

**PATTERNS OF NATURAL REGENERATION IN PINE AND HARDWOOD
FORESTS OF THE UPPER COASTAL PLAIN, VIRGINIA**

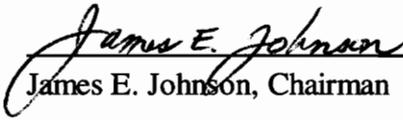
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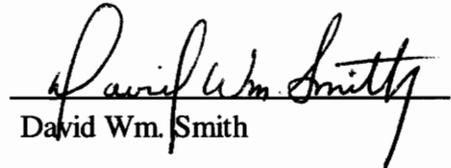
Polly-Anne Rantis

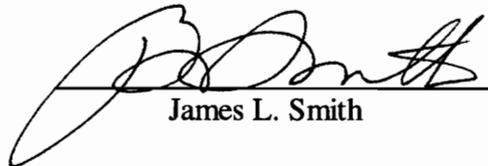
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by

Polly-Anne Rantis

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Forestry

(ABSTRACT)

Natural regeneration is the primary means of replacing mature forests of parks and preserves in the absence of forest management. There is growing concern from landowners about how these forests will regenerate. The objective of this study was to examine the pattern of natural regeneration in some unmanaged, mature forests in the Virginia Upper Coastal Plain. Twelve pairs of gap and non-gap areas in each of three cover types: 1) pine, 2) pine-hardwood, and 3) hardwood forests were studied. All levels of forest vegetation were inventoried and species importance values were calculated. Regeneration was categorized by shade tolerance classes for analysis. Soil and light conditions were the measured environmental variables.

Conditions in gap and non-gap areas within each cover type were compared using the paired-*t* test. There were few clear distinctions in sapling and seedling densities, or sapling heights between gap and non-gap areas in these forest cover types. Light conditions were significantly higher in the gap areas than the non-gap areas; but soil properties were often quite similar. Principal component and best subsets regression analysis were used to determine the relationships between environmental variables associated with gap and non-gap areas and the regeneration present. The principal component analysis showed no meaningful results for the gap and non-gap areas across the environmental data matrix. Few significant relationships were found relating environmental variables and shade tolerance seedling densities using best subsets

regression. Conclusive evidence as to which variables were most influential remains unclear. Light and litter depth were most often the significant factors among the forest cover types.

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INTRODUCTION

Unmanaged forests, such as parks and preserves, depend on natural regeneration to replace existing mature stands. Foresters often rely on natural regeneration of forest stands because it is frequently successful and economical. All silvicultural methods of regeneration, including clearcutting, shelterwood, seed tree, and selection, depend on natural regeneration from coppice sprouts and seedfall to replace forest stands if planting is not used. There is a growing demand to manage more mixed pine and hardwood stands in the Southeast. This shift will require forest managers to alter many of their management schemes to include more use of natural regeneration. Such management scenarios can provide a multitude of forest resource products and uses.

The success of the natural regeneration of forests in parks, preserves, and natural areas is becoming an important issue in the Southeast. Many of these forests date back to land abandonment from agriculture 50 to 100 years ago, and are classified as oak-hickory-pine forests, especially in the Piedmont and the Coastal Plain north of the Savannah River (Skeen et al. 1993). Currently, these forests are undergoing successional change from pine to pine-hardwood to hardwood forests in the absence of fire (Cooper 1989). A substantial amount of insect damage is present in these forests, most noticeably from the southern pine beetle (*Dendroctonus frontalis* Zimm.) and the gypsy moth (*Lymantria dispar* L.). Additional features of these forests may include: dense, tolerant understories that have built up due to fire suppression; heavy deer browsing; invasion by aggressive exotic species like Japanese honeysuckle (*Lonicera japonica* Thunberg) and tree-of-heaven (*Ailanthus altissima* (Miller) Swingle); and in recent years, frequent, recurrent droughts which have been linked to increased tree mortality (Clinton et al. 1993). Over two-thirds of commercial forest land in the southern oak-hickory-pine forest are privately owned and natural regeneration is the primary means of forest renewal (Skeen et al. 1993). Landowners and forest managers are rightfully concerned about how these forests

will regenerate, given the difficult conditions that persist in many areas in the region.

It is generally accepted that forests exhibit a cyclical regeneration pattern in which small scale disturbances are an integral part (Denslow 1980a, Whitmore 1989, Pickett and White 1985, Runkle 1985b, Hibbs 1982, Peet and Christensen 1987, Shugart 1984). Such disturbances include areas in the forest where death of a dominant canopy tree occurs as a result of windthrow, insect and/or disease damage, and senescence (Spies and Franklin 1989, Peet and Christensen 1987). These events create an opening in the forest canopy. It is in these small openings or gaps where the death of a canopy tree can enhance the growth of existing regeneration, as well as the germination of seed from new sources (McClure and Lee 1992). Ultimately, the forest cycle begins in these gaps where the future forest composition and structure is shaped (Whitmore 1989, Runkle 1989). Several studies have investigated patch dynamics in tropical forests (Brokaw and Scheiner 1989, Brokaw 1985, Denslow 1980a), and in temperate forests of the Northeast (Krasny and Whitmore 1991, Runkle 1990, Hibbs 1982), however little has been done in the pine-hardwood forests of the Southeast.

This study was conducted in the Petersburg National Battlefield in the Upper Coastal Plain of Virginia, and is typical of many pine, pine-hardwood, and hardwood natural forests of the Southeast. The study area remains unmanaged; there are no active silvicultural practices, with the exception of fire suppression. This study was initiated to examine the patterns of natural regeneration that have developed within these unmanaged, mature forests. Studying the changes in regeneration that occur as a result of small scale disturbances, such as the death of one or more dominant trees creating a gap in the canopy, is one way of achieving this goal. In addition, the environment of the gap and adjacent closed canopy areas were studied to better understand the dynamics of gap replacement. Through our understanding of how and what species replace a gap in these unmanaged forest ecosystems, managers will be better able to predict the composition and structure of future forests.

OBJECTIVES

1. To quantify the amount and type of regeneration associated with gap and adjacent non-gap areas in pine, pine-hardwood, and hardwood forests in the Upper Coastal Plain of Virginia.
2. To determine if light levels and soil conditions differ significantly between gap and adjacent non-gap areas in pine, pine-hardwood, and hardwood forests.
3. To determine the relationship between species and abundance of natural regeneration and environmental variables associated with gap and adjacent non-gap areas in pine, pine-hardwood, and hardwood forests.

LITERATURE REVIEW

Role of Natural Disturbance

Natural disturbance in forested ecosystems is a powerful event that modifies local environmental conditions both spatially and temporally. Disturbance can alter the relative amount and availability of resources such as sunlight, water, and nutrients (White and Pickett 1985, Vitousek and Denslow 1986, Mladenoff 1987). These changes in forest resource and structure may occur at all levels of ecological organization, affecting both plant and animal populations (Oliver and Larson 1990, Pickett and White 1985, Bazazz 1983).

Disturbance scales in forested ecosystems vary in size and frequency. Large disturbances are usually infrequent and are a result of exogenous forces such as fire, wind, ice, or human activity (White and Pickett 1985, Bormann and Likens 1979). These types of disturbances are discrete and are easily identified. The most visible impact large disturbance has on a forest is on species composition and structure. Normal successional processes in forests can be impeded by large disturbances, maintaining large populations of early successional forest tree species (Bazazz 1983). For example, West et al. (1981) concluded from tested forest dynamic simulations of the mixed oak-pine forests in Upland Arkansas, that fire is the primary regulator of species composition. With the fire regime loblolly pine (*Pinus taeda* L.) can dominate; without fire, loblolly pine eventually dies, is secondarily succeeded by sweetgum (*Liquidambar styraciflua* L.) and swamp pine (*Pinus serotina* Michx. f.), with eventual domination by southern red oak (*Quercus falcata* Michx.). Forman and Boerner (1981) showed a shift in species composition in the pine barrens in New Jersey away from pine as a result of a change in fire frequency. The impacts of large disturbances on the biotic and abiotic conditions of the forest have been well documented (Shugart 1984, Pickett and White 1985).

Smaller, more frequent disturbances, such as single or multiple tree deaths from windthrow, insect attacks, and senescence, are more difficult to classify. These disturbances are regarded as both exogenous and endogenous (White and Pickett 1985, Runkle 1985b, Bazazz 1983). The significance of these small disturbances in the forest ecosystem are less visible, but should not be underestimated.

Small disturbances have an important role in the regulation of ecosystem processes in the forest community. An opening in the forest canopy, a gap, is an area that can be significant for structural change and renewal in mature forests (Whitmore 1989, Canham 1989, Pickett and White 1985). Treefall gaps may alter the microclimatic conditions beneath them enough to allow the establishment of new species and enhance the growth of previously established species (Oliver and Larson 1990). The pattern and distribution of tree regeneration in the forest, therefore, is shaped by the pattern and distribution of gap formations (McClure and Lee 1993, Pickett and White 1985, Runkle 1981, Williamson 1975).

Gaps may also function as a source of renewed species richness (McClure and Lee 1993, Philips and Shure 1990, Brokaw and Scheiner 1989, Denslow 1980b) and increased genetic diversity within plant species (Denslow 1985, Bazazz 1983). Species composition is often associated with forest structure in describing forest dynamics. Treefall gaps can temporarily increase the variability of forest structure (Brokaw and Scheiner 1989), which is important for the maintenance of biodiversity. The longevity of the multi-aged forest is constant, for when the advanced regeneration in the understory of a gap reaches the forest canopy, other sections of the forest will assume a recruitment role at the next disturbance (Brokaw and Scheiner 1989, Lorimer 1989).

Disturbance Parameters

Disturbance events of all scales are unique. Parameters such as frequency, rate of

closure, size, and severity characterize disturbance in all types of ecosystems (Pickett and White 1985). In turn, these parameters affect the microenvironment within the disturbed area where tree regeneration develops (Denslow 1980a, Cho and Boerner 1991, Pickett and White 1985).

Frequency

The frequency of disturbance can influence the survival strategy of tree species. Species whose seeds arrive and germinate early are generally those which will dominate frequent disturbance areas (van der Valk 1992, Denslow 1980b). High recurrences of disturbance require species that are fast growing and can reproduce early; or have seeds that remain viable in the soil long enough for the next disturbance, such as several cherry species (*Prunus spp.*). There are several types of seed dormancy, the lengths of which could last for as little as a few days to many years before suitable conditions for germination occur (van der Valk 1992). Low disturbance frequencies allow the presence of species with a longer developmental period to reproductive maturity to persist (Bazzaz 1983). Further, Lorimer (1989) speculated that the relationship between large and small disturbance frequencies is inversely related. In natural forests where large disturbances are the primary disturbance pattern, the periods between these events are long and there are fewer small disturbances. Likewise, in forests where small disturbances are common, large disturbances are very infrequent.

Runkle (1982) found that rates of canopy gap-forming disturbances varied from 0.3-3.6 percent (mean 1.2-1.7 percent) of total land area per year in the southern Appalachians. A study conducted by Barden (1989) in the same region reported a rate of gap forming disturbance less than 0.4 percent. Gap formation rates were determined to be approximately 1 percent of total land area per year according to several studies in the eastern old-growth forests (Runkle 1982). Clinton et al. (1993) found a gap formation rate of 0.8 gaps per hectare per year in a southern Appalachian mixed oak (*Quercus spp.*) forest. These discrepancies reflect the need for standardized definitions of gap

terminology.

Small disturbance rates can be patterned as occurring in periods that are the approximate life spans of the dominant species. Runkle (1985b) estimates a 50-200 year time span between disturbances for a given site in the eastern forests. The natural rotation time of a gap, based on the average time a tree is in the canopy (defined as >25 cm dbh), is estimated as 100 years at a given site (Runkle 1982). In general, forests in the younger stages of development will have smaller openings than more mature forests that have trees with large expansive crowns (Busing 1995).

Rate of Closure

The rate at which a gap closes depends upon the above-mentioned parameters of the disturbance and upon the resiliency of the site (Clinton et al. 1993, Pickett and White 1985, Denslow 1985). Clinton et al. (1993) found the longevity of a gap in the southern Appalachian forests to be from 8-20 years. Closure of a gap occurs in several ways, primarily depending on the size of the gap. One way is through the lateral growth of branches from surrounding tree species. Northern red oak (*Quercus rubra* L.) has lateral extension rates of 14.0 to 17.0 cm/yr (Trimble and Tryon 1966, Hibbs 1982). Red maple (*Acer rubrum* L.) extension rates have been reported as 8.0 cm/yr (Hibbs 1982) and branch growth rates of tulip poplar (*Liriodendron tulipifera* L.) have been estimated as 9.0 cm/yr (Trimble and Tryon 1966, Hibbs 1982). Runkle (1985b) determined from the literature that average rates of lateral branch growth are 4.0-14.0 cm/yr. Small gaps created by a single tree death close primarily as a result of this process.

The second form of gap closure is through sapling ingrowth. This form of gap closure is usually a result of openings at least 5.0 m in radius (Hibbs 1982). Hibbs (1982) found that saplings grew 10.0-50.0 cm/yr in small gaps and 25.0-50.0 cm/yr in open fields. Runkle (1982) concluded from the literature that average height growth rates of saplings in the eastern deciduous forests are approximately 0.5-1.0 m/yr.

Gaps often close through the integration of both sapling ingrowth and branch

extension (Runkle 1985b). This regime allows understory saplings to receive a temporary release which allows certain saplings to better compete against species with faster growth rates in the next disturbance event. For some species, especially shade tolerant species such as American beech (*Fagus grandifolia* Ehrh.) and eastern hemlock (*Tsuga canadensis* (L.) Carr.), this sequence of multiple gap episodes is necessary for canopy status to be achieved (Runkle 1985b, 1990; Spies and Franklin 1989). Gaps are considered closed when saplings reach a certain height in the understory stratum. Runkle (1982) considered gap closure to occur when understory saplings reached 10-20 m in height; Barden (1981) used a range of 18-30 m.

Size

The opening size of a disturbance regulates forest composition (Pickett and White 1985, Hibbs 1982). Microsite conditions vary with the size of the opening and interact with species silvical characteristics to shape the species composition of the opening (McClure and Lee 1993, Denslow 1980b). Height of the trees surrounding an opening also regulates the duration of high light conditions within a gap; taller trees allow shorter periods of high light infiltration, where shorter trees allow longer periods of high light infiltration. In general, large gaps contain more shade intolerant species, with a mixture of shade tolerant species; smaller gaps allow more intermediate and shade tolerant species to persist (Phillips and Shure 1990, Pickett and White 1985, Denslow 1980a). For example, Runkle (1990) found white ash (*Fraxinus americana* L.) and tulip poplar to be important colonizing species in large gaps; American beech to persist in gaps of all sizes; and sugar maple (*Acer saccharum* Marsh.) important in small gaps. Minckler and Woerheide (1965) also found that opening size had a strong effect on species composition of regeneration in a study on mixed hardwood and oak-hickory forests in southern Illinois.

The age of a gap since formation, or gap age, can also influence the composition and abundance of regeneration. According to a study in the northern hardwood forest, gap age was found to be the most influential environmental variable on species

composition, above gap area, gap shape, soil, and slope (McClure and Lee 1993). Clinton et al. (1994), Runkle (1990), and Runkle and Yetter (1987) found that as gaps aged, species richness decreased and seedling density decreased. Generally, the numbers of oak, with the exception of northern red and black (*Quercus velutina* Lam.), were significantly more dense in five-year-old gaps compared to one-year-old gaps (Clinton et al. 1994). Environmental variables also change with gap age. For instance, soil moisture and light decreased with gap age in a gap dynamic study in a beech-maple forest (Moore and Vankat 1986).

Severity

Severity is a measure of impact a disturbance has on forest systems. The severity, or magnitude of a disturbance, can influence the species, seed origin (Connell 1989), and rate of subsequent revegetation within a gap (Runkle 1985b). The degree of severity is assessed by the level of forest floor and soil disturbance, and often by the disturbance size. (Oliver and Larson 1990, Pickett and White 1985). Type of disturbance may also reflect the disturbance severity. For example, gaps with standing-dead snags reflect minimal disturbance severity due to the lack of forest floor and soil disruption, thus advanced regeneration is favored (Clinton *et al.* 1994). These relationships are illustrated in Figure 1. The rate of revegetation may also be a function of the original substrate quality of the site. Severe disturbances can interrupt nutrient cycling, promote losses of nutrients through leaching (Oliver and Larson 1990, Runkle 1985b, Vitousek 1985), and prolong revegetation. Most small scale disturbances, however, leave the forest floor relatively intact, causing minor disturbance.

Disturbance Patterns in Southeastern Cove Forests

Many forest types reflecting different disturbance patterns are represented in southeastern forests. There are no studies on regeneration of small gaps in the

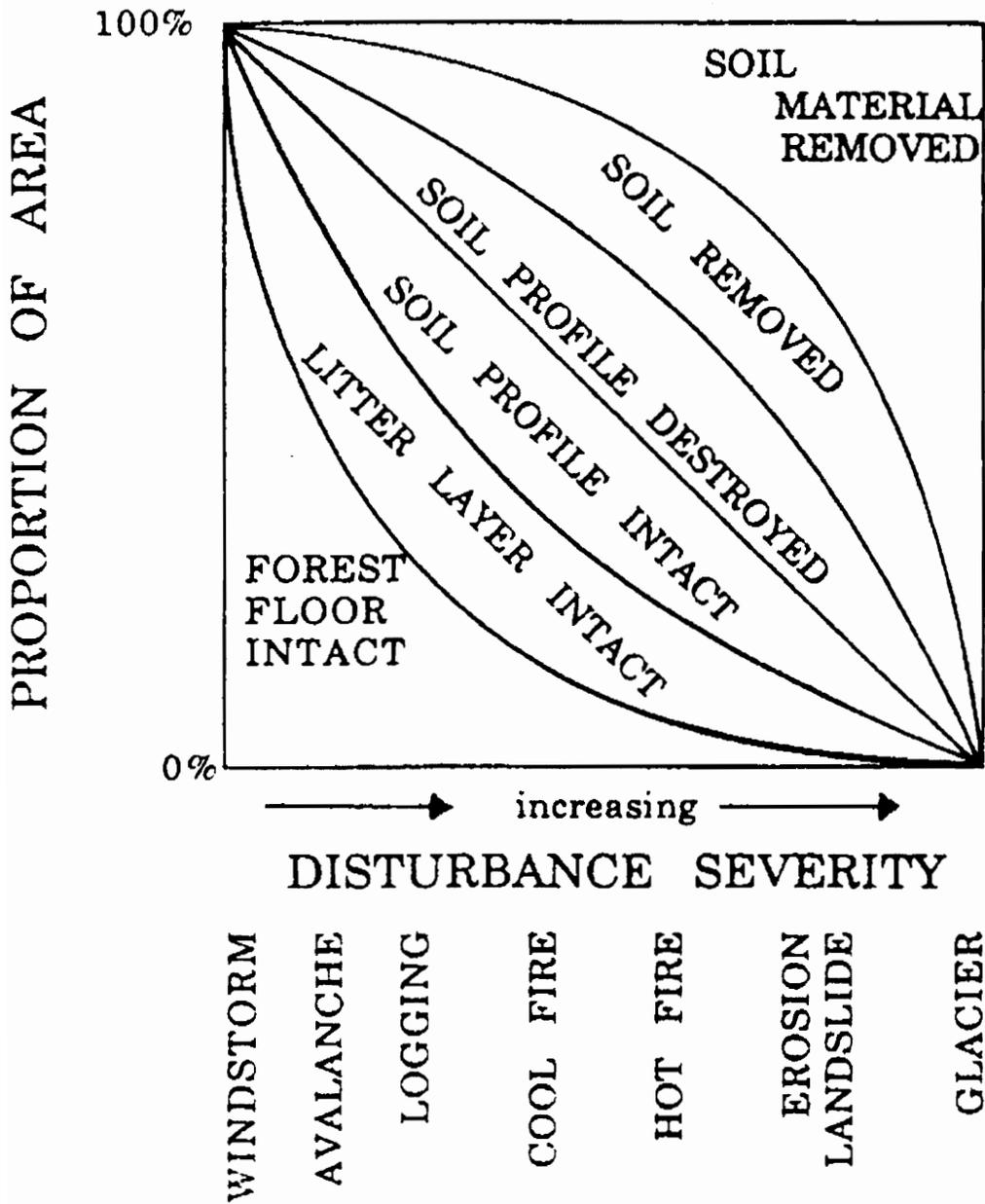


Figure 1. The relationship between type of disturbance, disturbance size, and area impacted (from Oliver and Larson 1990).

southeastern Coastal Plain. However, disturbance patterns of the southern Appalachian cove forests have been well studied by Runkle (1985b) and Runkle and Yetter (1987). In these forests, several mixtures of mesophytic tree species dominate, including: sugar maple, yellow buckeye (*Aesculus octandra* Marsh.), yellow birch (*Betula alleghaniensis* Michx. f.), American beech, and eastern hemlock. Although these species are quite different from those found in the Coastal Plain, the disturbance patterns are similar for comparison.

Southern Appalachian cove forests are mostly affected by small scale disturbances where single or few canopy trees die. High winds, ice, and lightning strikes are common types of small disturbances in Appalachian cove forests; hurricanes are the most common disturbance throughout the southeastern forest region (Table 1). Most of these disturbances are not severe, and often the forest floor is not disturbed except for some windthrown trees that are uprooted, exposing the mineral soil. The average gap size is 31 m² and disturbances are often repeated near previous openings. This pattern enhances those species that persist in the understory for long periods and can respond quickly during gap episodes. Species such as sugar maple, yellow buckeye, American beech, eastern hemlock, and some oaks are known to have this ability. White ash, black cherry (*Prunus serotina* Ehrh.), and red maple can live for a short time under dense canopies and longer under less dense canopies; tulip poplar and sweetgum can survive about a year under a dense canopy (Oliver and Larson 1990).

Site Characteristics and Regeneration in Canopy Gaps

Woody plant growth is regulated by the interaction of genetics and environmental conditions (Kozlowski et al. 1991). The environmental conditions control the degree of heredity that is expressed. Some tree species have varying regeneration strategies, which allows them to be more competitive than others following a disturbance. Species that have regeneration strategies that fit with the disturbance type are at a competitive

Table 1. Major disturbance types in the Southeastern forest region of the United States (Oliver and Larson 1990).

Disturbance Type	Occurrence (%)
hurricane	63
tornado	31
cyclone	6

advantage (Figure 2). For example, the ability to produce advance regeneration is a mechanism which allows some species like black cherry and many oaks to out-compete other germinants after less severe disturbances. The ability of a tree species to successfully establish itself is primarily dependent on seed supply, seedbed conditions, microclimate, and predators. This section will address the seedbed and microclimate variables.

Light

Canopy openings alter the light conditions in the understory (Canham 1988a, 1988b). Microenvironmental conditions within the gap may vary with height of adjacent trees, distance from the center of the opening, compass orientation, and the microtopography of the site (Collins and Pickett 1987). These conditions are strongly influenced by the frequency and severity of canopy disturbance (Cho and Boerner 1991). Jackson (1959) established the following light intensity categories for successful loblolly pine regeneration: < 20% light intensity is detrimental; between 30 and 55% is marginal; and > 55% is most favorable. In a study done in Central America, differences in light intensity had the greatest influence on species distribution, however, not on total seedling density (MacDougall and Kellman 1992). This trend was supported by Minckler and Woerheide (1965) who found that opening sizes ranging from a quarter to twice the height of the surrounding mixed hardwood and oak-hickory forests had little effect on seedling numbers.

A gap light index, which is an estimate of the amount of incident photosynthetically active radiation that is transmitted to the understory, was used by Canham et al. (1990) to determine the light regime in small gaps in temperate and tropical forests. They concluded that the penetration of light through the canopy is a function of canopy height and gap size: the taller the forest and the larger the opening, the greater the gap light index. Chazdon and Fetcher (1984) studied the variability of light conditions in various sizes of gaps in terms of photosynthetic photon flux density (PPFD) in a lowland

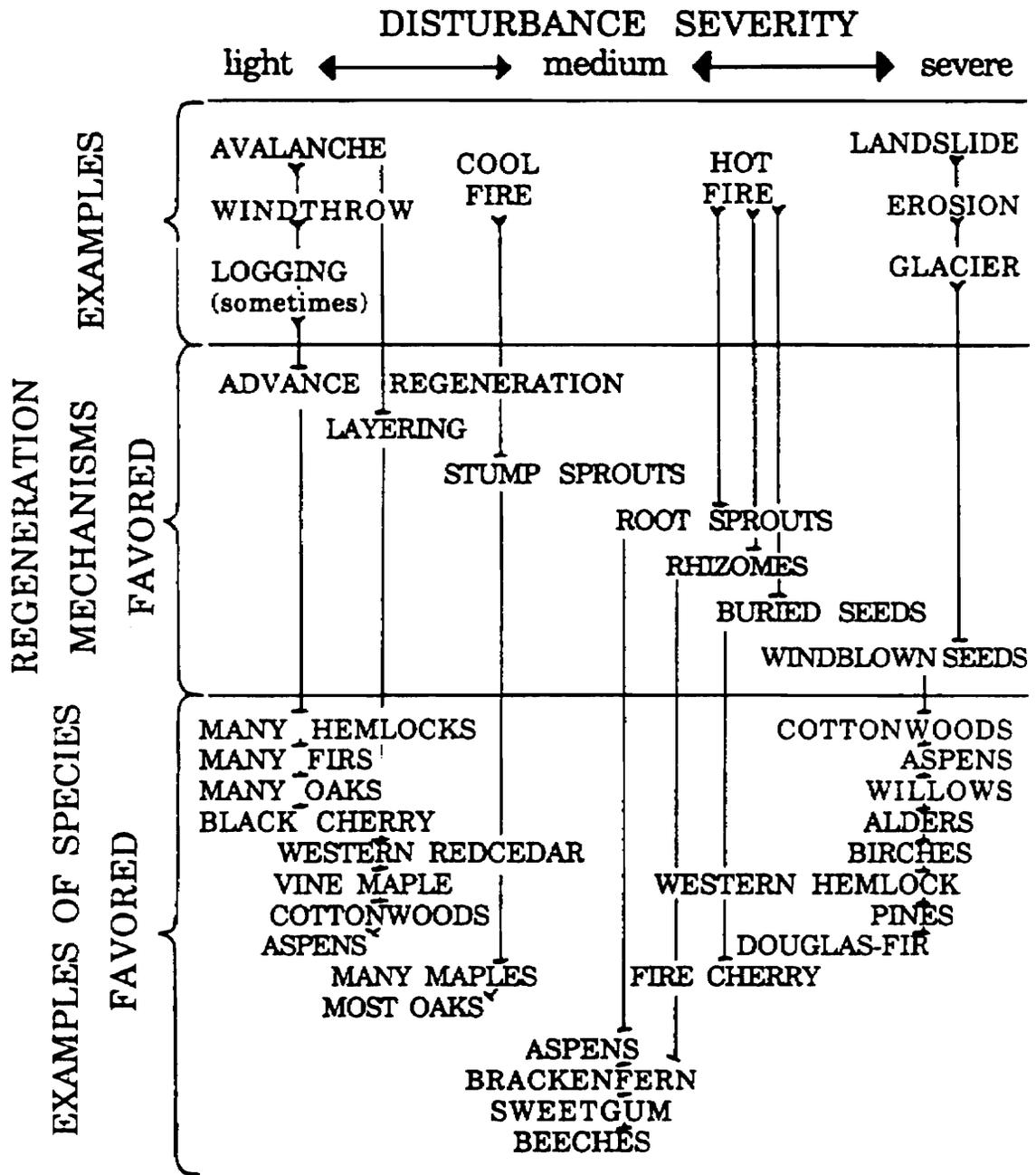


Figure 2. Disturbance severity and favored regeneration mechanisms (from Oliver and Larson 1990).

tropical rain forest. They concluded that large openings of 400 m² maintained 20-35% of total daily PPFD, openings of 200 m² maintained 9% of total daily PPFD, and the understory maintained 1-2% of total daily PPFD. Further, Chazdon and Fetcher (1984) noted that a small change in PPFD, like those that occur in small gaps, may have a larger effect on the carbon gain in understory species than those species present in large gaps. This can be explained by the species' relative photosynthetic efficiency under different light regimes. Species like red maple and American beech, which are associated with smaller openings in the forest, generally have lower light requirements due to their higher photosynthetic efficiency for growth, allowing them to persist in low light conditions (Kozlowski et al. 1991).

In addition to quantity of light, quality of light can have a significant influence on germination and light use efficiency. When light passes through the forest canopy, red, blue, and some green wavelengths are absorbed, resulting in an abundance of far-red radiation in the sub-canopy. A ratio of red to far-red radiation is often used as an index of shading (Kozlowski et al. 1991). Several genera have species whose germination patterns are sensitive to high ratios of red to far-red wavelengths, which is commonly found in unfiltered light. This seed germination dependency is most useful for shade intolerant species, like some of those in the genera *Pinus*, *Fraxinus*, and *Ulmus* (Kozlowski et al. 1991). The increased far-red wavelength signals shade intolerant seeds to initiate germination activities when the conditions are suitable. If conditions remain incompatible, shade intolerant seeds remain dormant.

The distribution of light in small gaps can be influenced by compass orientation and aspect. In a study located in old-growth deciduous forest of the eastern U.S., Poulson and Platt (1989) found that small overlapping gaps with a north-south compass orientation had higher light levels than those with east-west orientations. In addition, Canham et al. (1990) found the greatest gap light indices in gaps found on south-facing slopes in temperate forests. Light distribution within a gap may vary. For example, Poulson and Platt (1989) found the brightest light conditions along the northern edge of the opening and the least in

south edge of the opening.

It is generally accepted that the light environment within a gap shapes the regeneration that develops there. However, there are variables other than light that may be equally important to species establishment and composition. Some of these factors include changes in the seedbed conditions, such as temperature and moisture fluctuations, and the encroachment of root competition from the edge of an opening to the center after a small disturbance (McClure and Lee 1993).

Soil Moisture

Soil moisture, or available water holding capacity, is primarily a function of soil texture, organic matter content, and soil depth. Soils rich with organic matter and finer in texture have greater water holding capacities (Brady 1984). Water stress significantly slows the growth rate of seedlings and has negative implications on nutrient cycling, in addition to limiting leaf area development (Allen *et al.* 1990). Low soil moisture also impedes the accumulation of biomass, decreases the rate of decomposition, and reduces the soil microbial population. As a result, levels of available nitrogen and other nutrients may decrease.

Small gaps can alter the soil moisture regimes in localized areas beneath a canopy opening. Collins and Pickett (1987) found that soil moisture and temperature increased after gap formation as compared to the closed canopy environment in an Allegheny Plateau forest. There was no direct relationship to gap size. Another study conducted in upper Michigan, however, found a highly positive correlation between canopy opening and percent moisture in the soil (Mladenoff 1987). Oliver and Larson (1990) speculate, however, that after a windthrow, soil mixing with organic matter may occur, creating areas in the soil with poor water retaining ability. This emphasizes the patchy areas of available resources that can occur within small gaps which influences regeneration.

Soil Nutrient Availability

Nutrient availability can limit the growth rate of seedlings, depending on the supply and on the species involved (Chapin et al. 1986). Gap creation often modifies various components of the growth environment. More specifically, when the canopy leaf area decreases, light, water, and temperature of the forest floor increases. These increases enhance microbial activity and subsequent organic matter decomposition and mineralization, ultimately leading to an increase in soil nutrient availability (Lajtha 1994, Jokela et al. 1991, Oliver and Larson 1990, Waring and Schlesinger 1985). Species response to nutrient availability is dependent on physiological attributes; a low nutrient supply may or may not equate to a nutrient deficiency on the site (Chapin et al. 1986). Characterizing an area as nutrient deficient also depends upon the nutrient demand of the species.

Research is limited concerning soil nutrient dynamics in gap and non-gap environments in mixed temperate forests of the Southeast. Mladenoff (1987) measured several soil variables and found significantly lower levels of potassium and calcium in gap areas than adjacent non-gap areas in eastern hemlock and sugar maple stands. In addition, soil pH levels and nitrification were significantly greater in gaps. Vitousek and Denslow (1986) studied soil nutrient supply in three zones within treefall gaps: the root throw zone, the fallen trunk zone, and the crown fall zone. Microbial biomass and nitrogen were significantly greater in the crown zone of gaps than any other zone including the intact forest; whereas the rootfall zone had significantly lower nitrogen mineralization, phosphorous, carbon, and a higher pH than all other zones.

METHODS

Research Site Description

Location, Geology, and Soils

The study was conducted in the forests of the Petersburg National Battlefield (PNB) in Petersburg, Virginia. PNB is comprised of nearly 1,000 ha of mixed pasture and forest, scattered in 6 units in and around the city. Petersburg is located in the upper part of the Coastal Plain physiographic province, where the Appomattox River intersects the Fall Line (Frye 1986). The underlying rock in the Petersburg area is a combination of Petersburg granite, which is primarily composed of feldspar and quartz, and the late Pliocene Bacons Castle formation (Frye 1986). The soils are primarily composed of well-drained, sandy loams with a clay loam subsurface. The dominant soil series represented are the Emporia and Slagle series in the Ultisol soil order, which developed from a combination of marine sediments and residual parent materials from the Coastal Plain and Piedmont provinces, respectively.

Land Use and Vegetation

The PNB is one of many commemorative Civil War battlefields that are administered by the National Park Service. Historical use of the park land before its establishment in 1926 was primarily agricultural, with tobacco and cotton as principle crops (Wallace 1983). Today the park is maintained in a mixture of forest and open fields. Currently the forests are in the late consolidated and sub-climax successional sere, with loblolly pine, several oak species, sweetgum, and tulip poplar as the dominant canopy species. Primary vegetation in the understory includes tree seedlings and saplings, blueberries (*Vaccinium spp.* L.), huckleberries (*Gaylussacia spp.* L.), and common waxmyrtle (*Myrica cerifera* L.). Ground vegetation on the forest floor is dominated by

greenbrier (*Smilax rotundifolia* L.), muscadine grape (*Vitis rotundifolia* Michaux), and the invading Japanese honeysuckle.

No major disturbances in the forest have been reported in the park since its establishment, although there are many areas that have been heavily infested by the southern pine beetle. Other tree deaths are attributed to windthrow, disease, or senescence.

Field Procedures

Forest stands were selected for study if they met certain age and species criteria. Stands greater than forty years old, in three forest cover types as defined by (Sheffield et al. 1989), were included in this study:

Pine: species composition contains > 50% pine basal area, including loblolly pine, Virginia pine (*Pinus virginiana* Miller), and shortleaf pine (*Pinus echinata* Miller).

Pine-hardwood: species composition contains 20-50% pine basal area, with the remaining composed of any mixture of oak, hickory (*Carya spp.*), tulip poplar, sweetgum, or red maple.

Hardwood: species composition contains > 50% oak basal area, with the remaining composed of any mixture of pines, hickory, tulip poplar, sweetgum, or red maple.

Forest cover type maps for PNB were developed from aerial photographs and forest inventory data compiled during the summer of 1992. Within each of the three forest cover types described above, four stands were randomly identified for study.

Gaps were located in each stand based on the presence of a canopy opening and stocking levels. Associated non-gap areas were identified for paired comparisons at least 25 m from the center of each gap. Gaps were defined as canopy breaks within which the stocking level was below 60% (Roach and Gingrich 1968, USDA 1986). In each forest

cover type, 12 paired gap and non-gap plots were established randomly from the population of identified gaps, for a total of 36 in the study.

Site and Vegetation Sampling

Vegetation and site sampling were conducted within each gap and adjacent non-gap area. In the center of each gap a fixed, circular, overstory plot (0.04 ha), two fixed, circular, understory sub-plots (0.008 ha each) nested within the overstory plot, and four fixed, square, regeneration sub-sub-plots (1 m² each) within each understory sub-plot were established (Figure 3). A similar plot configuration was also randomly established in the adjacent forest to sample the non-gap areas.

Site Measurements

Within each overstory plot, slope percent and aspect were measured. Two lengths of each gap were measured from the base of the border trees surrounding the gap, and is consistent with the "expanded gap" definition used by Runkle (1981, 1982). Gap area was estimated using the formula for either a circle or an ellipse, depending upon gap shape (Runkle 1985a). Topographic landform was also noted.

Overstory Measurements

Woody stems over 5 m tall were measured as overstory trees in 0.04 ha, fixed, circular, overstory plots. All trees on the plot were recorded by species, dbh, and crown class. Overstory trees that bordered the gap were included in the overstory calculations of basal area and trees/ha for the gap plot when the base of the tree fell within the fixed area overstory plot. Two healthy, dominant border trees were bored to determine the age and approximate time of gap formation. Total height of these trees was also recorded. Tree density by species was calculated from the edge of the overstory plots of the gaps to an

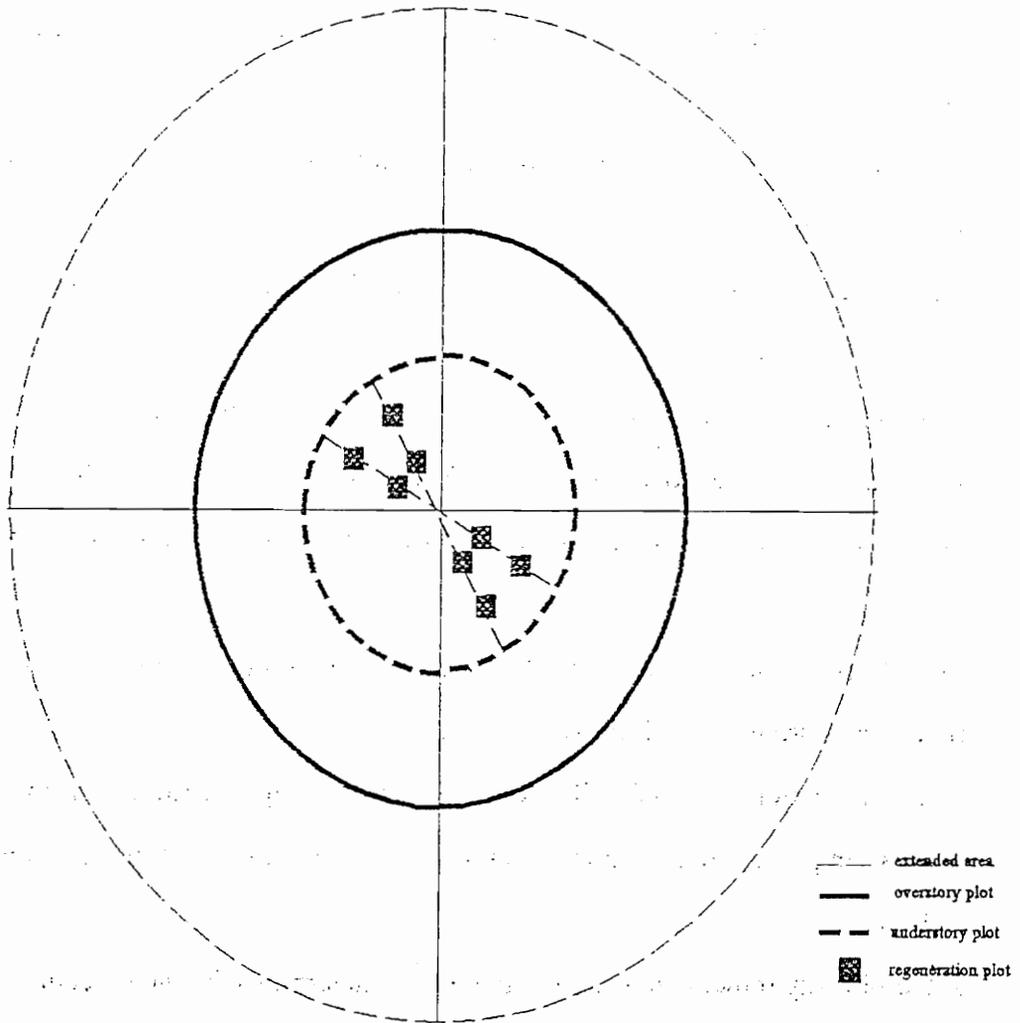


Figure 3. Vegetation plot layout. (Extended area radius = 20 m; overstory radius = 11.3 m; understory radii = 5 m; regeneration plots = 1 m².)

additional 8.7 m radius. This area is referred to as an extended gap area.

Understory Measurements

Each overstory plot was divided into four quadrants, of which two were randomly chosen as the understory sub-plots measuring 0.008 ha each (Figure 3). The understory consisted of woody stems between 1.3 and 5.0 m tall. Understory measurements included the number of stems by species, dbh, and total height for each sub-plot. Within each quadrant, a dominant understory sapling was chosen for an age measurement, felled, and the rings counted at ground level.

Regeneration Measurements

Nested within the understory sub-plots were four 1 m² regeneration plots. These sub-sub-plots were systematically located along 30° and 60° transects, 2 and 4 m from the plot center (Figure 3). All woody seedlings less than 1.3 m tall were counted by species. The tallest seedling was clipped at approximately 1 cm above the ground and aged by counting the rings in the lab. Basal diameter of each oak seedling was measured. In addition, the percent ground cover classes, by species, for both woody and herbaceous vegetation were estimated using the following percent cover classes: 1: 0%, 2: 1-15%, 3: 16-35%, 4: 36-65%, 5: 66-85%, 6: 85-99%, 7: 100%. Dominant ground cover species were also recorded.

Environmental Measurements

A leaf area index (LAI) estimation was taken at approximately the height of the tallest seedling in the center of each regeneration plot and in the center of each overstory plot using a LI-COR LAI-2000 Plant Canopy Analyzer. This was done in order to assess the canopy structure and distribution of leaves affecting the microsite. In addition, the overstory canopy density at the center of each overstory plot and at the center of each

regeneration plot was also estimated using a Spherical Densiometer (Lemon 1956).

Soil samples for describing both physical and chemical soil properties were taken from each regeneration plot. On each regeneration plot a loose soil sample to a depth of 30 cm was collected using a soil probe, and the surface horizon depth was measured. The eight samples for each plot were composited in the field. Associated with the loose soil samples, bulk density cores to a five cm depth were collected from within each regeneration sub-sub-plot using an impact core sampler. The depth of the forest floor was also measured in four locations in each regeneration plot and an average was computed.

Laboratory Procedures

Soil Sample Preparation

All loose soil samples were mixed in sample bags, air-dried, and ground to pass through a 2 mm sieve. Percent fine (< 2 mm) and coarse soil was calculated on a total soil basis. Moisture content after air-drying was determined gravimetrically.

Physical Analysis

Analysis of soil physical properties included organic matter content, available water holding capacity, and bulk density. Organic matter content was determined by two replications of each composite sample using a LECO CR12 Carbon Determinator.

Available water holding capacity was measured as the percent soil water held between field capacity at 0.33 bars and wilting point at 15.0 bars. A pressure plate was used to measure the amount of water held at field capacity and a pressure membrane apparatus was used to measure the amount of water held at wilting point. These measurements were determined for each regeneration sub-sub-plot, and averaged to yield one field capacity measurement and one wilting point measurement for each overstory plot. Bulk density was determined from the intact cores by weighing a known volume of

soil that was oven-dried at 105^o for 24 hours (Blake and Hartage 1986). One sample from each regeneration sub-sub-plot was analyzed and averaged for one bulk density measurement for each overstory plot.

Chemical Analysis

Analysis of soil chemical properties included total nitrogen, anaerobic nitrogen, cation availability, and soil pH. Total soil nitrogen was determined using the micro-Kjeldahl method (Bremner and Mulvaney 1982). Two replications were performed on each composite soil sample.

An index of nitrogen availability was determined using the anaerobic nitrogen incubation technique (Keeney 1982). With this procedure 5.0 g samples were incubated for 7 days at 40^o C, extracted with 3M KCl, and analyzed for total N using a Technicon autoanalyzer.

Phosphorous (P) and essential cations including calcium (Ca), potassium (K), magnesium (Mg), and manganese (Mn) were analyzed using a Jarrell-Ash inductively-coupled plasma emission spectrophotometer following a double acid extraction (0.025 N H₂SO₄ and 0.05 N HCl) (Olsen and Sommers 1982).

Soil pH was determined using a Mettler-D12 Titrator glass electrode in a mixture of 20 ml of water and 10.0 g of soil.

Data Analysis

Objective One: Vegetation Analysis

Differences in vegetation variables between gap and non-gap areas within each cover type were determined using the paired-*t* test for sample means at the 0.05 alpha level. Vegetation variables subjected to this statistical test included the numbers per hectare, collectively, by pine and hardwood groups, and by shade tolerance classes for the

seedling and sapling strata, mean height of saplings by species, and ground cover. To achieve the first objective, the following hypotheses were tested:

H₀: There is no difference in the total number of seedlings between gap and non-gap areas in pine, pine-hardwood, and hardwood cover types.

H₀: There is no difference in the total number of saplings between gap and non-gap areas in pine, pine-hardwood, and hardwood cover types.

H₀: There is no difference in the total number of pine and hardwood seedlings between gap and non-gap areas in pine, pine-hardwood, and hardwood cover types.

H₀: There is no difference in the total number of pine and hardwood saplings between gap and non-gap areas in pine, pine-hardwood, and hardwood cover types.

H₀: There is no difference in the heights of saplings in pine and hardwood groups between gap and non-gap areas in pine, pine-hardwood, and hardwood cover types.

H₀: There is no difference in the number of seedlings by shade tolerance classes between gap and non-gap areas in pine, pine-hardwood, and hardwood cover types.

H₀: There is no difference in the number of saplings by shade tolerance classes between gap and non-gap areas in pine, pine-hardwood, and hardwood cover types.

H₀: There is no difference in the heights of saplings by shade tolerance classes between gap and non-gap areas in pine, pine-hardwood, and hardwood cover types.

H₀: There is no difference in the percent ground cover between gap and non-gap areas in pine, pine-hardwood, and hardwood cover types.

Objective Two: Environmental Analysis

Differences in environmental variables between gap and non-gap areas within each

cover type were determined using the paired-*t* test for sample means at the 0.05 alpha level. Light and soil variables subjected to statistical testing included LAI, canopy density, soil bulk density, A horizon depth, available water holding capacity, organic matter content, total carbon, total soil nitrogen, available nitrogen, cation availability, and soil pH. With respect to the second objective, the following hypotheses were tested:

H₀: There is no difference in light conditions between gap and non-gap areas.

H₀: There is no difference in the soil conditions between gap and non-gap areas.

Objective Three: Environmental-Plant Relationships

Principal Component Analysis (PCA), an exploratory factor analysis technique, was used to reduce the size of the data matrix of environmental factors, and create a suite of independent variables from the original data set for use with multiple regression procedures (Minitab, Inc. 1994, Bernstein 1988, and Gauch 1982). All light, soil, and forest floor properties from gap and non-gap areas were included in the data matrix for the PCA in each cover type. Eigenvectors were computed from the correlation matrix because the variables were multi-scaled. The principal components used for interpretation and further analysis were chosen based on the explanation of 95% of the variation within the data set (Myers 1990, Bernstein 1988). The other components each explained less than 2% of the remaining variation, and were not considered important. Components were defined by the most important variables within the eigenvector, which were identified by coefficients greater than the absolute value of 0.3 (Bernstein 1988).

Multiple regression using the best subsets regression was employed to determine the best model for relating seedling density to environmental factors (Minitab Inc. 1994). For each cover type, three separate models were built. The seedling density of shade intolerant, intermediate, and tolerant classes were the response variables for the three models. The regressors for each model included the component scores from the PCA, the

standardized gap sizes, and the transformed density of the trees in the shade tolerance class that corresponds with the shade tolerance class of the response variable. For example, if the density of shade intolerant seedlings is the response variable, then the density of shade intolerant species in the overstory was used in the suite of regressors. Gap size was standardized over the entire cover type, using values of 0 for the non-gap sites and the formula: $[(X_i - \mu_i) / \sigma_i]$, where X_i is the observation, μ_i is the mean of the sample, and σ_i is the standard deviation of the sample. Densities were transformed by the formula: $[\log (X_i + 1)]$.

RESULTS AND DISCUSSION

Disturbance Parameters and Gap Characteristics

Two general types of disturbance can influence upper Coastal Plain forests. Large-scale disturbances, such as hurricanes, ice storms, and large insect outbreaks can cause tree mortality in several forest types. Small-scale disturbances that result in small canopy openings are caused when single trees, or small groups of trees die or are blown down. These disturbances are more common in the Southeast and until recently were often an unrecognized event in forest ecosystems. Hardwood stands generally exhibit blow downs and gradual tree death resulting in standing dead snags as the primary gap-forming processes, whereas canopy gaps in the pine stands are generally a result of over-maturity or southern pine beetle infestation. No studies have addressed small gap replacement in the pine-hardwood forests of the upper Coastal Plain.

Size and Age of Canopy Gaps

Gap size and age are helpful in explaining the presence and abundance of regeneration in the gap environment (Clinton *et al.* 1994). At Petersburg National Battlefield (PNB), the mean size of the canopy openings in each cover type were similar, ranging from 281 m² in the pine-hardwood cover type to 320 m² in the hardwood cover type (Table 2a).

Gap ages were estimated from interpretations of growth rings on border trees, and ages of understory trees growing in the gaps. From these ring counts, three gap age classes were developed: young (< 5 yrs.), intermediate (6 to 9 yrs.), and old (>10 yrs.). Within each cover type, the majority (58%) of the gaps were in the intermediate age class (Table 2b).

Table 2. Distribution and mean size (m²) of gaps by (a) cover type and (b) age class in pine, pine-hardwood, and hardwood forest cover types at Petersburg National Battlefield, Virginia.

(a)

Cover Type	Number	Area (m²)	Std. Dev. (m²)	Range (m²)
pine	12	308	110	93-474
pine-hardwood	12	281	115	138-665
hardwood	12	320	122	152-597
Total	36	---	---	---

(b)

Cover Type	Young		Intermediate		Old	
	Number	Area (m²)	Number	Area (m²)	Number	Area (m²)
pine	2	298	9	319	1	303
pine-hardwood	1	292	7	313	4	320
hardwood	0	---	5	299	7	335
Total	3	---	21	---	12	---

Site Characteristics

Light

Light conditions in the gap and non-gap areas were evaluated using leaf area index (LAI) and percent canopy cover. Although the gaps consistently had significantly lower percent canopy coverages and LAI's than the non-gap areas at the 0.05 alpha level, the values for the gaps were still higher than expected (Table 3). Overall, canopy coverage in the gaps averaged about 95%. The pine cover type had LAI's in the gap and non-gap areas of $4.7 \text{ m}^2 \text{ m}^{-2}$ and $5.0 \text{ m}^2 \text{ m}^{-2}$, respectively, which were higher than found in both the pine-hardwood and hardwood cover types (Table 3). This index is much higher than the estimated range of 1.5 and $3.0 \text{ m}^2 \text{ m}^{-2}$ for southern pine stands reported by Gholz (1986). However, the high LAI indicates that the pine stands have the foliar mass typical of productive southern pine stands estimated at $5.0 \text{ m}^2 \text{ m}^{-2}$ LAI (Allen *et al.* 1990, Gholz 1986). The high canopy coverage is generally due to the smaller sized gaps associated with single tree deaths and the large number of older gaps that have succumbed to the lateral branch extension of the surrounding canopy (Table 2b). Also, canopy and light measurements were made at the tallest seedling in each regeneration sub-sub-plot which were sometimes at the edges of the opening in the smaller gaps, therefore increasing the reported mean for the gaps.

A single tree gap can temporarily influence light levels and alter the forest floor and soil microenvironment in and around the gap, potentially regulating species and abundance of regeneration (Figures 1 and 2). For instance, resources may become more available as a result of a small gap through local decreased nutrient uptake, less shading and therefore increased light, and increased decomposition as a function of increased temperature and moisture beneath the opening (Runkle 1985b). Severity of the disturbance regulates the degree to which the availability of resources are expressed. For example, a windthrown, uprooted tree creates a more severe disturbance than a standing

Table 3. Canopy cover (a) and LAI (b) for the gap and non-gap areas in pine, pine-hardwood, and hardwood cover types at Petersburg National Battlefield, Virginia. Means within a row followed by the same uppercase letter are not significantly different ($\alpha = 0.05$); P values are listed in Appendix 2.

(a)

Cover Type	GAP ----- % canopy cover -----			NON-GAP ----- % canopy cover -----		
	Mean	Std. Dev.	Range	Mean	Std. Dev.	Range
Pine	94 A	4.3	85 - 99	98 B	1.5	95 - 100
Pine-hardwood	96 A	2.3	91 - 98	99 B	0.5	98 - 100
Hardwood	94 A	5.2	79 - 98	99 B	0.6	98 - 100

(b)

Cover Type	GAP ----- LAI (m ² m ⁻²) -----			NON-GAP ----- LAI (m ² m ⁻²) -----		
	Mean	Std. Dev.	Range	Mean	Std. Dev.	Range
Pine	4.7 A	0.8	3.1 - 6.2	5.0 A	1.2	2.9 - 6.4
Pine-hardwood	3.4 A	0.4	2.5 - 4.0	3.8 B	0.5	2.8 - 4.6
Hardwood	3.0 A	0.6	2.0 - 3.8	3.5 B	0.6	2.5 - 4.5

dead tree, although both disturbances are mild (Krasny and Whitmore 1992, Oliver and Larson 1990). Clinton *et al.* (1993) determined standing dead snags to be an influential component of second and third generation mixed forests shaping regeneration patterns. Water stress, which facilitates pathogen attacks, were the primary causes of the gradual death of several oak species in southern Appalachian mixed oak forests, resulting in standing dead snags (Clinton *et al.* 1993, Tainter *et al.* 1986).

Light levels tend to be higher in gaps with fallen trees than in gaps with standing dead trees, as the remaining branches cause some shading (Spies and Franklin 1989). Generally, there is more light in and around a gap, enhancing the successful regeneration of most tree species. For instance, Canham *et al.* (1990) found significantly higher photosynthetically-active radiation levels in the understory of small gaps than the understory beneath a closed canopy.

Light is the prominent factor in the survival of loblolly pine seedlings (March and Skeen 1976). Increased light levels are also linked with several site variables, which collectively influence the establishment success and survival of tree seedlings. For example, a decrease in canopy leaf area has been related to an increase in soil moisture and temperature. These variables have further been associated with more soil microbial activity, which in turn means an increased mineralization rate and subsequent nutrient availability to forest tree species (Binkley 1986, Waring and Schlesinger 1985). McClure and Lee (1993) suggest that for some species, like red maple, factors such as soil moisture and scarification may be more important than gap size (and therefore light) for successful regeneration. This is logical given the shade tolerance of red maple. Thus, the interaction of light and seedbed conditions coupled with a species' physiological traits will determine its survival.

Forest Floor Conditions

Litter Depth

The gaps in the pine cover type had significantly shallower litter depths than the non-gap areas at the 0.05 alpha level (Table 4). There was no significant difference in litter depth between gap and non-gap areas in the pine-hardwood and hardwood cover types. The average litter depth for both the gap and non-gap plots in the pine and pine-hardwood cover types was 43 mm, while the average litter depth for the gap and non-gap plots in the hardwood cover type was 36 mm (Table 4). The higher litter depths in the pine and pine-hardwood cover types is not unreasonable and is attributable to slower litter decomposition rates of the litter associated with each cover type. For example, pine litter decomposes at the slowest rate because of its resins and low nutrient content. Oak litter is also slow to decompose because of tannins in the leaves, but still faster than pine. Sweetgum and red maple, which dominate the pine-hardwood cover type, decompose at a more intermediate rate, and species, such as tulip poplar, hickory, and flowering dogwood (*Cornus florida* L.) which are more common in the hardwood cover type, decompose at the fastest rate because of the high nutrient content of the leaves (Burrows 1990).

The amount and quality of litter on the forest floor have many important functions. Two of the most important functions are that the litter layer serves to continually restore the nutrient pool with each litter fall, and it allows more water to infiltrate into the mineral soil, often preventing seed desiccation (Pritchett and Fisher 1987). Litter depth also affects the germination success of some tree species. For example, most pine, sweetgum, and tulip poplar prefer a shallow litter layer or a bare, mineral, seedbed for germination (Kozłowski *et al.* 1991, Burrows 1990). However, hickory and oaks such as black (*Quercus velutina* Lam.), white (*Quercus alba* L.), and willow (*Quercus phellos* L.) oaks, can persist in deeper litter depths because of their ability to produce deep taproots, which

Table 4. Litter depth (mm) and percent ground cover in gap and non-gap areas in pine, pine-hardwood, and hardwood cover types at Petersburg National Battlefield, Virginia. Means within a row followed by the same uppercase letter are not significantly different ($\alpha = 0.05$); *P* values are listed in Appendix 2.

Cover Type	Variable	GAP			NON-GAP		
		Mean	Std. Dev.	Range	Mean	Std. Dev.	Range
Pine	litter depth (mm)	43 A	4	34-49	46 B	5	38-55
	herbaceous cover (%)	1 A	3	0-27	0 A	0	0-0
	woody cover (%)	34 A	28	7-93	5 B	3	0-7
	total cover (%)	34 A	28	7-93	5 B	3	0-7
Pine-hardwood	litter depth (mm)	40 A	10	23-52	43 A	7	32-56
	herbaceous cover (%)	4 A	8	0-25	1 A	3	0-7
	woody cover (%)	20 A	17	7-50	6 B	2	0-7
	total cover (%)	31 A	22	7-75	10 B	8	0-25
Hardwood	litter depth (mm)	35 A	11	17-60	37 A	5	27-44
	herbaceous cover (%)	6 A	7	0-25	5 A	7	0-25
	woody cover (%)	19 A	17	7-50	9 B	5	7-25
	total cover (%)	34 A	18	7-75	18 B	13	7-50

are more capable of sequestering moisture from the soil surface (Kozlowski *et al.* 1991, Burrows 1990, Collins and Good 1987).

Ground Cover

Herbaceous, woody, and total cover followed the same pattern between gaps and non-gaps in the pine, pine-hardwood, and hardwood cover types, where gaps consistently had more ground cover than non-gaps. Herbaceous cover was not found to be significantly higher in gaps versus non-gaps in any cover type, although it was always numerically higher in gaps (Table 4). The generally low herbaceous cover is attributed to the large amount of woody cover in the regeneration stratum, which covered at least five times that of herbaceous cover, and was highly competitive for resources.

Woody cover and total cover were significantly higher in the gaps of each cover type at the 0.05 alpha level. Overall, total cover in the gaps was approximately 33%, regardless of cover type and was at least twice the coverage than present in the non-gaps (Table 4). Herbaceous and woody competition can outcompete smaller tree seedlings for soil moisture and nutrients, especially in limiting conditions (Morris and Campbell 1991, Oliver and Larson 1990, Poulson and Platt 1989). Collins and Good (1987), however, found that ground cover had minimal effect on the density of some tree seedlings. In fact, Collins and Good (1987) found white oak, willow oak, and sassafras (*Sassafras albidum* (Nutt.) Nees), can persist in areas with greater ground cover.

Soil Conditions

Soil conditions can greatly impact seedling survival (McClure and Lee 1993, Oliver and Larson 1990, Collins and Good 1987). The status of the soil physical and chemical properties, as well as their interactions, have both direct and indirect influences on regeneration success. Generally, there were few discriminations found in the soil parameters between gap and non-gap areas in the pine, pine-hardwood, and hardwood

cover types.

The soil conditions in the pine cover type were similar in the gap and non-gap locations. With the exception of the A horizon depth, where the A horizon was slightly deeper in the gaps, there were no significant differences in any of the soil physical properties between gaps and non-gaps at the 0.05 alpha level (Table 5). The gaps, however, did have nearly one cm more available water than the non-gaps, which was also noted by Collins and Pickett (1987) and Minckler *et al.* (1973). There were several discriminations found in the soil chemical properties. Soils in the pine cover type were generally acidic, with pH values of 4.7 and 4.6, respectively in gap and non-gap locations. Potassium (K), calcium (Ca), and magnesium (Mg) were all significantly lower in the gaps versus the associated non-gap areas in the pine cover type (Table 5). With the exception of Mg, these results are similar to those found in a treefall gap study in hemlock and hardwood forests in Michigan (Mladenoff 1987). The lower values of these nutrients in the gaps were attributed to increased leaching. This is logical if there is a decreased nutrient demand associated with the loss of a dominant tree, and there is increased decomposition and nutrient availability, which results from higher temperature and moisture in gaps (Lajtha 1994, Jokela *et al.* 1991, Oliver and Larson 1990, Vitousek 1985, Minckler *et al.* 1973). Phosphorous (P) and sulfur (S) on the other hand showed the opposite trend, where gaps had significantly more of each nutrient than the non-gap areas. In fact, P was almost twice as high in the gaps than the non-gap areas, with 0.7 kg/ha and 0.4 kg/ha, respectively (Table 5). These values indicate a phosphorous deficiency, and is not unexpected due to the relatively low organic matter content in the soils, which is the primary source for P, the generally acidic nature of the soils, which makes the P unavailable for plant use, and the P-fixing capacity consistent with many soils in the Southeast (Morris and Campbell 1991, Pritchett and Fisher 1987). Again, this is supported by Mladenoff (1987), who also found P levels to be twice as high in treefall gaps as in forested areas in hemlock and hardwood forests in Michigan. No differences

Table 5. Soil conditions in gap and non-gap areas in the pine cover type at Petersburg National Battlefield, Virginia. Means within a row followed by the same uppercase letter are not significantly different ($\alpha = 0.05$); *P* values are listed in Appendix 2.

Soil Variable	GAP			NON-GAP		
	Mean	Std. Dev.	Range	Mean	Std. Dev.	Range
available water (cm)	4.9 A	1.8	2 - 7	4.1 A	1.6	1 - 7
A horizon depth (mm)	40.0 A	10.0	25 - 57	35.0 B	8.0	24 - 47
bulk density (g/cm ³)	1.2 A	0.1	1.1 - 1.4	1.3 A	0.1	1.1 - 1.4
organic matter content (kg/ha)	28441 A	12961	7317 - 52393	28410 A	7773.0	9731 - 36532
pH	4.7 A	0.3	4.5 - 5.2	4.6 A	0.2	4.2 - 4.7
total soil nitrogen (kg/ha)	1370 A	584	355 - 2311	1227 A	422.0	546 - 2120
available nitrogen index (kg/ha)	38.0 A	19.0	14 - 69	36.0 A	16.0	19 - 65
carbon:nitrogen ratio	36:1 A	8.0	26 - 49	41:1 B	8.0	24 - 53
potassium (kg/ha)	15.0 A	5.0	6 - 28	20.0 B	15.0	7 - 61
phosphorous (kg/ha)	0.4 A	0.0	0 - 1	0.2 B	0.0	0 - 1
sulfur (kg/ha)	1073 A	306	685 - 1465	943 B	347.0	383 - 1618
calcium (kg/ha)	44.0 A	22.0	20 - 91	65.0 B	61.0	17 - 203
manganese (kg/ha)	11.0 A	6.0	4 - 20	11.0 A	7.0	4 - 20
magnesium (kg/ha)	7.0 A	3.0	3 - 15	16.0 B	22.0	4 - 72

were found in total or available nitrogen between the two areas where available nitrogen was minimally higher in the gaps, with 38 kg/ha compared to 36 kg/ha in the non-gap areas (Table 5). Another index of nitrogen availability, the ratio of carbon to nitrogen (C:N), however, was significantly lower in the gaps with a ratio of 36:1, than the non-gap areas, with a 41:1 ratio (Table 5). Generally, ratios closer to 10:1 indicate nitrogen is available for plant uptake, ratios higher than this indicate less decomposed litter, with the mineralized nitrogen being entirely used by the decomposer organisms (Morris and Campbell 1991, Burrows 1990, Pritchett and Fisher 1987, Waring and Schlesinger 1985). Thus, it appears that the decomposition rate was increased in the gaps of the pine cover type.

No discrimination was found in any of the measured soil physical properties between gaps and non-gaps in the pine-hardwood cover type (Table 6). With the exception of soil pH, no differences were found in the soil chemical properties. Soil pH was slightly more acidic in the gap plots versus the paired non-gap plots, though only by a tenth, and was weakly significant (Table 6). The most likely reason soil properties in the gap and non-gap environments did not show any significant differences in this study as was hypothesized, is because of the large range of gap sizes, where the range spanned over 500 m² (Table 2). This large range and older nature of the gaps in this cover type could easily have prevented any discriminations from being detected within the scope of this study.

The gaps in the hardwood cover type had significantly more available water than the non-gap areas, 5.3 cm compared to 4 cm (Table 7). In addition, the A horizon depths were deeper in the gaps than the non-gaps; this difference, however, is not believed to be a result of a gap formation, and is attributable to the highly variable nature of soils. None of the remaining soil physical properties were significantly different. This trend is similar to other studies that characterized differences between gap and closed canopy environments in hardwood forests (Collins and Pickett 1987, Moore and Vankat 1986, Minckler *et al.*

Table 6. Soil conditions in gap and non-gap areas in the pine-hardwood cover type at Petersburg National Battlefield, Virginia. Means within a row followed by the same uppercase letter are not significantly different ($\alpha = 0.05$); *P* values are listed in Appendix 2.

Soil Variable	GAP			NON-GAP		
	Mean	Std. Dev.	Range	Mean	Std. Dev.	Range
available water (cm)	6.0 A	2.9	2 - 12	6.5 A	1.2	5 - 8
A horizon depth (mm)	41.0 A	8.0	26 - 55	41.0 A	6.0	32 - 51
bulk density (g/cm ³)	1.1 A	0.1	1.0 - 1.3	1.1 A	0.1	0.9 - 1.3
organic matter content (kg/ha)	34496 A	8781	25391 - 53185	33125 A	7204	23338 - 48438
pH	4.6 A	0.3	4.1 - 5.0	4.7 B	0.4	4.2 - 5.6
total soil nitrogen (kg/ha)	1127 A	439.0	330 - 1619	1344 A	471	283 - 2150
available nitrogen index (kg/ha)	38.0 A	19.0	8 - 64	44.0 A	19.0	26 - 93
carbon:nitrogen ratio	69:1 A	53.0	31 - 185	50:1 A	31.0	30 - 140
potassium (kg/ha)	18.0 A	10.0	8 - 46	16.0 A	3.0	10 - 23
phosphorous (kg/ha)	0.4 A	1.0	0 - 2	0.3 A	0.0	0 - 1
sulfur (kg/ha)	928 A	335	382 - 1339	1006 A	227	627 - 1506
calcium (kg/ha)	38.0 A	23.0	13 - 84	62.0 A	77.0	17 - 297
manganese (kg/ha)	6.0 A	5.0	0 - 15	7.0 A	4.0	1 - 16
magnesium (kg/ha)	8.0 A	4.0	3 - 16	8.0 A	3.0	4 - 13

Table 7. Soil conditions in gap and non-gap areas in the hardwood cover type at Petersburg National Battlefield, Virginia. Means within a row followed by the same uppercase letter are not significantly different ($\alpha = 0.05$); *P* values are listed in Appendix 2.

Soil Variable	GAP			NON-GAP		
	Mean	Std. Dev.	Range	Mean	Std. Dev.	Range
available water (cm)	5.3 A	2.5	1 - 9	4.0 B	1.9	1 - 7
A horizon depth (mm)	53.0 A	31.0	8 - 110	41.0 B	14.0	16 - 62
bulk density (g/cm ³)	1.1 A	0.1	1.0 - 1.4	1.1 A	0.1	1.0 - 1.2
organic matter content (kg/ha)	41592 A	25244	24704 - 110249	38198 A	20085	21012 - 97902
pH	4.1 A	0.3	4.5 - 5.2	4.6 A	0.2	4.2 - 4.7
total soil nitrogen (kg/ha)	1520 A	467	696 - 2157	1499 A	523	729 - 2660
available nitrogen index (kg/ha)	64.0 A	34.0	21 - 125	50.0 B	36.0	16 - 122
carbon:nitrogen ratio	46:1 A	17.0	27 - 87	43:1 A	8.0	33 - 63
potassium (kg/ha)	19.0 A	6.0	12 - 29	18.0 A	4.0	8 - 24
phosphorous (kg/ha)	1.0 A	2.0	0 - 6	0.5 A	0.0	0 - 1
sulfur (kg/ha)	917 A	352	313 - 1350	704 B	319	329 - 1293
calcium (kg/ha)	70.0 A	73.0	12 - 224	39.0 A	18.0	16 - 70
manganese (kg/ha)	9.0 A	8.0	1 - 27	7.0 A	7.0	2 - 25
magnesium (kg/ha)	18.0 A	16.0	4 - 44	22.0 A	20.0	4 - 71

1973). Also, Mladenoff (1987) found significant positive correlations between canopy opening and moisture. Few discriminations were found in the soil chemical properties the hardwood cover type (Table 7). The C:N ratio did not significantly support this finding though. Vitousek and Denslow (1986) concluded that nitrogen concentrations were minimally impacted by treefall gaps in a gap study in Costa Rica. Sulfur was also found to be significantly greater in the gaps. The higher water availability and the higher pH, as pH is a general regulator of cation availability, logically explains the higher index of available nitrogen and sulfur in the gaps. It should be noted, however, that the soil parameters found to be significantly different between gap and non-gap areas could be a result of the difference in A horizon depth rather than a consequence of a gap.

Primary factors driving compositional change are the production and viability of seed fall throughout a disturbance, and its subsequent germination capacity leading to establishment (Shugart 1984, Good and Good 1972). Successful germination and seedling establishment depends heavily on the local growth environment and can be inhibited by minor fluctuations in the soil as a result of a small scale disturbance (Oliver and Larson 1990). For example, soil moisture is critical to seed germination, and seed desiccation is attributed to large seed crop losses, after predation. The nutrient status of soils usually does not impact initial seedling survival, as seedlings generally have low nutrient requirements anyway, although it will become more important once seedlings are established. Soil acidity is the only soil chemical property directly linked with seedling survival, where very basic soils were found to have a negative impact on the success of pine regeneration (Morris and Campbell 1991). The pH of the soils beneath all of the forest cover types ranged from slightly acidic to neutral.

If single tree gaps are truly patches of high resource availability in forests, it was not conclusively detected in this study. The lack of many soil differences between gaps and non-gaps can be explained by several possibilities. One is the smaller size and older nature of the gaps, which allowed enough time for surrounding plants to use any previously

released water or nutrients associated with the gaps. An example is soil moisture, where it has been found that as gaps age, the difference between the moisture levels in gaps and forested areas decreases, as the gaps are slowly becoming more and more similar to the surrounding forest (Runkle 1990). The second is that the disturbance was simply not severe enough to disturb the soil profile or the forest floor conditions in the first place, which is often the case with windstorm tree deaths, and even more so in gaps with standing dead snags (Figure 2) (Oliver and Larson 1990, Runkle 1985b). Third, perhaps the use of stocking values as a criteria for defining gap and non-gap areas was not discriminating enough. Based on the current soils information alone, it is difficult to draw many conclusions about the past or future species composition. It is an objective of this study, however, to provide a general, but holistic view of the environmental gradients interacting within gaps as they relate to species composition and abundance.

Vegetation Characteristics

Overstory Composition

The overstory of each cover type was characterized by the vegetation measurements on the non-gap plots. Canopy trees were delineated as those greater than 5 m tall. The pine cover type had the most diverse overstory, with 19 different overstory species, which composed a total of 31 m² of basal area/ha and 4,018 trees/ha (Table 8). Loblolly pine dominated the overstory with 12 m² of basal area/ha and 181 trees/ha. However, it ranked second in importance value because of the low relative density, reflecting a smaller number of large trees. Red maple and tulip poplar were ranked highest in importance, at 15% and 13%, because of their high relative densities, which equals nearly 40% of the total density. However, the respective low basal area of red maple and tulip poplar, with 2 and 5 m²/ha, reflects their abundance in the smaller diameter classes. Other associates included sweetgum, black oak, and northern red oak.

Table 8. Overstory density and basal area in the pine cover type at Petersburg National Battlefield, Virginia.

Species	Mean #/ha	Std. Dev.	Range	Basal Area (m²/ha)	Rel. Freq. (%)	Rel. Den. (%)	Imp. Val. (%)
red maple	791	1108	0-4401	2	11	20	15
tulip poplar	705	1589	0-4750	5	9	18	13
black oak	420	986	0-2759	2	4	10	7
northern red oak	279	774	0-2681	1	5	7	6
sweetgum	251	472	0-1402	3	12	6	9
eastern red cedar	224	420	0-1133	1	5	5	5
southern red oak	217	427	0-1133	1	5	5	5
loblolly pine	181	183	20-700	12	21	5	13
white oak	185	369	0-1133	1	5	5	5
blackgum	150	306	0-975	1	5	4	5
sourwood	117	291	0-936	0	4	3	3
pignut hickory	117	404	0-1398	0	2	3	2
scarlet oak	78	270	0-936	0	2	2	2
willow oak	78	270	0-936	0	2	2	2
white ash	71	247	0-856	0	2	2	2
slippery elm	56	209	0-725	0	2	1	2
water oak	45	156	0-539	0	2	1	1
sassafras	42	145	0-503	0	2	1	1
black cherry	11	39	0-135	0	2	0	1
Total	4018	---	---	31	102	100	99

Sweetgum was clearly the dominant species in the pine-hardwood cover type, composing 8 m² of basal area, 26% of the total density, and was ranked highest in importance (Table 9). Loblolly pine, while ranking third in importance, composed 17% of the basal area (5 m²/ha). Red maple had the second greatest density with 1,192 trees/ha, causing it to rank second in importance. Interestingly, mockernut hickory (*Carya tomentosa* (Poir.) Nutt.) was a stable component in the overstory. Other associated species, blackgum (*Nyssa sylvatica* Marsh), northern red oak, and tulip poplar, contributed to the total basal area of 29 m²/ha and 4,870 trees/ha in the pine-hardwood cover type.

The hardwood cover type had a total of 24 m²/ha of basal area, with 4,120 trees/ha (Table 10). Most of the smaller, suppressed stems were composed of blackgum, which composed over half of the total density, and had an importance value of 36%, well above any other species. This high proportion of blackgum is attributed to the fire suppression regime of 70 years, which allows thin-barked species like blackgum to thrive and persist in the suppressed canopy position, prolonging oak recruitment to the sapling stage (Orwig and Abrams 1994a). The largest trees were primarily white oak, with 5 m² of basal area/ha. Sweetgum followed with 3 m²/ha of basal area and 18% of the total density. Other species included hickory, red maple, and several oaks; pine was absent from the overstory.

Edge Trees in Gaps

Tree density remaining in the gap areas was often high because of the use of fixed area plots for sampling the overstory. Consequently, the overstory plot size was often larger than many of the gaps, and therefore overstory trees within the radius of the gap plots were included in the measurements characterizing gap areas. Total basal area and density in the gaps of the pine cover type were 16 m²/ha and 3,337 trees/ha, respectively (Table 11). Loblolly pine and sweetgum were prominent, composing 29% of the total density

Table 9. Overstory density and basal area in the pine-hardwood cover type at Petersburg National Battlefield, Virginia.

Species	Mean #/ha	Std. Dev.	Range	Basal Area (m²/ha)	Rel. Freq. (%)	Rel. Den. (%)	Imp. Val. (%)
sweetgum	1243	1382	0-3700	8	16	26	21
red maple	1192	2232	0-6247	3	9	25	17
mockernut hickory	652	1097	0-3269	2	10	13	12
blackgum	511	838	0-2348	3	7	10	9
northern red oak	391	924	0-2902	1	7	8	8
loblolly pine	226	598	0-2111	5	19	5	12
tulip poplar	226	652	0-2282	1	7	5	6
white oak	154	509	0-2241	1	4	3	3
f. dogwood	102	260	0-856	0	4	2	3
sassafras	56	193	0-670	0	2	1	1
willow oak	54	124	0-416	1	5	1	3
slippery elm	24	82	0-283	0	2	0	1
southern red oak	15	50	0-174	0	2	0	2
post oak	12	40	0-139	0	2	0	1
black oak	8	22	0-73	0	4	0	2
scarlet oak	4	14	0-49	0	2	0	1
Total	4870	---	---	29	102	99	102

Table 10. Overstory density and basal area in the hardwood cover type at Petersburg National Battlefield, Virginia.

Species	Mean #/ha	Std. Dev.	Range	Basal Area (m²/ha)	Rel. Freq. (%)	Rel. Den. (%)	Imp. Val. (%)
blackgum	2246	3463	0-11665	5	20	55	37
sweetgum	739	1752	0-6023	3	13	18	15
white oak	246	422	0-1261	5	20	6	13
mockernut hickory	288	791	0-2706	1	5	7	6
red maple	181	441	0-1383	1	5	4	5
white ash	86	490	0-1698	0	3	2	2
slippery elm	135	327	0-1133	0	5	3	4
f. dogwood	117	339	0-1174	1	5	3	4
tulip poplar	52	179	0-621	0	5	1	3
willow oak	14	42	0-146	2	8	0	4
pignut hickory	6	21	0-73	0	3	0	1
northern red oak	4	15	0-51	1	3	0	1
southern red oak	4	8	0-22	0	5	0	3
scarlet oak	2	7	0-25	1	3	0	1
Total	4120	---	---	24	103	99	99

Table 11. Overstory density and basal area of edge trees in gaps in pine, pine-hardwood, and hardwood cover types at Petersburg National Battlefield, Virginia.

Species	Pine		Pine-hardwood		Hardwood	
	Density #/ha	Basal Area (m ² /ha)	Density #/ha	Basal Area (m ² /ha)	Density #/ha	Basal Area (m ² /ha)
loblolly pine	406	4	9	1	0	0
sweetgum	561	4	407	3	738	5
red maple	562	2	0	0	65	0
southern red oak	312	2	329	1	0	0
tulip poplar	194	1	88	1	0	0
black oak	143	1	123	1	35	0
sourwood	236	1	78	0	0	0
willow oak	170	1	3	0	27	1
white oak	78	0	171	1	335	2
eastern red cedar	50	0	0	0	0	0
northern red oak	39	0	0	0	78	0
blackgum	0	0	142	1	302	1
mockernut hickory	315	0	111	0	55	1
pignut hickory	78	0	0	0	0	0
water oak	71	0	0	0	0	0
American holly	42	0	0	0	0	0
sassafras	33	0	61	0	0	0
black walnut	30	0	0	0	0	0
tree-of-heaven	8	0	0	0	0	0
scarlet oak	9	0	1	0	0	0
flowering dogwood	0	0	0	0	59	0
Total	3337	16	1523	9	1694	12

and half of the total basal area (Table 11). The high density in the gaps is related to the generally older mean age of the gaps in this cover type. Tulip poplar and tree-of-heaven were present in the gaps where none was noted in the surrounding forest canopy, this is also indicative of older, large gaps that have begun to close with such an invasive, fast growing species (Tables 8 and 11).

Gaps in the pine-hardwood cover type had 1,523 trees/ha and 9 m²/ha of basal area (Table 11). Sweetgum dominated, composing a third of the total basal area and the highest density, with 407 trees/ha. The oaks were a large component, with southern red oak, white oak, and black oak being 41% of the total density and another third of the basal area. Blackgum and mockernut hickory were other common associates in the canopy. Scattered, large trees of loblolly pine remained as edge trees in the gaps and will eventually drop out of the canopy unless a large disturbance occurs, allowing the pine to regenerate.

The primary species in the gaps of the hardwood cover type was sweetgum, which had the highest density, with 738 trees/ha, and more basal area than any other species (Table 11). White oak and blackgum were the secondary species, composing 38% of the total density, which was 1,694 trees/ha. Northern red oak, red maple, and flowering dogwood were other notable species present.

The total density in the gaps was usually at least half the density of the surrounding intact forest. The somewhat high density in the gaps is related to the large size of the fixed overstory plots and the generally small size of the actual gaps, which was often smaller than the overstory plot. This discrepancy automatically included some overstory trees, or edge trees, in the inventory figures. Also, as nearly all of the gaps surveyed were in the intermediate and old age classes, advanced regeneration present at the time of disturbance could have easily grown tall enough to be classified as a tree with 5 m height requirement, yet not large enough in diameter to contribute significantly to the basal area when the canopy status of the plot was determined.

The current forest canopy is the primary seed source, and therefore the most important determinant of forthcoming natural regeneration. Those canopy species closer in proximity to a gap will contribute more seeds to the seed pool in the gap than the seeds from other parent trees further away (Oliver and Larson 1990, Bazaaz 1983). This is especially true for forests with a random distribution of many tree species, which is typical of these forest cover types (Runkle 1981).

Understory Composition

Species compositional change occurs continuously in forest ecosystems. Whereas forest cover types are distinguished by species composition, they are at varying stages in succession, and change through time at different rates across the landscape. Land managers attempt to shape the direction of compositional change to fulfill certain objectives. Advanced regeneration provides the best insight to the future forest composition because it may comprise the future forest. Small gaps most effectively facilitate the growth of advanced regeneration for several reasons. Disturbances that create small gaps are generally mild in severity, often leaving saplings beneath it untouched and fully capable of using any newly available resource (Oliver and Larson 1990). Height, rather than density, determines the most probable successors of a canopy position. Tall species are more able to intercept more light and outcompete smaller tree seedlings (Huston and Smith 1986, Oliver and Larson 1990). Generally, it requires at least two gaps before saplings will reach the canopy (Runkle 1990, Runkle and Yetter 1987). Those species that can persist in between gap events will have the best probability of attaining canopy status.

Pine Cover Type

Saplings in the understory will comprise the forest canopy in the next forest cycle, with

the exception of small tree species such as flowering dogwood, redbud (*Cercis canadensis* L.), or viburnum (*Viburnum spp.*). Loblolly pine saplings dominated the gaps in the pine cover type with 150 stems/ha (Table 12). Sweetgum, black cherry, and sourwood (*Oxydendrum arboreum* (L.) DC.) were also abundant and are not unusual pine understory associates. In contrast, red maple was the most important species in the non-gap areas of the pine cover type, with 46 stems/ha. Loblolly pine was poorly represented in the non-gap areas, with only 25 stems/ha. In fact, red maple and loblolly pine were the only species significantly different between gaps and non-gaps ($P = 0.06$ and $P = 0.13$, respectively) at the 0.05 alpha level (Table 12). Sweetgum, American holly (*Ilex opaca* Ait.), and sassafras were also abundant in the non-gap locations in the pine cover type.

Regeneration in gaps were further analyzed by species groups. Species were delineated into groups of pine and hardwood, and shade tolerance classes in an effort to classify regeneration patterns. Pine density in the gaps was significantly higher than in the non-gap locations, with 150 stems/ha versus 38 stems/ha, respectively (Table 13). The hardwoods composed 85% of the total density in the non-gap understory, whereas the distribution of species was more evenly split in the gaps. Total density was higher in the gaps, with 342 saplings/ha compared to the 246 saplings/ha that composed the non-gap understory, but was not significant. The gaps in this cover type were predominantly older, allowing the sapling density to equilibrate, as gaps resemble associated non-gap understories over time. Runkle and Yetter (1987) found total sapling density declined as gaps aged in southern Appalachian forests. In an *Acer-Fagus* forest, sapling density was significantly less as gaps aged into the intermediate and old age classes (Runkle 1990).

In general, shade intolerant species usually capture light-enriched environments such as fields and canopy gaps. Only those species with very fast growth, such as tulip poplar, will survive into the sapling stage and eventually to the canopy in a gap environment (Beck 1990). In the pine stands the shade intolerant species indeed dominated the gaps, with 263 saplings/ha. The non-gap locations had a significantly lower density of intolerant

Table 12. Absolute and relative density, relative frequency, and importance values for saplings in gap and non-gap areas in the pine cover type at Petersburg National Battlefield, Virginia.

GAP						
Species	Mean #/ha	Std. Dev.	Range	Rel. Freq. (%)	Rel. Den. (%)	Imp. Val. (%)
loblolly pine*	150	267	0-750	11	44	28
sweetgum	42	63	0-200	14	12	13
black cherry	17	33	0-100	8	5	7
sourwood	17	33	0-100	8	5	7
tree-of-heaven	17	58	0-200	3	5	4
southern red oak	17	44	0-150	3	5	4
tulip poplar	13	23	0-50	8	4	6
flowering dogwood	13	31	0-100	6	4	5
northern red oak	8	19	0-50	6	2	4
willow oak	8	19	0-50	6	2	4
American holly	8	19	0-50	6	2	4
sassafras	8	19	0-50	6	2	4
blackgum	4	14	0-50	3	1	2
American sycamore	4	14	0-50	3	1	2
scarlet oak	4	14	0-50	3	1	2
red maple*	4	14	0-50	3	1	2
black oak	4	14	0-50	3	1	2
mockernut hickory	4	14	0-50	3	1	2
Total	342	---	---	100	100	100

NON-GAP						
red maple*	46	72	0-250	15	19	17
sweetgum	25	45	0-150	12	10	11
loblolly pine*	25	58	0-150	6	10	8
American holly	25	58	0-150	6	10	8
sassafras	21	58	0-200	6	8	7
tulip poplar	17	39	0-100	6	7	6
eastern red cedar	13	23	0-50	9	5	7
southern red oak	13	31	0-100	6	5	6
slippery elm	13	31	0-100	6	5	6
sourwood	13	43	0-150	3	5	4
black oak	4	14	0-50	3	2	2

Table 12. Continued.

NON-GAP						
Species	Mean #/ha	Std. Dev.	Range	Rel. Freq. (%)	Rel. Den. (%)	Imp. Val. (%)
northern red oak	4	14	0-50	3	2	2
mockernut hickory	4	14	0-50	3	2	2
common waxmyrtle	4	14	0-50	3	2	2
willow oak	4	14	0-50	3	2	2
white oak	4	14	0-50	3	2	2
black cherry	4	14	0-50	3	2	2
pignut hickory	4	14	0-50	3	2	2
scarlet oak	4	14	0-50	3	2	2
Total	247	---	---	102	102	98

*Mean absolute densities are significantly different between gap and non-gap areas at the 0.05 alpha level.

Table 13. Sapling density by species group and shade tolerance class in gap and non-gap areas in the pine cover type at Petersburg National Battlefield, Virginia. Means within a column followed by the same lowercase letter are not significantly different ($\alpha = 0.05$). Means within a row followed by the same uppercase letter are not significantly different ($\alpha = 0.05$). Species in each group are listed in Appendix 1; *P* values are listed in Appendix 2.

Species Group	Gap ----- #/ha -----	Non-gap ----- #/ha -----
Pine	150 aA	38 aB
Hardwood	192 aA	208 bA
Total	342 A	246 A

Shade Tolerance Class	Gap ----- #/ha -----	Non-gap ----- #/ha -----
Intolerant	263 A	120 B
Intermediate	54 A	54 A
Tolerant	25 A	71 A

species, with 120 stems/ha (Table 13). There were no significant differences in the densities of intermediate or shade tolerant species between the gap and non-gap locations, however, the density of shade tolerant species in the non-gap locations was numerically higher than the gaps, 71 stems/ha compared to 25 stems/ha, respectively (Table 13). This is most likely related to the low frequency and presence associated with both groups.

Species were stratified by mean height to serve as an additional expression of dominance, since taller saplings generally outcompete shorter saplings and seedlings for resources. Data presented on a species basis are the means of species present. Northern red oak was the tallest species throughout the understory of the pine cover type, averaging 4.9 m in height, although it was poorly represented, with only 8 saplings/ha in the gaps and 4 saplings/ha in the non-gap areas (Figure 4, Table 12). Scarlet oak (*Quercus coccinea* Muenchh.), blackgum, and sassafras, each averaging 4.4 m in height, were slightly shorter in the gaps. Species with the tallest individuals in the cover type differed in the location. American holly, tree-of-heaven, and sweetgum were the absolute tallest individuals in the gaps. In general, there was a wider distribution in height stratification in the non-gap understory. Mockernut hickory, averaging 4.1 m tall, was just under northern red oak in the non-gap understory, followed by red maple and eastern red-cedar (*Juniperus virginiana* L.). The mean height of loblolly pine was slightly taller in the non-gap locations, at 2.6 m, than the gaps, at 2.2 m (Figure 4). Loblolly pine, red maple, and American elm (*Ulmus americana* L.) were the absolute tallest individuals in the non-gap areas. The mean height of pine and hardwood groups did not differ significantly between the gap and non-gap locations, although species in the gaps were generally taller (Table 14). Within the gaps and non-gap areas, hardwoods were significantly taller than the pines. In fact, the hardwood saplings were three times as tall as the pine saplings (Table 14). These results show the early phases of the transitional sere in succession towards a pine-hardwood forest.

Like the analysis of the pine and hardwood heights, the heights of the shade tolerance

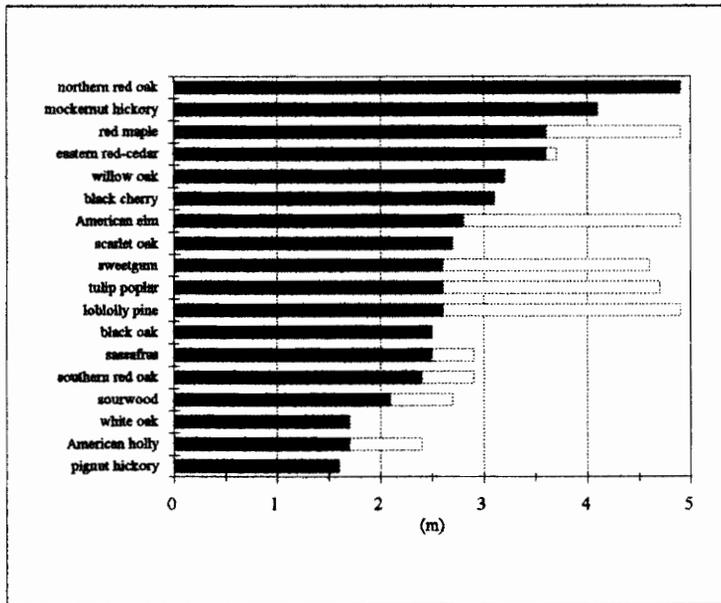
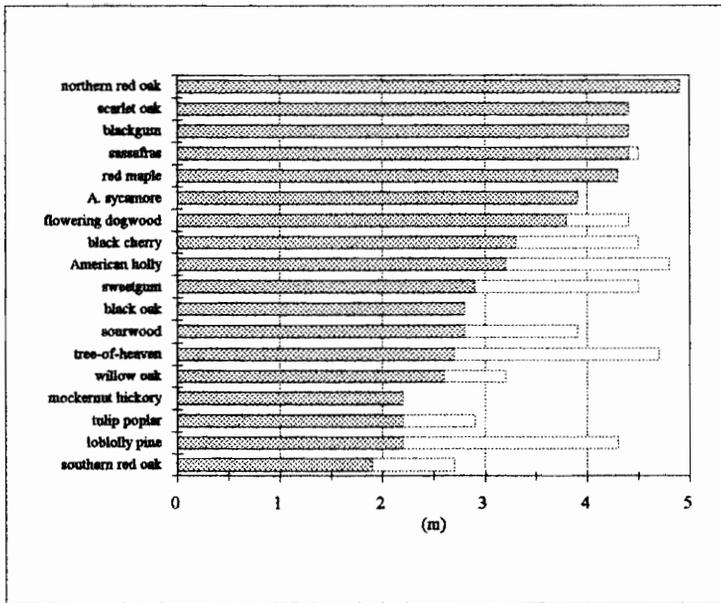


Figure 4. Mean and maximum height (- - -) of saplings in the gap (upper) and non-gap (lower) areas in the pine cover type at Petersburg National Battlefield, Virginia.

Table 14. Mean height of saplings by species group and shade tolerance class in gap and non-gap areas in the pine cover type at Petersburg National Battlefield, Virginia. Means within a column followed by the same lowercase letter are not significantly different ($\alpha = 0.05$). Means within a row followed by the same uppercase letter are not significantly different ($\alpha = 0.05$). Species in each group are listed in Appendix 1; *P* values are listed in Appendix 2.

Species Group	Gap ----- m -----	Non-gap
Pine	0.9 aA	0.7 aA
Hardwood	3.3 bA	2.7 bA

Shade Tolerance Class	Gap ----- m -----	Non-gap
Intolerant	2.4 A	2.1 A
Intermediate	2.2 A	2.7 A
Tolerant	1.1 A	0.3 A

classes are expressed on a plot-by-plot basis. No significant differences were detected between gap and non-gap areas in any of the shade tolerance classes in the pine understory (Table 14). Though not significant, both shade intolerant and tolerant species were taller on average in the gaps than the non-gap areas, and the shade intermediate species were taller in the non-gap understory (Table 14).

It is difficult to explain the presence of species currently in the understory based on a single evaluation of the forest conditions, as the ecosystem variables are continuously changing and highly variable. The high density of loblolly pine in the gaps of the pine cover type is not unexpected because of the large seed pool of loblolly pine in the surrounding forest, and as the edge trees in the gaps were predominantly pine (Tables 8 and 11). Runkle (1981) found highly significant interactions between canopy species and sapling composition in a gap regeneration study of old-growth forests in the eastern U.S. As most of the gaps were older, and therefore larger than at present, they probably functioned as a release, to which loblolly pine responds favorably, and can often outgrow its competitors (Baker and Langdon 1990). In contrast, red maple is undeniably the dominant species in the understory of the non-gap areas in height and in importance value. Red maple's dominance can be attributed to its prolific sprouting ability, high replacement rate of seeds, and tolerance of shade when young (Walters and Yawney 1990). This combination of characteristics, coupled with fire suppression, perpetuates the large red maple component in the understory.

Density alone does not predict the future composition of the forest, as most saplings will either die from shading or remain suppressed beneath a taller competitor. For example, Skeen (1980) found loblolly pine had less than 40% survival and tulip poplar had less than 8% survival of their original density in a single gap study after 7 years. As the taller competitors generally have faster growth rates and express more dominant traits, they have the highest probability of survival into the canopy (Connell 1989, Huston and Smith 1986). The understory of gaps in the pine cover type, although densely populated

with loblolly pine, were overtopped by hardwoods, specifically northern red oak, blackgum, and scarlet oak. Similarly, the large red maple component in the understory of the non-gaps was beneath northern red oak and mockernut hickory in mean height. The importance values of these oaks and hickories, however, were generally low throughout the pine understories. For example, southern red oak, the most important understory oak species, had an importance value of 4% in the gaps and 5% in the non-gap areas. This is in contrast to importance values of 28% and 8% for loblolly pine in the gap and non-gap areas, respectively (Table 12).

These longer-lived, more tolerant oaks and hickories compose the climax overstory vegetation in this area, and will probably require another gap episode before becoming dominant canopy species (Runkle 1990, Runkle and Yetter 1987). Further, as these species can remain in the understory for long periods of time, they will undoubtedly dominate the forest in its future successional stages, despite their current low importance (Oliver and Larson 1990, Sander 1990). This cover type is currently mature in age, and loblolly pine is beginning to die and phase out of dominance, barring another large disturbance. Many of the pine saplings will most likely be shaded out because of their height, although there are a few tall loblolly pine saplings noted throughout the understory that could survive into the canopy. As this transition occurs, loblolly pine will become more of an associate canopy species, and the cover type will move towards a mixed pine-hardwood forest. Red maple should continue to be prominent in the understory, and become less dense in the overstory, as it grows very slow with increasing competition for light (Walters and Yawney 1990).

Pine-hardwood Cover Type

The understory stratum of the pine-hardwood cover type was similar in composition to the pine cover type. Sweetgum, with 96 saplings/ha and an importance value of 33%, clearly dominated the gaps (Table 15). Loblolly pine, with 63 saplings/ha was the

Table 15. Absolute and relative density, relative frequency, and importance values for saplings in gap and non-gap areas in the pine-hardwood cover type at Petersburg National Battlefield, Virginia.

GAP						
Species ¹	Mean #/ha	Std. Dev.	Range	Rel. Freq. (%)	Rel. Den. (%)	Imp. Val. (%)
sweetgum	96	180	0-600	27	39	33
loblolly pine	63	217	0-750	5	26	15
red maple	25	45	0-150	14	10	12
southern red oak	21	58	0-200	9	9	9
American holly	8	19	0-50	9	3	6
tulip poplar	8	29	0-100	5	3	4
black oak	4	14	0-50	5	2	3
white oak	4	14	0-50	5	2	3
sourwood	4	14	0-50	5	2	3
blackgum	4	14	0-50	5	2	3
common waxmyrtle	4	14	0-50	5	2	3
water oak	4	14	0-50	5	2	3
eastern red cedar	4	14	0-50	5	2	3
Total	249	---	---	100	104	101

NON-GAP						
Species ¹	Mean #/ha	Std. Dev.	Range	Rel. Freq. (%)	Rel. Den. (%)	Imp. Val. (%)
sweetgum	117	159	0-400	21	35	28
blackgum	79	156	0-400	10	24	17
flowering dogwood	38	71	0-250	17	11	14
mockernut hickory	25	40	0-100	14	7	11
American holly	13	31	0-100	7	4	5
willow oak	13	23	0-50	7	4	5
black cherry	13	43	0-150	3	4	4
white oak	8	19	0-50	7	3	5
red maple	8	29	0-100	3	3	3
American elm	8	29	0-100	3	3	3
tulip poplar	8	19	0-50	3	3	3
common waxmyrtle	4	14	0-50	3	1	2
Total	334	---	---	100	100	100

¹ There are no significant differences in mean absolute density by species between gap and non-gap areas at the 0.05 alpha level.

secondary associate to sweetgum in the gaps of the pine-hardwood cover type. Red maple and southern red oak were also important species in the gaps. The oak component was relatively small, composing 13% of the total sapling density (Table 15). Sweetgum also dominated the understory of the non-gap locations in the pine-hardwood cover type, and was even slightly higher than in the gaps at 117 saplings/ha (Table 15). Blackgum, hickory, and willow oak were the secondary tree species growing in the understory. Small tree species and shrubs, such as flowering dogwood and American holly were also prominent. Oaks were minimally represented, with only 21 saplings/ha, and loblolly pine was entirely absent in the non-gap understories.

The overwhelming presence of sweetgum throughout the understory of the pine-hardwood cover type is justified primarily as a result of the species' dominance as both an edge tree around the gaps and an overstory tree in the surrounding forest canopy (Tables 9 and 11). This explosion of sweetgum saplings is more likely due to its vigorous sprouting ability from suppressed buds along parent tree root systems, rather than the germination of large seed influxes (Kormanik 1990). Species with this ability have the advantage over other species because of its access to the parent trees' carbon reserves. Once large enough, these sprouts will become independent individuals (Oliver and Larson 1990). In a long-term gap replacement study in the Georgia Piedmont, the relative density of sweetgum was found to increase with gap age, from 7% in a 4-year-old opening to 12% in an opening that was 7-years-old (Skeen 1980). In addition, sweetgum had high survivorship, with 92% survival after the second year inventory, and remained high by year 7 (Skeen 1976, 1980). These results suggest that sweetgum can temporarily remain dominant under a closing forest canopy, and has been observed in sweetgum saplings on preferred sites (Kormanik 1990).

Understory hardwood density was higher than pine density in both the gaps and the non-gap locations in the pine-hardwood cover type, although the difference was only significant in the non-gap locations, where no pine regeneration was present (Table 16).

Table 16. Sapling density by species group and shade tolerance class in gap and non-gap areas in the pine-hardwood cover type at Petersburg National Battlefield, Virginia. Means within a column followed by the same lowercase letter are not significantly different ($\alpha = 0.05$). Means within a row followed by the same uppercase letter are not significantly different ($\alpha = 0.05$). Species in each group are listed in Appendix 1; *P* values are listed in Appendix 2.

Species Group	Gap ----- #/ha -----	Non-gap -----
Pine	67 a	NA
Hardwood	183 aA	334 B
Total	250 A	334 A

Shade Tolerance Class	Gap ----- #/ha -----	Non-gap -----
Intolerant	175 A	175 A
Intermediate	42 A	100 A
Tolerant	33 A	58 A

The fact that hardwood density was nearly three times that of the pine density in the gaps, and still not significant is because of the high variation, since many plots had no pine regeneration. Hardwood density was nearly twice as high in the non-gap locations as compared to the gaps, and was significant at the 0.05 alpha level. This is largely due to the higher numbers of shade tolerant and intermediate species in the non-gap areas, such as flowering dogwood and blackgum, which were either not present in gaps, or much less abundant in the gaps. There was no significant difference in total sapling density between gaps and non-gaps in the pine-hardwood cover type (Table 16). Other studies support these results. For instance, Ehrenfeld (1980) also found no significant differences in understory density between small gap and control (non-gap sites) in a mature oak forest in New Jersey. In a small disturbance study in Ohio old-growth forests, no differences in total sapling density were found between gap and non-gap areas (Cho and Boerner 1991).

When species groups were analyzed by shade tolerance class, there was no discrimination found between gap and non-gap locations in the pine-hardwood cover type (Table 16). Shade intolerant species were as dense in gaps as non-gap areas, indicating that advanced regeneration may have been present in or near the gap areas before the gap formed. The intermediate and tolerant classes were each twice as dense in the non-gap locations than the gaps, although neither was significant. This finding is not surprising due the fact that shade tolerant and intermediate species in the overstory composed nearly half of the total density (Table 9). The lack of significance, again is most likely in response to the high variability associated among the groups. Some of these relationships were found by McClure and Lee (1993), where shade tolerant species were more dense in non-gap understories than in gaps, and shade intolerant species were more abundant in gaps. The gaps studied by McClure and Lee (1993), however, were slightly larger than the mean gap size found in this cover type, potentially allowing for a greater differentiation of shade tolerance species classes.

Mean height, determined by species present, averaged nearly 4 m in the gaps of the

pine-hardwood cover type. Black oak overtopped the understory stratum at 4.5 m, followed by water oak and blackgum (Figure 5). The importance values of all of these species were very low, at 3% each, so they will most likely remain a minor component in the future species composition (Table 15). Species individuals with the tallest absolute height were southern red oak, sweetgum, and red maple. Skeen (1981) found sweetgum to be prominent in nearly all height stratifications in an opening in Georgia. Along with being among the tallest individuals, these species were generally much more abundant and much more important, suggesting their probable co-dominant role in the future forest canopy. Loblolly pine saplings, although quite dense, were very short in stature, standing at less than 2 m tall and beneath all other hardwood competition. Given these circumstances, loblolly pine cannot outcompete the more shade tolerant hardwoods, but may persist in small patches where disturbances are severe enough for pine establishment. Loblolly pine had less than 40% survival and low regeneration in an opening in a hardwood forest in the Piedmont (Skeen 1980). In contrast, willow oak, sweetgum, and flowering dogwood were, on the average, the tallest saplings in the non-gap understories in the pine-hardwood cover type (Figure 5). Sweetgum was also one of the absolute tallest individuals, along with mockernut hickory and American elm. All of these species should become future canopy associates of the forest, along with those in gaps.

As analyzed on a plot-by-plot basis, hardwood saplings were significantly taller than pine saplings in the gaps; no pine regeneration was present in the non-gap locations (Table 17). In addition, the hardwoods in the non-gap areas were significantly taller, at 3.4 m, compared to those in the gaps, at 2.7 m in the pine-hardwood cover type. This further shows the shift in species composition of advanced regeneration away from pine to hardwood species that is common in many successional models.

Shade intolerant species were ironically found to be significantly taller in the non-gap understories than the associated gaps (Table 17). This is a result of the statistical procedure, where these groups were analyzed on a plot-by-plot basis. Essentially no

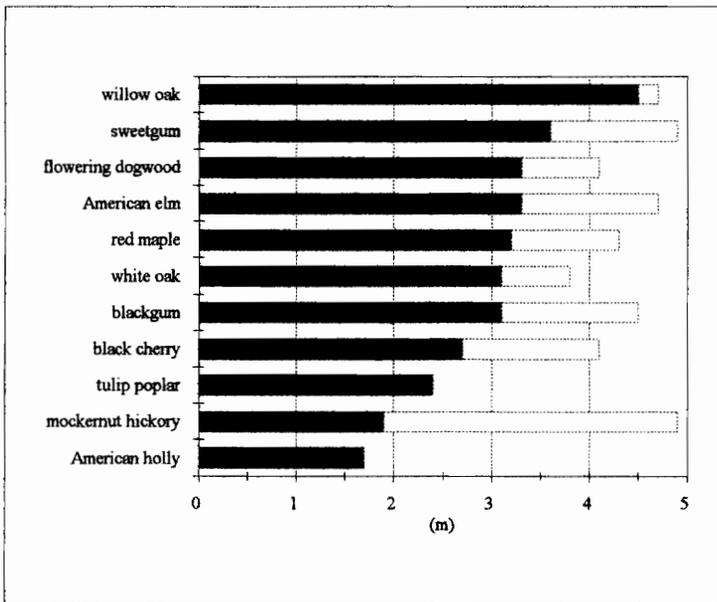
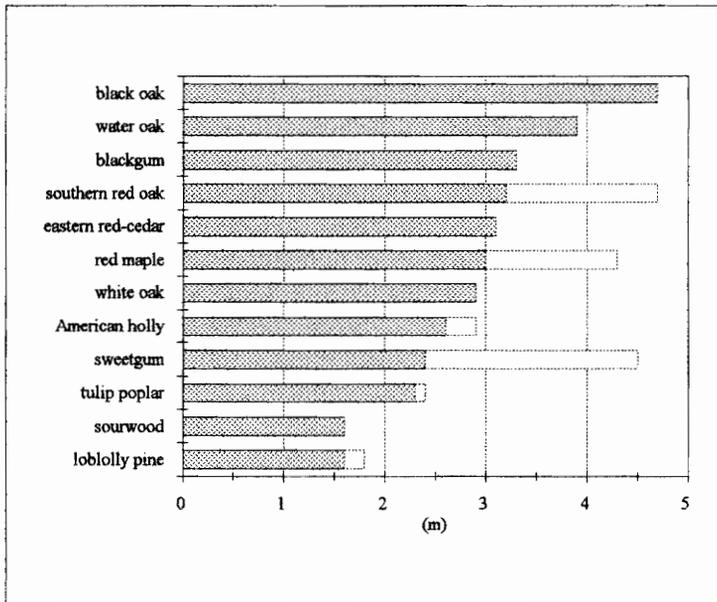


Figure 5. Mean and maximum height (- - -) of saplings in the gap (upper) and non-gap (lower) areas in the pine-hardwood cover type at Petersburg National Battlefield, Virginia.

Table 17. Mean height of saplings by species group and shade tolerance class in gap and non-gap areas in the pine-hardwood cover type at Petersburg National Battlefield, Virginia. Means within a column followed by the same lowercase letter are not significantly different ($\alpha = 0.05$). Means within a row followed by the same uppercase letter are not significantly different ($\alpha = 0.05$). Species in each group are listed in Appendix 1; *P* values are listed in Appendix 2.

Species Group	Gap	Non-gap
	----- m -----	
Pine	0.4 a	NA
Hardwood	2.7 bA	3.4 B

Shade Tolerance Class	Gap	Non-gap
	----- m -----	
Intolerant	1.0 A	2.5 B
Intermediate	2.1 A	1.3 A
Tolerant	0.6 A	1.6 A

differences in height existed between the remaining shade tolerance classes. These results show no clear shifts in species composition based on shade tolerance characteristics, unlike some other studies (Skeen 1980, McClure and Lee 1993).

The data presented clearly suggests that sweetgum will continue to be a dominant species in the canopy. This is not unusual as small gaps often perpetuate the canopy species through the next generation (Runkle 1981,1990). This cover type is in the late transitional sere of succession. Although sweetgum is generally considered a pioneer species, it is relatively long-lived, living for 200 to 300 years on good sites (Harlow *et al.* 1978). The fact that these forests are protected from fire, awards sweetgum another competitive advantage over other saplings. Oaks, such as black, willow, and southern red, and mockernut hickory and will slowly become more important species, although may require other gap episodes before reaching the canopy (Runkle and Yetter 1987). Blackgum should remain as an important sub-canopy species, but may continue to increase as a result of the fire protection practices (Orwig and Abrams 1994a). This trend also applies to flowering dogwood.

Hardwood Cover Type

The understory in the gaps of the hardwood cover type was composed of three species, sweetgum, blackgum and slippery elm (*Ulmus rubra* Muhl.), which collectively account for 80% of the total sapling density (Table 18). Loblolly pine, the hickories, and flowering dogwood were also minor components in this stratum. Oak saplings were practically non-existent, with only 8 saplings/ha (Table 18). Over half of the sapling density in the non-gap areas in the hardwood cover type were composed of sweetgum and blackgum. Hickories, elms, and red maple were the secondary component. Species, like sweetgum, that regenerate via vegetative processes have the ability to produce many sprouts under closed canopies and in gaps (Busing 1994, Kormanik 1990). This characteristic allows it to respond quickly to a temporary release of resources.

Table 18. Absolute and relative density, relative frequency, and importance values for saplings in gap and non-gap areas in the hardwood cover type at Petersburg National Battlefield, Virginia.

GAP						
Species ¹	Mean #/ha	Std. Dev.	Range	Rel. Freq. (%)	Rel. Den. (%)	Imp. Val. (%)
sweetgum	104	185	0-550	26	18	22
blackgum	58	156	0-550	21	13	17
slippery elm	50	158	0-550	11	22	16
loblolly pine	13	43	0-150	5	11	8
pignut hickory	13	43	0-150	5	11	8
flowering dogwood	8	29	0-100	5	7	6
mockernut hickory	4	14	0-50	5	4	4
tree-of-heaven	4	14	0-50	5	4	4
red maple	4	14	0-50	5	4	4
northern red oak	4	14	0-50	5	4	4
white oak	4	14	0-50	5	4	4
Total	266	---	---	100	100	100

NON-GAP						
sweetgum	75	112	0-300	20	28	24
blackgum	67	107	0-350	24	25	25
mockernut hickory	33	89	0-300	8	13	10
flowering dogwood	25	45	0-150	16	9	13
American elm	21	58	0-200	8	8	8
red maple	13	31	0-100	8	5	6
slippery elm	13	43	0-150	4	5	4
white ash	8	29	0-100	4	3	4
white oak	8	29	0-100	4	3	4
red mulberry	4	14	0-50	4	2	3
Total	267	---	---	100	100	100

¹ There are no significant differences in mean absolute density by species between gap and non-gap areas at the 0.05 alpha level.

The two most important sapling species in the understory were also the two most important species in the overstory and the two most abundant species in the gap edges (Tables 10 and 11). Runkle (1981) reported strong relationships between canopy species and sapling species in close proximity to one another. White oak, however, does not appear to follow this pattern. For example, the sapling component of white oak was very low, with 8 saplings/ha or less in both gap and non-gap areas, while in the overstory it was third in importance, and second in density as an edge tree in gaps (Tables 10 and 11). The relative density of oaks was comparable to those reported by Ehrenfeld (1980). The oaks in the gaps composed 8% of the relative density and 4% in the non-gap areas in this study, compared to 10% in small gaps and 12% under the canopy of a mature oak forest impacted by the gypsy moth (Ehrenfeld 1980). Cho and Boerner (1991) also reported few large oak saplings throughout an Ohio old-growth forest. In the Piedmont and Coastal Plain forests of Virginia, Orwig and Abrams (1994a) reported low recruitment of tall oak regeneration.

No significant differences were found in sapling density between gap and non-gap areas in either the pine or hardwood groups (Table 19). However, within the gaps and non-gap areas, the number of hardwoods was significantly higher than the number of pines, as there was virtually no advanced pine regeneration in the understory (Table 19). Total sapling density was nearly the same for both gap and non-gap areas, with about 267 saplings/ha. This suggests that there was little measurable response to gaps in the sapling layer, or if there was a response, the timing of this study was too late to detect it, as most of the gaps were old in this cover type (Table 2).

Shade intolerant species were more abundant in gaps of the hardwood cover type, with 138 saplings/ha, compared to the 108 saplings/ha in the non-gap areas, although no discrimination was detected (Table 19). Both the intermediate and intolerant classes were slightly more abundant in the non-gap areas, although neither were significant. These gaps appear to have favored the regeneration of shade intolerant species. Some shade

Table 19. Sapling density by species group and shade tolerance class in gap and non-gap areas in the hardwood cover type at Petersburg National Battlefield, Virginia. Means within a column followed by the same lowercase letter are not significantly different ($\alpha = 0.05$). Means within a row followed by the same uppercase letter are not significantly different ($\alpha = 0.05$). Species in each group are listed in Appendix 1; *P* values are listed in Appendix 2.

Species Group	Gap ----- #/ha -----	Non-gap ----- #/ha -----
Pine	13 a	NA
Hardwood	254 bA	267 bA
Total	267 A	267 A

Shade Tolerance Class	Gap ----- #/ha -----	Non-gap ----- #/ha -----
Intolerant	138 A	108 A
Intermediate	116 A	121 A
Tolerant	13 A	38 A

intolerant species can regenerate under forest canopies, but require a gap in the canopy for those species to reach maturity (Busing 1994, Whitmore 1989). Some intolerant oaks and sweetgum are examples of species with this attribute. Shade tolerant and intermediate species can regenerate in both gap and non-gap locations, but are more successful beneath forest canopies because they can persist for longer periods of time. Also, many of these species are more resource efficient in the use of short pulses of available resources than shade intolerant species in canopy gaps (Busing 1994, Canham and Marks 1985).

The taller saplings in the gaps of the hardwood cover type included northern red oak, red maple, and tree-of-heaven, all of which were approximately 3.5 to 4 m mean height (Figure 6). However, none of these species were abundant, where each species was represented by only 4 saplings/ha (Table 18). For example, tree-of-heaven, a shade intolerant species with very fast growth rates on a variety of soils, can often be found in the canopy, but is usually not dominant in mixed hardwood forests (Miller 1990). The absolute tallest individuals were sweetgum, blackgum, and pignut hickory (*Carya glabra* (Mill.) Sweet), which were all relatively abundant. Species height stratification in the non-gap understory was somewhat different than the gaps. In order of decreasing height, flowering dogwood, white ash, and blackgum were on average the tallest sapling species, and with slippery elm replacing white ash, were also the absolute tallest individual species (Figure 6).

As the pines were relatively low in frequency, the statistical mean height of the hardwood saplings was significantly taller than the pines in the gaps (Table 20). No pine regeneration was present in the non-gap areas to compare with the other groups. Also, the hardwood saplings in the non-gap areas were significantly taller than those in the gaps, at 3.2 m and 2.0 m, respectively. This is explained by a combination of factors. One is the nature of the statistical analysis, where shade tolerant species were relatively more frequent in the non-gap areas than the gaps, and therefore taller based on a plot-by-plot analysis. These species were also among the absolute tallest species present. Sapling

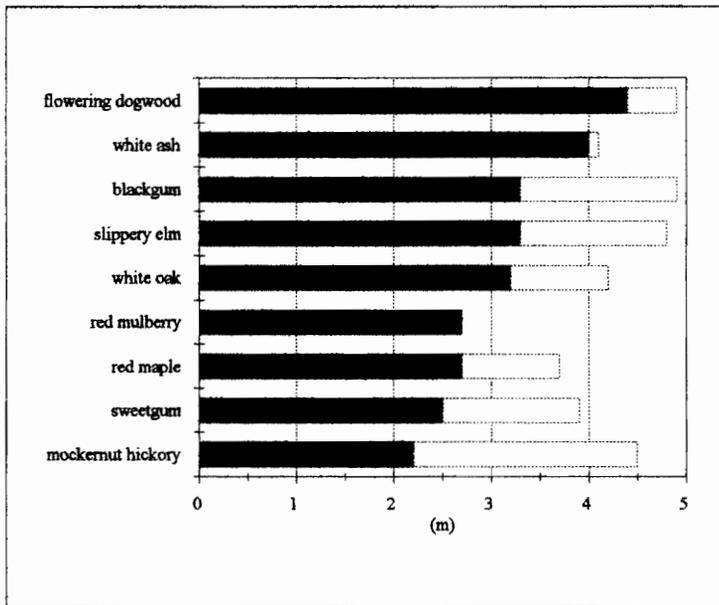
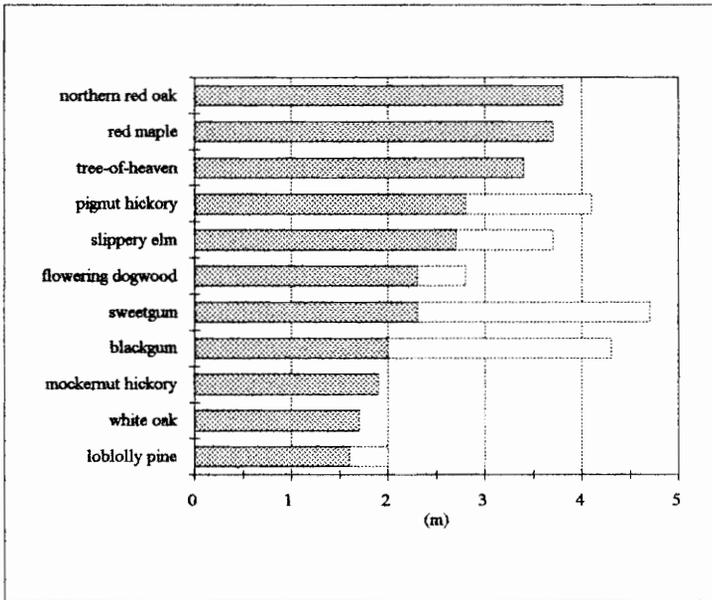


Figure 6. Mean and maximum height (- - -) of saplings in the gap (upper) and non-gap (lower) areas in the hardwood cover type at Petersburg National Battlefield, Virginia.

Table 20. Mean height of saplings by species group and shade tolerance class in gap and non-gap areas in the hardwood cover type at Petersburg National Battlefield, Virginia. Means within a column followed by the same lowercase letter are not significantly different ($\alpha = 0.05$). Means within a row followed by the same uppercase letter are not significantly different ($\alpha = 0.05$). Species in each group are listed in Appendix 1; *P* values listed in Appendix 2.

Species Group	Gap ----- m -----	Non-gap
Pine	0.1 a	NA
Hardwood	2.0 bA	3.2 B

Shade Tolerance Class	Gap ----- m -----	Non-gap
Intolerant	1.5 A	1.8 A
Intermediate	1.3 A	0.3 A
Tolerant	0.2 A	1.2 A

recruitment is consistent with the overstory, which is hardwood.

No significant differences were found in the height analysis of the shade tolerance classes in the hardwood cover type (Table 20). Shade intolerant species were abundant in the understory, and the mean height was virtually equal in both the gap and non-gap locations, at approximately 1.5 m, suggesting minimal growth response to the canopy opening. The intermediate class was almost twice as tall in the non-gap areas than in the gaps, and the same was true for the tolerant class. Based on this information, compositional shifts related to shade tolerant height classes remains unclear.

The hardwood cover type is currently in the late transitional sere. Based on the observations of the sapling composition, this forest probably will not shift completely into a sub-climax successional sere for some time, because of the generally low representation and small stature of the climax species present. Sweetgum and blackgum were the most abundant and were among the absolute tallest species in both the gap and non-gap understories. These species, including flowering dogwood, will remain important in the cover type, as they are common features of fire suppressed forests (Orwig and Abrams 1994a). Oaks were not adequately being recruited into the sapling stratum via gap replacement or beneath the intact canopy. Other studies have also documented the decline in tall oak recruitment (Cho and Boerner 1991, Orwig and Abrams 1994a). Runkle (1990) hypothesized that oak recruitment requires a disturbance from the understory, such as fire, to promote the species rather than a canopy disturbance. Cho and Boerner (1991) have suggested that the oak decline is related to increased competition, suppression, and associated pathogen/insect attack. Others have linked the oak decline to decreased occurrences of natural fires (Van Lear and Watt 1992, Orwig and Abrams 1994a). These fires act as an understory cleaning tool that eradicates persistent, shade tolerant and intermediate species, and thereby increasing recruitment of oaks to the sapling stratum (Lorimer 1993). For example, blackgum can remain in the understory for several decades with completely suppressed growth or very slow growth (Orwig and Abrams 1994b). The

latter hypothesis is most likely the process at work in these forests, given the fire restrictions of the park.

Regeneration Composition

Pine Cover Type

Seedlings, being younger and more fragile, are probably more sensitive to minor changes in the local environment as a result of a gap in the canopy than more established saplings. As such, the seedling stratum should best reflect species response patterns to gaps in the canopy and its associated array of environmental variables.

Loblolly pine, with 24,479 seedlings/ha, or 58% of the density, was clearly the most abundant and important source of regeneration in the gaps of the pine cover type (Table 21). Sweetgum, tulip poplar, and willow oak made up an additional 28% of the seedling density. Sassafras, sweetgum, and tulip poplar seedlings dominated the regeneration stratum in the non-gap areas, composing 58% of the seedling density, and loblolly pine regeneration was low at 521 seedlings/ha (Table 21). Collectively, the oaks were lower in importance in the gaps, with 13%, than the importance value of 27% in the non-gap areas. These results suggest that loblolly pine and willow oak were recruited primarily through the gaps in this cover type; willow oak was the only species found to be significantly more dense in the gaps than the non-gap areas (Table 21). There was no significant difference in total seedling density between the gap and non-gap locations of the pine cover type, although the gaps had four times the density, with 42,083 seedlings/ha, compared to 10,209 seedlings/ha in the non-gap areas (Table 22). This is a result of high species variability between plots.

Seedling regeneration analyzed by species group and shade tolerance class provided some additional insight on regeneration patterns. Although no significant differences were found in the pine or hardwood groups between gap and non-gap locations in the pine

Table 21. Absolute and relative density, relative frequency, and importance values for seedlings in the gap and non-gap areas in the pine cover type at Petersburg National Battlefield, Virginia.

GAP						
Species	Mean (#/ha)	Std. Dev.	Range	Rel. Freq. (%)	Rel. Den. (%)	Imp. Val. (%)
loblolly pine	24479	57064	0-201250	14	58	36
sweetgum	5208	8804	0-30000	13	12	12
tulip poplar	5000	13175	0-46250	9	12	10
willow oak*	1458	1671	0-5000	13	3	8
red maple	1250	1685	0-5000	11	3	7
sassafras	1146	2027	0-6250	9	3	6
sourwood	833	2519	0-8750	4	3	3
American holly	729	1245	0-3750	7	2	4
tree-of-heaven	625	2165	0-7500	2	1	2
southern red oak	417	814	0-2500	5	1	3
northern red oak	313	777	0-2500	4	1	2
black cherry	313	565	0-1250	4	0	2
pignut hickory	208	487	0-1250	5	1	3
blackgum	104	361	0-1250	2	0	1
Total	42083	---	---	100	101	100

NON-GAP						
Species	Mean (#/ha)	Std. Dev.	Range	Rel. Freq. (%)	Rel. Den. (%)	Imp. Val. (%)
sassafras	2500	7230	0-25000	6	24	18
sweetgum	1875	3825	0-12500	12	18	12
tulip poplar	1563	3620	0-12500	12	15	11
red maple	729	1550	0-5000	9	7	7
southern red oak	729	1245	0-3750	12	8	7
sourwood	625	1250	0-3750	9	6	7
loblolly pine	521	991	0-2500	9	5	6
black oak	417	1443	0-5000	3	4	6
pignut hickory	417	814	0-2500	9	4	6
willow oak*	313	777	0-2500	6	3	5
white oak	104	361	0-1250	3	1	3
water oak	104	361	0-1250	3	1	3
northern red oak	104	361	0-1250	3	1	3
eastern red cedar	104	361	0-1250	3	1	3
black cherry	104	361	0-1250	3	1	3
Total	10209	---	---	102	99	99

* Mean absolute density is significantly different between gap and non-gap areas at the 0.05 alpha level.

Table 22. Seedling regeneration by species group and shade tolerance class in gap and non-gap areas in the pine cover type at Petersburg National Battlefield, Virginia. Means within a column followed by the same lowercase letter are not significantly different ($\alpha = 0.05$). Means within a row followed by the same uppercase letter are not significantly different ($\alpha = 0.05$). Species in each group are listed in Appendix 1; *P* values are listed in Appendix 2.

Species Group	Gap ----- #/ha	Non-gap -----
Pine	24,479 aA	521 aA
Hardwood	17,604 aA	9,688 bA
Total	42,083 A	10,208 A

Shade Tolerance Class	Gap ----- #/ha	Non-gap -----
Intolerant	39,271 A	8,125 A
Intermediate	833 A	1,354 A
Tolerant	1,979 A	729 A

cover type, seedling density in the gaps greatly exceeded that in the non-gap locations for each group (Table 22). Differences were not detected because of the high variation and resource patchiness associated with regeneration in mature forests. Pine seedling density was higher than the hardwood density within the gaps, but was not significant (Table 22). In the non-gap locations, the hardwood seedling density was significantly higher than the pine density, with 9,688 seedlings/ha compared to 521 seedlings/ha (Table 22).

Statistical differences were not found in the density of any shade tolerance class between gap and non-gap areas, although the intolerant class in the gaps was about five times as dense as the non-gap areas (Table 22). Again, this is most likely due to the inherently high variation in seedling density.

In an effort to explain the relationships between seedling density classes and environmental factors in gap and non-gap areas, principal components analysis was performed. The components explaining 95% of the variation in the environmental variable matrix for the pine cover type were examined. The eigenvalues and eigenvectors for the first five principal components, which explained 82% of the variation, are presented in Table 23. Each principal component is defined by the weight of its eigenvector. For example, the first principal component, which explains 31% of the variation in the data matrix, is predominantly defined by available soil potassium (Table 23, Figure 7). However, the distribution of the data on the first component is difficult to interpret because of the lack of a definitive pattern. This indicates that perhaps there was not as clear a distinction in available soil potassium between gap and non-gap areas in the pine cover type, as the paired-*t* test indicated earlier (Figure 8, Table 5).

The distribution of gap and non-gap locations on the third principal component was the most definitive. Gaps were negatively and non-gap areas were positively weighted on the third component (Figure 8). This means that the gaps were associated with low canopy density, and non-gap areas were associated high canopy density, which confirms that the classification of sites into gap and non-gap areas was distinct. There were no meaningful

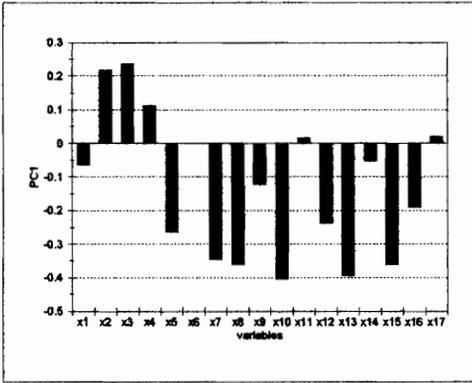
Table 23. Eigenvalues and eigenvectors for the first five principal components of the correlation matrix of environmental data for the pine cover type at Petersburg National Battlefield, Virginia.

Variable ¹	Eigenvector				
	1	2	3	4	5
x1	-0.06	0.31	0.26	-0.02	-0.46
x2	0.22	0.24	-0.22	-0.01	-0.19
x3	0.24	-0.18	0.26	-0.15	-0.48
x4	0.11	-0.36	0.28	-0.20	-0.20
x5	-0.26	-0.23	-0.11	-0.44	-0.19
x6	0.00	-0.42	-0.13	0.18	0.16
x7	-0.35	0.00	-0.25	-0.30	-0.06
x8	-0.36	0.01	-0.14	-0.05	-0.04
x9	-0.12	0.10	-0.29	0.57	-0.23
x10	-0.41	0.10	0.15	0.03	0.01
x11	0.02	-0.30	-0.12	-0.18	0.34
x12	-0.24	-0.32	-0.13	-0.01	-0.34
x13	-0.39	0.11	0.19	0.06	0.00
x14	-0.05	-0.34	-0.17	0.38	-0.32
x15	-0.36	0.15	0.27	0.01	0.10
x16	-0.19	-0.30	0.25	0.29	0.16
x17	0.02	-0.11	0.54	0.21	0.07
Eigenvalue	5.19	3.72	2.32	1.6	1.09
% of variation	30.5	21.9	13.6	9.4	6.4

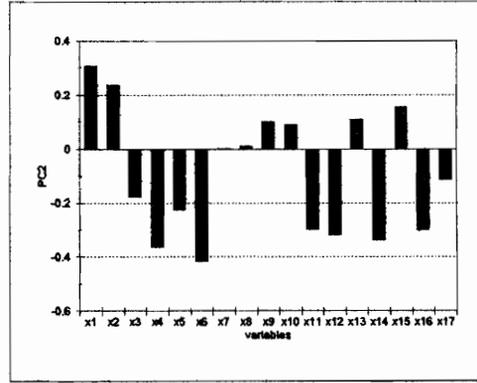
¹x1: bulk density (g/cm³)
x2: A horizon depth (mm)
x3: litter depth (mm)
x4: soil C:N ratio
x5: soil organic matter content (kg/ha)
x6: soil available water (cm)
x7: total soil nitrogen (kg/ha)
x8: available nitrogen index (kg/ha)
x9: soil pH

x10: potassium (kg/ha)
x11: phosphorous (kg/ha)
x12: sulfur (kg/ha)
x13: calcium (kg/ha)
x14: manganese (kg/ha)
x15: magnesium (kg/ha)
x16: LAI (m² m⁻²)
x17: overstory density (%).

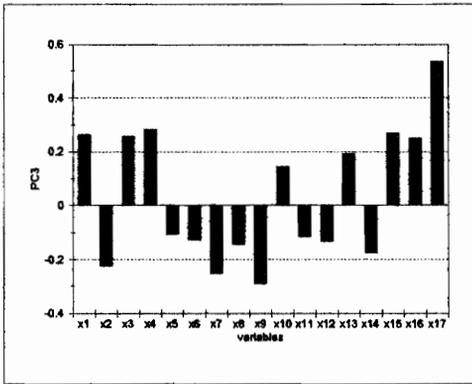
(a)



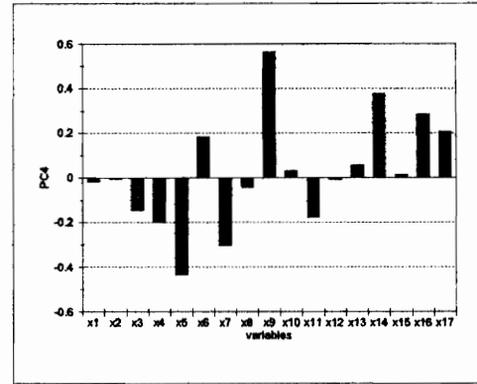
(b)



(c)



(d)



(e)

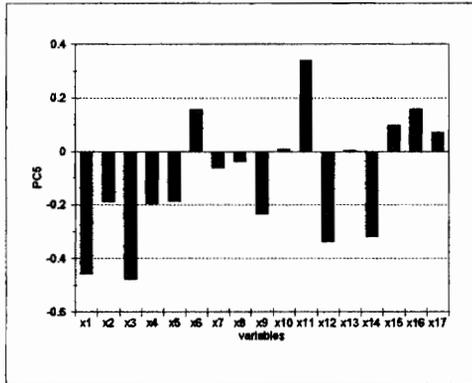


Figure 7. Plot of principal component loadings for the first five principal components of the environmental data for the pine cover type at Petersburg National Battlefield, Virginia. (a) component 1; (b) component 2; (c) component 3; (d) component 4; (e) component 5. Variables are defined in Table 23.

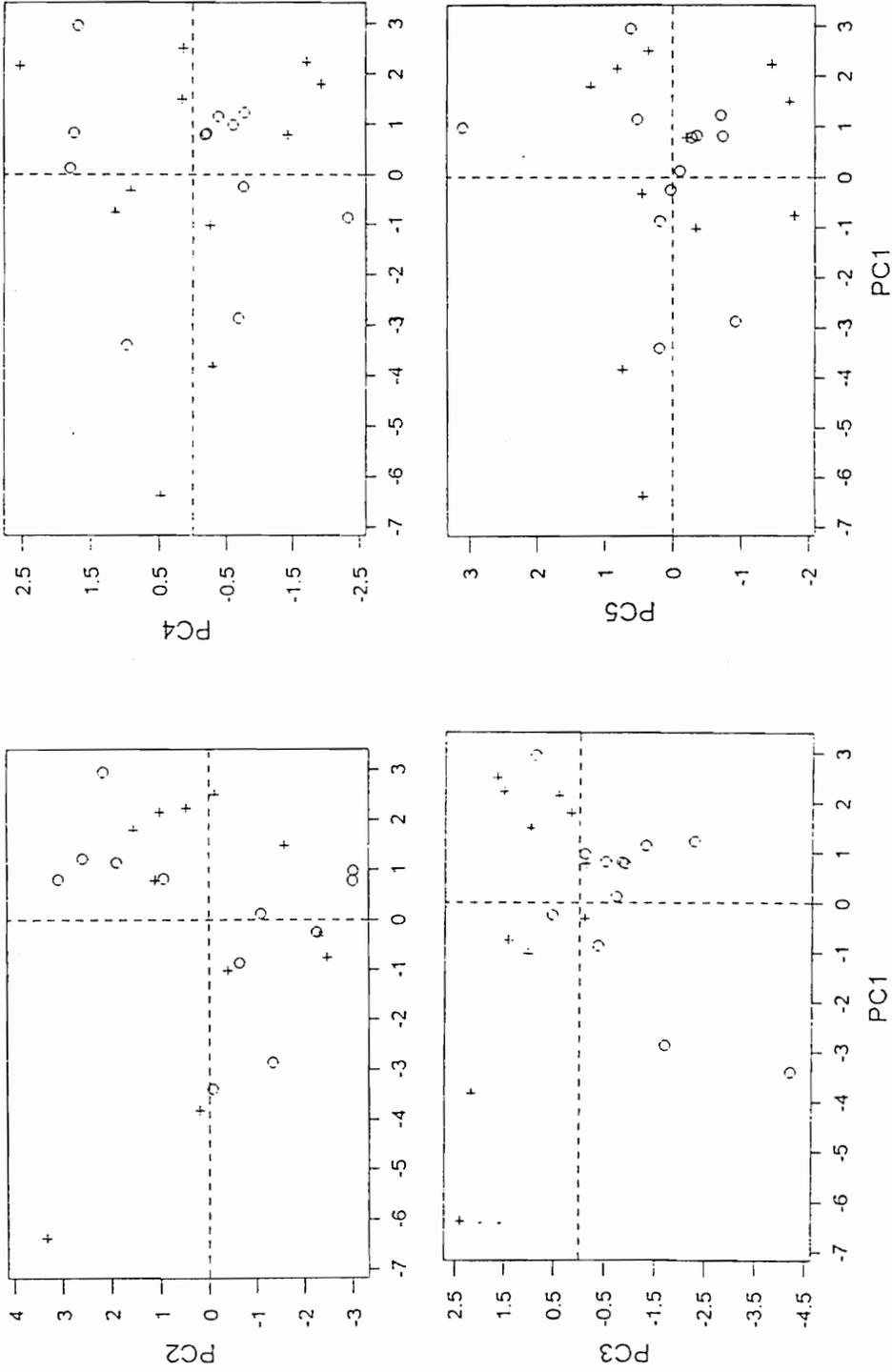


Figure 8. Distribution of gap (O) and non-gap (+) areas on five principal components in the pine cover type at Petersburg National Battlefield, Virginia.

relationships found in the distributions of gap and non-gap plots on any of the other principal components (Figure 8).

To answer the question how canopy openings shape regeneration patterns, the density of each shade tolerance class was used as the response variable, with surrounding tree density, gap size, and the component scores for the environmental data matrix as predictors in three, separate multiple regression models. Results of the Best Subsets Regression (BSR) showed that density of shade intolerant seedlings was best related to the principal components defined by the variables, % canopy density and litter depth ($P=0.000$, $r^2=0.62$; Table 24). This indicates that the success of shade intolerant seedlings are not only dependent on high light conditions, but also on shallow litter depths. These conditions appear to be facilitated by small canopy gaps in the pine cover type, where canopy density and litter depth were significantly less in gaps (Tables 3 and 4). A shallow litter depth increases the chances for seed germination of small seeded species, such as those of many shade intolerant species. For example, loblolly pine, tulip poplar, and sweetgum require the combination of mineral soil and high light for best germination (Burns and Honkala 1990). These species ranked highest in seedling abundance in the gaps (Table 21). The humus layer, although often prohibitive of small seed germination, enhances seedling growth after establishment (Canham and Marks 1985).

A very weak regression was found to explain the density of intermediate seedlings. BSR identified a regression model including the principal components defined by the variables, A horizon depth, bulk density, and K to be the best regressors ($P = 0.071$, $r^2 = 0.30$) (Table 24). Of these variables, the ones that were significantly different between gap and non-gap areas were A horizon depth, which was deeper in the gap areas, and K, which was higher in the non-gap areas (Table 5). There is no apparent ecological reason associated with small canopy openings to account for the difference in A horizon depth. The level of K was higher in the non-gap areas, most likely as a consequence of increased throughfall, as Mladenoff (1987) concluded in a northern hardwood forest. A more

Table 24. Set of best regression models describing the relationships between seedling density (seedlings/ha) by shade tolerance classes and environmental variables in the pine cover type at Petersburg National Battlefield, Virginia (n=23).

Response Variable	Regression Equation	r²	P	SS
Shade intolerant seedling density	$Y = 3.44 - 0.536 \text{ PC3} + 0.829 \text{ PC5}$	0.62	0.000	50.3
	<i>Portion explained by each variable:</i>			
	litter depth	0.33	0.000	16.5
	canopy density	0.29	0.001	14.6
Intermediate seedling density	$Y = 1.19 + 0.199 \text{ PC1} + 0.865 \text{ PC7} + 0.676 \text{ PC8}$	0.30	0.071	61.9
	<i>Portion explained by each variable:</i>			
	A horizon depth	0.15	0.06	9.1
	bulk density	0.08	0.15	5.1
	K	0.07	0.175	4.5
Shade tolerant seedling density	$Y = 1.23 - 0.473 \text{ PC2} - 0.397 \text{ PC4} + 0.514 \text{ PC5}$	0.46	0.007	65.4
	<i>Portion explained by each variable:</i>			
	available water	0.28	0.005	18.1
	litter depth	0.10	0.08	6.3
	pH	0.09	0.099	5.6

probable reason for the low intermediate seedling density in the gaps is that shade intolerant seedlings can simply compete better and grow faster in gap conditions. As the gaps close, many of the new shade intolerant germinants will die. Evidence of this trend can be found through the classification of gaps into age groups, as estimated by examining the growth rings of the border trees and the understory of the gaps. Intolerant seedling density decreased and tolerant seedling density increased as the gaps aged; intermediate species remained essentially unaffected in terms of density (Figure 9). The growth of species in the intermediate class, which consists of many of the oaks, should be enhanced and better able to surpass other competitors in the next gap disturbance.

The density of shade tolerant seedlings was best related to the principal components defined by available water, litter depth, and pH as regressors ($P = 0.007$, $r^2=0.46$). Available water was the most significant, explaining 28% of the variation (Table 24). The regression coefficients suggest that shade tolerant seedlings can grow more efficiently in drier, more shady, conditions with deeper litter layers than seedlings in other shade tolerance classes. This concept of resource use efficiency is described in detail by Canham and Marks (1985). In the pine cover type, tolerant seedlings consist of red maple and American holly, both of which were more abundant in the gaps (Table 21). Perhaps red maple seeds germinated better under gap conditions, which compare with the germination specifications for red maple reported by Walters and Yawney (1990).

In summary, small openings in the pine cover type function to stimulate germination of seeds in all shade tolerance classes. Shade intolerant seedlings, such as loblolly pine, responded the most in terms of germination, growth and establishment, to gaps in the canopy, where litter depth and light were significant. As canopy closure ensues, there is a reduction in this population of seedlings. Gaps also enhanced the growth of seedlings in the other tolerance classes, increasing the likelihood of attaining a canopy position via a subsequent small disturbance. There were no satisfactory relationships describing intermediate seedling density. Shade tolerant seedlings appear to be only minimally

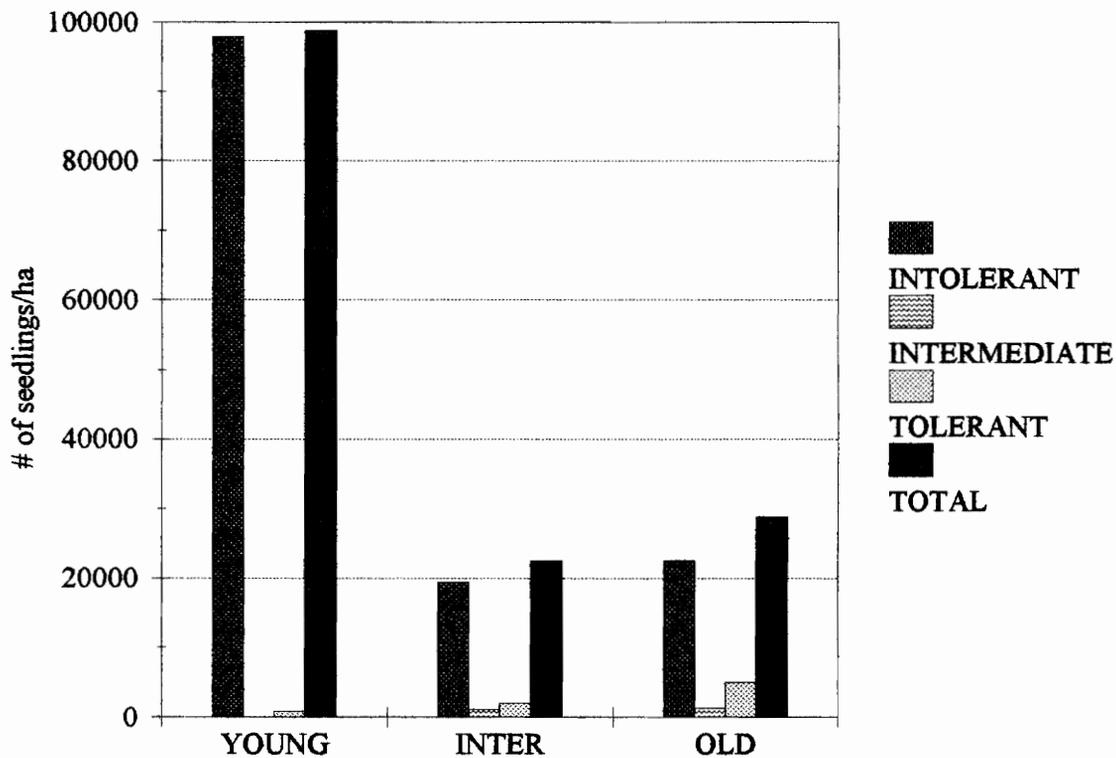


Figure 9. Seedling density per hectare by shade tolerance class in young (0-5 yrs.), intermediate (6-9 yrs.), and old (10-15 yrs.) gaps in the pine cover type at Petersburg National Battlefield, Virginia.

impacted by canopy openings and were most dense where other species cannot compete.

Pine-hardwood Cover Type

The regeneration in the gaps in the pine-hardwood cover type were dominated by loblolly pine and sweetgum seedlings which composed 60% of the total density (Table 25). Tulip poplar, red maple, and scarlet oak were primary associates. The oak component was also substantial, with 8,500 seedlings/ha. Total seedling density of 67,083 seedlings/ha in the gaps was significantly greater than the non-gap areas, with 21,250 seedlings/ha (Table 25). Sweetgum dominated the regeneration of the non-gap areas, with 6,771 seedlings/ha and was the most important species at 23%. Oaks composed 20% of the regeneration. Regeneration of loblolly pine was low with only 5% of the seedling density in the non-gap locations, and was significantly less dense than in the gaps (Table 25). Both the pine and hardwood groups were significantly more dense in the gaps than the non-gap areas in the pine-hardwood cover type (Table 26). Likewise, the hardwood component was significantly more dense than the pine group within both the gap and non-gap locations. Pine regeneration was low, but was still recruited in the gaps of the pine-hardwood cover type, where loblolly pine was the most important seedling species (Table 25). Otherwise, the seedling population appears to be steadily shifting towards the hardwood group. Total seedling density was significantly higher in the gaps than the non-gap areas, by approximately three times (Table 26). As was suggested in the pine cover type, small gaps facilitate the growth of shade intolerant species. Shade intolerant species including, loblolly pine, tulip poplar, and southern red oak were significantly more dense in the gaps than the non-gap areas (Table 25).

All shade tolerance classes were more dense in the gaps compared to the non-gap areas, but only the shade intolerant class was significant, with 55,313 seedlings/ha versus 14,792 (Table 26). Principal component analysis was used to examine the relationships between shade tolerance classes and the environmental data associated with gap and non-

Table 25. Absolute and relative density, relative frequency, and importance values for seedlings in gap and non-gap areas in the pine-hardwood cover type at Petersburg National Battlefield, Virginia.

GAP						
Species	Mean (#/ha)	Std. Dev.	Range	Rel. Freq. (%)	Rel. Den. (%)	Imp. Val. (%)
loblolly pine*	22708	28036	0-81250	11	34	23
sweetgum	17708	24511	0-87500	14	26	20
tulip poplar*	5521	7375	0-25000	11	8	10
red maple*	5521	8798	0-23750	8	8	8
scarlet oak	3333	6853	0-20000	4	5	4
blackgum	2188	3659	0-12500	8	3	5
southern red oak*	2083	2837	0-8750	9	3	6
sassafras	1771	2793	0-7500	8	3	5
downy serviceberry	1458	5052	0-17500	1	2	2
white oak	1354	2162	0-6250	5	2	4
willow oak	1250	1994	0-6250	6	2	4
black oak	521	1245	0-3750	3	1	2
pignut hickory	521	1456	0-5000	3	1	2
mockernut hickory	417	814	0-2500	4	0	2
black cherry	313	777	0-2500	3	0	1
e. hophornbeam	208	722	0-2500	1	0	1
American holly	104	361	0-1250	1	0	1
sourwood	104	361	0-1250	1	0	1
Total*	67083	---	---	100	99	100

NON-GAP						
sweetgum	6771	9675	0-31250	14	32	23
tulip poplar*	1875	4379	0-15000	6	9	7
white oak	1667	2735	0-8750	8	8	8
blackgum	1563	3204	0-11250	8	7	8
red maple*	1458	1909	0-6250	9	7	8
loblolly pine*	1458	3146	0-11250	9	7	8
scarlet oak	1458	2656	0-8750	6	7	6
cherry	1250	2261	0-5000	5	6	5
sassafras	1042	1754	0-5000	6	5	5
willow oak	521	991	0-2500	5	3	4
mockernut hickory	625	1250	0-3750	5	3	4

Table 25. Continued.

NON-GAP						
Species	Mean (#/ha)	Std. Dev.	Range	Rel. Freq. (%)	Rel. Den. (%)	Imp. Val. (%)
sourwood	313	565	0-1250	5	2	4
black cherry	313	560	0-1250	5	2	4
southern red oak*	313	777	0-2500	3	2	3
flowering dogwood	208	487	0-1250	3	1	2
downy serviceberry	104	361	0-1250	1	0	1
black oak	104	361	0-1250	1	0	1
pignut hickory	104	361	0-1250	1	0	1
northern red oak	104	361	0-1250	1	0	1
Total*	21251	---	---	101	101	100

* Mean absolute densities are significantly different between gap and non-gap areas at the 0.05 alpha level.

Table 26. Seedling regeneration by species group and shade tolerance class in gap and non-gap areas in the pine-hardwood cover type at Petersburg National Battlefield, Virginia. Means within a column followed by the same lowercase letter are not significantly different ($\alpha = 0.05$). Means within a row followed by the same uppercase letter are not significantly different ($\alpha = 0.05$). Species in each group are listed in Appendix 1; *P* values are listed in Appendix 2.

Species Group	Gap -----#/ha-----	Non-gap
Pine	22,708 aA	1,458 aB
Hardwood	44,375 bA	19,792 bB
Total	67,083 A	21,250 B

Shade Tolerance Class	Gap -----#/ha-----	Non-gap
Intolerant	55,313 A	14,792 B
Intermediate	5,208 A	4,271 A
Tolerant	5,936 A	1,667 A

gap areas in the pine-hardwood cover type. The first six components explained 83% of the variation within the data matrix (Table 27). Variables with the highest loading defined each component; however, many of the components were defined by more than one variable (Figure 10). No meaningful relationships were found from the distribution of gap and non-gap areas on the first five principal components (Figure 11). This suggests that all of the gap and non-gap areas may not have been distinctly different, although they may have appeared different upon visual inspection and according to the classification criteria set forth.

The BSR did not determine many strong relationships between the density of shade tolerance classes and the PCA results for the pine-hardwood cover type. In order to keep 23 observations in the BSR analysis, surrounding canopy density, or edge trees in the gaps were not included because of missing data for one plot. The size of the gap explained the most variation in the density of the shade intolerant species in the regression model that also included the principal components defined by canopy density and soil C:N ratio, to explain 45% of the observed variation ($P = 0.008$) (Table 28). The regression suggested a positive relationship between intolerant seedling density and each regressor variable. Larger gaps tended to also be the older gaps, which perhaps experienced a more severe disturbance prolonging its closure, such that there was an increase in the number of intolerant seedlings from young to old gaps in the pine-hardwood cover type (Table 2, Figure 12). McClure and Lee (1993) found a high correlation between the density of shade intolerant species and large gaps in a natural disturbance regeneration study located in upper Michigan, as did Runkle (1982). The soil C:N ratio was not significantly different between gap and non-gap areas (Table 6), but was significantly related to the shade intolerant seedling density found in the best regression model (Table 28). This suggests that some species in the class are not only dependent on light for survival, but also on the availability of nutrients, based on the decomposition rate that the soil C:N ratio indexes. For example, loblolly pine may be more of a light demanding species, where it

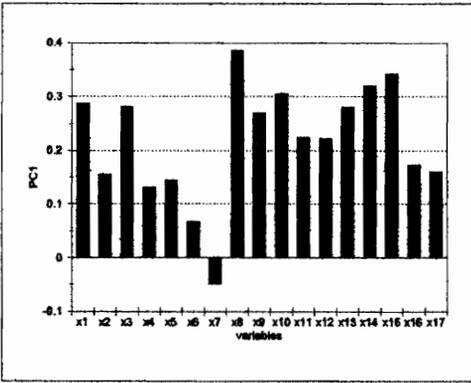
Table 27. Eigenvalues and eigenvectors for the first six principal components of the correlation matrix of environmental data for the pine-hardwood cover type at Petersburg National Battlefield, Virginia.

Variable ¹	Eigenvector				
	1	2	3	4	5
x1	0.29	0.03	0.06	0.21	0.17
x2	0.16	-0.05	0.13	-0.56	-0.34
x3	0.28	-0.06	0.14	-0.26	-0.42
x4	0.13	0.13	-0.59	0.03	0.07
x5	0.14	0.45	0.06	-0.10	0.25
x6	0.07	-0.42	-0.14	-0.14	0.37
x7	-0.05	-0.04	0.58	0.03	0.11
x8	0.39	-0.18	0.03	-0.03	0.17
x9	0.27	-0.45	0.07	-0.01	-0.04
x10	0.31	0.27	-0.06	-0.26	0.20
x11	0.23	0.43	0.12	-0.05	-0.01
x12	0.22	-0.12	-0.34	-0.17	0.12
x13	0.28	-0.22	0.20	0.29	0.25
x14	0.32	-0.03	-0.12	-0.01	-0.23
x15	0.34	0.16	0.22	0.14	0.08
x16	0.17	-0.03	-0.09	0.46	-0.49
x17	0.16	0.14	-0.09	0.36	-0.13
Eigenvalue	5.42	2.57	2.25	1.64	1.10
% of variation	31.9	15.1	13.3	9.7	6.5

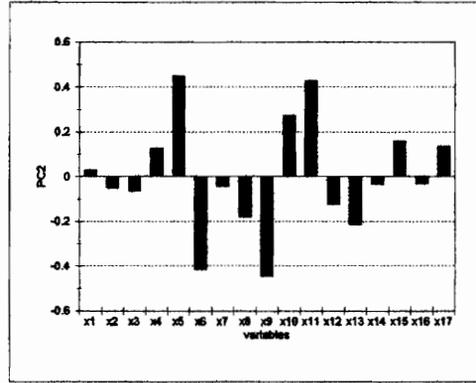
¹x1: bulk density (g/cm³)
x2: A horizon depth (mm)
x3: litter depth (mm)
x4: soil C:N ratio
x5: soil organic matter content (kg/ha)
x6: soil available water (cm)
x7: total soil nitrogen (kg/ha)
x8: available nitrogen index (kg/ha)
x9: soil pH

x10: potassium (kg/ha)
x11: phosphorous (kg/ha)
x12: sulfur (kg/ha)
x13: calcium (kg/ha)
x14: manganese (kg/ha)
x15: magnesium (kg/ha)
x16: LAI (m² m⁻²)
x17: overstory density (%).

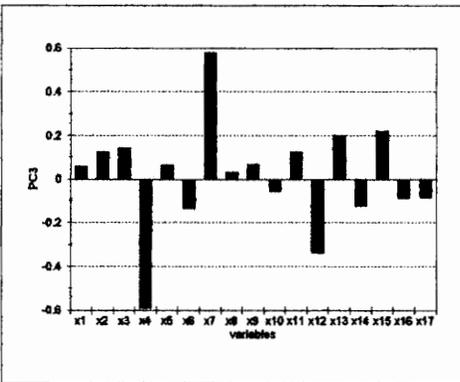
(a)



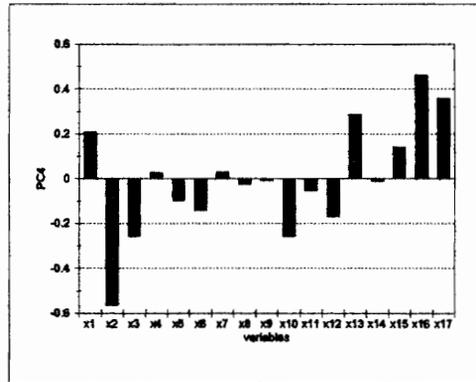
(b)



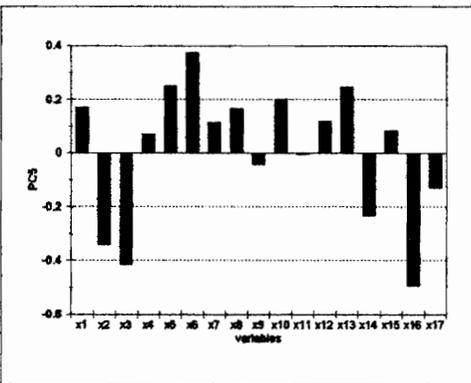
(c)



(d)



(e)



(f)

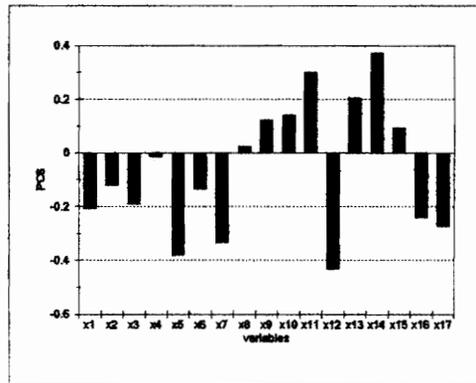


Figure 10. Plot of principal component loadings for the first six principal components of the environmental data for the pine-hardwood cover type at Petersburg National Battlefield, Virginia. (a) component 1; (b) component 2; (c) component 3; (d) component 4; (e) component 5; (f) component 6. Variables are defined in Table 27.

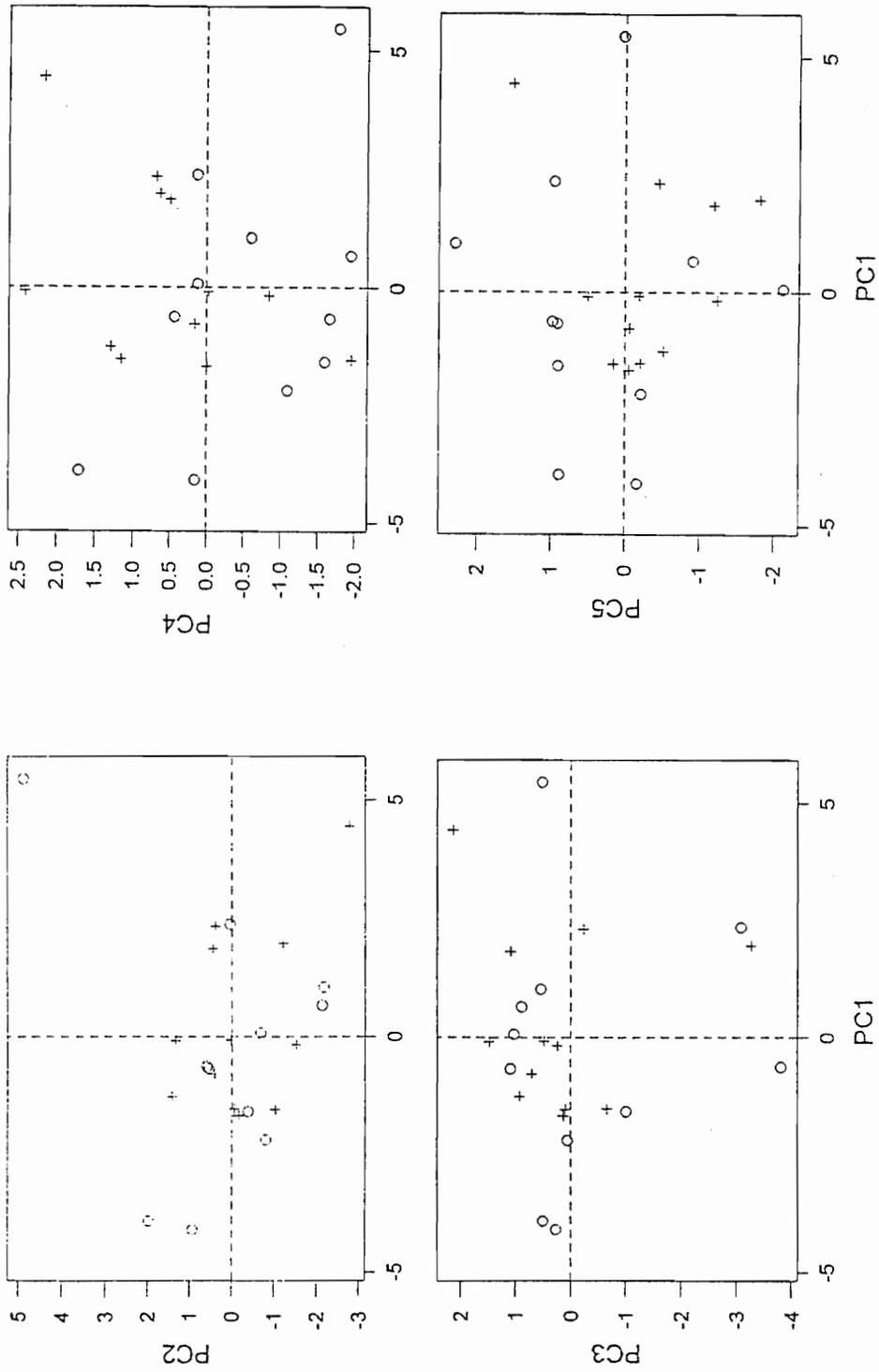


Figure 11. Distribution of gap (O) and non-gap (+) areas on five principal components in the pine-hardwood cover type at Petersburg National Battlefield, Virginia.

Table 28. Set of best regression models describing the relationships between seedling density (seedlings/ha) by shade tolerance classes and environmental variables in the pine-hardwood cover type at Petersburg National Battlefield, Virginia (n=23).

Response Variable	Regression Equation	r²	P	SS
Shade intolerant seedling density	$Y = 4.31 + 0.104 \text{ PC3} + 0.136 \text{ PC5} + 0.198 \text{ size}$	0.45	0.008	4.5
	<i>Portion explained by each variable:</i>			
	gap size	0.18	0.022	0.8
	C:N	0.11	0.057	0.5
	canopy density	0.16	0.085	0.7
Intermediate seedling density	$Y = 3.04 + 0.174 \text{ PC1} + 0.501 \text{ PC5}$	0.21	0.098	46.8
	<i>Portion explained by each variable:</i>			
	canopy density	0.13	0.085	6.1
	mineralizeable nitrogen	0.08	0.177	3.6
Shade tolerant seedling density	$Y = 1.84 - 0.317 \text{ PC1} - 0.711 \text{ PC7} - 0.906 \text{ PC8}$	0.45	0.009	73.7
	<i>Portion explained by each variable:</i>			
	mineralizeable nitrogen	0.16	0.029	12.0
	LAI	0.14	0.039	10.5
	S	0.14	0.039	10.6

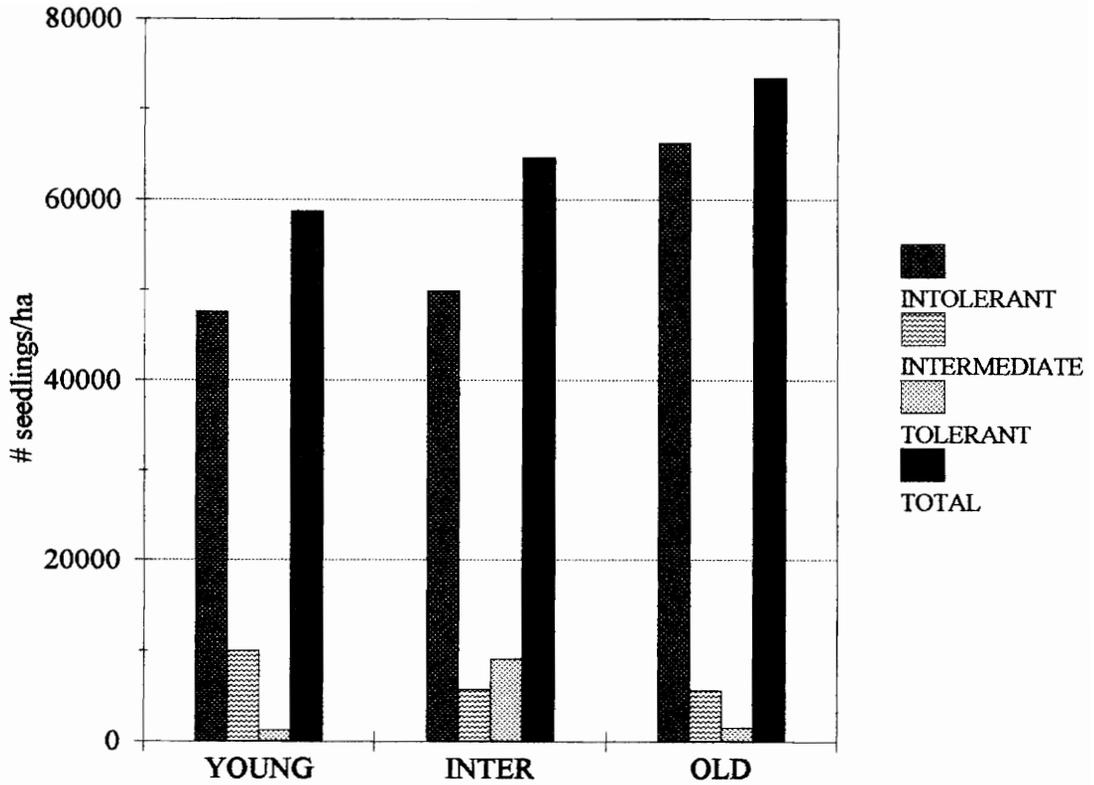


Figure 12. Seedling density per hectare by shade tolerance class in young (0-5 yrs.), intermediate (6-9 yrs.), and old (10-15 yrs.) gaps in the pine-hardwood cover type at Petersburg National Battlefield, Virginia.

thrives in the gaps, compared to sweetgum which is also a shade intolerant species that performs well in areas with lower light and a nutrient rich medium, indexed by the soil C:N ratios like those in the non-gap areas (Tables 25 and 5). Kormanik (1990) commented on the ability of sweetgum to grow under shade in its preferred conditions of moist, alluvial clay.

An extremely weak regression explained the variation of intermediate seedling density. Principal components defined by canopy density and mineralizable nitrogen were the significant regressors in the model ($r^2 = 0.21$, $P = 0.098$) (Table 28). The component defined by light was the most significant regressor, which was significantly higher in the gap areas, explaining the higher seedling density in the gaps (Tables 3 and 26). Mineralizable nitrogen was higher in the non-gap areas, though not significantly, perhaps explaining the large number of intermediate seedlings in the non-gap areas (Tables 6 and 26). Thus, no conclusions can be drawn from this analysis that firmly explains the abundance of intermediate seedling density. This is most likely due to the non-extreme nature of both the disturbances in this cover type, and the species' life history that compose the intermediate class.

A fairly weak regression, including in order of significance, components defined by mineralizable nitrogen, LAI, and soil S, explained 45% of the observed variation in the shade tolerant seedling density ($P = 0.009$) (Table 28). The regression coefficients for each variable in the model were negative, which could be interpreted as: shade tolerant species are associated with lower available nitrogen, soil S, and LAI (which equates to more light). All of these conditions were associated with the non-gap areas (Tables 3 and 6). Available nitrogen was the most significant regressor, where it explained 16% of total variation. Increased light, enhanced the growth of the tolerant seedlings in the gaps, accounting for their high numbers in the gap areas of the pine-hardwood cover type. For example, red maple density was significantly higher in the gaps, perhaps showing higher germination success in those conditions facilitated by the gaps (Table 25). The

macronutrient S is usually not deficient in forest soils, and functions in protein synthesis (Binkley 1986, Binkley and Vitousek 1989, Kramer and Kozlowski 1979). Sulfur was not significantly different between gap and non-gap areas in this cover type (Table 6).

The gaps in the pine-hardwood cover type recruits shade intolerant species, primarily as a function of increased light conditions. Secondary to light, there appears to be an underlying relationship between density of each seedling tolerance class and available nitrogen, which does not appear to be a consequence of gaps in the forest canopy in the pine-hardwood cover type. However, the results suggest the possibility of nitrogen exerting greater influence on regeneration immediately after the death of a canopy dominant.

Hardwood Cover Type

The gaps in the hardwood cover type had prolific and diverse regeneration with nearly 87,000 seedlings/ha, representing 19 different species (Table 29). Oak regeneration was the most abundant in the gaps of the hardwood cover type, with nearly 50,000 seedlings/ha, and white oak dominated with 38,854 seedlings/ha and northern red, willow, and scarlet oak as primary associates in the group (Table 29). Sweetgum was the second most important species, with 18,646 seedlings/ha. Loblolly pine was a minor species, composing only 4% of the regeneration. Total seedling density did not significantly differ between gap and non-gap areas, in fact, the regeneration in the non-gap locations was very similar to that found in the gaps of the hardwood cover type (Tables 20 and 29). White oak also dominated the non-gap locations, with a slightly higher density and greater species importance, 34%, than in the gap areas (Table 29). Sweetgum, red maple, and willow oak followed in kind. Loblolly pine, with an importance value of 5%, was a very minor component, making up only 3% of the regeneration.

No discrimination was found in the densities of either the pine or hardwood groups between the gap and non-gap locations in the hardwood cover type (Table 30). However,

Table 29. Absolute and relative density, relative frequency, and importance values for seedlings in the gap and non-gap areas in the hardwood cover type at Petersburg National Battlefield, Virginia.

GAP						
Species¹	Mean (#/ha)	Std. Dev.	Range	Rel. Freq. (%)	Rel. Den. (%)	Imp. Val. (%)
white oak	38854	63524	0-193750	9	45	27
sweetgum	18646	25285	0-78750	13	22	18
northern red oak	5208	12176	0-38750	5	6	6
red maple	4375	5778	0-17500	9	5	7
willow oak	3854	4781	0-13750	8	4	6
loblolly pine	3646	4781	0-11250	8	4	6
sassafras	2500	6418	0-22500	5	3	4
tulip poplar	1458	2313	0-7500	6	2	4
scarlet oak	1354	4691	0-16250	1	2	2
flowering dogwood	1354	4691	0-16250	1	2	2
blackgum	1146	1550	0-3750	6	1	4
black cherry	833	1539	0-3750	4	1	3
mockernut hickory	625	1460	0-3750	3	1	2
downy serviceberry	521	1456	0-5000	3	1	2
cherry	521	1245	0-3750	3	1	2
pignut hickory	313	565	0-1250	4	0	2
slippery elm	313	1083	0-3750	1	0	1
southern red oak	208	487	0-1250	3	0	1
black oak	208	487	0-1250	3	0	1
sourwood	208	722	0-2500	1	0	1
sweet bay	208	722	0-2500	1	0	1
e. hophornbeam	104	361	0-1250	1	0	1
common persimmon	104	361	0-1250	1	0	1
Total	86561	---	---	100	100	100

NON-GAP						
white oak	40625	66432	0-180000	13	54	34
sweetgum	13750	18640	0-60000	14	18	16
red maple	5521	10122	0-37500	9	7	8
willow oak	2708	5379	0-18750	9	4	6
loblolly pine	2500	5085	0-17500	7	3	5
blackgum	1875	2845	0-10000	10	3	6

Table 29. Continued.

NON-GAP						
Species	Mean (#/ha)	Std. Dev.	Range	Rel. Freq. (%)	Rel. Den. (%)	Imp. Val. (%)
tulip poplar	1667	1794	0-5000	10	2	6
cherry	1667	4036	0-12500	3	2	3
black cherry	1458	3027	0-7500	4	2	3
pignut hickory	729	1881	0-6250	3	1	2
southern red oak	417	814	0-2500	4	1	2
sassafras	417	973	0-2500	3	1	2
scarlet oak	417	1443	0-5000	1	1	1
northern red oak	417	1443	0-5000	1	1	1
mockernut hickory	208	487	0-1250	3	0	2
slippery elm	104	361	0-1250	1	0	1
downy serviceberry	104	361	0-1250	1	0	1
e. hophornbeam	104	361	0-1250	1	0	1
American holly	104	361	0-1250	1	0	1
Total	74792	---	---	98	100	101

¹ There are no statistical differences in mean absolute density between gap and non-gap areas at the 0.05 alpha level.

Table 30. Seedling regeneration by species group and shade tolerance class in gap and non-gap areas in the hardwood cover type at Petersburg National Battlefield, Virginia. Means within a column followed by the same lowercase letter are not significantly different ($\alpha = 0.05$). Means within a row followed by the same uppercase letter are not significantly different ($\alpha = 0.05$). Species in each group are listed in Appendix 1; *P* values are listed in Appendix 2.

Species Group	Gap -----#/ha-----	Non-gap
Pine	3,646 aA	2,500 aA
Hardwood	82,917 bA	72,396 bA
Total	86,563 A	74,896 A

Shade Tolerance Class	Gap -----#/ha-----	Non-gap
Intolerant	34,271 A	25,417 A
Intermediate	46,146 A	43,750 A
Tolerant	6,146 A	5,729 A

the density of the hardwood group was significantly higher than the pine group within each of the gap and non-gap areas. So, the pine group, as supported by these results and classic successional theory, have dropped out of importance in this early sub-climax forest.

The analysis of the seedling density by shade tolerance classes showed no statistical differences in any of the classes between gap and non-gap areas, although the gaps consistently had higher densities of seedlings (Table 30). Analysis by age class showed similar trends as seen in the gaps of the pine-hardwood cover type, where the density of the intolerant and intermediate seedlings was higher in the older gaps (Figure 13). Again, this is attributed to the larger sized gaps that happened to be older (Table 2). Runkle (1982) determined the same relationship of increasing numbers with increasing gap size. McClure and Lee (1993) found a high correlation between presence of intolerant species and large gaps in a natural disturbance regeneration study located in upper Michigan. In addition, gap age was reported as the most important variable explaining the variance in the density of shade tolerance classes (McClure and Lee 1993).

The first five principal components explained 82% of the variation in the environmental data matrix in the hardwood cover type (Table 31). The variable accounting for the most variation within each eigenvector was defined by the highest component loading (Figure 14). Often there was more than one variable defining a particular component, which made interpretation difficult. The distribution of gap and non-gap areas on each principal component proved fruitless, as there were no clear patterns in the data (Figure 15). This suggests that among the environmental data, there were no variables distinctly defining gaps separate from non-gap areas.

Strong regressions were built using the principal component scores, gap size, and surrounding canopy density. In order of significance, litter depth, soil pH, and organic matter content defined the components which explained 60% of the variation in shade intolerant seedling density in the hardwood cover type ($P = 0.000$) (Table 32). It is interesting to note that contrary to what was expected, light was not a significant variable

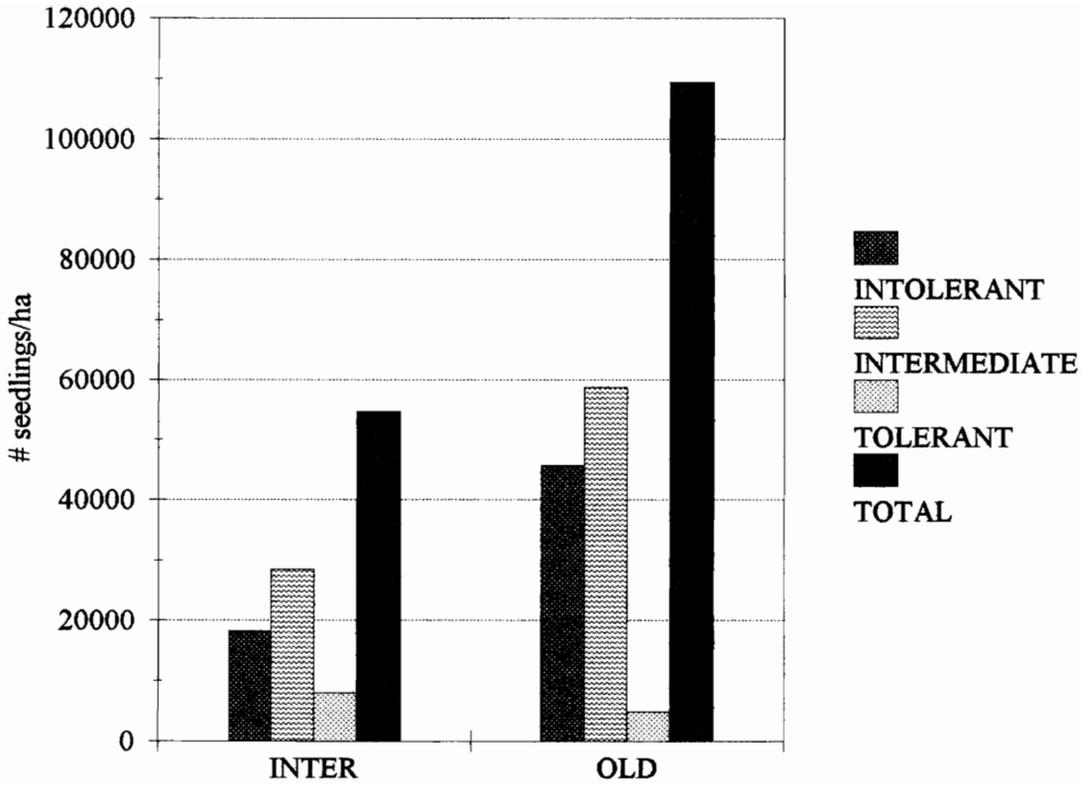


Figure 13. Seedling density per hectare by shade tolerance class in intermediate (6-9 yrs.) and old (10-15 yrs.) gaps in the hardwood cover type at Petersburg National Battlefield, Virginia.

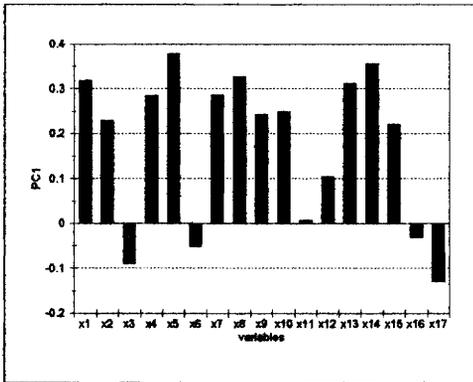
Table 31. Eigenvalues and eigenvectors for the first five principal components of the correlation matrix of environmental data for the hardwood cover type at Petersburg National Battlefield, Virginia.

Variable ¹	Eigenvector				
	1	2	3	4	5
x1	0.32	-0.04	0.13	0.43	-0.07
x2	0.23	0.34	-0.22	0.05	-0.13
x3	-0.09	0.13	0.55	0.08	0.17
x4	0.28	0.22	0.07	0.11	-0.30
x5	0.38	-0.01	0.10	-0.16	-0.29
x6	0.05	0.45	-0.15	0.00	0.25
x7	0.29	-0.22	0.09	-0.36	-0.11
x8	0.33	-0.08	-0.20	-0.30	-0.11
x9	0.24	-0.10	-0.05	0.53	0.18
x10	0.25	0.20	0.35	-0.24	0.06
x11	0.01	0.24	0.49	-0.13	0.10
x12	0.10	0.45	0.09	0.19	-0.13
x13	0.31	-0.18	0.05	0.23	0.35
x14	0.36	-0.12	-0.07	-0.01	0.01
x15	0.22	-0.12	-0.02	-0.16	0.63
x16	-0.03	-0.30	0.38	-0.05	-0.33
x17	-0.13	-0.31	0.17	0.27	-0.07
Eigenvalue	5.68	3.47	2.30	1.46	1.02
% of variation	33.4	20.4	13.5	8.6	6.0

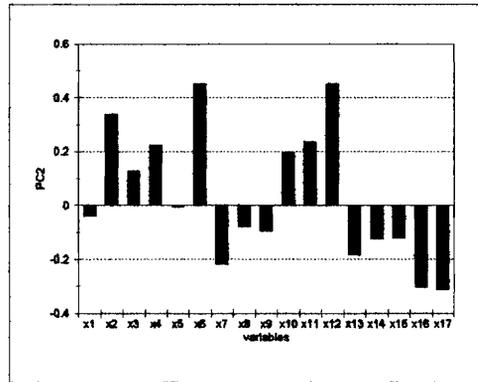
¹x1: bulk density (g/cm³)
x2: A horizon depth (mm)
x3: litter depth (mm)
x4: soil C:N ratio
x5: soil organic matter content (kg/ha)
x6: soil available water (cm)
x7: total soil nitrogen (kg/ha)
x8: available nitrogen index (kg/ha)
x9: soil pH

x10: potassium (kg/ha)
x11: phosphorous (kg/ha)
x12: sulfur (kg/ha)
x13: calcium (kg/ha)
x14: manganese (kg/ha)
x15: magnesium (kg/ha)
x16: LAI (m² m⁻²)
x17: overstory density (%).

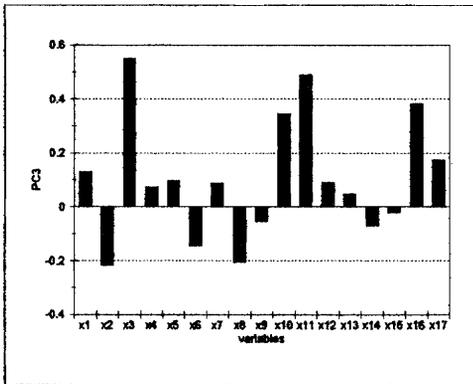
(a)



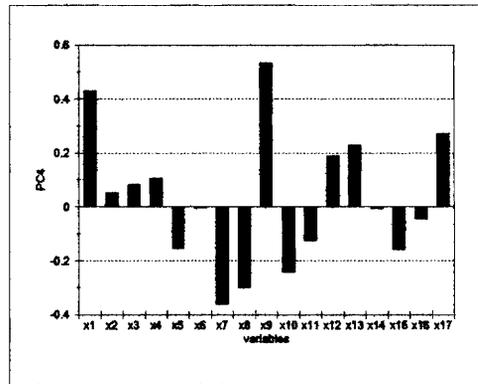
(b)



(c)



(d)



(e)

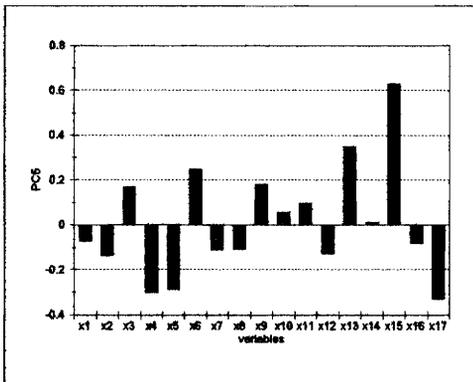


Figure 14. Plot of principal component loadings for the first five principal components of the environmental data for the hardwood cover type at Petersburg National Battlefield, Virginia. (a) component 1; (b) component 2; (c) component 3; (d) component 4; (e) component 5. Variables are defined in Table 31.

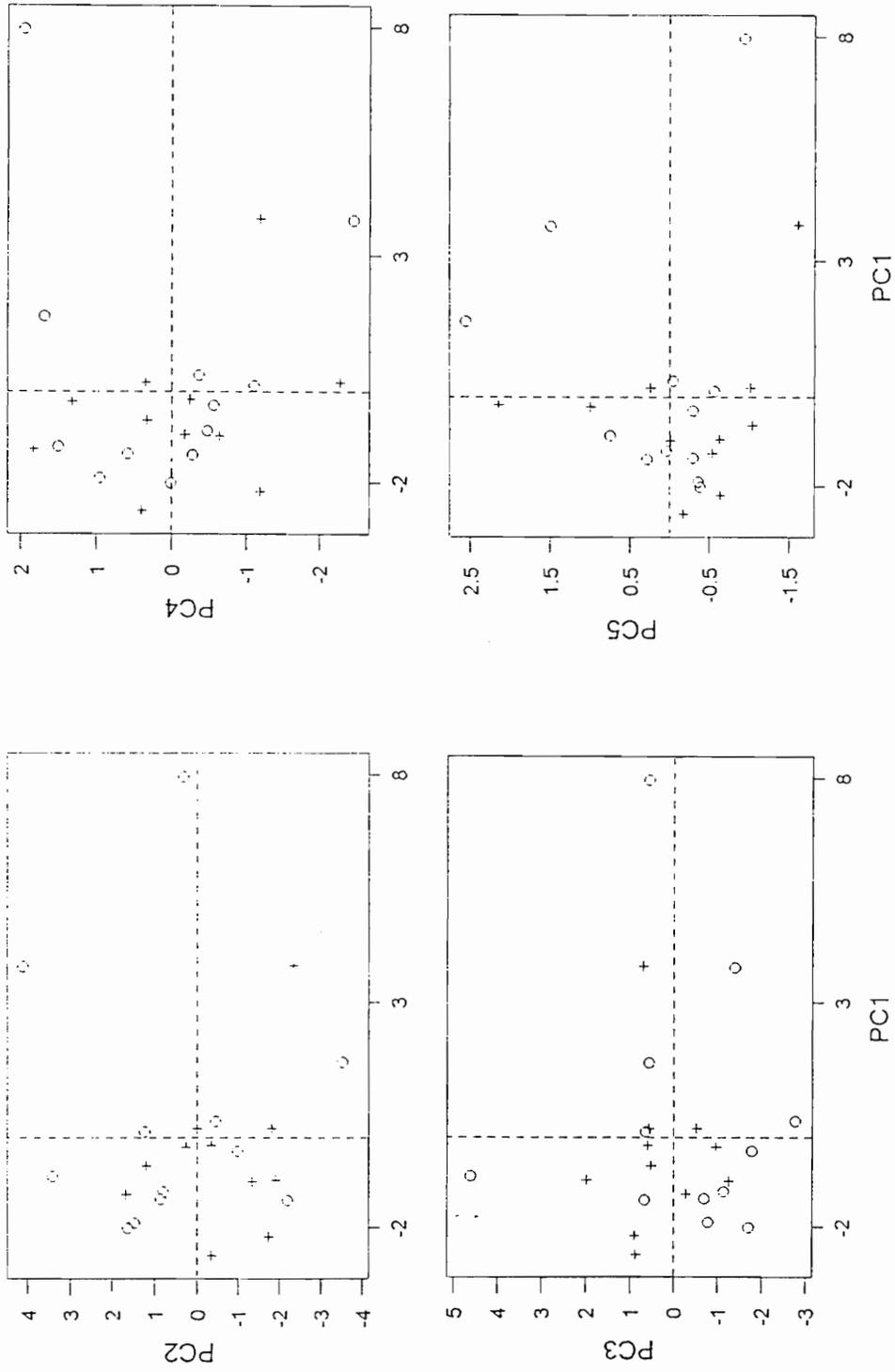


Figure 15. Distribution of gap (O) and non-gap (+) areas on five principal components in the hardwood cover type at Petersburg National Battlefield, Virginia.

Table 32. Set of best regression models describing the relationships between seedling density (seedlings/ha) by shade tolerance class and environmental variables in the hardwood cover type at Petersburg National Battlefield, Virginia (n=23).

Response Variable	Regression Equation	r²	P	SS
Shade intolerant seedling density	Y = 4.38 + 0.03 PC1 - 0.11 PC3 - 0.13 PC4	0.60	0.000	2.0
	<i>Portion explained by each variable:</i>			
	litter depth	0.29	0.001	0.6
	pH	0.25	0.003	0.5
	organic matter	0.06	0.098	0.1
Intermediate seedling density	Y = 3.5 - 0.24 PC1 + 0.49 PC3 + 0.80 PC4	0.48	0.006	84.2
	<i>Portion explained by each variable:</i>			
	pH	0.25	0.007	20.8
	litter depth	0.14	0.034	12.2
	organic matter	0.09	0.095	7.2
Shade tolerant seedling density	Y = 2.43 + 0.82 PC4 + 1.52 PC8 + 0.878 size	0.62	0.000	77.5
	<i>Portion explained by each variable:</i>			
	pH	0.28	0.001	21.7
	K	0.14	0.002	11.2
	gap size	0.20	0.006	15.1

affecting the abundance of intolerant seedlings, but rather litter depth was most significant, and negative. Litter depth was indeed significantly shallower, and the shade intolerant seedlings were more dense in the gaps, and can be interpreted as being a function of a gap formation in the canopy (Tables 4 and 30). Soil pH was highly significant and explained a considerable amount of variation, but was not significantly different between gap and non-gap areas (Tables 32 and 7). As many of the shade intolerant species are adaptive of a range of soil conditions and given this data set has a narrow range of pH values, it is difficult to report definitive conclusions based on this variable. The coefficients in the regression model suggests a negative relationship between soil pH and shade intolerant density, which is plausible for loblolly pine, but more questionable for other shade intolerant species (Table 32). Mladenoff (1987) found a negative relationship between hemlock importance value and pH, which supports the relationship, although hemlock is a shade tolerant species. Primary shade intolerant species in the hardwood cover type included sweetgum, willow oak, loblolly pine, and sassafras, all of which prefer seedbed conditions with shallow litter. In fact, the seedbed conditions were optimum for willow oak regeneration, which are soil pH between 4.5 and 5.5, about a 25 mm litter layer, and high organic matter (Schlaegel 1990).

The same variables significant in the shade intolerant regression model were significant in the best model for intermediate seedlings; however, the regression was much weaker and the order of significance among variables was different ($r^2 = 0.48$, $P = 0.006$) (Table 32). Soil pH was most significant, explaining 25% of the observed variation, followed by litter depth and organic matter. In this model, the regression showed a positive relationship between soil pH and intermediate density, which corresponds with the more basic, nutrient rich soils demanded by many oak species that compose the majority of the intermediate shade tolerance class. This corresponds with the positive signs of the remaining regression coefficients (Table 32).

A strong regression including, in order of percent variation explained, pH, K, and gap

size related the best to shade tolerant seedling density ($r^2 = 0.62$, $P = 0.000$) (Table 32). Soil pH was the most significant variable, explaining 28% of the total observed variation. Again, there was no difference in soil pH or K between gap and non-gap areas (Table 7). The regression indicates positive relationships between all of the regressors and response variables (Table 32). The pH and K trends are difficult to support or refute, given the ubiquitous nature of the shade tolerant species, red maple and American holly. However, the remaining species, flowering dogwood, supports all of the positive relationships through its preference to more basic soils (McLemore 1990). Gap size explained the final 20% of the total observed variation and was also positive (Table 32). This makes sense as shade tolerant species, relative to itself, performs better in conditions associated with gaps than in shady conditions; this is supported by the results of this study where shade tolerant density was higher in the gaps (Table 30) (Canham and Marks 1985).

Thus, unlike the other cover types, light was not a prominent factor related to the abundance of any of the shade tolerance classes; however, this may be a consequence of the older nature of the gaps, where when they were younger, light may have been more of a dominant force. Litter depth and soil pH were the primary factors associated with both shade intolerant and intermediate classes of regeneration. Shade tolerant species appeared to be enhanced by higher soil pH and increased light, similar to what characterized the gaps. Gaps of the sizes found in the hardwood cover type were associated with the trends suggested by the regression analysis.

SUMMARY

Mature forests in the Upper Coastal Plain of Virginia were evaluated to determine the pattern of natural regeneration in pine, pine-hardwood, and hardwood forest cover types. Environmental and vegetative data were collected in small canopy openings (gap) and adjacent forested areas (non-gap) in order to quantify and classify the regeneration in these forest cover types. Small canopy openings were generally created by southern pine beetle infestations in the pine cover type and windthrow from hurricanes or senescence in the hardwood cover type. The mean gap size in these forests was 300 m², and ages ranged from 1 years to 15 years since gap formation.

There were few dramatic differences in environmental variables between the gap and non-gap areas. Generally, there was more light in the gap areas. Forest floor litter depth and vegetative ground cover were similar in all three cover types, but within the pine cover type, litter depth was significantly thinner in the gaps. Few discriminations existed in soil conditions in the pine-hardwood and hardwood cover types. Delineations in the soil conditions between the gap and non-gap areas in the pine cover type were the most discrete. Abundance and composition of regeneration were influenced by a collection of environmental variables. However, it is difficult to clearly state the causal relationships between species composition and any particular environmental variable.

Pine Cover Type

The sapling stratum of the pine cover type was dominated by loblolly pine and red maple in the gap areas, whereas sassafras and sweetgum dominated the non-gap areas. Shade intolerant species and pine density were significantly greater in the gap areas as compared to the non-gap areas. Oak and hickory were among the tallest saplings.

The forest floor conditions created by canopy gaps appeared to facilitate the recruitment of loblolly pine and willow oak in the seedling stratum, where these species

were significantly more dense than the non-gap areas. No statistical differences were found in total seedling density or the density of any of the shade tolerance classes between gap and non-gap areas.

Principal component analysis showed a clear distinction between gap and non-gap areas based on the component defined by the light variable. The best subsets regression analysis determined the density of shade intolerant species to be most related to the component scores defined by canopy density and litter depth ($P = 0.001$, $r^2 = 0.62$). There were no strong relationships determined for the shade intermediate and tolerant classes.

Pine-hardwood Cover Type

The understory of the pine-hardwood cover type was dominated by sweetgum and loblolly pine in the gap areas, and sweetgum and blackgum in the non-gap areas. There were no differences in total sapling density, or any of the sapling shade tolerance class densities between gap and non-gap areas. Oak and sweetgum were the tallest saplings in the understory.

Total seedling density, shade intolerant density, as well as pine and hardwood groups were significantly greater in the gap areas compared to the non-gap areas of this cover type. Loblolly pine dominated the gap areas, where there was no pine regeneration in the adjacent forested areas; sweetgum was prominent in both sites.

There were no meaningful relationships found in the principal components analysis, indicating that the distinctions (over all of the environmental variables) between gap and non-gap areas were indiscernible. The components described by gap size, canopy density, and the soil C:N ratio were found to be significant regressors for the model explaining the density of shade intolerant species ($P = 0.008$; $r^2 = 0.45$). Other shade tolerance regressions were inconclusive.

Hardwood Cover Type

Sweetgum and blackgum dominated both the gap and non-gap understories in the hardwood cover type. Although oak saplings were infrequent, northern red oak was among the tallest saplings in the gap areas, whereas blackgum was the tallest species in the non-gap areas. There were no differences in total or shade tolerance sapling densities, or heights between gap and non-gap areas. Seedling densities followed the same trends as the saplings, where white oak was the dominant species in both areas.

Results from the principal components analysis were unmeaningful, again suggesting vague delineations between gap and non-gap areas. Best subsets regression determined the components defined by litter depth, soil pH, and organic matter for the best model explaining shade intolerant seedling density ($P = 0.000$; $r^2 = 0.60$). In addition, shade tolerant seedling density was best explained by the regression model with the components defined by soil pH, potassium, and gap size ($P = 0.000$; $r^2 = 0.62$).

Small canopy openings in these forests appear to favor the growth of shade intolerant species, primarily as a function of light and the creation of unoccupied growing space. Studies of vegetation dynamics within small gaps that span the entire gap period are needed. The results of this study do not refute, but suggest the possibility of soil chemical properties playing a more regulatory role in species composition than previously believed. A study examining the changes in small gaps immediately after gap formation would be better suited to determine if soil chemical properties have a significant influence on regeneration.

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Appendix 1. Common names of species pine and hardwood groups, and shade tolerance classes (according to Kramer and Kozlowski 1979, Burns and Honkala 1990).

Pine: loblolly pine, eastern red cedar.

Hardwood: willow, northern red, southern red, white, black, scarlet, and water oaks, sassafras, red maple, sourwood, black gum, sweetgum, tulip poplar, American holly, tree-of-heaven, pignut and mockernut hickory, downy serviceberry, sweet bay, flowering dogwood, eastern hophornbeam, slippery elm, and common persimmon.

Intolerant: loblolly pine, tulip poplar, sweetgum, black cherry, pignut and mockernut hickory, willow, water, post and scarlet oaks, sassafras, downy serviceberry, American sycamore.

Intermediate: northern red, southern red, white, and black oaks, white ash, elm, black gum, and sourwood.

Tolerant: red maple, flowering dogwood, American beech, American holly, eastern hophornbeam, and common persimmon.

Appendix 2. *P* values for all paired-*t* test statistical analyses for the pine, pine-hardwood, and hardwood forest cover types at Petersburg National Battlefield, Virginia.

		Pine	Pine- hardwood	Hardwood
Analysis	Table No.	<i>P</i> value	<i>P</i> value	<i>P</i> value
% canopy cover	3a	0.012	0.000	0.008
LAI (m ² m ⁻²)	3b	0.109	0.005	0.032
litter depth (mm)	4	0.029	0.197	0.585
% herbaceous cover	4	0.167	0.123	0.339
% woody cover	4	0.006	0.036	0.060
% total cover	4	0.006	0.006	0.006
available water (cm)	5, 6, 7	0.189	0.522	0.056
A horizon depth (mm)	5, 6, 7	0.111	0.885	0.119
bulk density (g/cm ³)	5, 6, 7	0.251	0.669	0.746
organic matter (kg/ha)	5, 6, 7	0.994	0.668	0.726
pH	5, 6, 7	0.170	0.027	0.163
total soil nitrogen (kg/ha)	5, 6, 7	0.408	0.170	0.903
available nitrogen index (kg/ha)	5, 6, 7	0.777	0.242	0.144
carbon:nitrogen ratio	5, 6, 7	0.067	0.241	0.585
potassium (kg/ha)	5, 6, 7	0.138	0.459	0.900
phosphorous (kg/ha)	5, 6, 7	0.102	0.576	0.212
sulfur (kg/ha)	5, 6, 7	0.025	0.425	0.048
calcium (kg/ha)	5, 6, 7	0.108	0.1924	0.178
manganese (kg/ha)	5, 6, 7	0.903	0.615	0.438
magnesium (kg/ha)	5, 6, 7	0.138	0.762	0.637
loblolly pine saplings (#/ha)	12	0.132	NA	NA
red maple saplings (#/ha)	12	0.064	NA	NA
pine saplings (#/ha)	13, 16, 19	0.174	0.307	0.339
hardwood saplings (#/ha)	13, 16, 19	0.762	0.043	0.881
pine vs. hardwood saplings in gaps (#/ha)	13, 16, 19	0.582	0.195	0.008
pine vs. hardwood saplings in non-gaps (#/ha)	13, 16, 19	0.001	0.000	0.000
shade intolerant saplings (#/ha)	13, 16, 19	0.161	1.000	0.632
shade intermediate saplings (#/ha)	13, 16, 19	1.000	0.235	0.937
shade tolerant saplings (#/ha)	13, 16, 19	0.111	0.420	0.236
total saplings (#/ha)	13, 16, 19	0.349	0.409	1.000

Appendix 2. (continued)

		Pine	Pine- hardwood	Hardwood
Analysis	Table No.	<i>P</i> value	<i>P</i> value	<i>P</i> value
height of pine saplings (m)	14, 17, 20	0.751	NA	NA
height of hardwood saplings (m)	14, 17, 20	0.237	0.061	0.026
height of pine vs. hardwood saplings in gaps (m)	14, 17, 20	0.001	0.000	0.001
height of pine vs. hardwood saplings in non-gaps (m)	14, 17, 20	0.01	NA	NA
height of shade intolerant saplings (m)	14, 17, 20	0.611	0.019	0.334
height of shade intermediate saplings (m)	14, 17, 20	0.494	0.199	0.122
height of shade tolerant saplings (m)	14, 17, 20	0.095	0.067	0.140
loblolly pine seedlings (#/ha)	21, 25	NA	0.025	NA
willow oak seedlings (#/ha)	21	0.034	NA	NA
tulip poplar seedlings (#/ha)	25	NA	0.103	NA
red maple seedlings (#/ha)	25	NA	0.094	NA
southern red oak seedlings (#/ha)	25	NA	0.016	NA
pine seedlings (#/ha)	22, 26, 30	0.175	0.019	0.595
hardwood seedlings (#/ha)	22, 26, 30	0.271	0.011	0.383
pine vs. hardwood seedlings in gaps (#/ha)	22, 26, 30	0.664	0.013	0.005
pine vs. hardwood seedlings in non-gaps (#/ha)	22, 26, 30	0.017	0.000	0.007
shade intolerant seedlings (#/ha)	22, 26, 30	0.145	0.006	0.240
shade intermediate seedlings (#/ha)	22, 26, 30	0.546	0.605	0.729
shade tolerant seedlings (#/ha)	22, 26, 30	0.074	0.118	0.899
total seedlings (#/ha)	22, 26, 30	0.133	0.005	0.263

VITA

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