	-410.7 + (3.05) coiv + (34.44) candep - (701.78) par + (16.61) blgm - (41.21) sass
NW / J61	-257.46 + (3.05) coiv + (34.44) candep - (701.78) par + (16.61) blgm - (41.21) sass
RT / J61	-350.12 + (3.05) coiv + (34.44) candep - (701.78) par + (16.61) blgm - (41.21) sass
SE / J61	-359.94 + (3.05) coiv + (34.44) candep - (701.78) par + (16.61) blgm - (41.21) sass

- NW, SE, RT = northwest, southeast aspect at midslope position, and ridge top position
- J11, J12, J21, J51, J52, J61 = soil associations
- coiv = chestnut oak importance value
- candep = average total canopy depth (m)
- par = average photosynthetically active radiation below the canopy
- Blgm = total number of blackgum in the 4th size class
- sass = total number of sassafras in the 4th size class

Table 10. Significant model variables for chestnut oak regeneration, all size classes.

Y-variable	Model Variables	R-square	P-value
Total	LFPos Soil Coiv Candep Par Blgm Sass	69.6%	.0041
1st Size Class	LFPos Soil Coiv Candep Blgm	58.9%	.0117
2nd Size Class	LFPos Soil Coiv Dogw	72.4%	.0001
3rd Size Class	LFPos Soil Par Ypiv Dogw	62%	.0060
4th Size Class	LFPos Soil Litdep Coiv Hickiv Sass	78.4%	<.0001

- LFPos = landform position
- Soil = soil association
- Coiv = chestnut oak importance value
- Candep = average canopy depth (m)
- Par = average photosynthetically active radiation, below the canopy
- Blgm = total number of blackgum saplings in 4th size class
- Sass = total number of sassafras saplings in 4th size class
- Hickiv = hickory importance value
- Ypiv = yellow-poplar importance value

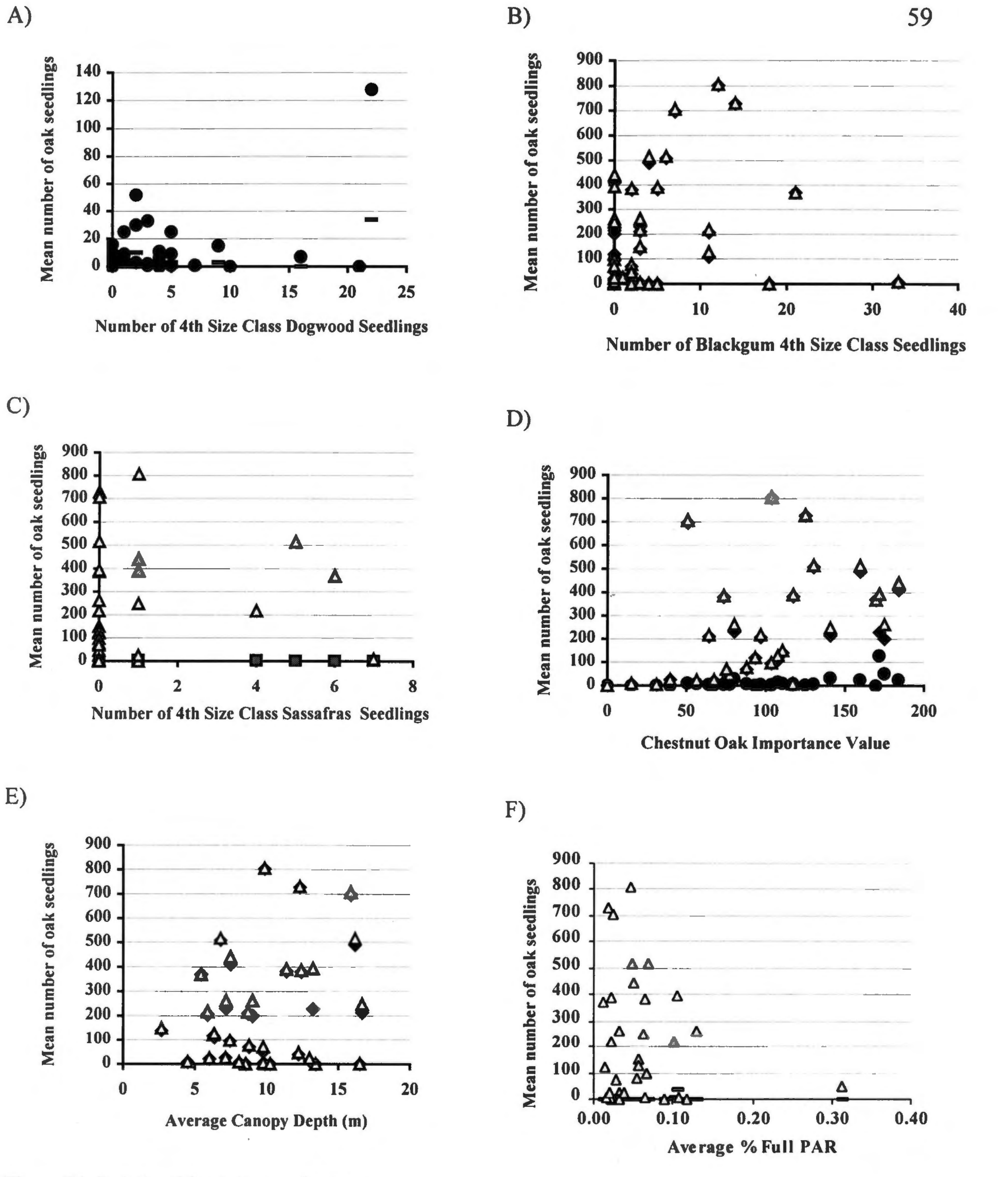


Figure 21. Relationships between the mean number of chestnut oak seedlings of all size classes and (A) number of 4th size class dogwood seedlings, (B) number of 4th size class blackgum seedlings, (C) number of 4th size class sassafras seedlings, (D) chestnut oak importance value, (E) average canopy depth, and (F) average % full PAR.

potential competitors. An increased number of dogwood saplings generally accompanies a negative trend in 2nd and 3rd size class chestnut oak seedlings. Although it is a weak relationship, the total number of blackgum saplings in the 4th size class is positively related to an increase in 1st size class chestnut oak seedlings. The relationship between 4th size class chestnut oak seedlings and the number of sassafras saplings present is unclear. Chestnut oak importance value appears to be positively associated with the number of 1st and 2nd size class chestnut oak, but for the 3rd size class the negative relationship with yellow-poplar importance value became important (Figure 21D). Average canopy depth appeared in the 1st size class model, but failed to be a significant variable for any other size class. The scatter-plot for this relationship shows a weakly positive relationship between the variables (Figure 21E). While average percent full PAR has a negative relationship to the total number of chestnut oak seedlings present, there is an unclear relationship between percent full PAR and the number of 4th size class seedlings (Figure 21F).

Black Oak

A total of 1,303 black oak seedlings were tallied over all of the sample sites. The 1st size class comprised 79% of the total number of black oak seedlings, while the 4th size class comprised only 1.8% of the total. On average, black oak seedlings were most common on the NW/J52 and RT/J11 landform position and soil association combinations (Figure 22). In general, the J51 soil association had the fewest black oak seedlings on all landform positions. First size class black oak seedlings were most abundant on both the NW/ J52 combination and the RT/ J11 combination and least abundant on the NW/ J51

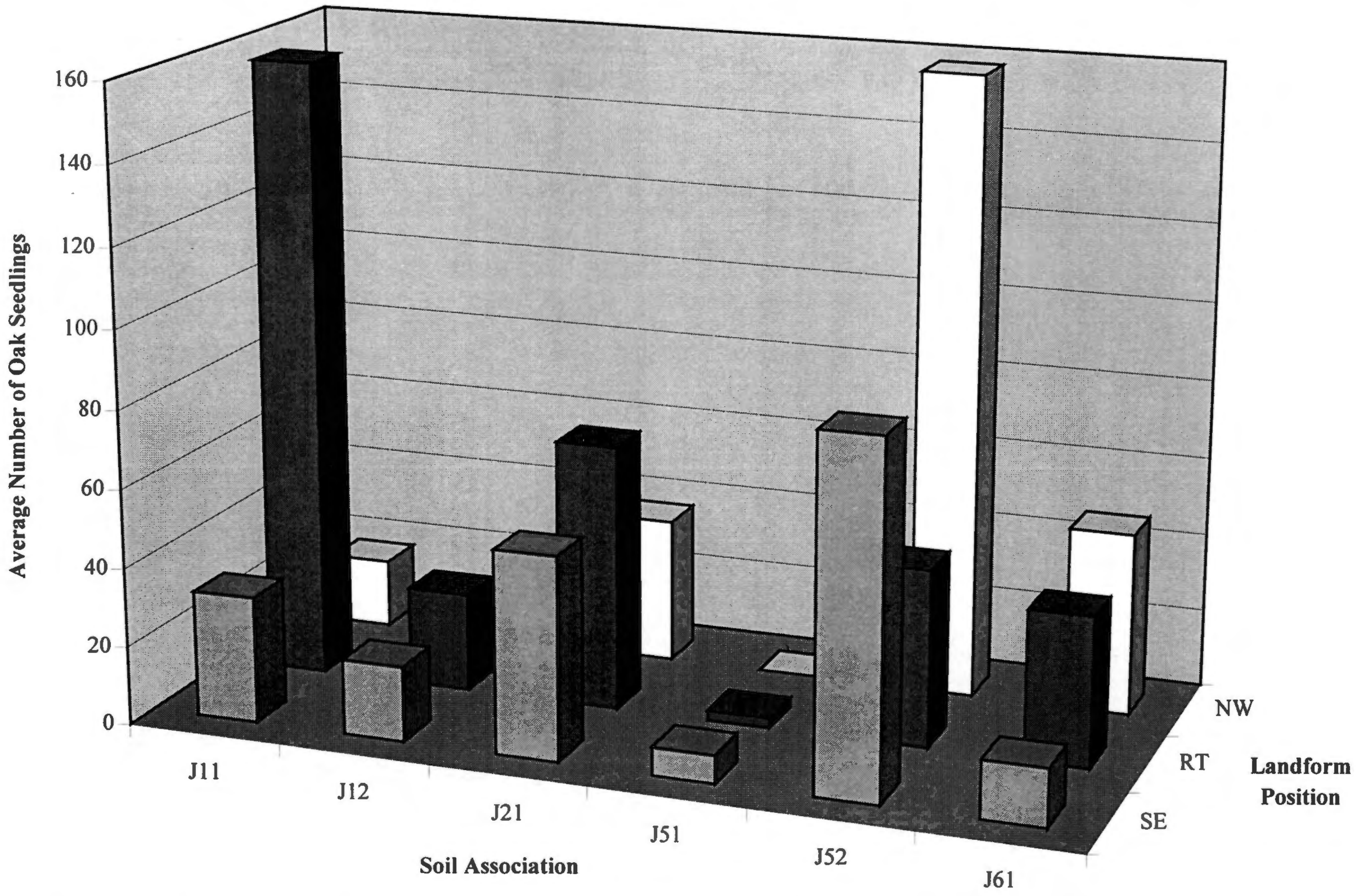


Figure 22. Number of black oak seedlings (all size classes combined) by landform position and soil association combination.

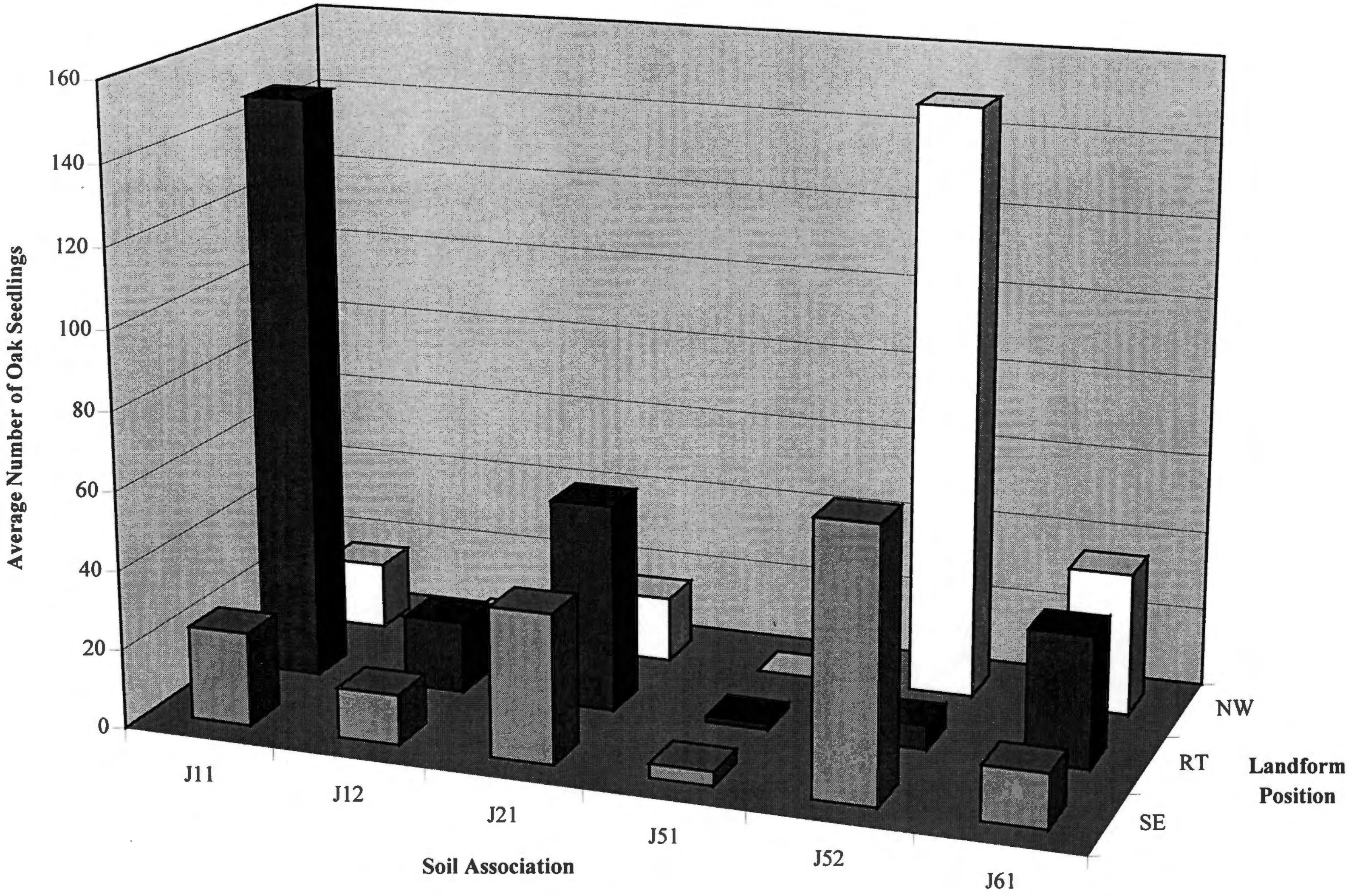


Figure 23. Number of 1st size class black oak seedlings by landform position and soil association combination.

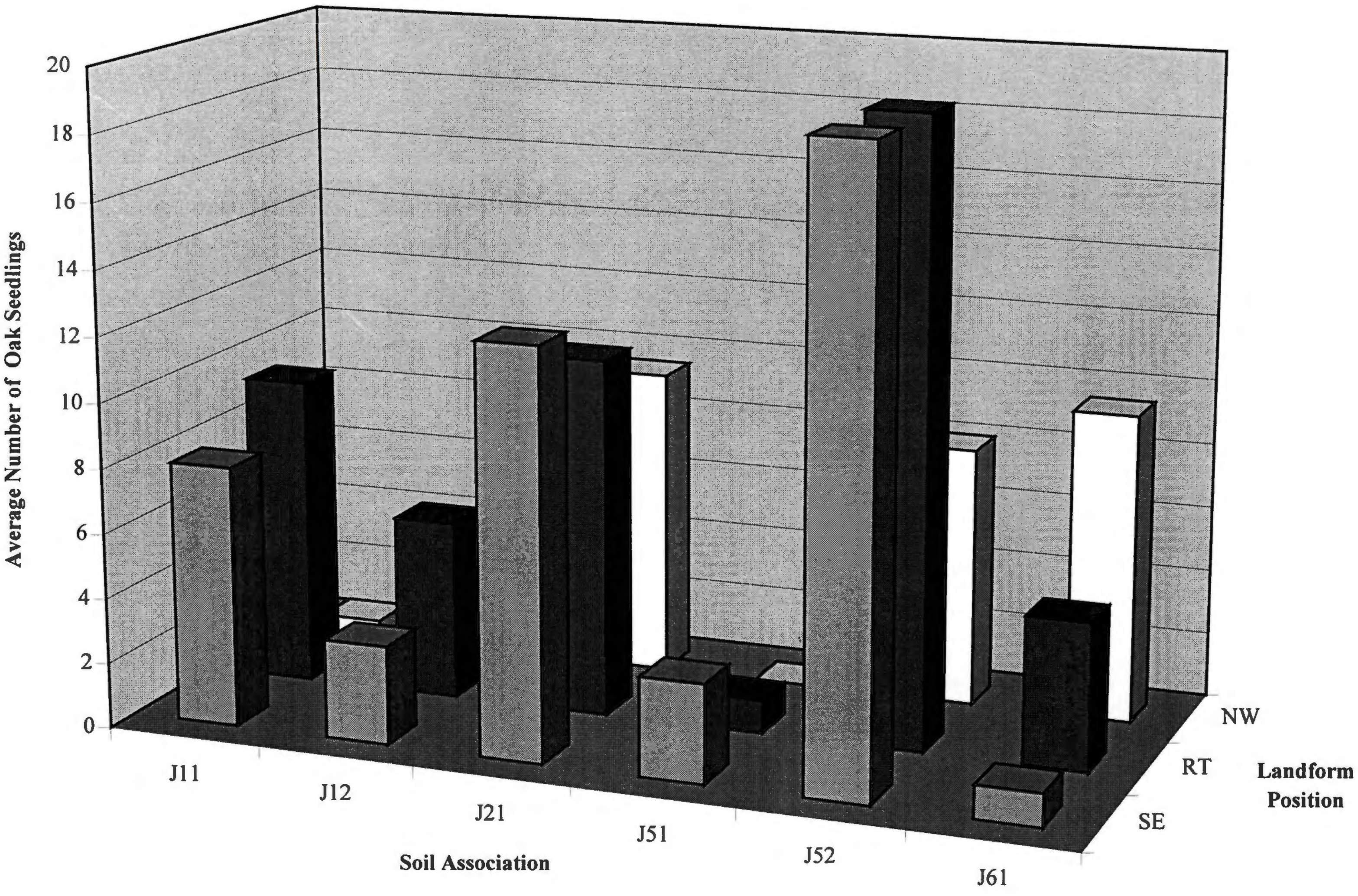


Figure 24. Number of 2nd size class black oak seedlings by landform position and soil association combination.

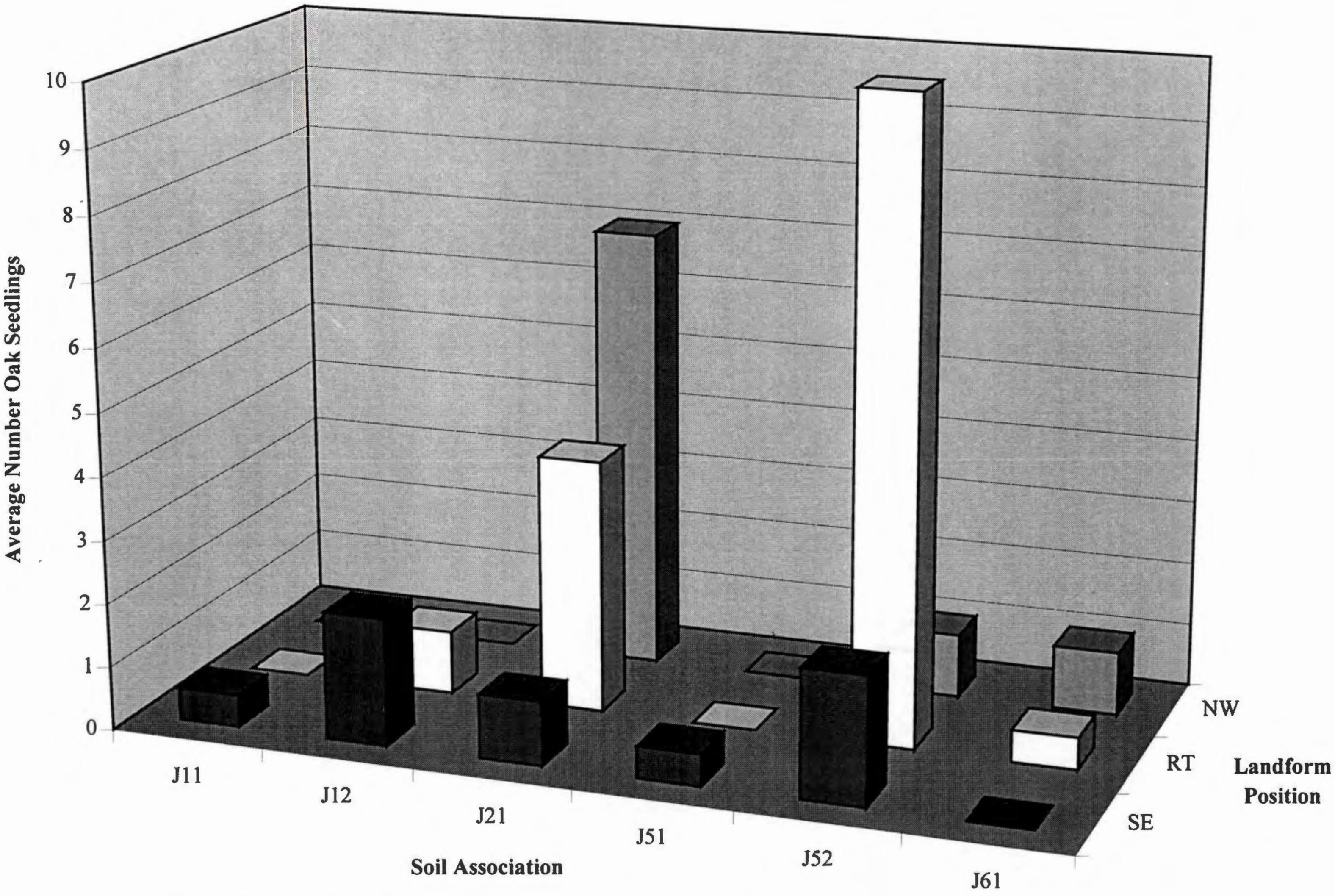


Figure 25. Number of 3rd size class black oak seedlings by landform position and soil association combination.

combination (Figure 23). The 2nd and 3rd size class black oak seedlings were greatest in number on the J52 combinations (Figures 24 & 25). The RT/ J52 landform position-soil association combination contained the highest average number of black oak seedlings 4th size class (Figure 26).

Estimated regression equations for total black oak regeneration are located in Table 11. The equations show that as black oak importance value and pine importance value increase, the number of black oak seedlings increase (R-square = 73.2%; P=<.0001). The intercepts indicate a general trend toward greatest abundance of black oak on the ridge top landform position.

The models that best explain the number of black oak seedlings for each size class are located in Table 12. Black oak importance value and hickory importance value were common variables in the models. The relationship between black oak seedlings and black oak importance value was slightly positive, whereas hickory importance value proved to have a negative relationship with only the first size class seedlings (Figures 27A and 27B). The number of dogwood saplings in the 4th size class was important in the 3rd and 4th size class models, having a slightly negative relationship with both size classes (Figure 27C). Pine importance value was shown to have a positive relationship with both the total number of black oak seedlings and the number of 2nd size class seedlings (Figure 27D).

Northern Red Oak

A total of 1,108 northern red oak seedlings were tallied over all of the sample sites. Seventy-three percent of the total number of northern red oak seedlings was in the

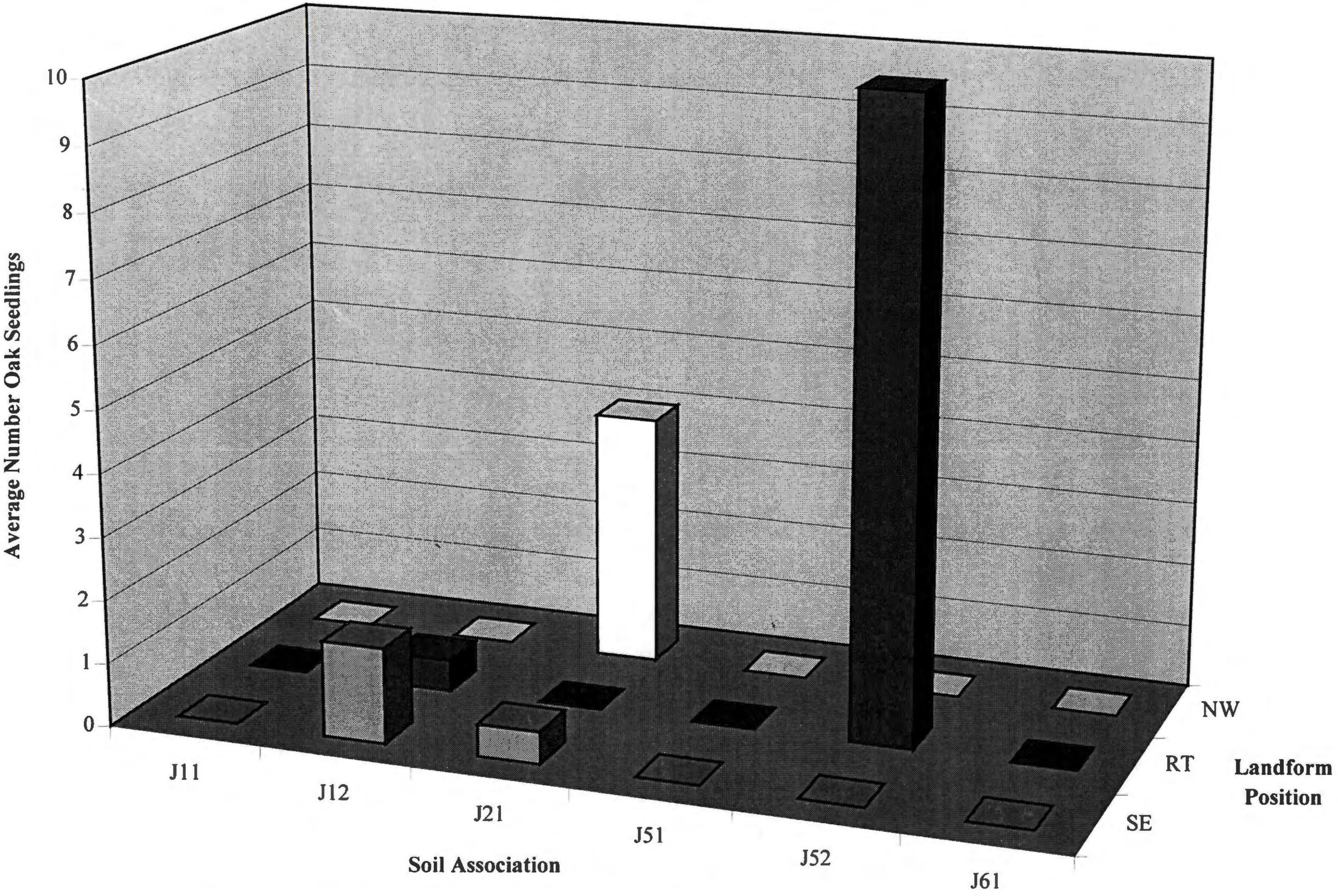


Figure 26. Number of 4th size class black oak seedlings by landform position and soil association combination.

Table 11. Equations for all size classes of black oak regeneration combined, by landform position/ soil association combination. R-square was 73.2% (P<.0001) for these equations.

Landform Position / Soil Association	Equation
NW / J11	21.43 + (0.45) pineiv + (1.92) boiv
RT / J11	47.19 + (0.45) pineiv + (1.92) boiv
SE / J11	15.32 + (0.45) pineiv + (1.92) boiv
NW / J12	3.59 + (0.45) pineiv + (1.92) boiv
RT / J12	29.34 + (0.45) pineiv + (1.92) boiv
SE / J12	-2.53 + (0.45) pineiv + (1.92) boiv
NW / J21	36.38 + (0.45) pineiv + (1.92) boiv
RT / J21	62.14 + (0.45) pineiv + (1.92) boiv
SE / J21	30.27 + (0.45) pineiv + (1.92) boiv
NW / J51	-16.13 + (0.45) pineiv + (1.92) boiv
RT / J51	9.63 + (0.45) pineiv + (1.92) boiv
SE / J51	-22.24 + (0.45) pineiv + (1.92) boiv
NW / J52	-8.38+ (0.45) pineiv + (1.92) boiv
RT / J52	17.38 + (0.45) pineiv + (1.92) boiv
SE / J52	-14.49 + (0.45) pineiv + (1.92) boiv
NW / J61	4.67 + (0.45) pineiv + (1.92) boiv
RT / J61	30.43 + (0.45) pineiv + (1.92) boiv
SE / J61	-1.44+ (0.45) pineiv + (1.92) boiv

- NW, SE, RT = northwest, southeast facing aspects at midslope position, or ridge top position
- J11, J12, J21, J51, J52, J61 = soil associations
- pineiv = pine importance value
- boiv = black oak importance value

Table 12. Significant model variables for black oak regeneration for all size classes.

Y-variable	Model	R-square	P-value
Total	LFPos Soil Pineiv Boiv	73.2%	<.0001
1st Size Class	LFPos Soil Hickiv Boiv	73.5%	<.0001
2nd Size Class	LFPos Soil Pineiv Boiv	48.7%	.0418
3rd Size Class	LFPos Soil Boiv Hickiv Dogw Rbud Total	73.8%	.0012
4th Size Class	LFPos Soil Slope Dogw Hickiv Sass	69.2%	.0021

- LFPos = landform position
- Soil = soil association
- Pineiv = pine importance value
- Boiv = black oak importance value
- Hickiv = hickory importance value
- Dogw = total number of dogwood saplings in 4th size class
- Rbud = total number of redbud saplings in 4th size class
- Total = total number of competing species in the 4th size class
- Slope = average percent slope
- Sass = total number of sassafras saplings in the 4th size class

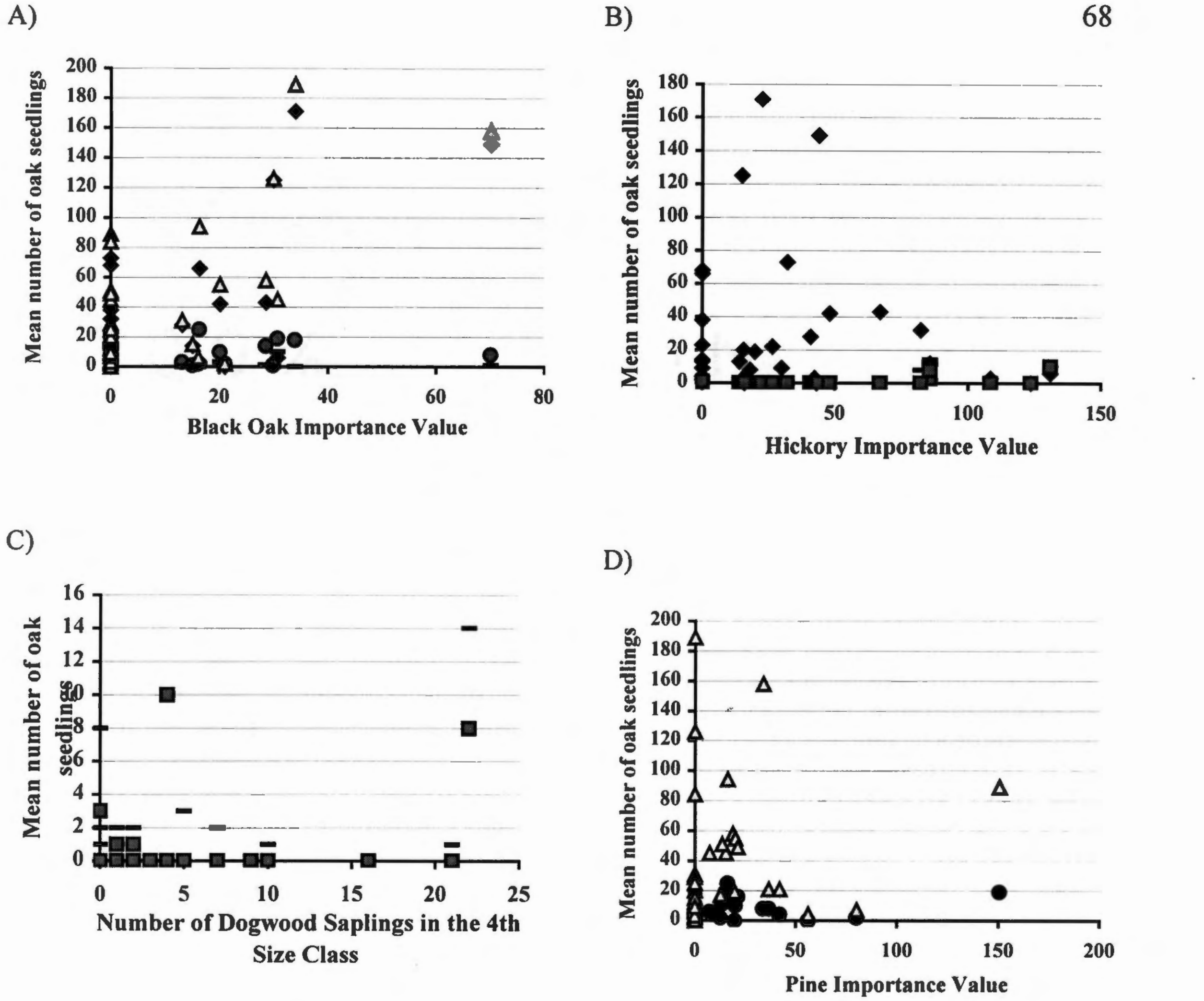


Figure 27. Relationships between mean number of black oak seedlings and (A) black oak importance value, (B) hickory importance value, (C) number of 4th size class dogwood seedlings, and (D) pine importance value.

1st size class, while only 1.5% was in the 4th size class. On average, northern red oak seedlings were most common on the NW/ J51 landform position-soil association combination and least abundant on the SE / J11 combination (Figure 28). First size class seedlings were most abundant on the NW / J51 combination, while seedlings were least abundant on the SE / J11 combination (Figure 29). On average, the NW / J61 landform position/soil association combination had the highest number of 2nd size class northern red oak seedlings, while the SE / J11 and NW / J51 had the least (Figure 30). The SE / J12 and SE / J52 landform position-soil association combinations had the greatest number of 3rd size class seedlings (Figure 31). The NW / J21 combination had the highest average number of northern red oak seedlings in the 4th size class (Figure 32).

Estimated regression equations for total northern red oak regeneration are found in Table 13. The equations show that as average mid-canopy depth, white oak importance value, and sassafras importance value increase, the number of northern red oak seedlings decrease. As northern red oak importance value and blackgum importance value increase, the number of northern red oak seedlings increase (R-square = 61%; P= .0280).

The models that best explain the number of northern red oak seedlings for each size class are located in Table 14. The number of dogwood saplings in the 4th size class is an important variable in the 1st,2nd, and 3rd size classes, showing a slight negative trend as the number of dogwood saplings increase (Figure 33A). Hickory importance values are important in determining the number of northern red oak seedlings in the 2nd, 3rd, and 4th size classes. Although the relationships are very slight, there is a positive relationship between hickory importance value and the number of northern red oak seedlings in these size classes (Figure 33B). Average canopy cover percent has a significant effect on the

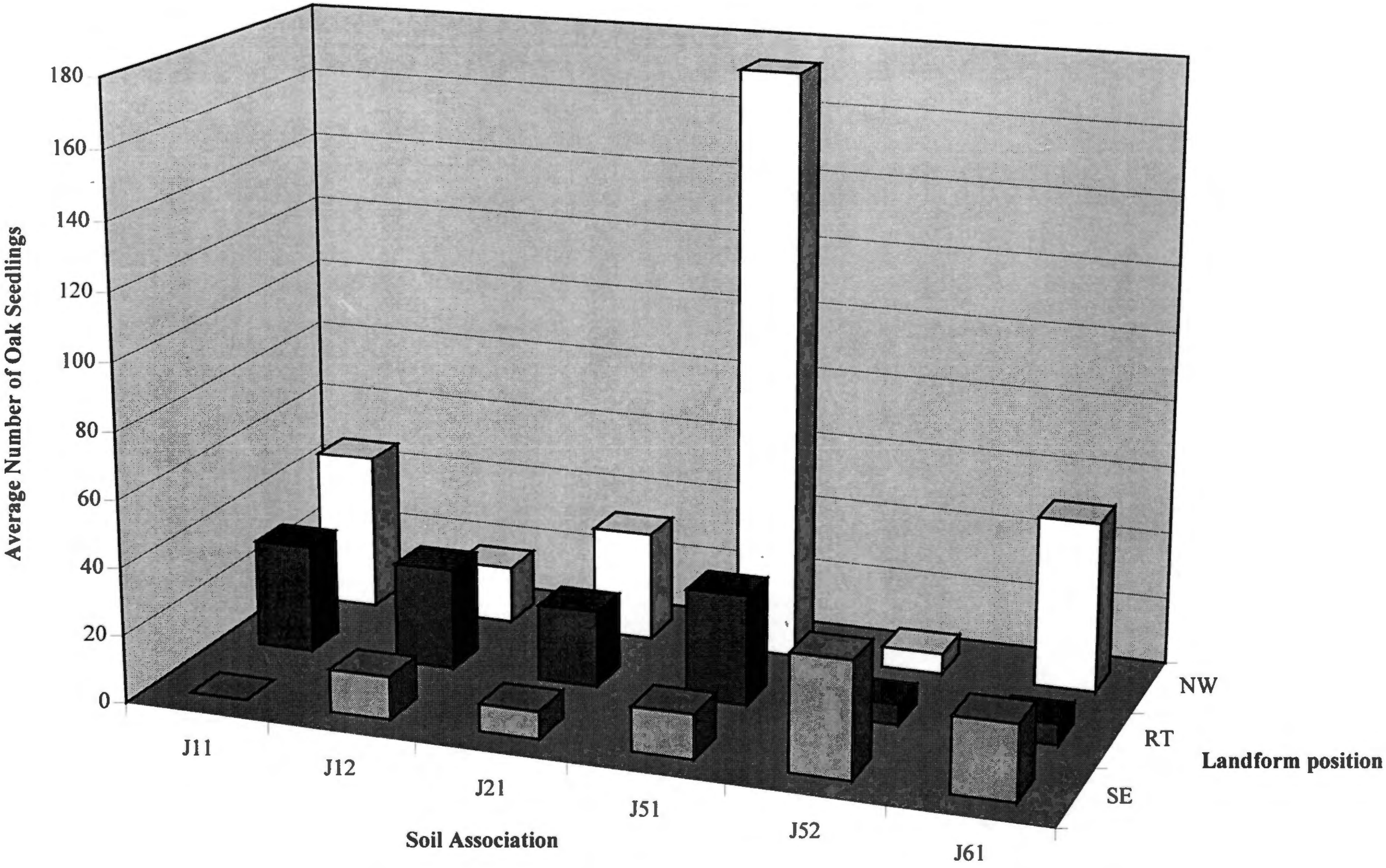


Figure 28. Number of northern red oak seedlings (all sizes combined) by landform position and soil association combination.

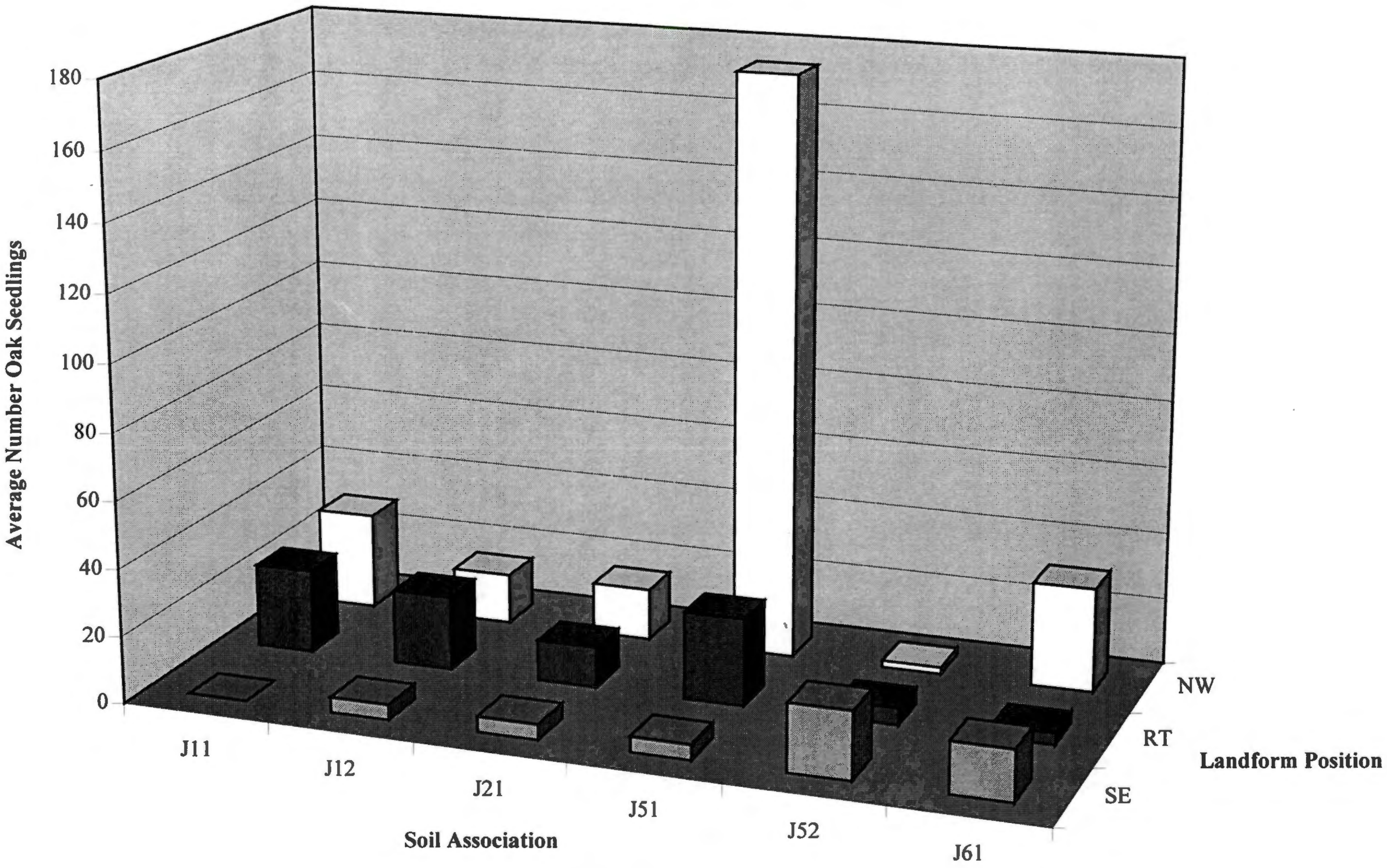


Figure 29. Number of 1st size class northern red oak seedlings by landform position and soil association combination.

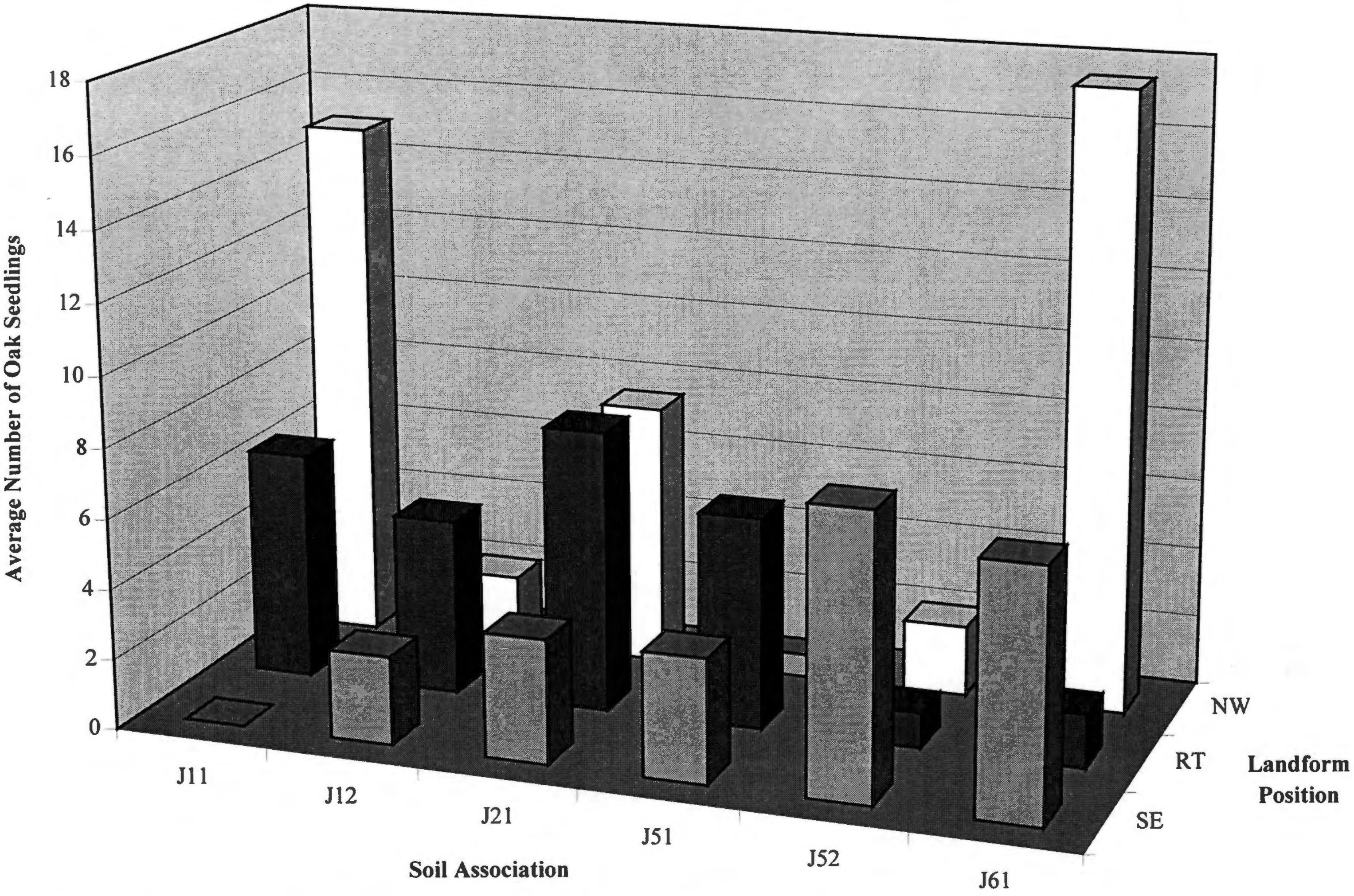


Figure 30. Number of 2nd size class northern red oak seedlings by landform position and soil association combination.

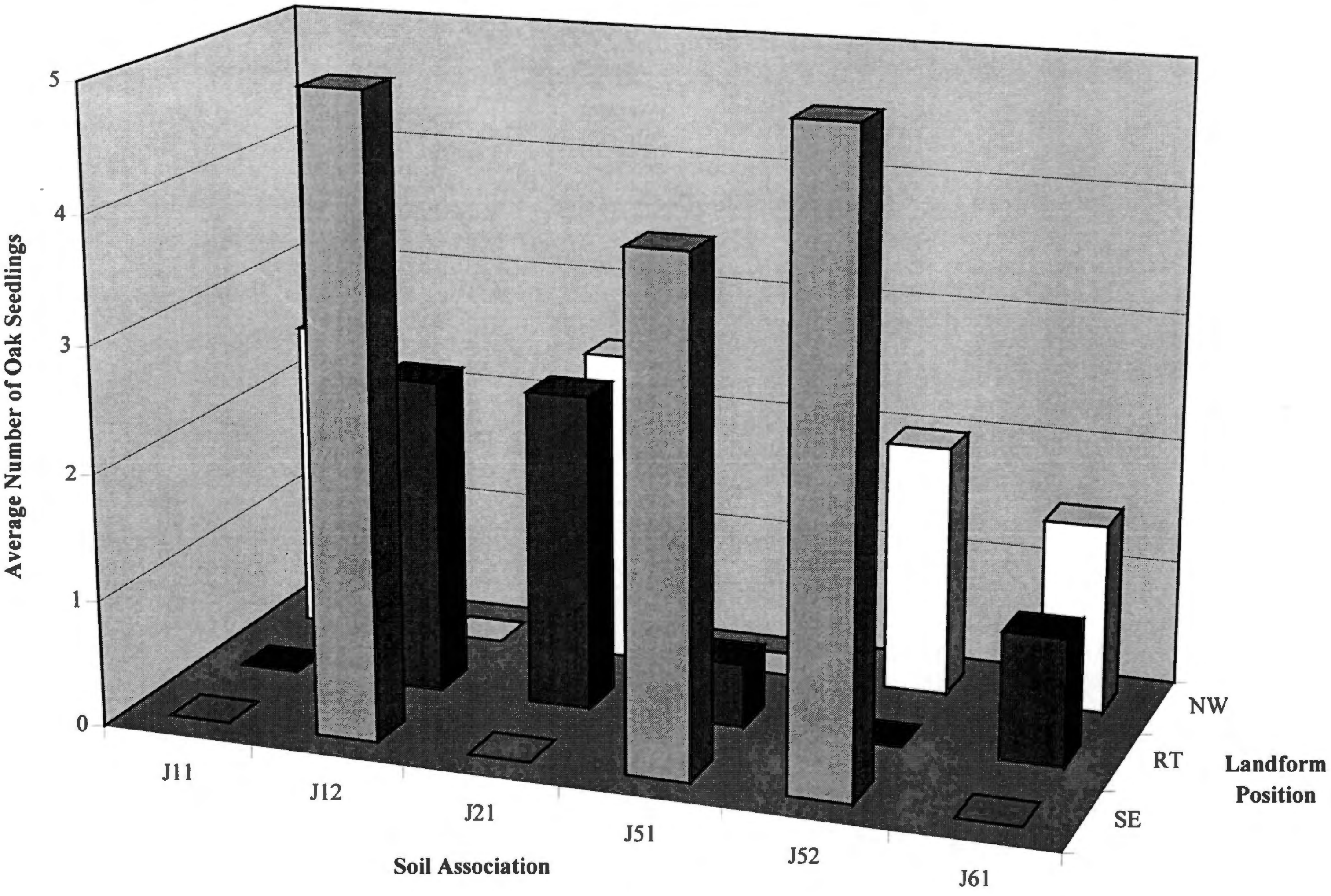


Figure 31. Number of 3rd size class northern red oak seedlings by landform position and soil association combination.

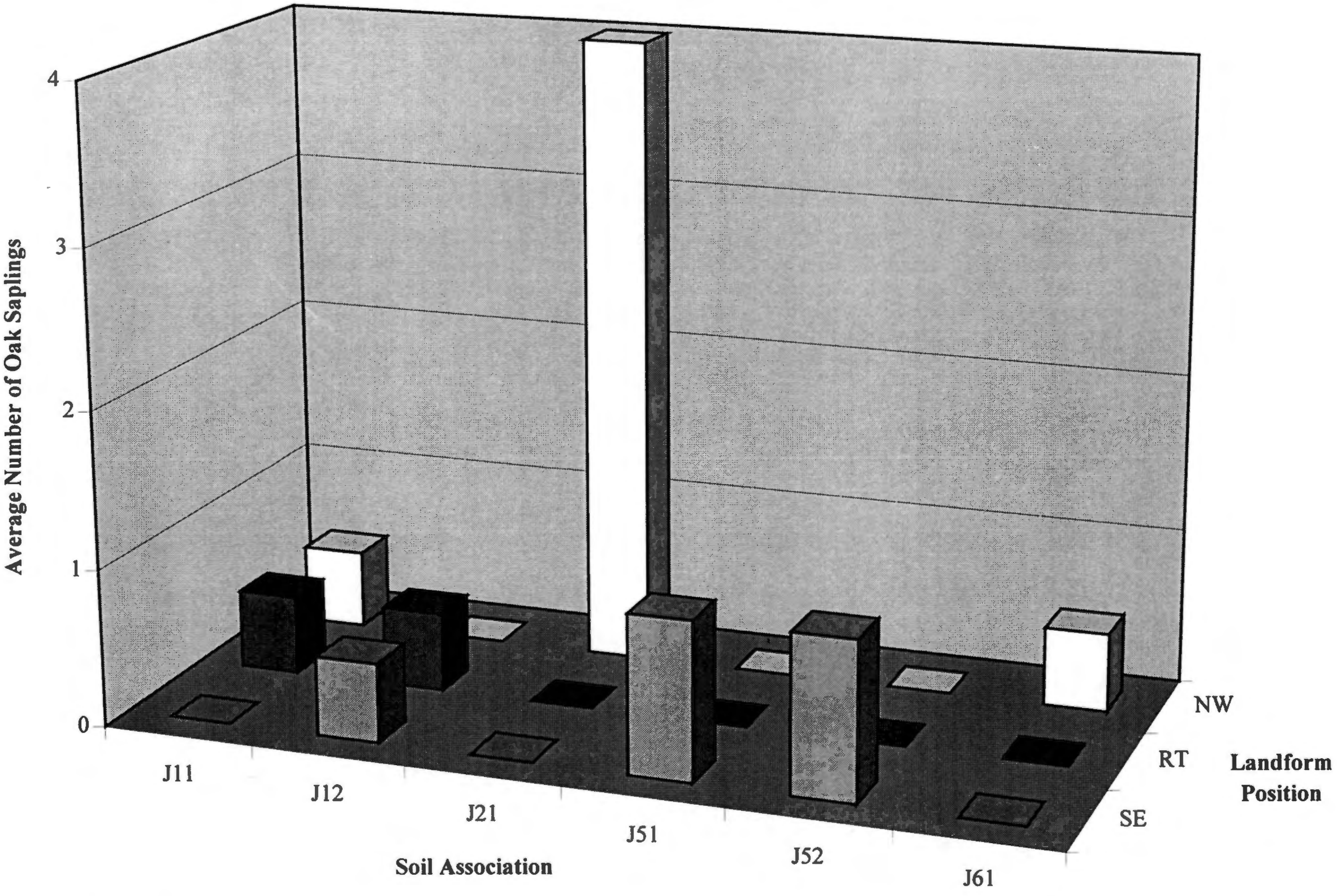


Figure 32. Number of 4th size class northern red oak seedlings by landform position and soil association combination.

Table 13. Equations for all size classes of northern red oak regeneration combined by landform position/ soil association combination. R-square was 61% (P= .0280) for this group of equations.

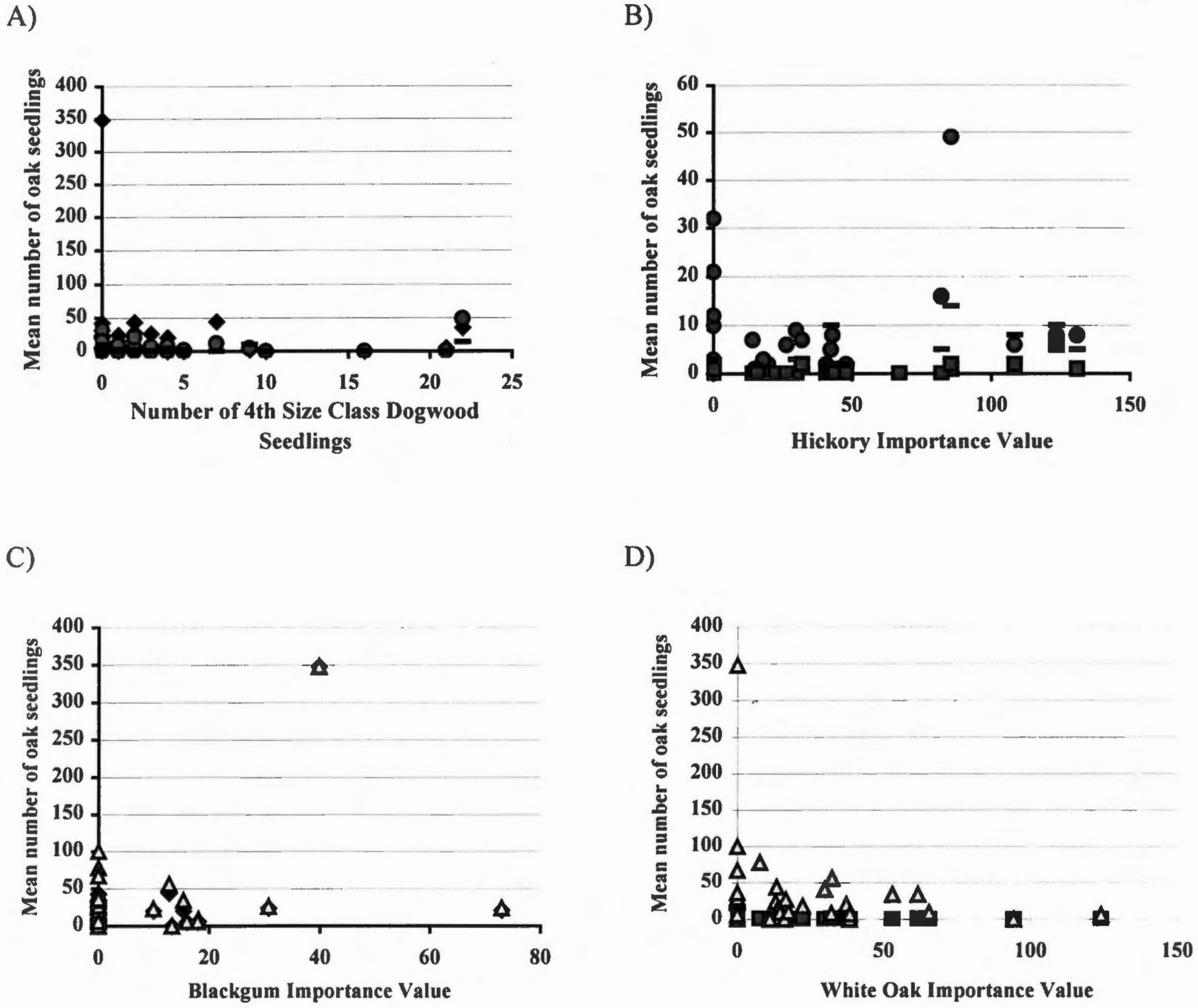
Landform Position / Soil Association	Equation
NW / J11	118.25 – (9.20) midcan + (1.73) nroiv – (0.63) woiv + (1.81) blgmiv – (4.37) sassiv
RT / J11	84.34 – (9.20) midcan + (1.73) nroiv – (0.63) woiv + (1.81) blgmiv – (4.37) sassiv
SE / J11	98.79 – (9.20) midcan + (1.73) nroiv – (0.63) woiv + (1.81) blgmiv – (4.37) sassiv
NW / J12	38.83 – (9.20) midcan + (1.73) nroiv – (0.63) woiv + (1.81) blgmiv – (4.37) sassiv
RT / J12	4.92 – (9.20) midcan + (1.73) nroiv – (0.63) woiv + (1.81) blgmiv – (4.37) sassiv
SE / J12	19.37 – (9.20) midcan + (1.73) nroiv – (0.63) woiv + (1.81) blgmiv – (4.37) sassiv
NW / J21	75.78 – (9.20) midcan + (1.73) nroiv – (0.63) woiv + (1.81) blgmiv – (4.37) sassiv
RT / J21	38.83 – (9.20) midcan + (1.73) nroiv – (0.63) woiv + (1.81) blgmiv – (4.37) sassiv
SE / J21	56.32 – (9.20) midcan + (1.73) nroiv – (0.63) woiv + (1.81) blgmiv – (4.37) sassiv
NW / J51	79.70 – (9.20) midcan + (1.73) nroiv – (0.63) woiv + (1.81) blgmiv – (4.37) sassiv
RT / J51	45.79 – (9.20) midcan + (1.73) nroiv – (0.63) woiv + (1.81) blgmiv – (4.37) sassiv
SE / J51	60.24 – (9.20) midcan + (1.73) nroiv – (0.63) woiv + (1.81) blgmiv – (4.37) sassiv
NW / J52	47.22– (9.20) midcan + (1.73) nroiv – (0.63) woiv + (1.81) blgmiv – (4.37) sassiv
RT / J52	13.31 – (9.20) midcan + (1.73) nroiv – (0.63) woiv + (1.81) blgmiv – (4.37) sassiv
SE / J52	27.77 – (9.20) midcan + (1.73) nroiv – (0.63) woiv + (1.81) blgmiv – (4.37) sassiv
NW / J61	49.46 – (9.20) midcan + (1.73) nroiv – (0.63) woiv + (1.81) blgmiv – (4.37) sassiv
RT / J61	15.55 – (9.20) midcan + (1.73) nroiv – (0.63) woiv + (1.81) blgmiv – (4.37) sassiv
SE / J61	30.00 – (9.20) midcan + (1.73) nroiv – (0.63) woiv + (1.81) blgmiv – (4.37) sassiv

- NW, SE, RT = northwest, southeast facing aspects at midslope positions, or ridge top position
- J11, J12, J21, J51, J52, J61 = soil associations
- midcan = average mid-canopy depth (m)
- nroiv = northern red oak importance value
- woiv = white oak importance value
- blgmiv = blackgum importance value
- sassiv = sassafras importance value

Table 14. Significant model variables for northern red oak, for all size classes.

Y-variable	Model	R-square	P-value
Total	LFPos Soil Midcan Nroiv Woiv Blgmiv Sassiv	61%	.0280
1st Size Class	LFPos Soil Scsroiv Blgmiv Dogw	51.2%	.0492
2nd Size Class	LFPos Soil Dogw Pineiv Hickiv	69.6%	.0008
3rd Size Class	LFPos Soil Dogw Coiv Hickiv Total	80%	<.0001
4th Size Class	LFPos Soil Avecc Hickiv Woiv	60.3%	.0087

- LFPos = landform position
- Soil = soil association
- Midcan = average mid-canopy depth (m)
- Nroiv = northern red oak importance value
- Blgmiv = blackgum importance value
- Woiv = white oak importance value
- Sassiv = sassafras importance value
- Scsroiv = scarlet and southern red oak importance value
- Dogw = total number of dogwood saplings in 4th size class
- Hickiv = hickory importance value



Figures 33. Relationships between mean number of northern red oak seedlings and (A) number of 4th size class dogwood seedlings, (B) hickory importance value, (C) blackgum importance value, and (D) white oak importance value.

amount of northern red oak in the 4th size class. Blackgum importance value is important in the 1st size class model and shows a positive relationship with the number of northern red oak seedlings (Figure 33C). The 4th size class northern red oak seedlings were only slightly negatively related to white oak importance value (Figure 33D).

Scarlet and Southern Red Oak

A total of 510 scarlet and southern red oak seedlings were tallied over all of the sample sites. Ninety percent of the total number of scarlet and southern red oak seedlings was in the 1st size class and no seedlings were tallied in the 4th size class. On average, scarlet and southern red oak seedlings were most common on the J21/ SE landform position-soil association combination (Figure 34). First size class seedlings were most abundant on the J21/ SE combination, on average (Figure 35). The J21/ NW and J52/ SE landform position/soil association combination had the most 2nd size class scarlet and southern red oak seedlings (Figure 36). The J52/ SE combination contained the highest average number of scarlet and southern red oak seedlings in the 3rd size class (Figure 37).

Estimated regression equations for total scarlet and southern red oak regeneration are located in Table 15. The equations show a negative relationship between total scarlet and southern red oak seedlings and average PAR and black oak importance value. As the importance value for scarlet and southern red oak increase, the number of scarlet and southern red oak seedlings increase (R-square = 86.9%; P=<.0001). There is a general negative trend toward a decrease in the number of scarlet and southern red oak seedlings as the site changes from NW to RT to SE landform positions.

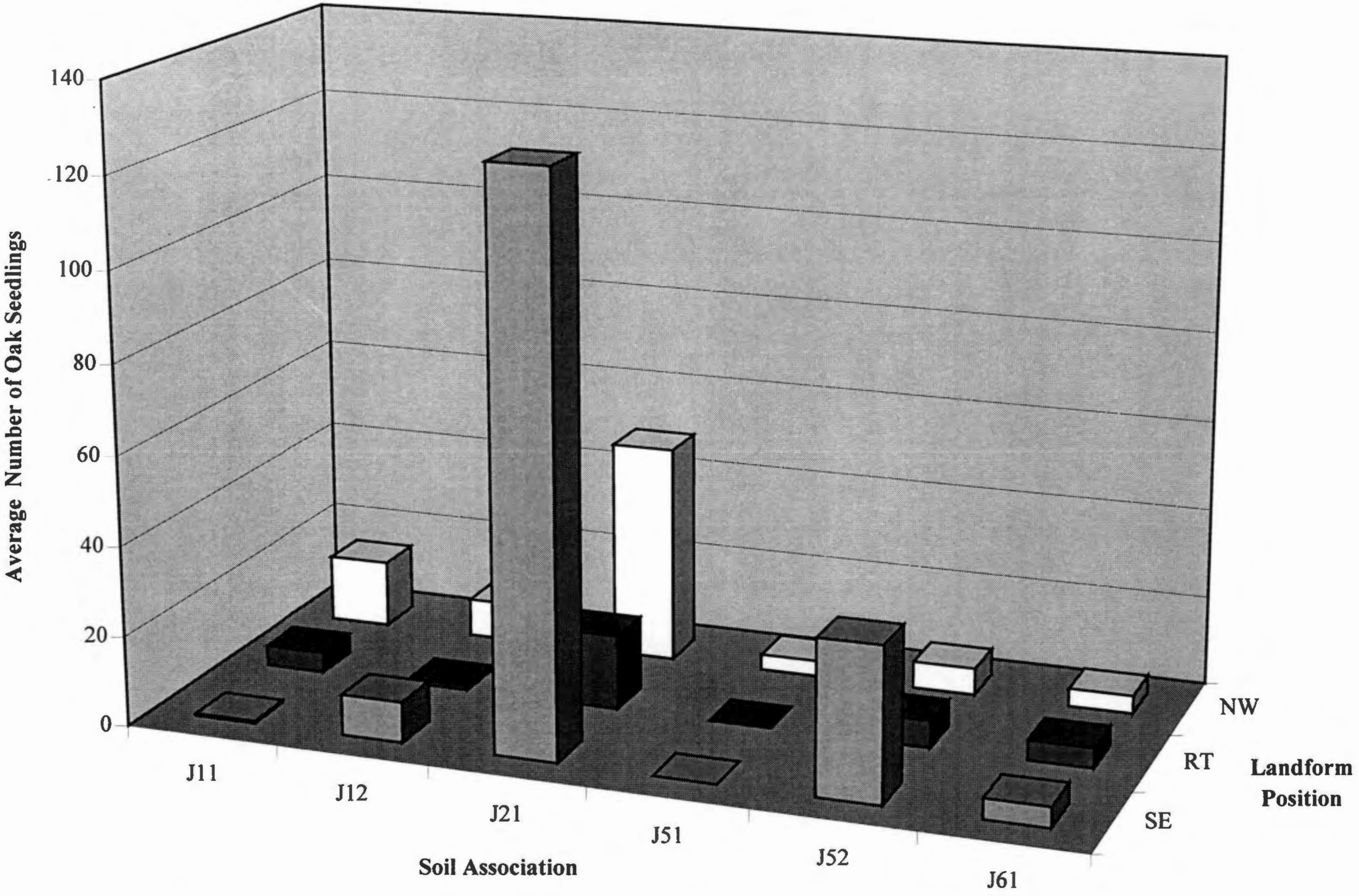


Figure 34. Number of scarlet and southern red oak seedlings (all size classes combined) by landform position and soil association combination.

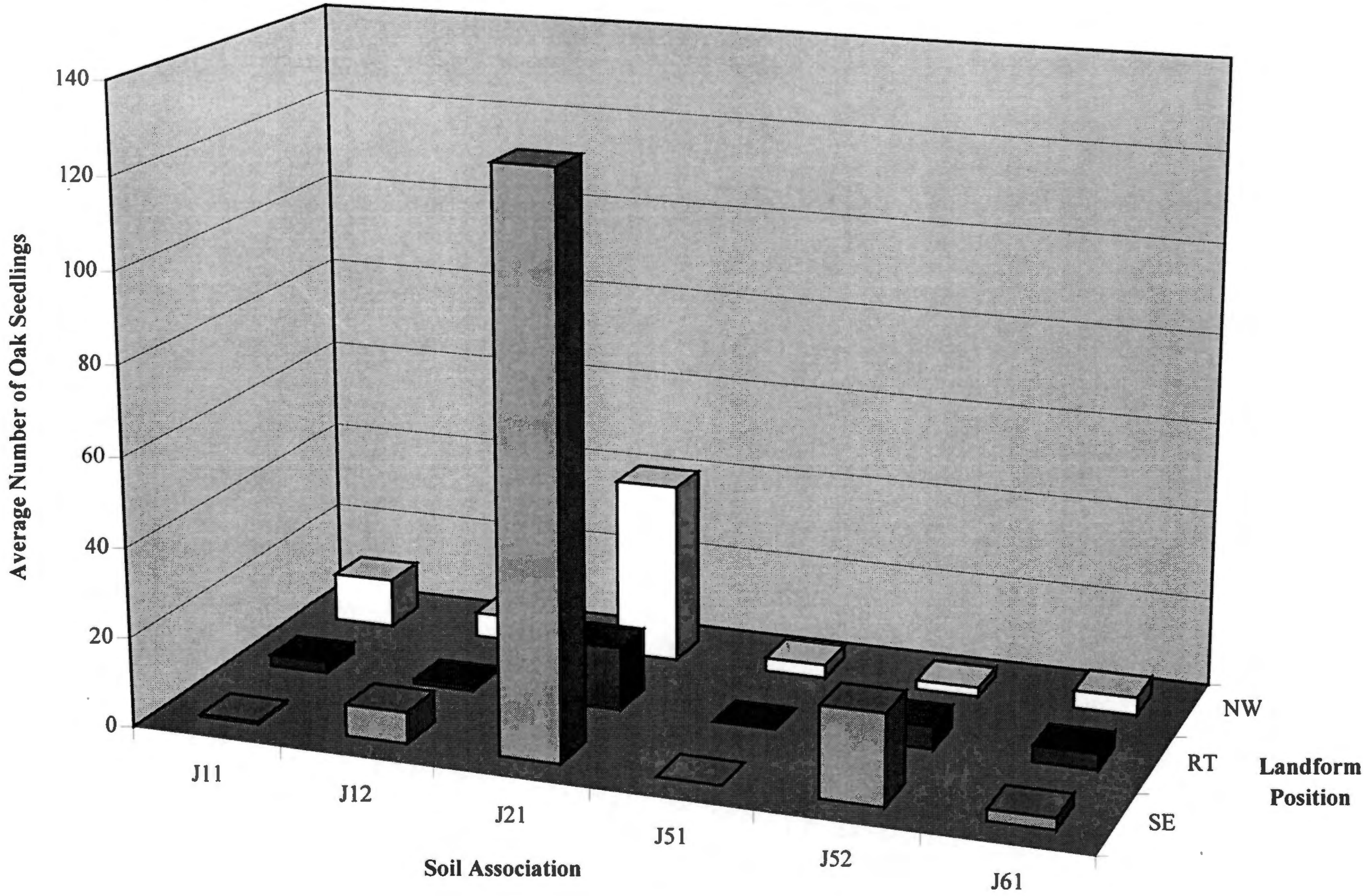


Figure 35. Number of 1st size class scarlet and southern red oak seedlings by landform position and soil association combination.

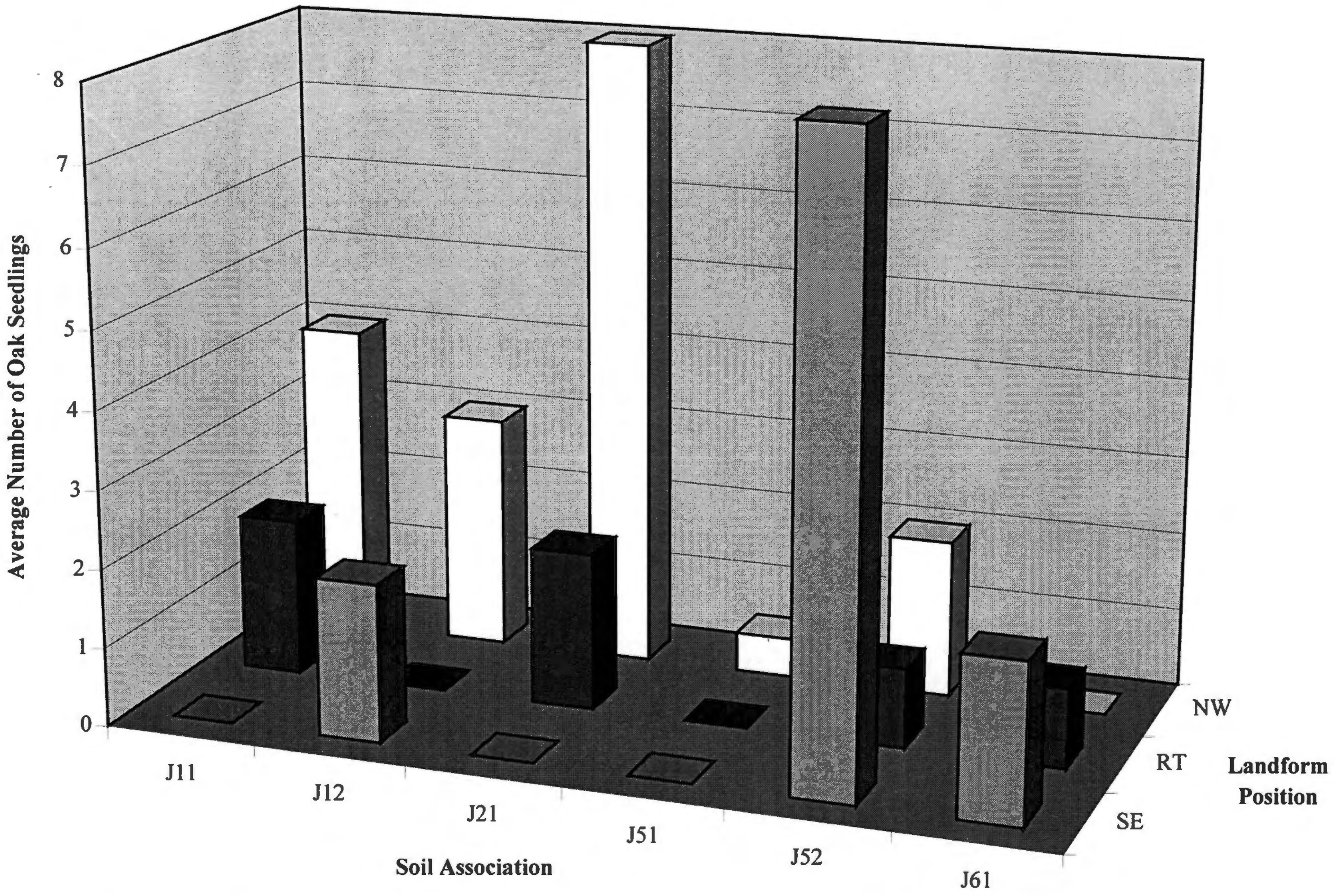


Figure 36. Number of 2nd size class scarlet adn southern red oak seedlings by landform position and soil association combination.

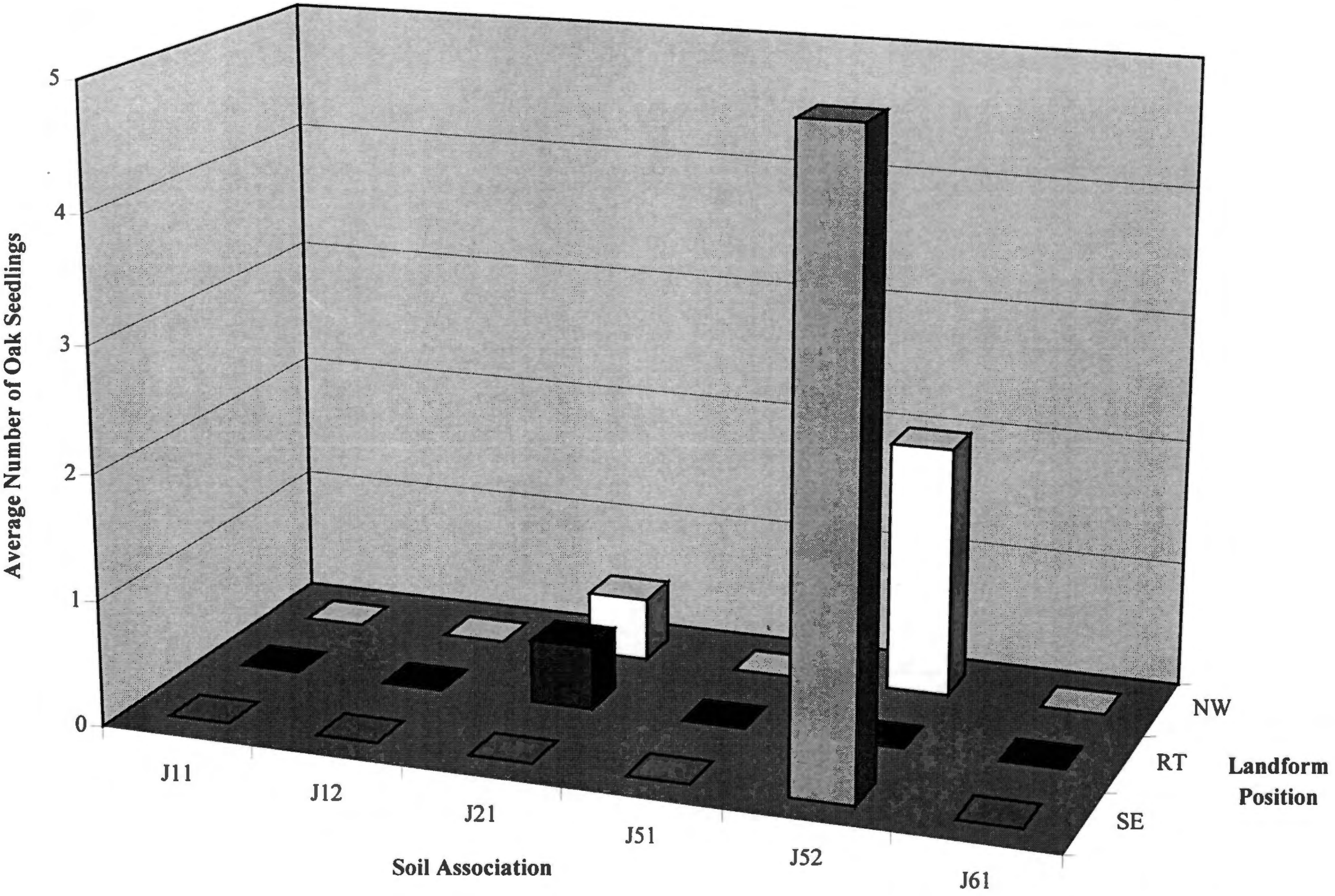


Figure 37. Average number of 3rd size class scarlet and southern red oak seedlings by landform position/soil association combination.

Table 15. Equations for all size classes of scarlet and southern red oak combined, by landform position/ soil association combination. R-square was 71.1% (P=.0005) for these equations.

Landform Position / Soil Association	Equation
NW / J11	95.11 + (.609) scsroiv – (237.03) par – (2.03) boiv
RT / J11	89.20 + (.609) scsroiv – (237.03) par – (2.03) boiv
SE / J11	79.85 + (.609) scsroiv – (237.03) par – (2.03) boiv
NW / J12	2.23 + (.609) scsroiv – (237.03) par – (2.03) boiv
RT / J12	-3.68 + (.609) scsroiv – (237.03) par – (2.03) boiv
SE / J12	-13.03 + (.609) scsroiv – (237.03) par – (2.03) boiv
NW / J21	9.92 + (.609) scsroiv – (237.03) par – (2.03) boiv
RT / J21	4.01 + (.609) scsroiv – (237.03) par – (2.03) boiv
SE / J21	-5.34 + (.609) scsroiv – (237.03) par – (2.03) boiv
NW / J51	27.44 + (.609) scsroiv – (237.03) par – (2.03) boiv
RT / J51	21.53 + (.609) scsroiv – (237.03) par – (2.03) boiv
SE / J51	12.18 + (.609) scsroiv – (237.03) par – (2.03) boiv
NW / J52	72.54 + (.609) scsroiv – (237.03) par – (2.03) boiv
RT / J52	66.63 + (.609) scsroiv – (237.03) par – (2.03) boiv
SE / J52	57.28 + (.609) scsroiv – (237.03) par – (2.03) boiv
NW / J61	13.38+ (.609) scsroiv – (237.03) par – (2.03) boiv
RT / J61	7.47 + (.609) scsroiv – (237.03) par – (2.03) boiv
SE / J61	-1.88 + (.609) scsroiv – (237.03) par – (2.03) boiv

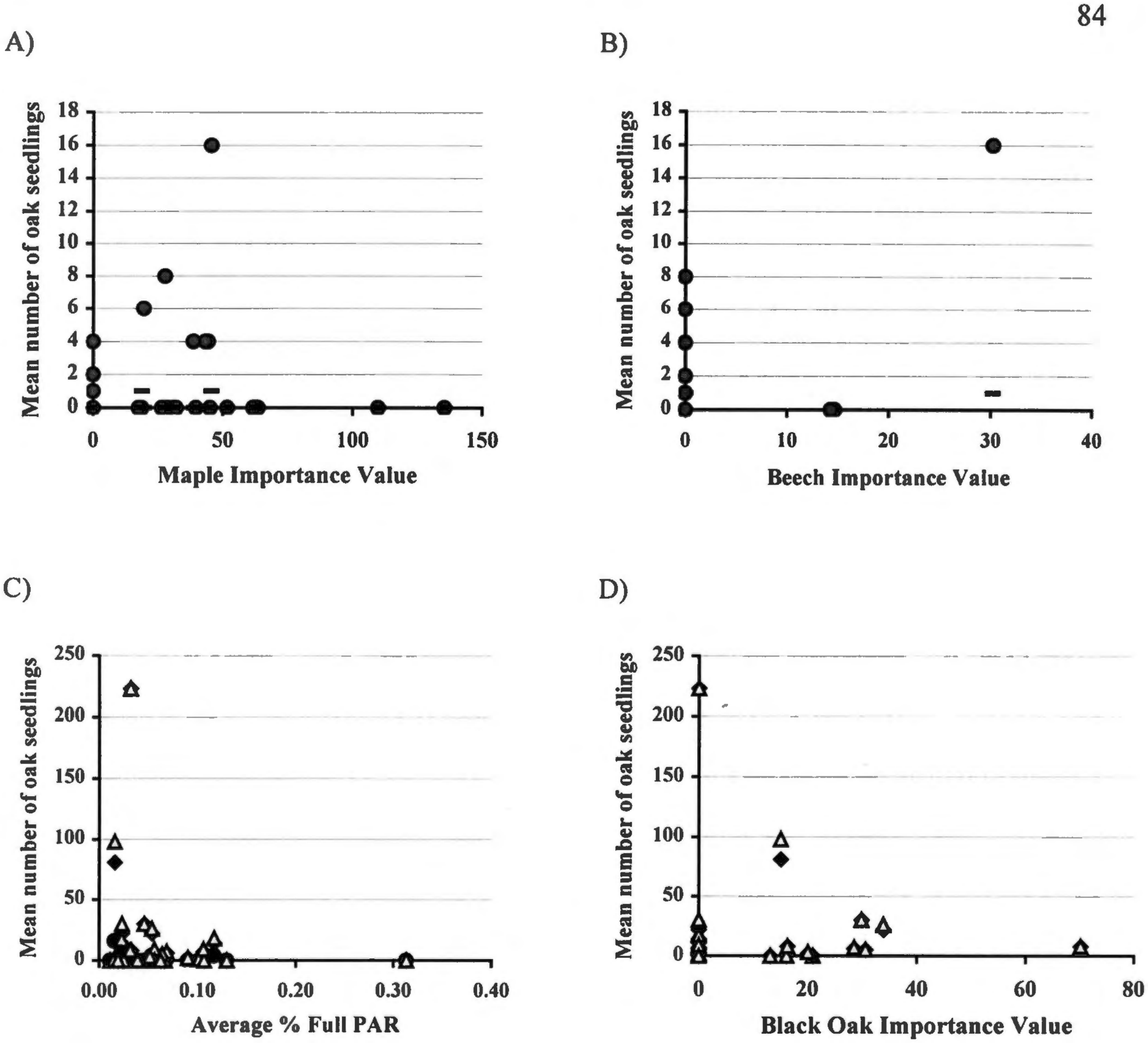
- NW, SE, RT = northwest, southeast aspect at midslope position, and ridge top position
- J11, J12, J21, J51, J52, J61 = soil associations
- scsroiv = scarlet and southern red oak importance value
- par = average photosynthetically active radiation below the canopy
- boiv = black oak importance value

Table 16. Significant model variables for Scarlet and southern red oak regeneration.

y-variable	Model	R-square	P-value
Total	LFPos Soil Scsroiv Par Boiv	71.1%	.0005
1st Size Class	LFPos Soil Scsroiv Par Boiv	69%	.0009
2nd Size Class	LFPos Soil Par Mapiv Bchiv Total	71.5%	.0010
3rd Size Class	LFPos Soil Candep Mapiv Bchiv	63.1%	.0045 *n.n.

- LFPos = Landform position
- Soil = soil association
- Scsroiv = scarlet and southern red oak importance value
- Par = average photosynthetically active radiation below canopy
- Boiv = black oak importance value
- Mapiv = maple importance value
- Total = total number of competing species in the 4th size class
- Bchiv = American beech importance value

The models that best explain the number of scarlet and southern red oak seedlings for each size class are in Table 16. Scarlet and southern red oak importance value is important for 1st size class seedlings, but is not present in the models for larger size classes. Maple and beech importance value are significant variables in the 2nd and 3rd size classes. While the exact relationship of beech importance value to the 2nd and 3rd size class scarlet and southern red oak seedlings is slightly positive, the relationship with maple importance value is slightly negative (Figures 38A and 38B). Average PAR had a slightly negative relationship with the number of 1st and 2nd size class scarlet and southern red oak seedlings (Figure 38C). With increasing values of black oak importance, there was a slight decrease in the number of total and 1st size class scarlet and southern red oak seedlings (Figure 38D). The data for the 3rd size class scarlet and southern red oak seedlings do not have a normal distribution.



Figures 38. Relationships between mean number of scarlet and southern red oak seedlings and (A) maple importance value, (B) beech importance value, (C) average % full PAR, and (D) black oak importance value.

◆ 1st Size Class
■ 4th Size Class
● 2nd Size Class
△ All Size Classes
▬ 3rd Size Class

IV. Discussion

Landform Position and Soil Association

Regardless of soil association, the smaller size classes of all species of oak, except chestnut oak and scarlet/southern red oak, were more abundant on the northwest landform positions. This suggests that conditions for germination and early survival may be best on northwest sites. Although the prevailing wind direction is from the west, which can increase evapotranspiration, the lower amount of radiation received on the northwest aspect than the southeast aspect may override the effect of wind, resulting in a cooler, moister microclimate. The occurrence of larger size classes on the drier southeastern and ridgetop positions is consistent with past studies that determined oaks are better adapted to droughty conditions than many other hardwoods and therefore may out compete other hardwood species on the drier, poorer sites (Abrams, 1990; Thor et al., 1969).

The abundance of chestnut oak seedlings was greatest on the ridge top landform positions in all size classes, which is consistent with previous studies that suggest that chestnut oak is well adapted to dry ridgetops and upper slopes with shallow soils (McQuilkin, 1990). The scarlet/southern red oak group seedlings are more abundant on the southeastern aspects, which is consistent with findings that scarlet oak appears to out compete other species on southern exposures and southern red oak typically grows on upper slopes with southern or western exposures (Johnson, 1990; Belanger, 1990).

The patterns of greater abundance of small seedlings of all oak species, except black oak and northern red oak, on more productive soils and the larger size classes being more common on slightly less productive soils indicates that conditions required by seedlings may change as the seedlings grow into larger size classes. Conditions associated with productive sites may be most important during the germination and early seedling stages, and the importance of these conditions may decrease as time progresses relative to the importance of competition for light. The shade tolerance of younger seedlings is often greater than that of older saplings in many hardwood species (Burns and Honkala, 1990).

Black oak is consistently more abundant on the J52 soil association in all size classes, and this soil association has moderately productive soils with large amounts of rock fragments and low water holding capacity (Springer and Elder, 1980). Northern red oak varies in its soil preferences, with each size class being more abundant on a different soil association.

Overall, the combined effect of soil association and landform position on reproduction of all oak species supports the hypothesis of oaks being better adapted to poorer quality sites (Weitzman and Trimble, 1957; Abrams, 1990; Barnes and Van Lear, 1998). When seedlings are more abundant on more productive soils, the combined landform position is usually southeastern or ridgetop, which would tend to be drier.

Canopy Structure

The positive relationships between canopy depth and oak regeneration for various species of oak and in many oak reproduction size classes were unexpected. These relationships may be explained by the generally higher shade tolerance of oak seedlings when they are young. The fact that the positive relationship occurred in the white oak and chestnut oak species, which are generally more shade tolerant than the red oaks, is consistent with this explanation. The greater shade tolerance of the white oak group would also explain the overall lack of regeneration of the red oak group on these sites with closed canopies. Northern red oak was the only species to increase in number as mid-canopy depth decreased, which is consistent with the degree of northern red oak shade tolerance previously reported (Sander, 1990).

Potentially Competing Saplings

The positive relationship found between the number of blackgum saplings and white oak seedlings of all size classes and 1st size class chestnut oak seedlings contradicts current thinking on how oak reacts to competition. This relationship may be due an affinity of blackgum for the same site conditions as oak. The negative relationship between total amount of oak regeneration and the number of largest size class hickory seedlings, as well as the negative relationship between the various size class seedlings of chestnut oak, black oak, and northern red oak and number of 4th size class dogwood seedlings, supports the current hypothesis that the amount of oak regeneration would decrease with increasing abundance of potential competitors (Lorimer, 1992; Hodges and Gardiner, 1992). A possible reason for the differing effects of blackgum and dogwood on oak regeneration may be due to differences in crown architecture. Dogwoods typically have numerous, wide spreading branches with dense foliage, whereas blackgum tends to be rather narrow and open (Hardin et al., 2001). Thus, blackgum may not shade smaller oaks to the same extent as dogwood.

Potentially Competing Mature Canopy Trees

The importance of seed source to oak regeneration is illustrated by the continual occurrence of the importance value of mature oaks of the same species as regenerating oak seedlings in the smaller size class models. In the analysis of the larger oak seedling size classes, the importance value of seed sources tends to drop out of the regression models, while the importance values of the species other than oaks tend to enter the models. Again, potential effects of competitors appear to increase with time. The presence of hickory in the overstory is positively associated with all species of oak, except scarlet and southern red oak, suggesting similar site requirements between the oaks and the hickories. This result is understandable due to the common co-occurrence of oaks and hickories in the widespread oak-hickory forest type in the central hardwood region.

The high frequency of chestnut oak in the models explaining reproduction for all species and size classes may be the result of the great abundance of chestnut oak throughout the region. The negative relationships that are occurring between northern red oak and white oak and also between the scarlet and southern red oak group and black oak can be explained in two ways. First, there could be competition between these oak species. Black oak may impede the number of total and 1st size class scarlet and southern red oak seedlings because of the preference of drier site conditions by both species. Although they share similar site preferences, white oak is more tolerant of shade than northern red oak, and therefore may be able to out compete northern red oak when in the understory and inhibit the growth of 4th size class northern red oak seedlings. A second potential explanation is the possibility of niche differences between these oak species.

Species of oak may either have separate distributions along a slope gradient, where one species occurs only on the lower or mid-slopes and the other occurs on the ridgetops and upper slopes. Even if their distributions overlap, they might not be competing for the same level of nutrients, light, or space (Racine, 1971).

The negative relationship between maple in the overstory and scarlet and southern red oak reinforces the shade intolerance of the scarlet and southern red oak species. This relationship is corroborated by past studies that suggest maple is replacing oak in many oak-dominated forests. The positive relationship between black oak and pine importance values was reasonable because both species are adapted to similar dry and poor soil-site conditions.

Photosynthetically Active Radiation

Hypothetically, greater PAR levels should promote the establishment of a greater number of oak seedlings on a site due to the importance of light to the maintenance of oak seedlings over time. The few times PAR was a significant variable, a negative relationship was indicated between PAR and chestnut oak and the scarlet and southern red oak group. Under high PAR conditions, it is possible that other tree species may outcompete oak for below-ground resources and space. Another reason for this discrepancy may be the limitations of the techniques used to collect PAR data. PAR was measured at one point during one time of the day, which does not account for changes in light flecks over the course of the day. Gaps adjacent to the transects, but not sampled within the transects, could have significantly impacted the light regime within the transect.

Slope

The positive relationships found between slope and 4th size class black oak, as well as the positive relationship between slope and the 3rd and 4th size classes of all species of oak regeneration combined, suggests that oak regeneration is enhanced on steep terrain. Shallow, very well-drained soils are characteristic of steep slopes, and may limit the establishment of the more drought sensitive competitors of oak. Thor et al. (1969) found that a greater number of scarlet and black oak seedlings were typically found on thinner, more acidic soils in the Cumberland Mountains of Tennessee.

V. Conclusion

The smallest size classes of oak seedlings of all species were most abundant on the moister, better landform positions, soils, and combinations, while the abundance of seedlings in the larger size classes was greater on the drier, poorer landform positions, soils, and combinations. This suggests that the relative importance of different site factors appear to change across seedling size classes. Although fewer seedlings may establish on the drier, poorer landform positions and soil associations, it appears that their survival rate into the largest size class may be greater than for seedlings on the cooler, moister, and richer combinations. Thus, moist, fertile conditions may be important for germination and early growth of oak seedlings, but less important than competition for light as seedlings grow into larger size classes.

Some competing species consistently played an important role in influencing the number of oak seedlings. Dogwood and hickory saplings likely inhibit the growth of oak seedlings. A mature seed source was important for all species of small size class oak seedlings.

The positive relationship found between oak seedlings and canopy depth, as well as the negative relationship between oak seedlings and percent full PAR, was unexpected, but could be explained by seedling shade tolerance and perhaps limitations of the technique used to sample PAR. The percent slope was not as important as expected, but when this variable was included in a model through the variable selection procedure, there was a positive relationship between steeper slopes and a greater abundance of oak seedlings.

The regression equations developed in this study could be used to predict the abundance of oak regeneration in the Ridge and Valley Province. However, the predictions are of limited value in other Physiographic provinces of the state, and should be further refined and tested for reliability before they are used to make management decisions. The real value of the modeling process was to identify variables that are important in the oak regeneration. Based on the results, managers should focus regeneration efforts on the drier sites in the Ridge and Valley region, where drought sensitive competitors are limited and growth of oak is adequate. Oak reproduction did occur on the more productive sites, but it appears that treatments to reduce the abundance of competitors may be necessary. Assuming adequate growth, less money, time, and effort would be used in managing for oak on the moderate sites. Among species groups, the red oak group appeared to be less tolerant of shaded conditions and competition than the white oak group. Therefore, stronger competition control efforts may be needed to stimulate red oak regeneration.

Gaps in information suggested by this study include regeneration patterns in forests that have had more recent and heavy disturbance, and oak regeneration in stands that lack oak in the present canopy. This study could be expanded in the future to incorporate such sites and conditions on all soil associations in the region.

References

Abrams, M. D. 1990. Adaptations and responses to drought in *Quercus* species of North America. Tree Phys. 7(1-4):227-238.

Abrams, M. D. 1992. Fire and the development of oak forests. Bioscience 42(5): 346-353.

Araman, P. A. 1988. The changing hardwood export market and research to keep the U.S. competitive. P. 168-177 *in* Proc. 16th Annual Hardwood Symp. Hardwood Res. Council.

Ashton, P.M.S. and G.P. Berlyn. 1994. A comparison of leaf physiology and anatomy of *Quercus* (section *Erythrobalanus*-Fagaceae) species in different light environments. Am. J. Botany 81(5): 589-597.

Axelsson, L., B. Klockare, and C. Sundquist. 1979. Oak seedlings grown in different light qualities: I. Morphological development. Physiol. Plant. 45: 387-392.

Barnes, T.A. and D.H. Van Lear. 1998. Prescribed fire effects on advanced regeneration in mixed hardwood stands. South. J. Applied For. 22 (3): 138-142.

Beck, D. E. 1970. Effect of competition on survival and height growth of red oak seedlings. USDA For. Serv. Res. Pap. SE-56. 7p.

Beck, D. E. 1977. Twelve-year acorn yield in southern Appalachian oaks. USDA For. Serv. Res. Note SE-244. 8p.

Beck, D.E. 1993. Acorns and oak regeneration. P. 96-104 *in* D.L. Loftis and C.E. McGee (eds.) Proceedings of Oak Regeneration: serious Problems, Practical Recommendations. USDA For. Serv. Gen. Tech. Rep. SE-84.

Beck, D. E. and David F. Olsen. 1968. Seed production in Southern Appalachian oak stands. USDA For. Serv. Res. Note SE-91. 7p.

Beck, D.E., and R.M. Hooper. 1986. Development of a southern Appalachian hardwood stand after clearcutting. South. J. Appl. For. 10: 168-172.

Belanger, R. P. 1990. Southern red oak (*Quercus falcata*). P 640-649 *in* Burns, R.M. and B.H. Honkala (eds.). Silvics of North America Vol. 2: Hardwoods USDA For. Serv., Agric. Handbook 654.

Brose, P.H. and D.H. Van Lear. 1998. Responses of hardwood advanced regeneration to seasonal prescribed fires in oak-dominated shelterwood stands. Can. J. For. Res. 28: 331-339.

Brose, P., D. Van Lear, and R. Cooper. 1999. Using shelterwood harvests and prescribed fire to regenerate oak stands on productive upland sites. For. Ecol. Manage. 113: 125-141.

Burns, R.M. and B.H. Honkala. 1990. Silvics of North America. Volume 2: Hardwoods. USDA For Serv. Agric. Handbook 654. 877p.

Burns, Y.P., and D.M. Christisen. 1954. Acorn production in the Missouri Ozarks. Res. Note Bull. No. 611. Agric. Exp. Sta., Univ. Missouri, College of Agriculture.

Campbell, R. W. and R. J. Sloan. 1977. Forest stand responses to defoliation by the gypsy moth. For. Sci. Monogr. 19. 34p.

Carvell, K.L. and E.H. Tryon. 1961. The effect of environmental factors on the abundance of oak regeneration beneath mature oak stands. For. Sci. 7(2): 98-105.

Clark, F.B. 1986. The hardwood resource. P. 13-18 *in* Robertson, D. and J.L. White (eds.) Eastern hardwoods: The resource, the industry, and the markets. Hardwood Research Council, Forest Products Research Society.

Clark, F. B. 1993. An historical perspective of oak regeneration. P. 3-13 *in* Loftis, D.L. and C.E. McGee (eds.) Proc. of Oak Regeneration: Serious Problems, Practical Recommendations. USDA For. Ser. Gen. Tech. Rep. SE-84.

Cook, J.E., T. L. Sharik, and D.W. Smith. 1998. Oak regeneration in the Southern Appalachians: Potential problems and possible solutions. South. J. Applied For. 22(1): 11-18.

Crow, T.R. 1988. Reproductive mode and mechanisms for self-replacement of northern red oak (*Quercus rubra*) – a review. For. Sci. 34(1): 19-40.

DeVivo, M.S. 1991. Indian use of fire and land clearance in the Southern Appalachians. P. 306-312 *in* Waldrop, T. and S. Nodvin (eds.) Proc. Intl. Symp. Fire and the Environment: Ecological and Cultural Perspectives. USDA For. Ser. Gen. Tech. Rep. SE-69.

Dickson, R. E. 1991. Episodic growth and carbon physiology in northern red oak. P. 117-124 *in* S.B> Laursen and J.F. De Boe (eds.) The oak resource in the upper Midwest: implications for management. Minnesota Ext. Serv. Univ. Minn.

Drake, W.E. 1991.Evaluation of an approach to improve acorn production during thinning. P. 429-441 *in* McCormick, L.H. and K.W. Gottschalk (eds.) Proc. 8th Central Hardwood For. Conf. USDA For. Serv. Gen. Tech. Rep. NE-148.

Galford, J. R. 1986. Primary infestation of sprouting chestnut, red, and white oak acorns by *Valentinia glandulella (Lepidoptera: Blastobasidae)*. Entomol. News 97(3): 109-112.

Gammon, A.D., V.J. Rudolph, and J.L. Arend. 1960. Regeneration following clearcutting of oak during a seed year. J. For. 58: 711-715.

Gardiner, E.S. and J.D. Hodges. 1998. Growth and biomass distribution of cherrybark oak (*Quercus pagoda* G.) seedlings as influenced by light availability. For. Ecol. Manage. 108: 127-134.

Gibson, L. P. 1982. Insects that damage white oak acorns. USDA For. Serv. Res. Pap. NE-220. Upper Darby, PA, 7pp.

Gill, J.D., J.W. Thomas, W.M. Healy, J.C. Pack, and H.R. Sanderson. 1975. Comparison of seven forest types for game in West Virginia. J. Wildl. Manage. 39(4): 762-768.

Goodrum, P.H., V.H. Reid, and C.E. Boyd. 1971. Acorn yields, characteristics, and management criteria of oaks for wildlife. J. Wildl. Manage. 35: 520-532.

Gottschalk, K.W., D.A. Ganser, and M.J. Twery. 1989. Impacts of gypsy moth on oak timber resources or will there be oak in 2001? P.11-22 *in* Proc. 17th Annual Hdwd. Symp. Hdwd. Res. Council.

Gysel, L. W. 1957. Acorn production on good, medium, and poor sites in southern Michigan. J. For. 55: 570-574.

Hardin, J.W., D.J. Leopold, and F.M. White. 2001.Harlow and Harrar's textbook of dendrology, 9th edition. McGraw-Hill Companies, Inc. New York. 534p.

Harrod, J.C. and R.D. White. 1999. Age structure and radial growth in xeric pine-oak forests in western Great Smokey Mountains National Park. J. Tor. Bot. Soc. 126(2): 139-146.

Healy, W. M. 1997. Influence of deer on the structure and composition of oak forests in central Massachusetts. P.249-266 *in* McShea, W.J., H.B. Underwood, and J.H. Rappole (eds.) The science of overabundance: deer ecology and population management.

Hodges, J.D. and E.S. Gardiner. 1993. Ecology and physiology of oak regeneration. P.54-65 *in* Loftis, D.L. and C.E. McGee (eds.) Proceedings of Oak Regeneration: Serious Problems, Practical Recommendations. USDA For. Serv. Gen. Tech. Rep. SE-84.

Horsley, S.B. and D.A. Marquis. 1983. Interference by weeds and deer with Allegheny hardwood reproduction. Can. J. For. Res. 13: 61-69.

Idassi, J., J. Huarachi, P. Winistorfer, and B. English. 1998. Economic impacts of the forestry and forest products industries on the Tennessee economy. Tenn. For. Prod. Center Rep. 5.

Immel, M.J., R.L. Rumsey, and S.B. Carpenter. 1978. Comparative growth responses of northern red oak and chestnut oak seedlings to varying photoperiods. For. Sci. 24(4): 544-560.

Johnson, A.S., J.M. Wentworth and P.E. Hale. 1989. Cumulative mast needs of forest wildlife. P. 18-23 *in* Proc. Workshop Southern Appalachian mast management. USDA For. Serv. and Univ. Tenn., Knoxville.

Johnson, A.S., P.E. Hale, W.M. Ford, J.M. Wentworth, J.R. French, O.F. Anderson, and G.B. Pullen. 1995. White-tailed deer foraging in relation to successional stage, overstory type, and management of southern Appalachian forests. Am. Midl. Nat. 133: 18-35

Johnson, P. S. 1976. Eight-year performance of interplanted hardwoods in southern Wisconsin oak clearcuts. USDA For. Serv. Res. Paper NC-126. 9pp.

Johnson, P. S. 1990. Scarlet oak (*Quercus coccinea*). P. 625-630 *in* R.M.Burns and B.H. Honkala (eds.) Silvics of North America Vol. 2: Hardwoods. USDA For. Serv. Agric. Handbook 654.

Johnson, R. L. 1979. Adequate oak regeneration - A problem without a solution? P. 59-65 *in* Proc. 7th Annual Hdwd. Symp. Hdwd. Res. Council.

Korstian, C.F. 1927. Factors controlling germination and early survival in oaks. Yale Univ. Sch. For. Bull.19. 115 p.

Krebs, C.J. 1985. Ecology: The experimental analysis of distribution and abundance, 3rd Edition. Harper and Row Publishers New York. 800 p.

Loach, K. 1967. Shade tolerance in tree seedlings. I. Leaf photosynthesis and respiration in plants raised under artificial shade. New Phytol. 66: 607-621.

LeBlanc, D. C. 1998. Interactive effects of acidic deposition, drought, and insect attacks on oak populations in the Midwestern United States. Can. J. For. Res. 28: 1184-1197.

Lorimer, C. C. 1984. Development of the red maple understory in northeastern oak forests. For. Sci. 30(1): 3-22.

Lorimer, C.G. 1985. The role of fire in the perpetuation of oak forests. P. 8-25 *in* Proc. Challenges in Oak Management and Utilization.

Lorimer, C. G. 1989. The oak regeneration problem: New evidence on causes and possible solutions. Seventeenth Ann. Symp. Hardwood Res. Council, Merrimac, Wisconsin p. 23-39.

Lorimer, C. G. 1993. Causes of the oak regeneration problem. P. 14-39 *in* D.L. Loftis and C.E. McGee (eds.) Proc. Oak Regeneration: Serious Problems, Practical Recommendations. USDA For. Serv. Gen. Tech. Rep. SE-84.

Lorimer, C.G., J.W. Chapman, and W.D. Lambert. 1994. Tall understory vegetation as a factor in the poor development of oak seedlings beneath mature stands. J. Ecol. 82: 227-237.

Luppold, W. G. 1983. The effects of changes in lumber and furniture prices on wood furniture manufacturers' lumber usage. USDA For. Serv. Res. Paper NE-514.

Luppold, W. G. 1997. Regional changes in price of red oak lumber. P. 229-236 *in* Proc. 26th Southern Forest Economics Workshop: Redefining roles in forest economics research.

Luther, E. T. 1977. Our restless earth: the geologic regions of Tennessee. Univ. Tennessee Press, Knoxville, TN. 94p.

Marquis, D. A. 1981. Effect of deer browsing on timber production in Allegheny hardwood forests of northwestern Pennsylvania. USDA For. Serv. Res. Paper NE-475.

Marquis, D.A., P.L. Eckert, and B.A. Roach. 1976. Acorn weevils, rodents, and deer all contribute to oak-regeneration difficulties in Pennsylvania. USDA For. Serv. Res. Paper NE-356.

Marquis, D.A. and R. Brenneman. 1981. The impact of deer on forest vegetation in Pennsylvania. USDA For. Serv. Gen. Tech. Rep. NE-65.

Martin, A.C., H.S. Zim, and A.L. Nelson. 1951. American wildlife and plants: A guide to wildlife food habits. Dover Publications, Inc., New York. 500p.

McGee, C.E. and R.M. Hooper. 1975. Regeneration trends 10 years after clearcutting of an Appalachian hardwood stand. USDA For. Serv. Res. Note SE-227.

McGee, C.E. 1975, Change in forest canopy affects phenology and development of northern red and scarlet oak seedlings. For. Sci. 21(2): 175-179.

McGee, C.E. 1984. Heavy mortality and succession in a virgin mixed mesophytic forest. USDA For. Serv. Res. Paper SO-209.

McGee, C. E. 1986. Budbreak for twenty-three upland hardwoods compared under forest canopies and in recent clearcuts. For. Sci. 23(4): 924-935.

McQuilken, R. A. 1990. Chestnut oak (*Quercus prinus*). P. 721-726 *in* H.M. Burns and B.H. Honkala (eds.) Silvics of North America Vol. 2: Hardwoods. USDA For. Serv. Agric. Handbook 654.

Meiners, T.M., D.W. Smith, T.L. Sharik, and C.E. Beck. 1984. Soil and plant water stress in an Appalachian oak forest in relation to topography and stand age. Plant and Soil 80: 171-179.

Meredieu, C., D. Arrouays, M. Goulard, and D. Auclair. 1996. Short range soil variability and its effects on red oak growth (*Quercus rubra* L.). Soil Sci. 161(1): 29-38.

Oak, S. W. 1993. Insects and diseases affecting oak regeneration success. P. 105-111 *in* Loftis, D.L. and C.E. McGee (eds.) Proc. Oak Regeneration: Serious Problems, Practical Recommendations. USDA For. Serv. Gen. Tech. Rep. SE-84.

Owenby J.R. and D.S. Ezell. 1992. Monthly station normals of temperature, precipitation, and heating and cooling degree days, 1961-1990. U.S. Dept. of Commerce, NOAA, NCDC. Asheville, NC.

Pack, J.C., R.P. Burkert, W.K. Igo, and D.J. Pybus.1980. Habitat utilized by wild turkey broods within oak-hickory forests of West Virginia. P. 213-224 *in* Proc. Fourth National Wild Turkey Symp. Little Rock, AK. Edgefield, S.C.: National Wild Turkey Federation.

Probst, J. R. 1979. Oak forest bird communities in Proceedings Management of North Central and Northeastern forests for nongame birds. USDA For. Serv. Gen. Tech. Rep. NC-51.

Racine, C. H. 1971. Reproduction of three species of oak in relation to vegetational and environmental gradients in the southern Blue Ridge. Bull. Tor. Bot. Club 98(6): 297-310.

Rogers, R. and R.S. Johnson. 1998. Approaches to modeling natural regeneration in oak-dominated forests. For. Ecol. Manage. 106: 45-54.

SAS Institute, Inc. 1999. The SAS System OnlineDoc., Version 8. CD-ROM. SAS Institute, Cary, NC.

Sander, I. L. 1971. Height growth of new oak sprouts depends on size of advance reproduction. J. For. 69: 809-811.

Sander, I. L. 1972. Size of oak advance reproduction: key to growth following harvest cutting. USDA For. Serv. Res. Paper NC-79.

Sander, I. L. 1990. Northern red oak (*Quercus rubra*). P. 727-733 *in* H.M.Burns and B.H. Honkala (eds.) Silvics of North America Vol. 2: Hardwoods. USDA For. Serv. Agric. Handbook 654.

Schweitzer, C. J. 2000a. Forest Statistics for East Tennessee, 1999. USDA For. Serv. South. Res. Stat. Res. Bull. SRS-51.

Schweitzer, C. J. 2000b. Forest statistics for Tennessee, 1999. USDA For. Ser. South Res. Stat. Res. Bull. SRS-52.

Springer, M.E. and J.A. Elder. 1980. Soils of Tennessee. Univ.Tennessee Agric. Exp. Sta., Knoxville and USDA .

Stevenson, A.G. 1981. Flower and fruit abortion: proximate causes and ultimate functions. Ann. Rev. Ecol. Syst. 12:253-279.

Stratton, D. and R. C. Wright. 1999. Tennessee's timber industry- An assessment of timber product output and use, 1997. USDA For. Serv. Res. Bull. SRS-42.

Strole, T. A. and R. C. Anderson. 1992. White-tailed deer browsing: Species preferences and implications for Central Illinois forests. Nat. Areas J. 12(3): 139-144.

Teskey, R.O. and R.B. Shrestha 1985. A relationship between carbon dioxide, photosynthetic efficiency, and shade tolerance. Physiol. Plant 63(1): 126-132.

Thor, E., H.R. DeSelm, and W.H. Martin. 1969. Natural reproduction on upland sites in the Cumberland Mountains of Tennessee. J. Tenn. Acad. Sci. 44(4): 96-100.

Tilghman, N. G. 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. J. Wildl. Manage. 53(3): 524-532.

Trimble, G.R. and G. Hart. 1961. An appraisal of early reproduction after cutting in northern Appalachian hardwood stands. USDA For. Serv. Northeastern Stat Paper – 162.

Trumball, V.L., E.J. Zielinski, and E.C. Aharrah. 1989. The impact of deer browsing on the Allegheny forest type. N. J. Appl. For. 6: 162-165.

Tryon, E.H. and K.L. Carvell 1958. Regneration under oak stands. Bull. 24T. Morgantown: West Virginia University, Agric. Exp. Stat. 22pp.

USDA. 1969. Soil survey interpretations for woodlands in the Cumberland Plateau and Mountains and the Southern Appalachian Ridges and Valley of Alabama, Georgia, and Tennessee. Progress Report W-11. Soil Conservation Services, Fort Worth, TX. 30 pp.

USDA. 1974. Seeds of woody plants in the United States. Agriculture Handbook 450. Washington, DC: USDA. 883pp.

Van Dersal, William R. 1940. Utilization of oaks by birds and mammals. J. Wildl. Manage. 4(4): 404-428.

Van Lear, D.H. 1991. Fire and oak regeneration in the Southern Appalachians. P.15-21 *in* Nodvin, Stephen C.; Waldrop, Thomas A. (eds.) Fire and the Environment: Ecological and Cultural Perspectives. USDA For. Serv. Gen. Tech. Rep. SE-69.

Van Lear, D.H. and J.M. Watt. 1993. The role of fire in oak regeneration. P. 66-78 *in* D.L. Loftis and C.E. McGee (eds.) Proc. Oak Regeneration: Serious Problems, Practical Recommendations. USDA For. Serv. Gen. Tech. Rep. SE-84.

Van Lear, D.H., and T.A. Waldrop. 1989. History, uses, and effects of fire in the Appalachians. USDA For. Serv. Gen. Tech. Rep. SE-54.

Vissage, J. S. and K.L. Duncan.1990. Forest statistics for Tennessee counties – 1989. USDA For. Serv. Res. Bull. SO-148.

Waldrop, T. A. and T. F. Lloyd. 1991. Forty years of prescribed fire on the Santee fire plots: effects on overstory and midstory vegetation. P. 45-50 *in* S.C. Nodvin and T.A. Waldrop (eds.) Fire and the Environment: Ecological and Cultural Perspectives. USDA For. Serv. Gen. Tech. Rep. SE-69.

Weitzman, S., and G.R. Trimble Jr. 1957. Some natural factors that govern the management of oaks. USDA For. Serv. Northeastern For. Exp. Stat. Paper - 88.

White, D.L., T.A. Waldrop, and S.M. Jones. 1991. Forty years of prescribed fire on the Santee fire plots: effects on understory vegetation. P. 51-59 *in* S.C. Nodvin and T.A. Waldrop (eds.) Fire and the Environment: Ecological and Cultural Perspectives. USDA For. Serv. Gen. Tech. Rep. SE-69.

Woods, D.B. and N.C. Turner. 1971. Stomatal response to changing light by four tree species of varying shade tolerance. New Phytol. 70: 77-84.

VITA

Leslie Chadwell was born in Greensboro, North Carolina on December 30, 1975. She was raised in Atlanta, Georgia along with six brothers and sisters. She graduated from St. Pius X Catholic High School in 1994. In the summer of 1994, she entered Clemson University, Clemson, South Carolina and graduated with a Bachelor of Science in Forest Resource Management in May, 1998. In July of 1999 she entered the Master's program in Forestry at the University of Tennessee, Knoxville. The Master's degree was received in August, 2001.