

POPULATION ECOLOGY OF PINUS FUNGENS
IN PINE-OAK FORESTS OF SOUTHWESTERN VIRGINIA

by

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(ABSTRACT)

I studied aspects of the population ecology of table mountain pine, Pinus pungens, in pine-oak forests on Brush Mountain, Montgomery County, Virginia. The objective of this study was to examine the age structure and recruitment dynamics of P. pungens, a fire-adapted conifer, and to determine whether P. pungens populations would persist in the absence of fire. The age distributions of P. pungens on the Brush Mountain study sites were bimodal, with peaks in seedling and canopy age classes and a major trough in the sapling and understory age classes. Age and diameter of P. pungens understory and canopy trees were positively related, but diameter was a poor predictor of age. The sparse representation of P. pungens in the seedling, sapling, and understory strata of the Brush Mountain sites strongly indicates that under current disturbance regimes, maintenance of P. pungens populations is unlikely. The prevalence of oak advance regeneration and other gap-exploiting woody species such as Sassafras albidum and Nyssa sylvatica suggests that gap replacement processes would favor these species and not P. pungens.

Recruitment of *P. pungens* was not limited by seedfall from serotinous cones or from seed predation by animals. Seedfall occurred throughout the year at low levels and was concentrated in the spring and summer months. The unavailability of seedling habitat strongly limited recruitment of *P. pungens* seedlings. Litter depth and type were important determinants of *P. pungens* seedling habitat; seedlings occurred almost exclusively in shallow pine litter. There was little overlap between the distributions of habitat variables for seedlings and random points in the forest, indicating that suitable seedling habitat was rare. Summer drought and substrate were important factors influencing the establishment and survivorship of seedlings.

Greenhouse studies were conducted to determine the influence of leaf litter and water regime on early establishment of *P. pungens*. Emergence of seedlings was consistently highest in pine litter and lowest in hardwood litter at all water regimes and in litter-free treatments at low watering intervals. Survival of seedlings was enhanced by litter at low water regimes. Significant litter/water interactions indicated that the effects of litter and water regime were not independent; litter significantly decreased the loss of soil moisture from experimental treatments. Evidence suggests that depression of *P. pungens* seedling emergence in hardwood litter was due to physical-mechanical effects.

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to the development and implementation of the greenhouse study reported herein.

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I. INTRODUCTION

Table mountain pine, *Pinus pungens* Lambert, is a conifer endemic to the central and southern Appalachian Mountains of the eastern United States (Zobel 1969). Fire appears to play a major role in the regeneration and maintenance of *P. pungens* (Zobel 1969; Harmon 1982) and McCune (1988) has classified it as a fire-resilient species. *P. pungens* is shade-intolerant and typically bears serotinous cones throughout most of its geographical range (McIntyre 1929; Zobel 1969, 1970; Barden 1979). In the absence of fire, competition with hardwoods, potentially low seed rain, and poor seedbed conditions may limit the ability of *P. pungens* to persist on some sites (Zobel 1969). Fire thus appears not only important but central for the maintenance of this species in parts of the landscape.

Despite the apparent importance of fire in the life history of *P. pungens*, this species may produce self-maintaining, non-successional populations on dry, steep sites (Whittaker 1956; Zobel 1969; Barden 1977, 1988). Such populations appear to persist in the absence of disturbance and have even been classified as topographic or edaphic climaxes (Whittaker 1956). Self-maintenance is unusual among pines of the eastern United States and reports of non-successional pine populations are infrequent (Burns 1983; Stephenson et al. 1986; Bergeron and Gagnon 1987). Typically, pine forests in this region are replaced in time by mixed oak-pine or oak-dominated forest. In most cases, fire or equivalent disturbance is essential for maintenance of

eastern pines (Little and Moore 1949; Crutchfield and Trew 1961; Olson and McAlpine 1973; Stoneburner 1978).

Recent evidence suggests that table mountain pine may be decreasing in importance in portions of its range (White 1987). Altered disturbance regimes, particularly fire suppression practices, have greatly decreased the areal extent of table mountain pine in some parts of the southern Appalachians (Harmon 1982; White 1987). For example, the mean fire interval in the western portion of the Great Smoky Mountains National Park is estimated to have been 12.7 years for the period of 1856 to 1940, but after the Park was founded, estimated fire rotations in pine forests increased to over 2000 years (Harmon 1982). Infrequent fire has also been implicated in the decline of other fire-dependent pines of the eastern United States (e.g., Little 1979; Milne 1985; Myers 1985).

Prior to settlement, forests dominated by table mountain pine were thought to have been restricted to xeric, exposed sites where competition from other trees was minimal (Barden and Woods 1976). Lightning-generated fires probably initiated little pine reproduction owing to their infrequency and lack of intensity (Barden and Woods 1973, 1976). Under drought conditions however, intense, lightning-initiated fires of large areal extent may have facilitated the spread of *P. pungens* into other parts of the landscape. Similarly, greater fire frequency and clearing by humans after settlement probably increased habitat suitable for *P. pungens* regeneration. Thus the areal

decreases in forests dominated by P. pungens observed at present reflect human-induced changes in a system whose spread was also partly anthropogenic.

Little is known about the population ecology of table mountain pine in the southern Appalachians. In particular, information concerning recruitment processes under low disturbance regimes is greatly lacking. Whittaker (1956) suggested that in the absence of fire, gap replacement processes contribute to maintenance of P. pungens populations but to date there are few data to support his hypothesis (e.g., Barden 1988). More recently, Whitney and Johnson (1984) found that reproduction of table mountain pine was apparently stimulated by ice storm damage. Therefore recruitment of P. pungens seedlings under fire-free conditions may be possible at two scales: in small gaps created by the death of a single tree and larger canopy gaps created by ice storms. Finally, evidence suggests that outbreaks of southern pine beetle, Dendroctonus frontalis, may either hasten succession to hardwoods by killing overstory pines, or facilitate pine regeneration through increased fuel loading and the hotter fires that result (Nicholas and White 1984; White 1987). High temperature forest fires favor pines by eliminating hardwood competition (Williamson and Black 1981). Thus one or several factors may limit or contribute to maintenance of P. pungens on a given site under low disturbance regimes.

This dissertation reports studies of the population ecology of *P. pungens* in the forests of southwestern Virginia. The major objective was to examine the prospects for maintenance of table mountain pine populations in the absence of fire or other large-scale disturbance. The chapters that follow comprise three related manuscripts that address specific aspects of the population ecology of *P. pungens* with respect to population maintenance. Chapter III describes the age structure of *P. pungens* populations on the southwestern Virginia study sites and examines the potential for maintenance on these sites. Chapter IV describes the demography of seedling populations on the study sites and examines factors that may limit recruitment of *P. pungens* seedlings under field conditions, particularly seed rain, the availability of safe sites for seed germination and seedling establishment, and the effects of seed predation. Finally, Chapter V describes the results of a greenhouse study designed to examine the effects of litter type and water regime on early establishment of *P. pungens* seedlings.

II. LOCATION AND DESCRIPTION OF STUDY SITES

The study sites were located approximately 2 km NW of Blacksburg, Montgomery County, Virginia (37°11' N; 80°25' W) on Brush Mountain in the Jefferson National Forest. Brush Mountain is in the Ridge and Valley Physiographic Province of the Appalachian Mountains. This province is typified by gently rolling valleys underlain by Cambrian and Ordovician limestones and shales, and high, narrow ridges of Silurian sandstone (Hoffman 1977). Brush Mountain is oriented in a northeast to southwest manner which is typical of ridges in the Ridge and Valley Province. The eastern portion of Brush Mountain near the study sites is bordered on the southeast by Blacksburg and on the northwest by Poverty Hollow. Most of the western portion is contained within the National Forest and studies were restricted to that side of the mountain where *P. pungens* is most abundant. Brush Mountain lies within the Appalachian oak forest type of Kuchler (1964).

Pine forests on Brush Mountain occur primarily on spur-ridges of southwest aspect and form discrete coniferous patches in an oak-hickory forest matrix. *P. pungens* dominates the canopy of the Brush Mountain study sites (Table 2.1). Less important canopy species include pitch pine (*Pinus rigida*), chestnut oak (*Quercus prinus*), scarlet oak (*Q. coccinea*) and red oak (*Q. rubra*). The understory stratum is dominated by black gum (*Nyssa sylvatica*). A well-developed but patchy shrub stratum composed of *Vaccinium* spp., *Gaylussaccia* spp., and *Kalmia latifolia* also occurs on the sites. Detailed descriptions

of the vegetation on the spur-ridges of Brush Mountain can be found in Lipscomb (1986) and in Chapter III.

The soils on the Brush Mountain sites are well-drained, shallow, and of the Berks and Weikert series (Creggar et al. 1985). Berks and Weikert soils are typically low in nutrients and organic matter, have a high permeability and low available water capacity, and are strongly acid (Creggar et al. 1985). See Feret et al. (1979) for a general description of the nutrient content of soils that support pine-oak forests on Brush Mountain.

The disturbance history of Brush Mountain is poorly documented. Although Brush Mountain was acquired by the Forest Service in the 1920's, fire records for the area are only available from the 1960's to the present (E. Leonard, USFS, Blacksburg District, pers. comm.). Fire-scarred trees and the presence of charcoal in spur-ridge soils indicates a past history of fires, but there is no evidence of recent fires on the study sites nor have fires occurred to any appreciable extent in any of the Brush Mountain pine forests since the 1960's (E. Leonard, pers. comm.). Clearcut logging and fuelwood cutting occur to varying degrees on Brush Mountain but the study sites show no evidence of recent cutting. The steep slopes of spur-ridges greatly limit access and the use of most logging equipment, and the sites are classified as unsuitable for timber production by the Forest Service (E. Leonard, pers. comm.).

Portions of the Ridge and Valley Province in southwestern Virginia are heavily grazed by cattle and sheep, but it appears unlikely that the Brush Mountain sites were grazed to any great extent in the past. The Berks and Weikert soils are extremely poor for growth of pasture grasses (Creggar et al. 1985) and the sites are steep and subject to substantial erosion if grazed. Neither pasture grasses nor evidence of livestock trails or related erosion occur on the Brush Mountain spur-ridges. Moreover, the absence of pasture and agricultural weeds in soil seed pool samples on Brush Mountain spur-ridges further suggests little or no past grazing pressure on these sites (P. Schiffman, pers. comm.). In contrast, the southeastern side of Brush Mountain, which is mostly in private ownership, is frequently grazed. Pasture grasses grow well on the Groseclose soils of the eastern side (Creggar et al. 1985) and the more moderate slopes are less susceptible to erosion.

Table 2.1. Characteristics for the three *Pinus pungens* study sites on Brush Mt., Montgomery County, Virginia (TMP = *P. pungens*).

Site	Elevation (m)	Aspect	Stand basal area (m ² /ha)	TMP basal area (%)	Can- opy cover (%)	Ground cover (%)	Slope
1	740	235°	25.6	70	78.1	32.2	26°
2	750	245°	29.0	81	75.2	40.5	26°
3	765	250°	29.5	76	80.9	37.9	27°

III. AGE STRUCTURE AND THE MAINTENANCE OF PINUS PUNGENS POPULATIONS ON BRUSH MOUNTAIN, MONTGOMERY COUNTY, VIRGINIA

III.1 Introduction

Age structure can provide important information about the potential stability of a population over time. In forest trees, three distinct types of age distributions are recognized (Leak 1975): a linear relationship of stems vs. age indicative of a stationary population of a long-lived species (Hett 1971); a concave or negative exponential age distribution characteristic of an increasing or self-maintaining population (Parker and Peet 1984; Parker 1986; Holla and Knowles 1988); and a convex or bell-shaped distribution representative of a declining population with low recruitment (e.g., Auclair and Cottam 1971). Disturbance-dependent, shade-intolerant trees such as pines typically exhibit the last form of age distribution. Often the age structure of a disturbance-dependent conifer is bimodal or polymodal, reflecting pulses of recruitment associated with fire, land abandonment or other large-scale disturbance (e.g., Christensen and Peet 1984; Clark 1986).

Maintenance of fire-dependent conifers is unusual in the absence of fire and is often associated with peculiar edaphic or climatic factors that reduce competition from more shade-tolerant, late-successional trees (Barden 1977, 1988; Despain 1983; Parker 1986; Bergeron and Gagnon 1987). Whittaker (1956) and others (Zobel 1969; Barden 1977, 1988) have suggested that some populations of table mountain pine, Pinus pungens, a shade-intolerant, serotinous species

endemic to the Appalachian Mountains, are capable of maintenance in the absence of exogenous disturbance. Xeric rock outcrops appear to be the most likely sites on which populations of *P. pungens* may persist (Zobel 1969; Barden 1977, 1988) although Whittaker (1956) suggested that maintenance of *P. pungens* is also possible in pine-oak forests by gap-replacement processes.

Stands of *P. pungens* on steep ridges in the southern Appalachians often occur as physiognomically distinct patches in a matrix of hardwoods (White 1987). This repeating pattern is well-developed on the southwest slopes of spur-ridges (secondary ridges) of Brush Mountain in Montgomery County, Virginia. Stands of *P. pungens* on Brush Mountain are juxtaposed with oak-dominated, northeast-facing slopes for many kilometers along major ridges. This pattern suggests the topographic or edaphic climax that Whittaker (1956) envisioned for *P. pungens* on dry sites.

This study examines the hypothesis that *P. pungens* populations occurring on Brush Mountain are self-maintaining. If *P. pungens* populations are self-maintaining on these sites, then population age distributions should depict a negative exponential decline of stems with age or show other evidence that recruitment is occurring. Underrepresentation of young age classes in age distributions of forest trees typically indicates inability for replacement (Harcombe and Marks 1978). Therefore, the self-maintenance hypothesis was tested by examining the age distributions of *P. pungens* populations.

Additionally, the composition and structure of woody vegetation growing with *P. pungens* populations was determined in order to predict potential changes in forest composition if the hypothesis of self-maintenance is rejected.

III.2 Materials and methods

III.2.1 Vegetation

A 0.25 ha study area, divided into 25 contiguous 10 X 10 m plots, was established on each of the three Brush Mountain study sites. Species and diameter of large (stems \geq 10 cm dbh) and small trees (stems \geq 2.5 cm but $<$ 10 cm dbh) were recorded for all plots. Tree saplings (stems $<$ 2.5 cm dbh and $>$ 1.0 m in height) and seedlings (stems \leq 1.0 m in height) were sampled in 2 X 2 m plots, one of which was located randomly in each 10 X 10 m plot. No attempt was made to determine whether seedlings were of sprout or seed origin. Ground cover was estimated visually within each seedling/sapling plot and overstory density was estimated at the center of each 10 X 10 m plot with a spherical densiometer (Lemmon 1956, 1957).

Density (number of stems/ha), basal area (m^2/ha), and frequency (percent occurrence in plots) were determined for small and large trees. To describe the relative importance of small and large trees in the study sites, importance values (relative density + relative basal area + relative frequency) were calculated for each species (Curtis and McIntosh 1951) and are presented as average percentages of the total. Importance values for tree saplings and seedlings were

calculated as average percentages of relative densities and frequencies (Adams and Stephenson 1983).

III.2.2 Age determination of P. pungens

An increment core was taken from the base (ca. 40-50 cm above ground) of each P. pungens tree large enough to core (stems > 2.5 cm dbh). Ages of seedlings and most saplings were determined by counting terminal bud scars in the field with the aid of a 10 X hand lens (see Chapter IV). Saplings that could not be aged by bud scars were cored with a micro-borer similar to that described by Sharik et al. (1983).

Increment cores were dried and mounted in wooden channels, and an X-acto wood chisel was used to expose a flat, smooth surface on each core to facilitate age determination. Annual rings were counted under a binocular dissecting microscope, and for those cores lacking a central pith the number of missing growth rings was estimated by the curvature of adjacent rings (Arno and Sneek 1977). Increment cores having decayed centers (n = 12) were eliminated from analysis.

The relationship between age and diameter of P. pungens trees (\geq 2.5 cm dbh) on each site was examined by regression analysis. Because the slopes of the age-diameter regressions did not differ significantly among study sites (analysis of covariance, $P > 0.05$), the data were pooled for analysis.

III.3 Results

III.3.1 Vegetation

Nine species were found in the large tree stratum of the three sites (Table 3.1). Based on importance values, *P. pungens* dominated the large tree stratum of each site (Table 3.1). Chestnut oak, *Quercus prinus*, was second in importance in each stand. Three other oak species were recorded from the large tree strata: scarlet oak (*Q. coccinea*), black oak (*Q. velutina*), and red oak (*Q. rubra*), but these species were considerably less important than *Q. prinus*. Pitch pine, *P. rigida*, occurred at low levels in the three stands. The remaining species, *Nyssa sylvatica*, *Acer rubrum*, and *Robinia pseudoacacia*, were of little importance in the large tree stratum. These species rarely achieve canopy status in dry pine-oak forests (Ross et al. 1982).

Sixteen woody species were recorded from the small tree strata of the three stands, and except for oaks, few species common in this stratum were also present in the large tree stratum (Table 3.2). For example, black gum, *Nyssa sylvatica*, was the dominant small tree on the Brush Mountain sites. *N. sylvatica* is a ubiquitous, long-lived species that often dominates the subcanopy of dry pine-oak forests in the southern Appalachians (Ross et al. 1982). Oaks, particularly *Q. prinus* and *Q. coccinea*, constituted an important component of the small tree stratum on each site. Most notably, *P. pungens* was considerably less important in the small tree stratum than in the canopy and varied in importance among the three sites.

The seedling and sapling strata of the study sites contained thirteen species (Table 3.3), and were strongly dominated by *Nyssa*

sylvatica and Sassafras albidum. S. albidum was the most important seedling species but was not particularly common as a sapling, whereas N. sylvatica was the dominant sapling species and was less common as a seedling. Both Nyssa and Sassafras sprout prolifically in dry pine-oak forests and function as dominants in the shrub layer (Ross et al. 1982). Oaks, and sprouts of American chestnut, Castanea dentata, were important components of the sapling and seedling strata of the study sites. Most oaks also appeared to be of sprout origin. Seedlings and saplings of P. pungens were uncommon.

Diameter distributions for Q. prinus and Q. coccinea were unimodal with peaks in the smallest diameter classes (Figs. 3.1 - 3.2). The diameter distributions for both oaks were skewed toward the larger size classes. In contrast, diameter distributions for P. pungens were bimodal (Fig. 3.3). Major peaks were in the 5 and 20 cm diameter classes. Q. prinus had the largest number of stems in the smallest age class (ranging from 648 - 1764 stems/ha) followed by P. pungens (200 - 296 stems/ha) and Q. coccinea (72 - 104 stems/ha). P. pungens dominated all diameter classes above 15 cm.

III.3.2 Age structure of P. pungens populations

The age distribution of P. pungens on all three study sites was bimodal with peaks in the seedling and canopy age classes (Figs. 3.4 - 3.6). Major peaks occurred in the 45 and 50 year age classes for site 1, the 75 year age class for site 2, and the 80 year age class for site 3. Secondary peaks occurred in the 10 year age class for all

sites. A major trough occurred in the 20 to 35 year age classes, the age range which corresponds to the sapling and small tree strata.

Mean stem ages among sites were similar in the seedling/sapling and small tree strata but differed in the large tree layer (Table 3.4). Large trees on site 1 were younger (avg. 56.1 years) than either site 2 (avg. 74.5 years) or site 3 (avg. 69.7 years). Estimates of stem ages ranged from 1 to 124 years for sites 1 and 3, and from 1 to 104 years for site 2.

Age and diameter of *P. pungens* stems (> 2.5 cm dbh) were positively related ($P < 0.0001$) but diameter was a moderate predictor of age (Fig. 3.7). The r^2 for the composite data was 0.45.

III.4 Discussion

The bimodal age distributions indicate that *P. pungens* populations on the Brush Mountain study sites are not self-maintaining. Seedlings and large trees on these sites can be viewed as two unimodal subpopulations linked by a small tree component in which recruitment to and from is strongly limited. Low recruitment into the small tree age classes may be due to several factors including low survival of seedlings, inadequate seed rain, and limited microsites for seedling establishment (see Chapter IV). In addition, low survivorship and suppression of small trees may limit recruitment into the large tree stratum. Suppression may explain the weak association between age and diameter observed in the study sites.

Whittaker (1956) hypothesized that gap-phase replacement may function in the maintenance of *P. pungens* populations in the absence of fire. Gaps produced by the death of a canopy tree may either be colonized by seedlings dispersed into the gap as seeds or by the release of established seedlings in the vicinity of the gap. For several reasons, neither is likely on the Brush Mountain sites.

First, adequate conditions for seedling establishment must occur within canopy gaps. Establishment of *P. pungens* seedlings on the Brush Mountain is strongly limited by microsite availability (Chapter IV). Thus the probability that suitable seedling habitat may exist within a gap is small. Second, *P. pungens* seedlings and understory trees established under the forest canopy typically grow poorly due to suppression. Release of suppressed age classes of yellow pines is often unsuccessful (Little and Somes 1964), and regeneration from suppressed seedlings and saplings may be limited. Finally, the prevalence of advance regeneration of oaks and other gap-exploiting woody species (e.g., *Sassafras* and *Nyssa*) suggests that these species and not *P. pungens* would quickly dominate new canopy gaps (Hewlette 1977; Ross et al. 1982).

Gap replacement by *P. pungens*, although unlikely on the Brush Mountain sites, may be important in the maintenance of populations on more xeric sites. Barden (1977, 1988) has documented a self-maintaining *P. pungens* population in the Blue Ridge of North Carolina that exhibits a polymodal age structure. Pulses of recruitment in this

population correlate with climatic conditions favorable for seedling establishment. Recruitment of P. pungens in xeric pine forests of the Ridge and Valley Province in southwestern Virginia may also be facilitated by ice storms. Reproduction of pines, including P. pungens, was apparently stimulated after damage to the forest canopy by an ice storm (Whitney and Johnson 1984). Damage by ice storms is usually localized and dependent upon topography and microclimate (Boerner et al. 1988), thus canopy removal by ice storms does not appear to be as frequent an event in the life of a P. pungens population as the death of a canopy tree.

The spread of P. pungens populations in the southern Appalachians has been attributed to human disturbance, particularly clearing and fires (Harmon 1982; White 1987). Sargent (1884) mentions that in 1880, the forest cover of inaccessible ridges in southwestern Virginia was extensive. However, by the turn of the century, much of the southern Appalachian Mountains had been logged to varied degrees (Wilson 1902). The age structure of P. pungens populations of Brush Mountain indicate that they also had their origin during the early portion of this century.

Peaks in the 75 and 80 year age classes of pines on sites 2 and 3 suggest a pulse of recruitment during the early 1900's. The oldest P. pungens trees on these sites today are over 120 years of age and would have been of seed-bearing age at or before the turn of the century. "Seed trees", particularly pines, are often left standing in

pine-oak clearcuts in southwestern Virginia even at present (e.g., Conner et al. 1979). Thus it is reasonable to assume that the oldest P. pungens trees on the study sites may have been left by loggers because of poor form and (or) low value (Wilson 1902; Frothingham 1931; Smith and Linnartz 1980). If logging slash were burned, seedbed conditions and copious seedfall from seed trees would facilitate P. pungens regeneration. McIntyre (1929) stated that P. pungens was a silvicultural problem in parts of Pennsylvania where it quickly colonized logged areas and excluded more valuable species. Rapid regeneration of P. pungens on the dry, southwest slopes of Brush Mountain spur-ridges was probably made possible by fire and the generally poor growing conditions for hardwoods on these sites. Regeneration of hardwoods in Appalachian pine-oak forests on dry, exposed sites following fire is considerably slower than pines (pers. obs.).

Population genetics studies of P. pungens in southwestern Virginia provide support for the "seed tree regeneration hypothesis". Feret (1974) found significant differences in isozyme frequencies and morphological characteristics among three P. pungens populations in southwestern Virginia. He hypothesized that observed differences among the stands may be due to a founder effect caused by the colonization of sites by progeny from a few seed trees.

In the absence of fire, P. pungens should decline in importance in the pine-oak forests of Brush Mountain. Abundant advance

regeneration and the importance of oaks in the overstory suggest that future forests will be dominated primarily by chestnut and scarlet oaks, common climax species on dry sites in the southern Appalachians (Smith and Linnartz 1980). However, because longevity in *P. pungens* approaches 200 years (Zobel 1969), this species will likely continue to be a component of these forests for some time.

Table 3.1. Importance values (scaled to total 100.0) of large trees (stems \geq 10 cm dbh) on the Brush Mt. study sites.

<u>Species</u>	<u>Site 1</u>	<u>Site 2</u>	<u>Site 3</u>
<u>Pinus pungens</u>	59.58	74.61	63.40
<u>P. rigida</u>	5.06	2.34	2.36
<u>Quercus prinus</u>	25.80	18.55	20.90
<u>Q. coccinea</u>	7.25	2.42	7.18
<u>Q. velutina</u>	1.59	1.05	4.76
<u>Q. rubra</u>	--	--	0.69
<u>Nyssa sylvatica</u>	0.72	--	--
<u>Acer rubrum</u>	--	1.04	--
<u>Robinia pseudoacacia</u>	--	--	0.72

Table 3.2. Importance values (scaled to total 100.0) of small trees (stems \geq 2.5 cm dbh but $<$ 10 cm dbh) on the Brush Mt. study sites.

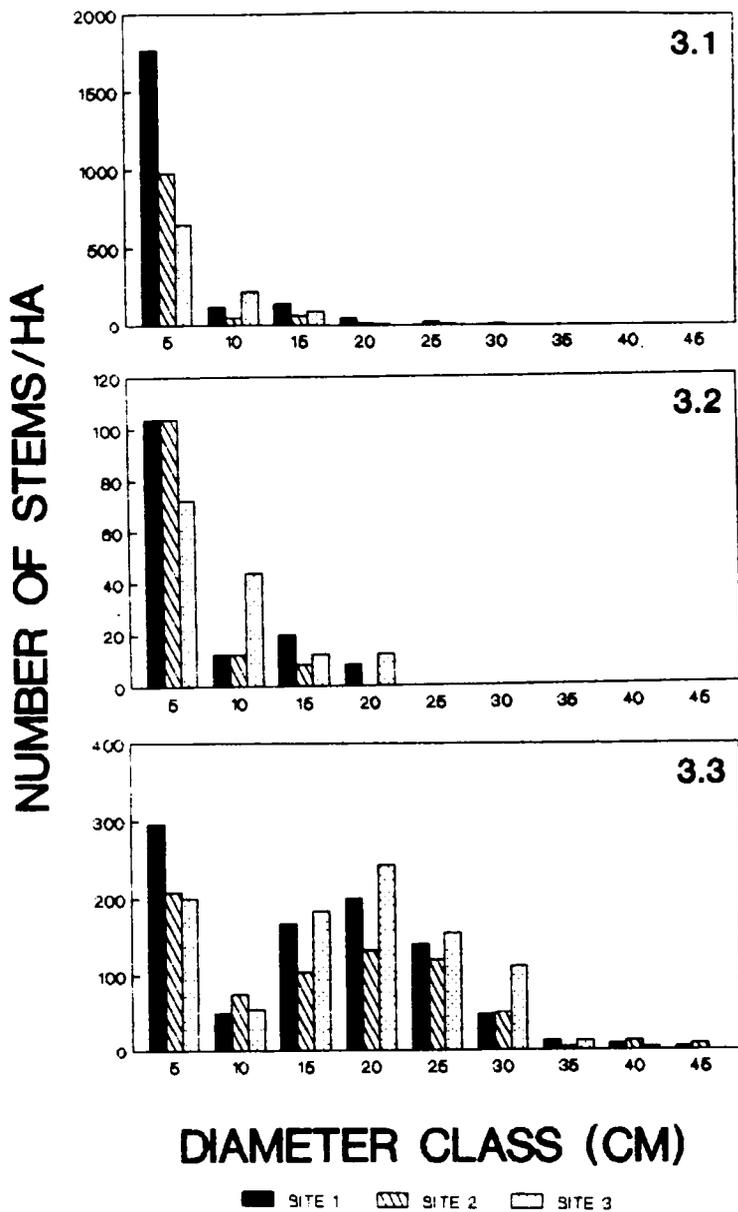
<u>Species</u>	<u>Site 1</u>	<u>Site 2</u>	<u>Site 3</u>
<u>Nyssa sylvatica</u>	46.53	36.80	22.47
<u>Quercus prinus</u>	16.07	13.20	19.02
<u>Q. coccinea</u>	9.77	12.30	7.17
<u>Q. velutina</u>	2.73	2.80	3.31
<u>Q. rubra</u>	--	--	2.00
<u>Q. alba</u>	0.72	3.90	0.59
<u>Castanea dentata</u>	7.20	10.60	4.63
<u>Pinus pungens</u>	10.17	2.50	8.49
<u>P. rigida</u>	0.80	--	0.89
<u>Carya tomentosa</u>	--	0.57	--
<u>Sassafras albidum</u>	--	1.03	--
<u>Acer rubrum</u>	4.00	15.40	24.94
<u>A. pensylvanicum</u>	0.80	--	--
<u>Amelanchier arborea</u>	0.63	0.93	3.90
<u>Robinea pseudoacacia</u>	0.66	--	2.17
<u>Cornus florida</u>	--	--	0.45

Table 3.3. Importance values (scaled to total 100.0) of sapling (sap) (stems < 2.5 cm dbh and > 1 m but < 2 m in height) and seedling (seed) (stems < 1 m in height) species on the Brush Mt. study sites.

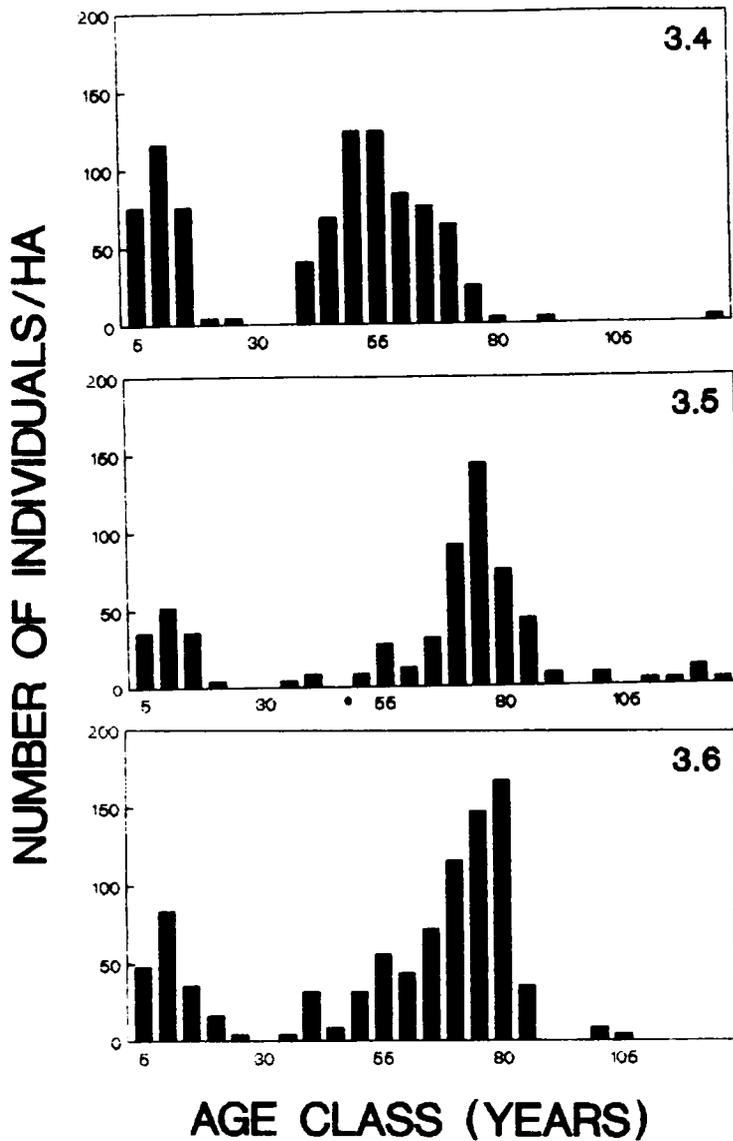
<u>Species</u>	<u>Site 1</u>		<u>Site 2</u>		<u>Site 3</u>	
	<u>seed</u>	<u>sap</u>	<u>seed</u>	<u>sap</u>	<u>seed</u>	<u>sap</u>
<u>Nyssa sylvatica</u>	14.33	73.60	2.23	31.28	4.85	36.81
<u>Quercus prinus</u>	11.10	--	15.24	5.22	5.96	3.36
<u>Q. rubra</u>	14.87	11.20	14.30	5.22	17.98	10.06
<u>Q. alba</u>	--	--	--	--	2.63	6.70
<u>Q. marilandica</u>	--	--	--	--	2.63	--
<u>Castanea dentata</u>	--	9.20	9.85	35.78	7.88	16.76
<u>Sassafras albidum</u>	46.18	3.10	29.80	12.03	29.19	--
<u>Acer rubrum</u>	7.58	--	17.80	5.22	10.51	10.06
<u>A. pensylvanicum</u>	--	3.10	--	--	2.63	--
<u>Pinus pungens</u>	3.79	--	3.17	--	13.13	6.21
<u>Amelanchier arborea</u>	1.08	--	5.40	--	--	6.70
<u>Carva tomentosa</u>	--	--	2.23	--	--	--
<u>Robinea pseudoacacia</u>	--	--	--	5.22	2.63	3.36

Table 3.4. Mean ages in years of seedling/saplings (seed/sap), understory and canopy Pinus pungens by site (as of March 1989). Mean age by site and grand mean by stratum are also presented.

<u>Site</u>	<u>seed/sap</u>	<u>small trees</u>	<u>large trees</u>	<u>total</u>
1	8.4 (n = 64)	41.1 (n = 15)	56.1 (n = 139)	35.2
2	7.9 (n = 32)	46.5 (n = 6)	74.5 (n = 115)	43.0
3	7.8 (n = 40)	43.7 (n = 15)	69.7 (n = 166)	40.4
Grand Mean	8.0	43.8	66.8	



Figures 3.1 - 3.3. Diameter distributions of major tree species on the Brush Mountain study sites. 3.1 - *Quercus prinus*. 3.2 - *Q. coccinea*. 3.3 - *Pinus pungens*. Note: Y-axis scales differ.



Figures 3.4 - 3.6. Age distributions of *Pinus pungens* populations/ha on Brush Mountain, Montgomery Co, Virginia as of March 1989. Fig. 3.1 - Site. Fig. 3.2 - Site 2. Fig. 3.3 - Site 3.

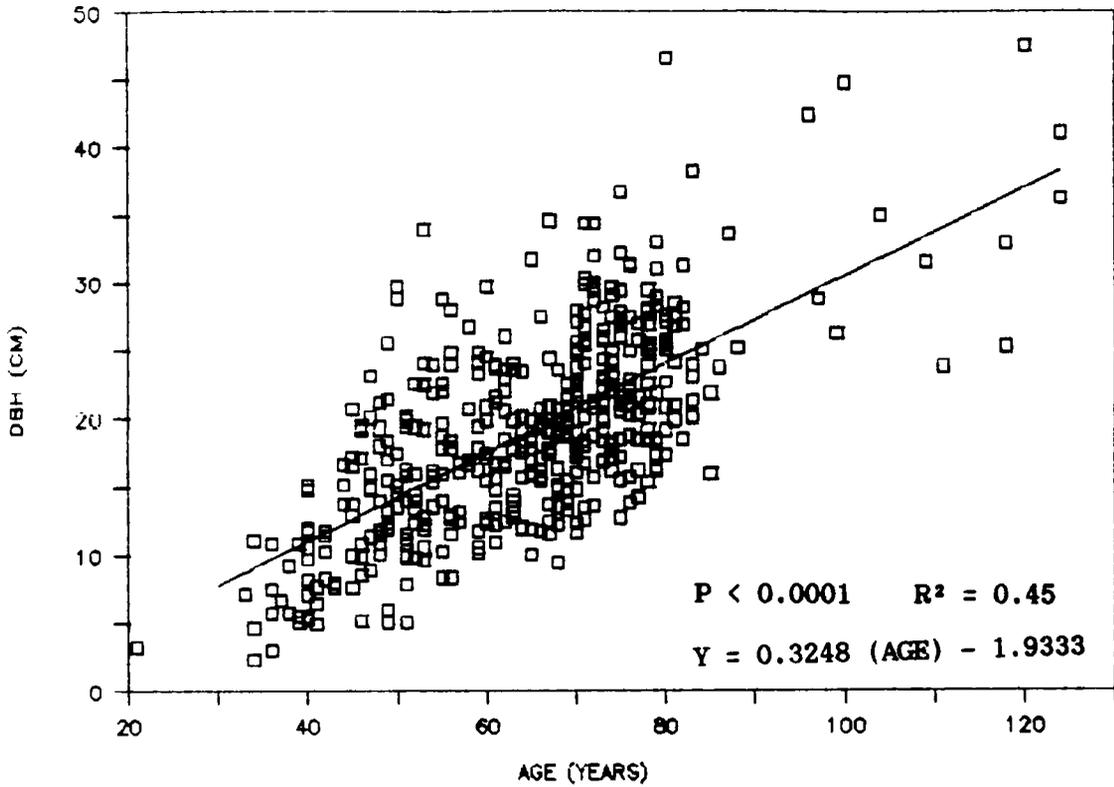


Figure 3.7. Composite age-diameter relations for *Pinus pungens* trees (> 2.5 cm dbh) on Brush Mountain, Montgomery Co., Virginia.

IV. FACTORS AFFECTING RECRUITMENT OF SEEDLINGS OF PINUS PUNGENS IN PINE-OAK FORESTS OF SOUTHWESTERN VIRGINIA

IV.1 INTRODUCTION

The maintenance of a plant population ultimately depends on the successful recruitment of seedlings (Harper 1977). Seedling recruitment may be limited by several factors including adequate seed dispersal (Johnson et al. 1981; McClanahan 1986), seed predation by animals (Gashwiler 1967, 1970; Johnson and Webb 1989), abiotic stresses such as drought (Hough 1937; Wood 1938), and availability of suitable microsites for seed germination and seedling establishment (Fowler 1986).

Seedling establishment and recruitment in yellow pines [subgenus Pinus (Little and Critchfield 1969)] of the eastern United States is usually associated with disturbance, particularly fire. Post-fire conditions generally favor pine regeneration; exposed mineral soil and lack of competition from other plants provide an optimal environment for seedling establishment (Fowells 1965). In closed-cone or serotinous pines of the eastern U.S., such as pitch (P. rigida), table mountain (P. pungens), and pond (P. serotina) pines, regeneration from seed may require fire as a stimulus for cone opening. Thus, serotinous pines may face two major limits to regeneration under low fire regimes: lack of suitable seedling habitat and limited release of seeds.

In this chapter I examine factors that may limit recruitment of *P. pungens* in pine-oak forests of southwest Virginia. The age structure of *P. pungens* in these forests suggests low recruitment of seedlings (Chapter III), and maintenance of *P. pungens* on these sites is questioned. This problem was addressed by asking several questions concerning the seedling ecology of *P. pungens* as related to recruitment and population maintenance in the absence of fire: 1) is seedling recruitment limited by lack of seedfall from serotinous cones? (seed limitation hypothesis); 2) does the availability of suitable microsites for seed germination and seedling establishment limit recruitment? (microsite limitation hypothesis); 3) if seedfall occurs at adequate rates, does seed predation play a role in limiting recruitment? (seed predation hypothesis); and 4) is limited recruitment the result of low levels of seedling establishment and survival due to the interactions of environmental factors such as herbivory, summer drought, substrate, and forest overstory conditions? (environmental limitation hypothesis).

IV.2 MATERIALS AND METHODS

IV.2.1 Measurement of *P. pungens* seedfall

Twenty-five 0.5 X 0.5 m seed traps were installed on each of the three Brush Mt. study sites in July 1987. A seed trap was positioned randomly in each of the twenty-five 10 X 10 plots within the study sites (see Chapter III). Seeds were collected at weekly or biweekly intervals throughout the study except when weather conditions limited

access to the study sites. After collection, seeds were counted and then stored at 4°C. *P. pungens* seeds were germinated at monthly intervals on moistened filter paper in plastic petri dishes at ca. 22°C. Seeds of *P. pungens* remain viable for at least nine years in cold storage (Schopmeyer 1974), thus I assumed that cold storage of seeds for one month did not affect germinability. Viability of filled, non-germinated seeds was assessed by tetrazolium staining.

IV.2.2 Characterization of seedling habitat

P. pungens seedling habitat was characterized using an approach similar to that of Collins and Good (1987) and Gibson and Good (1987). In late May 1988, 25 newly emerged *P. pungens* seedlings were selected at random at each of the three 0.25 ha study sites. In addition, 25 random points were selected within each study site using stratified random sampling. A random number table was used to select X-Y coordinates for each plot in the study sites. The random point was then located in the plot by pacing off the coordinates.

Seven habitat variables were recorded within a 14 cm diameter circular plot centered on each seedling and random point (Table 4.1). Canopy cover was estimated with a spherical densiometer (Lemmon 1956, 1957) and ground cover within plots was estimated visually. Litter depth was measured with a thin metal rule inserted to the soil surface. Enumeration of habitat variables for random points provided a basis for comparison with seedling points to determine if seedling habitat was significantly different from random points in the forest.

Statistical differences for continuous habitat variables between seedling and random points were examined with one-way ANOVA. Because there were no significant differences within seedling and random points among the three study sites, the data were pooled for analysis. Percentage data were transformed using the arcsin function and other continuous variables were log-transformed to ensure normality (Sokal and Rohlf 1981). Categorical variables were analyzed by median tests (Mood 1950; Zar 1984), a variant of the chi-square test.

Principal components analysis (PCA) was used to graphically display potential differences in seedling habitat and random points along derived habitat gradients. PCA is a multivariate technique that attempts to explain the total variation in a data set with as few factors as possible (Kleinbaum and Kupper 1978). Habitat gradients were derived from a data matrix containing 150 samples (25 seedling points and 25 random points pooled each from each of the three sites) by seven habitat variables. The PCA was derived from a correlation matrix of the seven habitat variables.

Stepwise discriminant function analysis was used to identify assemblages of habitat variables that could be used to distinguish seedling microsites from random points. The goal of stepwise discriminant function analysis is similar to that of classical multiple regression (i.e., the construction of a linear model that describes the relationship between a dependent and several independent variables), but discriminant analysis involves a nominal dependent

variable (e.g., seedlings, random points) whereas regression considers a continuous dependent variable (Kleinbaum and Kupper 1978).

IV.2.3 Experimental recruitment/predation plots

To assess the influence of canopy type (pine, oak), substrate (litter removed or intact) and predation on early establishment and survival of *P. pungens* seedlings, experimental recruitment/predation plots were installed on Sites 2 and 3. An experimental site (hereafter called a demosite) consisted of four 0.5 X 0.5 m plots situated in a 2 X 2 array: two plots in which litter was removed to mineral soil, and two plots in which litter was left intact. One plot of each litter treatment at all demosites was enclosed with a hardware mesh cage (1.2 cm openings) to exclude seed predators.

Five demosites were established for each canopy type (i.e., pine or oak), and plots within the demosites were positioned randomly. Twenty-five *P. pungens* seeds (seed lot viability = 89%) were sown and lightly worked into each plot during mid-June 1987. Upon emergence, seedlings in these plots were tagged with numbered plastic bird bands (National Band and Tag Co., Newport, KY) to track the fate of individuals. Seedling emergence and mortality were monitored at weekly intervals from June 1987 to December 1989. Potential causes of seedling mortality (e.g., predation, dessication) were recorded when possible.

Data were analyzed by two-way ANOVA with canopy type, substrate and interaction (canopy X substrate) as treatment variables. Data were

transformed before analysis (square root of $X + 0.5$) to stabilize variances (Sokal and Rohlf 1981). Statistical differences in treatment variables between sites precluded pooling. Individual differences in treatment means among sites was determined by Duncan's Multiple Range Test. Statistical analysis was not performed on the 1987 data because of extremely low seedling emergence.

IV.2.4 Demography of *P. pungens* seedlings in natural populations

All *P. pungens* seedlings (≤ 1 m in height) on each of the three study sites were tagged and aged. Seedling age was determined in the field by counting terminal bud scars with the aid of a 10X hand lens. To determine the accuracy of this method, 60 *P. pungens* seedlings were collected near each study site (20 seedlings/site area) and aged initially by counting bud scars and then by counting annual rings in stem cross-sections. There were no statistically significant differences in the distribution of differences of seedling ages between the two methods (paired t-test, $P > 0.99$), thus bud scar counts were considered a reliable method of aging *P. pungens* seedlings in the field.

Seedlings were first tagged in mid-June 1987, and censuses were conducted at frequent intervals through March 1989 (Table 4.2). At each census, study sites were thoroughly searched for previously tagged and newly established *P. pungens* seedlings, and the latter were tagged upon discovery. The status and condition (alive, dead, grazed)

of each tagged seedling were recorded at all censuses. Seedlings not relocated in three consecutive censuses were considered dead.

IV.3. RESULTS

IV.3.1 Seedfall of Pinus pungens

Seedfall of *P. pungens* occurred throughout the year but was concentrated in the spring and summer months (Figs. 4.1 - 4.3). The three study sites generally showed similar seedfall phenologies, but seed inputs varied among sites (Table 4.3; Figs. 4.1 - 4.3). Total input among study sites during March to August 1988 ranged from 5.8 to 10.4 seeds/m² and percent viability varied from 45 to 64% (Table 4.3). Seedfall also exhibited secondary peaks in the fall. Total seedfall and viable seedfall in autumn 1987 was greater than seedfall recorded during the same period in 1988 (Table 4.3).

Total inputs of *P. pungens* seeds during 1988 ranged from 7.8 to 13.1 seeds/m². Viable seedfall was generally half that of the total and viability ranged from 44% to 53%. Estimates of total seedfall for 1987 are unavailable as seed trapping did not begin until July. However, total and viable seedfall during July to December 1987 was substantially greater than the same period in 1988 (July to December 1988 seedfall 3.9 to 7.8 seeds/m², seed viability 49 to 68%). Thus total seed inputs may have varied between the years, assuming rates of seedfall for the rest of 1987 are comparable with those observed in 1988, with greater total seedfall occurring in 1987.

IV.3.2 Seedling habitat of Pinus pungens

Five of the seven habitat variables were significantly different for seedlings and random points (Table 4.4). Seedlings were found in microsites characterized by lower litter depth, ground cover, and canopy cover, and by greater nearest neighbor distances than occurred at random. Seedlings also occurred disproportionately often in pine litter (Table 4.4; Fig. 4.4 - 4.5). Only canopy type and nearest neighbor growth form were non-significant habitat variables (table 4.4; Figs. 4.6 - 4.7).

PCA showed that seedling and random points constitute two relatively homogeneous groups with little overlap (Fig. 4.8). The first two principal components defined habitat gradients that separated seedling and random points. These PCA axes had eigenvalues greater than 1.0 and accounted for 55% of the total variation in the original data matrix (Table 4.5). Axis 1 was a gradient from low to high ground cover, canopy cover, and litter depth. Axis 2 was a gradient from pine to oak canopy and high to low nearest neighbor distance. The difference in spatial distributions of seedling and random points was especially evident along axis 1. Random points occurred in habitats dominated by mixed and hardwood litters and further typified by greater litter depth, and higher ground and canopy covers. In contrast, seedlings tended to occur in habitats characterized by shallow pine litter, lower ground and canopy cover, pine canopy, and larger nearest neighbor distances than occurred at random.

There was little overlap in the distributions of significant habitat variables between seedling and random points (Table 4.6; Fig. 4.4, 4.5). The percentage of random points that occurred within 95% (two standard errors) of the means for seedling habitat variables was low, ranging from 0% occurrence in the litter depth interval to 16% occurrence in the interval for nearest neighbor distance. Leaf litter at random points was significantly deeper across all types than litter in the vicinity of seedlings (Table 4.7) and there was little overlap in the distributions of seedling and random points by litter depth classes (Fig. 4.4).

Stepwise discriminant function analysis identified a three variable model that best described seedling habitat and a two variable model that defined random points (Table 4.8). Litter depth was the only statistically significant variable that entered in the model for seedling habitat. Canopy type and canopy cover also entered in the model but were not significant. Based on significance levels, litter depth was the most important variable that defined seedling habitat. For random points, nearest neighbor distance and ground cover were variables that entered into the discriminant model, but only nearest neighbor distance was significant.

IV.3.3 Experimental recruitment/predation plots

Emergence of *P. pungens* seedlings from seeded plots was extremely low in 1987 (Table 4.9; Figs. 4.9-4.10). Emergence occurred almost exclusively in litter-free plots and was similar among caged

and uncaged treatments. Seedling emergence occurred from late June to mid-July but by 30 July all seedlings were dead. No further seedling emergence from these seeded plots was recorded in 1987. Low seedling emergence and survival coincided with a drought that lasted much of the summer, thus low seedling emergence and survival are potentially a result of low soil moisture that occurred during the vulnerable early establishment stage. Dead and dying seedlings typically appeared brown and wilted. There was little evidence of herbivory during 1987.

Emergence of *P. pungens* seedlings from seeded plots in 1988 was considerably higher than that recorded the previous year (Table 4.10; Figs. 4.9 - 4.10). Seedling emergence was first noted in mid-April and continued until mid-June 1988. Total seedling emergence differed between the two sites (three-way ANOVA, $P = 0.001$); a greater number of seedlings emerged in plots on site 2 than on site 3 (Figs. 4.9 - 4.10).

The significance of treatment effects for seedling emergence varied between sites (Tables 4.11, 4.12). For site 2, substrate treatment was significant but canopy, and the interaction of canopy and substrate, had no significant effects upon seedling emergence. Both canopy and substrate had significant effects upon seedling emergence on site 3 but the interaction of these two factors was not significant. Seedling emergence in site 3 plots was greater under canopies dominated by pine than under oak canopies (two-way ANOVA, $P = 0.015$; Fig. 4.10).

There was considerable overlap in mean seedling emergence among substrate treatments within sites (Table 4.10). Seedling emergence was generally higher in plots in which litter was removed although a significant litter effect was observed only in pine demsites on site 3 (Table 4.10). There was no significant difference in seedling emergence between caged and uncaged treatments except in oak demsites on site 2. Seedling emergence in oak demsites of site 2 was lower in caged, litter intact treatments, thus lowered emergence was probably not the result of seed predation but from shading or barrier effect by cages. Canopy cover was high over oak demsites (Table 4.13) and any further decrease in light levels caused by caging could have influenced seedling emergence.

There were no significant differences in seedling emergence between pine and oak canopies on site 2 (Table 4.12) or between pine canopies on sites 2 and 3 (two-way ANOVA, $P = 0.08$) so the respective data were pooled for analysis. Results indicate a strong litter effect for both pooled data sets (Table 4.14). Mean seedling emergence in both cases was greatest in the litter-free treatments and there was no difference in emergence between caged and uncaged substrate treatments. Thus the presence of litter appeared to have an important impact on the emergence of *P. pungens* seedlings whereas seed predation had little or no effect. Litter depth in demplots varied between canopy types but not between sites. Mean litter depth was significantly greater under oak than pine canopies but litter depths

under both canopies were deeper than the mean litter depth in which most *P. pungens* seedlings naturally establish (Table 4.4).

Survival and mortality of *P. pungens* seedlings did not differ between sites and canopy type or among substrate treatments (Table 4.11) but failure to reject the effect of substrate upon seedling mortality was marginal. Analysis of seedling mortality via single factor ANOVA also resulted in marginal failure to reject the null hypothesis ($P = 0.0527$) and this was reflected by the considerable overlap in treatment means (Table 4.15). In general, mortality was higher in plots containing litter than in those in which litter was removed. As in 1987, mortality of seedlings appeared to be the result of dessication, and evidence of herbivory was negligible.

IV.3.4 Demography of seedlings in natural populations

The age structure of *P. pungens* seedlings (≤ 1 m in height) was similar among sites but age distributions varied between the census periods (Figs. 4.11 - 4.13). Age distributions were generally unimodal or Gaussian-like. Seedling numbers were highest in the middle age classes and lowest at the tails of the age class range. The age distributions for seedlings as of March 1989 were bimodal with peaks in the youngest and middle age classes (Figs. 4.14 - 4.16). The lowest numbers of seedlings occurred in the oldest age classes and in the 2 to 5 year age range.

Mortality of *P. pungens* seedlings varied between years and among age classes (Tables 4.16 - 4.17; Fig 4.17). Seedling mortality was

highest across all age classes in 1987-88 censuses. The overall mean mortality of seedlings during 1987-88 was 31.9%. Seedling mortality during 1988-89 was considerably less, averaging 12.4%. Seedling mortality during both census periods was concentrated in the youngest age classes and was particularly high in seedlings up to one year in age (Tables 4.16-4.17; Fig. 4.17). A secondary peak in mortality also occurred in the oldest age classes in 1987-88 but the magnitude of the peak was substantially less than that observed in the youngest age classes.

Seedling mortality was generally highest during the summer months (Tables 4.16 - 4.17). Most mortality of newly emerged seedlings occurred during early to mid-summer, and in 1988, seedling mortality had stabilized by late July (Fig. 4.18). Growth-limiting water stress levels usually begin in late July and continue for the rest of the growing season in the Ridge and Valley of southwestern Virginia (Meiners et al. 1984). In contrast, mortality of seedlings in older age classes occurred sporadically throughout the census period (1988-89) or during late fall and early winter (1987-88). Mortality in newly emerged seedlings appeared to be primarily due to desiccation. Seedlings in older age classes that died in 1987-88 also appeared to have succumbed to drought. Needles of seedlings that died in the fall and winter typically began browning in late summer.

IV.4 DISCUSSION

IV.4.1 Seed limitation hypothesis

As dispersal of viable seeds of *P. pungens* occurred throughout the year at low levels, seed availability does not directly appear to be limiting recruitment. Assuming an average of 560 *P. pungens* trees/ha (≥ 10 cm dbh; computed from data in Table 3.4), seedfall would be more than adequate to replace these trees (viable seed inputs would range from 35,000 to 69,000 seeds/ha). Seed dispersal in the absence of fire has been noted for other serotinous conifers (Crutchfield and Trew 1961; Fowells 1965; McMaster and Zedler 1981) but rates of seedfall are unavailable for comparison.

Seedfall rates in non-serotinous pines are considerably higher than that recorded for *P. pungens* during this study. For example, seedfall of loblolly pine, *P. taeda*, may reach 225 seeds m^2 during years of good cone crops (Fowells 1965). Total seedfall of *P. pungens* recorded in this study ranged from 3 to 6% of this value. Mast seeding may decrease the impacts of seed predators through inundation and satiation (Silvertown 1980), but equally important, large seed inputs may increase the probability that seeds reach safe germination sites (e.g., Geritz et al. 1984). Low seed inputs in the absence of fire are advantageous for serotinous conifers as this provides some opportunity for colonizing open sites while retaining the majority of seed for colonizing sites after fire (Christiansen 1985). However, seed predation and the availability of microsites may be major limitations for recruitment when seed inputs are low. The probability that a seed

may reach a suitable microsite is lessened when seed inputs are low and predation is high.

IV.4.2 Microsite limitation hypothesis

The seedling habitat of *P. pungens* in pine-oak forest is distinct and there is little overlap of habitat variables with random points in the forest. This suggests that availability of microsites may be a significant factor limiting recruitment of *P. pungens*.

Litter depth and type strongly affects germination and success of *P. pungens*. Condition of seedbeds is a major consideration in conifer regeneration, and increased litter depths typically result in decreased seedling emergence and survival (Fowells 1965; Chrosiewicz 1974). Less is known about the effects of different litter types on emergence and survival of pine seedlings but experimental evidence suggests that emergence of *P. pungens* seedlings is greater in shallow pine litter than in hardwood litter of the same depth (Chapter V). Establishment in litter may be a trade-off between mechanical and chemical factors that restrict emergence and factors that enhance survival such as lower evaporation of soil moisture (Koroleff 1954; Blow 1955; McPherson and Thompson 1972; Sydes and Grime 1981b). Hardwood litter in particular has been reported to reduce seedling establishment through interference with radical penetration into the soil (Koroleff 1954; Ahlgren 1959; McPherson and Thompson 1972).

The seedbed provided by shallow pine litter may be functionally similar to those produced by fire. Fire-modified seedbeds vary by site

but typically consist of a layer of compacted organic matter and ash a few centimeters thick (Ahlgren 1959). The absorption and retention of water by organic matter/ash seedbeds is good, and provides ideal conditions for the establishment of many tree species including pines (Ahlgren 1959). The retention of water by soils overlain by shallow pine litter is also good (Chapter V) and the thin, linear needles of pine provide little barrier for radical penetration into the soil. Preferential establishment of *P. pungens* seedlings in shallow pine litter probably reflects a narrow tolerance of seedbed conditions selected in part by reliance on fire for regeneration.

Light quality and quantity may have substantial impacts on the survival of shade-intolerant pine seedlings (Kramer et al. 1952). Photosynthetically active radiation (PAR) was not measured in this study but is undoubtedly of importance in defining the regeneration niche of a plant (Grubb 1977). Previous studies of seedling habitats in pine-oak forest (Collins and Good 1987; Gibson and Good 1987) used instantaneous point measurements of PAR taken above seedlings. While this may provide an estimate of PAR at a given time, point estimates do not provide an integrated measure of total PAR received during the day. Open canopy conditions above seedlings probably provided more light to seedlings than would be received at random points. Hemispherical photographs of the canopy above each seedling projected onto solar tracks (Selter et al. 1986) would provide a better measure of insolation regime than point measurements of PAR.

Seedling habitat was also defined by larger distances to neighboring plants than occurred at random. Adjacent vegetation may compete for essential resources such as light, moisture, and nutrients. Woody vegetation, particularly shrubs, may also accumulate litter in their vicinity (Sydes and Grime 1981b); increased litter depths may limit establishment of *P. pungens* seedlings. Thus nearest neighbor distance may not only be a total function of resource competition, but also of interference with seedling establishment.

IV.4.3 Seed predation hypothesis

Post-dispersal seed predation by birds and mammals has been implicated in low seed survivorship and regeneration failures in many species of conifers (Smith and Aldous 1947; Tevis 1953; Abbott 1961; Ahlgren 1966; Abbott and Quink 1970; Radvanyi 1970). Seed predation by vertebrates varies with habitat (Mittelbach and Gross 1984; Webb and Wilson 1985) and appears to be higher in cutover and (or) burned forests (Ahlgren 1966; Buchholz 1983) than in undisturbed stands (Yeaton 1983).

There was no evidence that seed predation had a significant effect on seedling recruitment in *P. pungens* during this study. Establishment of seedlings did not differ between caged and uncaged demoplots, but the apparent lack of seed removal from plots may not reflect potential seed predation in undisturbed forest. Shrub and ground layer vegetation within all plots was removed, and the removal of leaf litter from some substrate treatments, created an exposed

environment unlike that in much of the adjacent forest. Small mammals such as Peromyscus are sensitive to differences in microhabitat and avoid open areas as small as 1 m in diameter (Rosenzweig 1973; Mittelbach and Gross 1984). Thus the apparent lack of predation of P. pungens seeds may reflect avoidance of demsites by seed predators, particularly small mammals.

To assess the effects of seed predation on recruitment of P. pungens seedlings, rates of seed predation must be examined in several microhabitats within pine-oak forests. For example, seed predation may differ in undisturbed vegetation, in disturbed microsites such as animal diggings, or in different types and depths of leaf litter. In addition, small mammals should be censused during periods of peak P. pungens seedfall (mid-summer and autumn) to determine population sizes and the species present.

Pre-dispersal predation of P. pungens seeds was not considered in this study but it may play a role in reducing the size of the arboreal seed pool. Reductions in seed pool size by pre-dispersal predation would also result in lowered seed inputs. The major pre-dispersal predators of P. pungens seeds include the red squirrel, Tamiasciurus hudsonicus (Mollenhauer 1939), larvae of the mountain pine coneworm, Dioryctria yatesi (Lepidoptera: Pyralidae), and the shield-backed pine seed bug, Tetyra bipunctata (Hemiptera: Pentatomidae) (Hedlin et al. 1981). All of these seed predators occur on Brush Mountain (pers. obs.).

IV.4.4 Environmental limitation hypothesis

The seedling environment consists of biotic and abiotic factors that may have positive, negative, or neutral effects upon survival. The environmental limitation hypothesis is a catchall for biotic and abiotic factors and their interactions that may influence establishment and survival of *P. pungens* seedlings. As such, there is some overlap of the factors considered by this hypothesis with those of the others. The environmental limitation hypothesis considers biotic and larger-scale abiotic factors such as drought, herbivory, substrate, and forest overstory.

Summer drought can have significant impacts on the establishment and survival of tree seedlings (Hough 1937; Selter et al. 1986) especially on southerly slopes where soil moisture is usually low (Mowbray and Costing 1968; Meiners et al. 1984). Barden (1988) suggested that summer drought limits recruitment and shapes the age distributions of self-maintaining populations of *P. pungens* primarily through high mortality of young age classes. Seedling age distributions of *P. pungens* during this study were noticeably influenced by the drought of 1987. Emergence and survival of *P. pungens* during the late spring and early summer of 1987 were extremely low. Moreover, older age classes also experienced greater mortality than in 1988 when moisture availability was higher. Repeated spring and summer droughts may have a large impact on the age structure of a *P. pungens* population, resulting in polymodal age distributions: peaks

in age classes experiencing drought during less susceptible stages of the life cycle and troughs in age classes that succumb to drought. Recruitment and thus the maintenance of *P. pungens* populations may be determined by drought duration, recurrence, and site factors which influence the intensity of drought.

Substrate and overstory are two factors that may influence seedling survival during drought. For example, evapotranspiration is often greater in a canopy gap than under a dense canopy, and this may cause surface soil moisture to be lower in gaps (Lee 1978). Leaf litter generally increases retention of soil moisture (Blow 1955; Chapter V). Therefore, litter-free sites under sparse canopies may be less favorable for seedling survival during drought than sites with litter or those under a denser canopy.

Low emergence and complete mortality of seedlings in demoplots during 1987 precluded the testing of these hypotheses but substantial seedling emergence and a less intense summer drought in 1988 provided some opportunities. The presence of litter decreased seedling emergence relative to litter-free plots and there is some indication that mortality was slightly higher in plots containing litter. Overall survivorship of seedlings in demoplots was similar to that of naturally occurring seedlings, thus substrate and canopy effects did not influence survival in 1988. This suggests that for newly emerged *P. pungens* seedlings there are few sites in pine-oak forests that provide shelter from drought.

Herbivory was not a significant factor in the establishment and survival of *P. pungens* seedlings. Seedlings in older age classes sustained nominal damage from pine webworm (*Tetralopha robustella*) and European pine sawfly (*Neodiprion sertifer*) in both 1987 and 1988, but no mortality could be attributed to herbivory. Infestation levels in seedlings among sites was less than 10%. Nominal levels of herbivory, however, reduce net carbon gain and may result in further loss of fitness in seedlings growing under forest canopies.

IV.4.5 Limits to recruitment and population maintenance in *Pinus pungens*

The limited recruitment of *P. pungens* seedlings in the pine-oak forests of Brush Mountain cannot be attributed to any single factor. Rather, several factors that influence the establishment and survival of seedlings may operate in tandem. Dispersal of viable seeds of *P. pungens* occurred throughout the year at low levels, thus seed availability does not directly appear to be limiting recruitment. However, seedling habitat is rare and low rates of seedfall may further decrease the probability that a seed reaches these limited sites. The influence of seed predation is at present unknown but may further reduce seed supply. Summer droughts have a major impact on the establishment and survival of seedlings, particularly those in young age classes, and may strongly influence the age structure of populations.

Maintenance of *P. pungens* populations on Brush Mountain in the absence of fire is doubtful. Although *P. pungens* will continue to be a canopy component of Brush Mountain forests for some time in the future, the prominence of hardwoods in the seedling, sapling and small tree strata of these forests suggests future oak-domination (Lipecomb and Nilsen, manuscript; Chapter III).

Table 4.1. The seven variables used to describe the seedling habitat of newly emerged *Pinus pungens* seedlings on the Brush Mt. study sites.

<u>Variable</u>	<u>measurement</u>
Litter depth	depth of litter (cm) adjacent to each seedling
Nearest neighbor distance	distance (cm) from the seedling to the nearest plant
Ground cover	estimate of percent cover of the ground layer vegetation in a 14 cm diameter circular plot centered on each seedling
Canopy cover	estimate of percent cover of the canopy vegetation over each seedling
Litter type	a categorical variable that identified the type of litter (1 = pine, 2 = mixed, 3 = deciduous) in which each seedling was found growing
Canopy type	a categorical variable that identified the type of canopy (1 = pine, 2 = mixed, 3 = deciduous) under which each seedling was growing
Nearest neighbor type	a categorical variable that identifies the type of plant growing nearest each seedling (1 = prostrate shrub, 2 = small shrub, 3 = tree seedling, 4 = vine, 5 = herb, 6 = large shrub)

Table 4.2. Census dates for demography studies of *Pinus pangens* seedlings, 1987-89.

<u>Date</u>	<u>Objectives</u>
18 June 1987	first seedling census
10 August 1987	further tagging of seedlings; previously tagged seedlings relocated
1 December 1987	previously tagged seedlings relocated
37 March 1988	previously tagged seedlings relocated
28 May 1988	1988 cohort tagged; previously tagged seedlings relocated
31 July 1988	previously tagged seedlings relocated
9 October 1988	previously tagged seedlings relocated
18 March 1989	previously tagged seedlings relocated

Table 4.3. Inputs of *Pinus pungens* seeds into the study sites, July 1987 to December 1988. Tot. = total seedfall/m², Via. = viable seedfall m², % = percent viability of total seedfall. Seed trapping began in July 1987 thus the total for this year is unavailable.

<u>Date</u>	<u>Site</u>								
	<u>1</u>			<u>2</u>			<u>3</u>		
	<u>Tot.</u>	<u>Via.</u>	<u>%</u>	<u>Tot.</u>	<u>Via.</u>	<u>%</u>	<u>Tot.</u>	<u>Via.</u>	<u>%</u>
1987									
July to Dec.	7.8	5.4	69	10.2	6.7	66	7.8	6.2	80
Oct. to Nov.	4.0	2.2	55	4.7	2.6	55	3.0	1.6	53
1988									
Mar. to Aug.	5.8	2.6	45	10.4	6.6	64	5.8	3.4	59
Oct. to Nov.	1.6	0.6	38	1.6	0.2	13	1.3	0.5	39
Jan. to Dec.	8.0	3.5	44	13.1	6.9	53	7.8	3.8	49

Table 4.4. Means, standard errors (continuous variables), and medians (categorical variables) of the seven habitat variables for newly emerged seedlings of *Pinus ginseng* and random points. The significance of continuous variables was tested by ANOVA whereas significance of categorical variables was determined by median tests.

<u>Continuous variables</u>	<u>Seedling</u>	<u>Random</u>	<u>P</u>
litter depth (cm)	1.71 ± 0.11	7.00 ± 0.35	< 0.0001
nearest neighbor distance (cm)	10.06 ± 0.97	5.19 ± 0.48	< 0.0001
ground cover (%)	6.48 ± 1.26	20.00 ± 2.71	< 0.0001
canopy cover (%)	82.76 ± 0.58	89.83 ± 0.40	< 0.001

<u>Categorical variables</u>	<u>Seedling</u>	<u>Random</u>	<u>P</u>
litter type	1.0	2.0	< 0.001
canopy type	2.0	2.0	0.05 < P < 0.10
nearest neighbor type	2.0	2.0	0.25 < P < 0.50

Table 4.5. Principal components analysis of the correlation matrix of the seven habitat variables measured for *Pinus pangens* seedlings and random points.

Variable	PCA axis	
	I	II
Litter depth	0.53	-0.08
Litter type	0.47	0.14
Nearest neighbor distance	-0.29	0.37
Nearest neighbor type	0.17	-0.39
Ground cover	0.39	-0.42
Canopy cover	0.43	0.40
Canopy type	0.23	0.59
Variance	33.86	21.14
Eigenvalue	2.37	1.48

Table 4.6. Percentage of random points occurring within two standard errors of the means for *Pinus pungens* seedling habitat variables.

<u>Variable</u>	<u>interval</u>	<u>% random points in interval</u>
Litter depth (cm)	1.60 - 1.82	0
Nearest neighbor distance (cm)	9.09 - 11.03	16
Ground cover (%)	3.96 - 9.00	8
Canopy cover (%)	81.60 - 83.92	8

Tables 4.7. Summary of stepwise discriminant function analysis for *Pinus pungens* seedling habitat and random points.

<u>Seedlings</u>		
<u>Variables</u>	F	P
Litter depth (cm)	14.19	0.0001
Canopy type	2.58	0.0826
Canopy cover (%)	2.23	0.1148
<u>Random points</u>		
<u>Variables</u>	F	P
Nearest neighbor distance (cm)	6.55	0.0024
Ground cover (%)	2.88	0.0629

Table 4.8. Summary of litter depth by type for *Pinus pungens* seedlings and random points. Means bearing the same letter are not significantly different (Duncan's multiple range test, $P \leq 0.05$).

<u>Litter type</u>	\bar{X} depth of litter (cm)		
	<u>Seedling</u>	<u>Random</u>	<u>P</u>
Pine	1.46a	6.35b	0.0001
Mixed	2.48a	6.94b	0.0001
Hardwood	1.50a	7.45b	0.0001

Table 4.9. Summary of treatment means for percent germination, survival, and mortality of *Pinus pungens* seedlings in experimental establishment plots during 1987. Treatments: NL = litter removed, L = litter intact, CNL = caged litter removed, CL = caged litter intact (emer. = emergence, surv. = survival, mort. = mortality).

<u>Oak canopy 1987</u>						
	<u>Spur-ridge 2</u>			<u>Spur-ridge 3</u>		
<u>Treatment</u>	% Emer.	% Surv.	% Mort.	% Emer.	% Surv.	% Mort.
NL	6.4	0.0	100.0	0.0	---	---
L	0.0	---	---	0.0	---	---
CNL	8.0	0.0	100.0	0.8	0.0	100.0
CL	0.8	0.0	100.0	0.0	---	---

<u>Pine canopy 1987</u>						
	<u>Spur-ridge 2</u>			<u>Spur-ridge 3</u>		
<u>Treatment</u>	% Emer.	% Surv.	% Mort.	% Emer.	% Surv.	% Mort.
NL	3.2	0.0	100.0	4.0	0.0	100.0
L	0.0	---	---	0.0	---	---
CNL	2.4	0.0	100.0	4.0	0.0	100.0
CL	0.0	---	---	0.0	---	---

Table 4.10. Summary of treatment means for percent germination, survival, and mortality of *Pinus pungens* seedlings in experimental establishment plots during 1988. Means bearing the same letter are not significantly different (Duncan's Multiple Range Test, $P \leq 0.05$). ANOVAs for percent survival and mortality were not significant ($P > 0.05$). Treatments: NL = litter removed, L = litter intact, CNL = caged litter removed, CL = caged litter intact (emer. = emergence, surv. = survival, mort. = mortality).

<u>Oak canopy 1988</u>						
	<u>Spur-ridge 2</u>			<u>Spur-ridge 3</u>		
<u>Treatment</u>	% Emer.	% Surv.	% Mort.	% Emer.	% Surv.	% Mort.
NL	28.0a	6.7	93.3	12.8a	0.0	100.0
L	20.0a	0.0	100.0	6.4a	0.0	100.0
CNL	28.0a	15.8	80.2	17.6a	16.7	83.3
CL	5.6b	0.0	100.0	6.4a	0.0	100.0

<u>Pine canopy 1988</u>						
	<u>Spur-ridge 2</u>			<u>Spur-ridge 3</u>		
<u>Treatment</u>	% Emer.	% Surv.	% Mort.	% Emer.	% Surv.	% Mort.
NL	42.4a	11.4	88.6	33.6a	8.4	91.6
L	12.0ab	0.0	100.0	10.4b	3.6	96.4
CNL	32.8ab	6.2	93.8	23.2a	5.7	95.3
CL	22.4ab	11.8	88.2	8.0b	0.0	100.0

Table 4.11. Analysis of variance of percent emergence, survival and mortality of *Pinus pungens* seedlings by site, canopy type and treatment for the 1988 demography plot data.

<u>% Emergence</u>				
<u>Source of variation</u>	<u>df</u>	<u>ss</u>	<u>F</u>	<u>P</u>
Site	1	1172.2102	10.83	0.0015
Canopy	1	693.7831	6.41	0.0135
Treatment (substrate)	3	3780.0412	11.64	0.0001
Error (plots)	74	8007.6421	—	—

<u>% Survival</u>				
<u>Source of variation</u>	<u>df</u>	<u>ss</u>	<u>F</u>	<u>P</u>
Site	1	77.4106	0.47	0.4948
Canopy	1	112.5933	0.69	0.4107
Treatment (substrate)	3	987.6600	2.00	0.1220
Error (plots)	74	10673.5879	—	—

<u>% Mortality</u>				
<u>Source of variation</u>	<u>df</u>	<u>ss</u>	<u>F</u>	<u>P</u>
Site	1	130.9424	0.79	0.3769
Canopy	1	52.2354	0.32	0.5761
Treatment (substrate)	3	1289.4923	2.60	0.0597
Error (plots)	74	10751.7266	—	—

Table 4.12. Analysis of variance of percent emergence of *Pinus pungens* seedlings in demoplots by site during 1988.

<u>Spur-ridge 2</u>				
<u>Source of variation</u>	<u>df</u>	<u>ss</u>	<u>F</u>	<u>P</u>
Canopy	1	169.4145	1.47	0.2348
Treatment	3	2094.5874	6.04	0.0022
Canopy X treatment	3	608.9073	1.76	0.1752
Error (plots)	32	3696.8456	--	--

<u>Spur-ridge 3</u>				
<u>Source of variation</u>	<u>df</u>	<u>ss</u>	<u>F</u>	<u>P</u>
Canopy	1	587.2923	5.57	0.0245
Treatment	3	1701.6612	5.38	0.0041
Canopy X treatment	3	250.3958	0.79	0.5074
Error (plots)	32	3372.3622	--	--

Table 4.13. Mean litter depth and canopy cover of *Pinus pungens* demoplots by study site and canopy type. Means bearing the same letter are not significantly different (Duncans multiple range test, $P \leq 0.05$). Litter depth did not differ significantly between caged and uncaged treatments thus means represent combined values for both.

<u>Variable</u>	<u>Spur-ridge 2</u>		<u>Spur-ridge 3</u>	
	oak	pine	oak	pine
Litter depth (cm)	5.0a	3.6b	5.0a	4.7b
Canopy cover (%)	91.0a	77.0b	90.2a	77.8b

Table 4.14. Summary of pooled treatment means for Pinus pungens seedling emergence. Means bearing the same letters are not significantly different (Duncan's multiple range test, $P < 0.05$). Mean seedling emergence did not differ significantly between oak and pine canopy on site 2 (two-way ANOVA, $P = 0.26$) or between pine canopies on sites 2 and 3 (two-way ANOVA, $P = 0.08$).

<u>Treatment</u>	<u>Site and canopy type</u>	
	Site 2 oak and pine	Sites 2 and 3 pine
Litter removed	35.6a	38.0a
Litter intact	16.0b	11.2b
Caged litter removed	30.4a	28.0a
Caged litter intact	14.0b	15.2b

Table 4.15. Composite summary of 1988 mean mortality of *Pinus pungens* seedlings by substrate treatment for both sites and canopy types. Means bearing the same letter are not significantly different (Duncan's multiple range test, $P \leq 0.05$). Failure to reject the null hypothesis via one-way ANOVA was marginal ($P = 0.0527$).

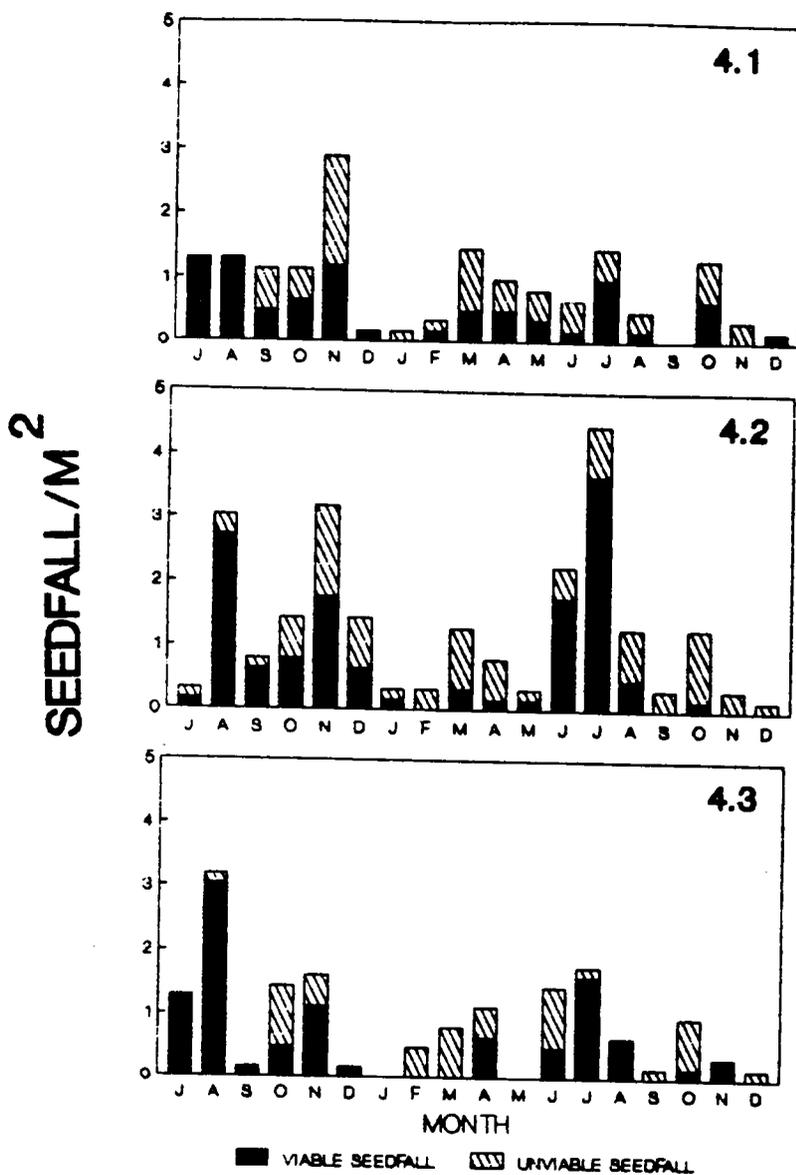
<u>Treatment</u>	<u>Mean mortality (%)</u>	<u>Number of plots</u>
Litter intact	99.3a	19
Caged litter intact	96.6ab	14
Litter removed	93.4ab	20
Caged litter removed	88.4b	18

Table 4.16. Composite population statistics for *Pinus pungens* seedlings (≤ 1 m in height) based on age-classes, June 1987 to March 1988 (l_x = number alive at census, dx = number dead at census).

Age class	June		August		Dec.		March		Percent mortality
	l_x	dx	l_x	dx	l_x	dx	l_x	dx	
0-1	25	27	3	9	18	6	3	76.0	
2-3	15	15	0	10	5	10	0	33.3	
4-5	18	18	0	15	3	15	0	16.7	
6-7	31	31	0	27	4	27	0	12.9	
8-9	31	31	0	28	3	27	1	12.9	
10-11	21	21	0	18	3	18	0	14.3	
12-13	18	17	1	14	3	13	1	27.8	
14-15	4	4	0	3	1	3	0	25.0	
16-17	2	1	1	0	1	0	1	100.0	
18-19	1	1	0	1	0	1	0	0.0	
Average mortality across classes:								31.9	

Table 4.17. Composite population statistics for *Pinus pungens* seedlings (≤ 1 m in height) based on age-classes, May 1988 to March 1989 (lx = number alive at census, dx = number dead at census).

Age class	May lx	July		October		March		Percent mortality
		lx	dx	lx	dx	lx	dx	
0-1	205	38	167	25	13	21	4	89.8
2-3	11	10	1	10	0	10	0	9.1
4-5	9	9	0	9	0	9	0	0.0
6-7	25	25	0	25	0	24	1	4.0
8-9	28	27	1	26	1	25	1	10.7
10-11	21	21	0	21	0	20	1	4.8
12-13	17	16	1	16	0	16	0	5.9
14-15	7	7	0	7	0	7	0	0.0
16-17	1	1	0	1	0	1	0	0.0
18-19	1	1	0	1	0	1	0	0.0
Average mortality across classes:								12.4



Figures 4.1 - 4.3 - Total and viable seedfall of *Pinus pungens*, July 1987 to December 1988. 4.1 - Site 1. 4.2 - Site 2. 4.3 - site 3. Height of bars = total seedfall/m².

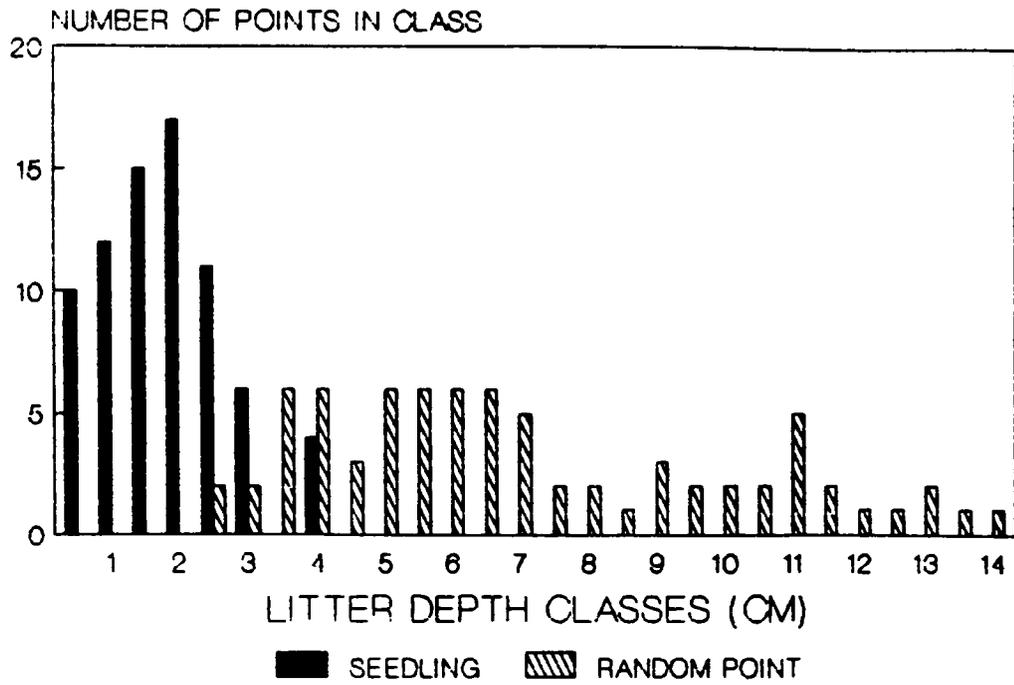
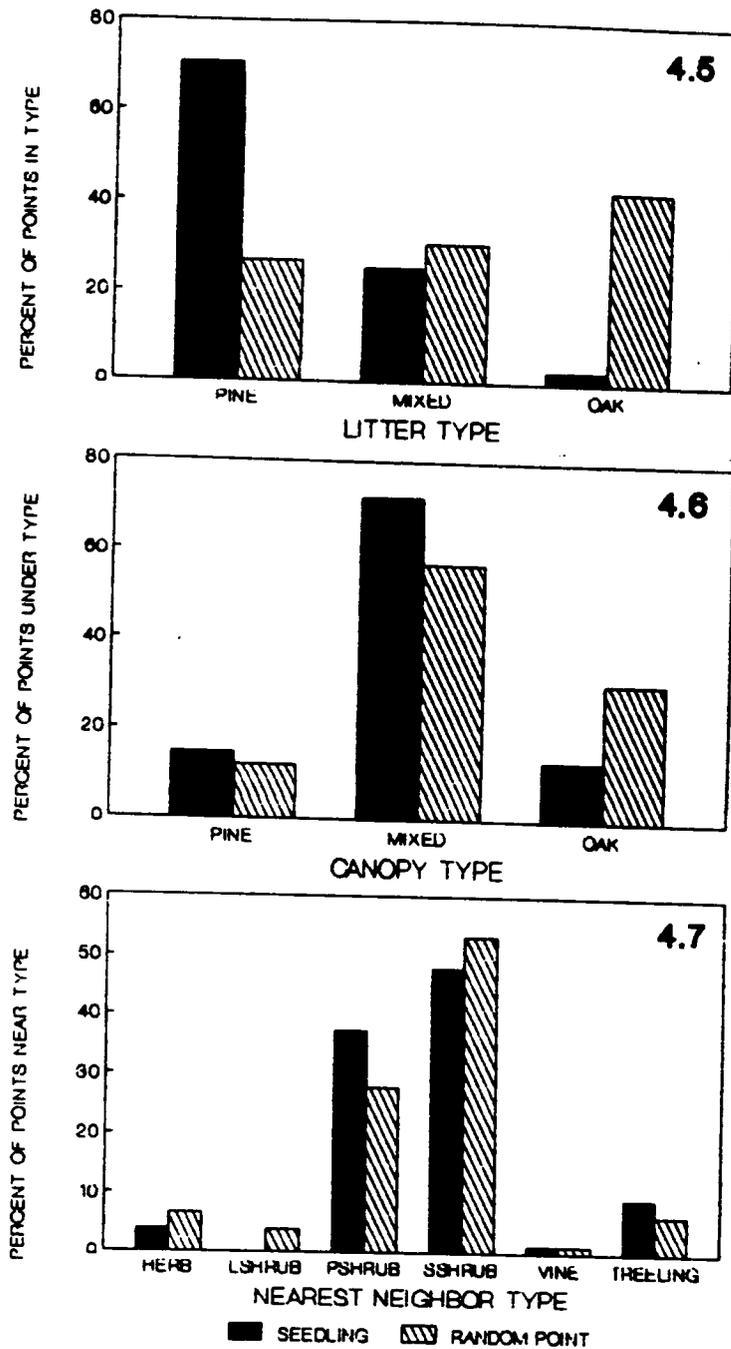


Figure 4.4 - Litter depth by class (0.5 cm intervals) for *Pinus pungens* seedlings and random points.



Figures 4.5 - 4.7 - Distributions of categorical habitat variables for *Pinus pungens* seedlings and random points. 4.5 - Litter type. 4.6 - Canopy type. 4.7 - Nearest neighbor type.

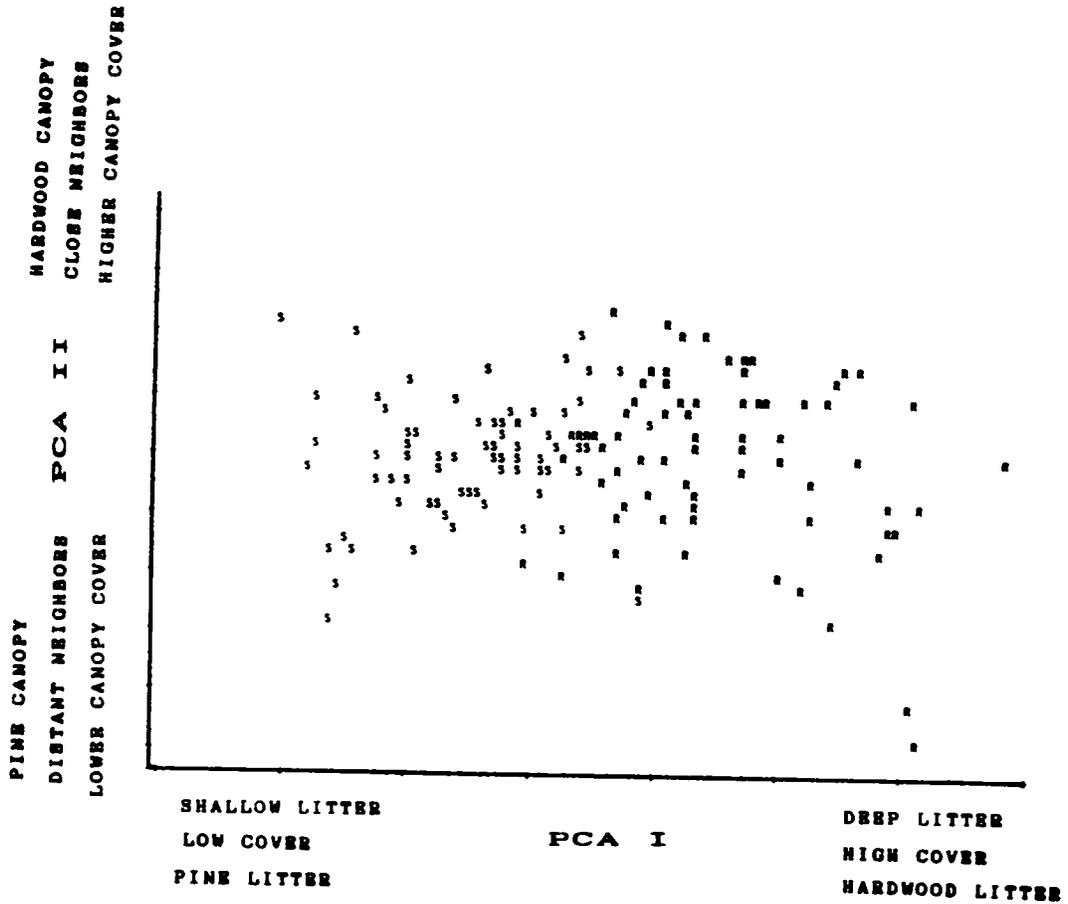
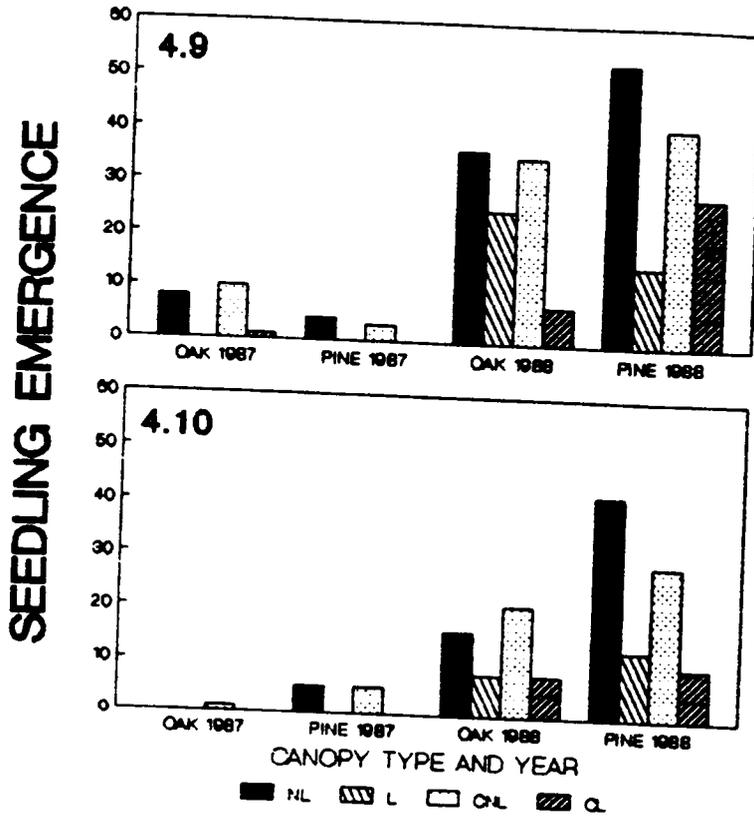
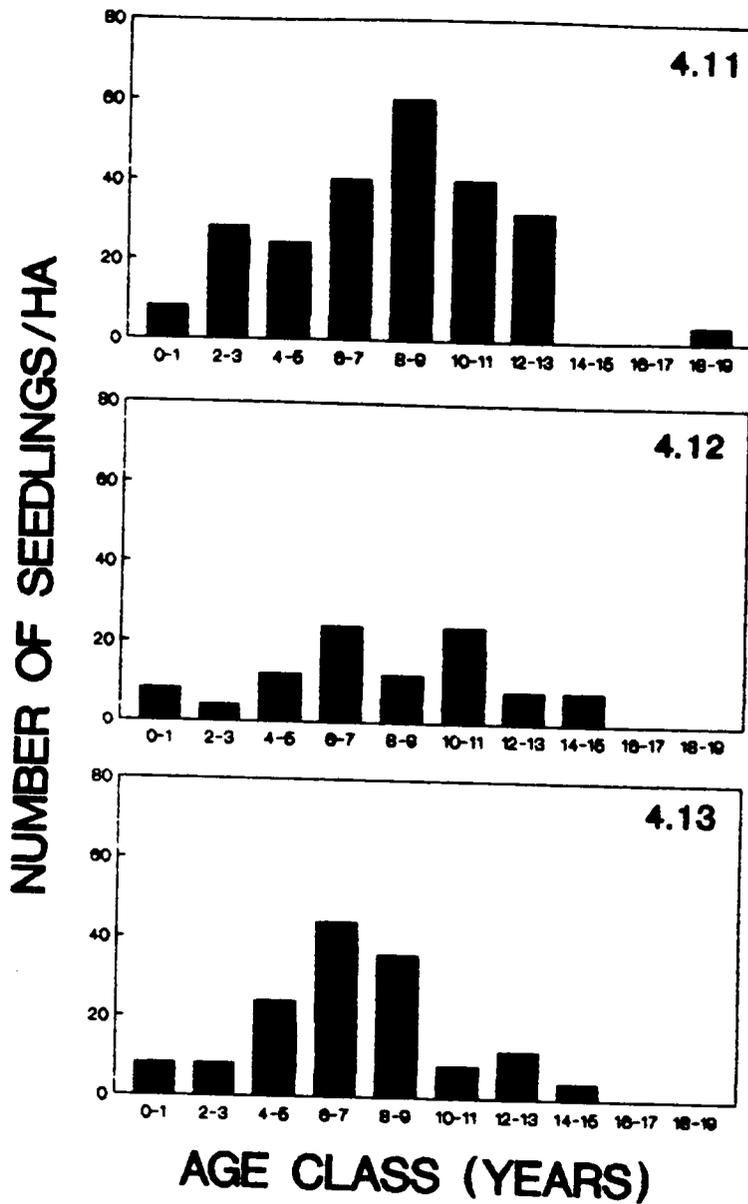


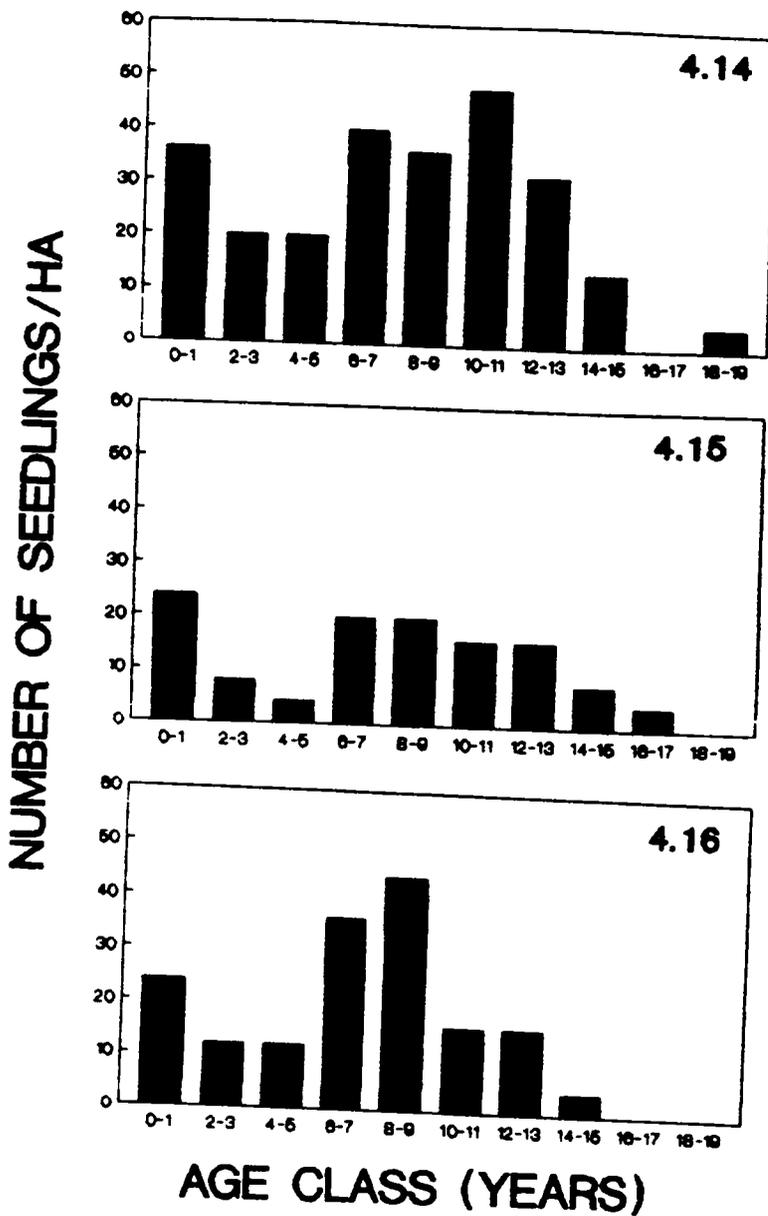
Figure 4.8 - Principle components analysis for *Pinus pungens* seedlings (S) and random points (R).



Figures 4.9 - 4.10 - Emergence of *Pinus pungens* seedlings from demoplots. 4.9 - Site 2. 4.10 - Site 3.



Figures 4.11 - 4.13. Age distribution of *Pinus pungens* seedlings/ha during March 1988. Fig. 4.11 - Site 1. Fig. 4.12 - Site 2. Fig. 4.13 Site 3.



Figures 4.14 - 4.16. Age distribution of *Pinus pungens* seedlings/ha during March 1989. Fig. 4.14 - Site 1. Fig. 4.15 - Site 2. Fig. 4.16 Site 3.

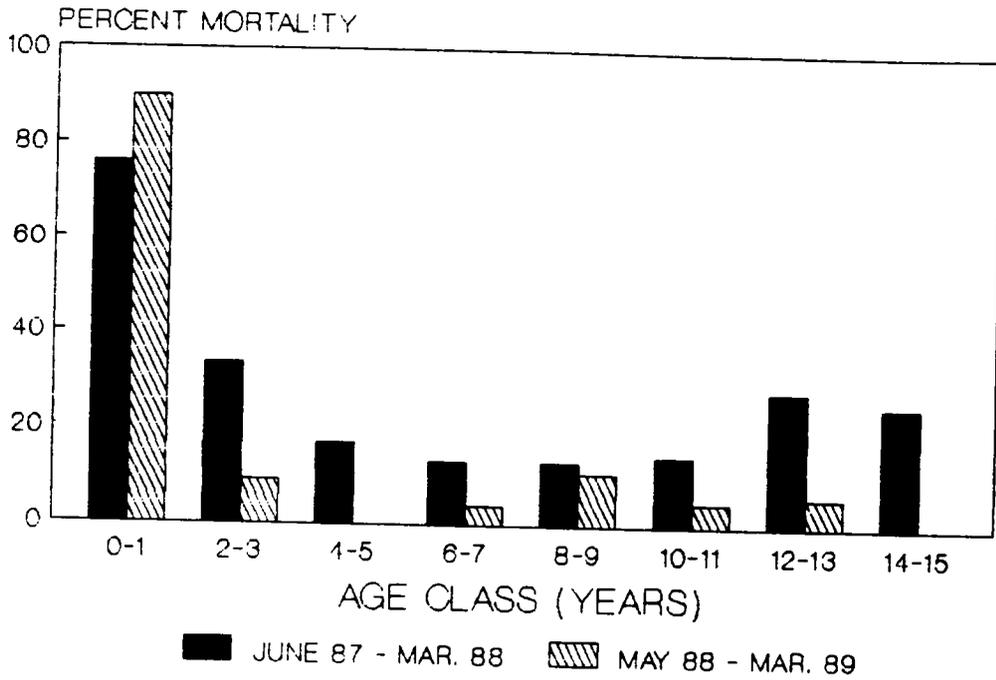


Figure 4.17 - Mortality of *Pinus pungens* seedlings by age class. June 1987 to March 1988, May 1988 to March 1989.

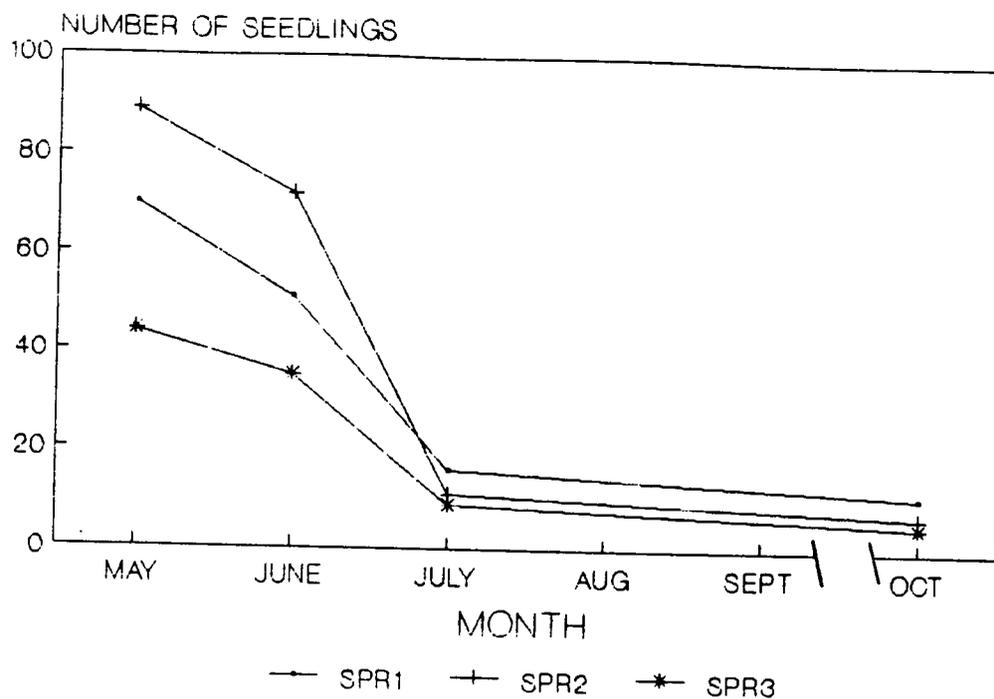


Figure 4.18 - Survival of newly emerged *Pinus pungens* seedlings May 1988 to March 1989.

V. INFLUENCE OF LEAF LITTER AND WATER REGIME ON EARLY ESTABLISHMENT OF PINUS PUNGENS

V.1. INTRODUCTION

Leaf litter is a conspicuous and ecologically important component of temperate forest ecosystems. For example, leaf litter type and quantity may strongly influence edaphic characteristics of forests particularly soil moisture, temperature, and nutrient content (Blow 1955). Leaf litter may also have a major impact on the spatial distribution, population size and recruitment abilities of forest herbs and tree seedlings (Koroleff 1954; McPherson and Thompson 1972; Sydes and Grime 1981a and b; Beatty and Sholes 1988) and evidence suggests that leaf litter may be a major determinant of species composition in the ground layer vegetation of some forest communities (Sydes and Grime 1981b).

Recruitment, and the maintenance or persistence of tree seedlings and ground layer species in forests, may be enhanced or restricted by leaf litter (Pitelka et al. 1980; Hughes et al. 1988). Litter may limit recruitment mechanically by interfering with root penetration into the soil (Koroleff 1954) and (or) by blocking light (Koroleff 1954; McPherson and Thompson 1972), or through the chemical inhibition of germination and growth (Al-Naib and Rice 1971; Lodhi 1978). Survivorship of some plant species may be increased by the presence of leaf litter. Litter may slow evaporation of water from forest soils (Blow 1955) and decrease the probability of death by desiccation (Fowler 1986). Thus plant establishment in leaf litter may

be a trade-off between factors that enhance survival and those that limit recruitment.

Seedlings of table mountain pine, Pinus pungens, establish in specific microsites within mature pine-oak forests in southwestern Virginia (Chapter IV). Litter appears to be a major determinant of P. pungens seedling habitat; significantly greater numbers of seedlings establish in shallow pine litter than in deep pine litter or hardwood litter of any depth. Few litter-free sites exist in mature pine-oak forests, and increased inputs of hardwood litter are expected as oaks and other deciduous trees increase in importance in the absence of fire. Thus leaf litter may be a key factor that restricts recruitment and maintenance of P. pungens in pine-oak forest.

The objective of this study was to examine the influence of leaf litter and water regime on early establishment of P. pungens. Although litter type and depth appear to be important determinants of P. pungens seedling habitat in field situations (Chapter IV), nothing is known about the ability of P. pungens to establish in different litter types or of the interaction of litter and soil moisture. The interaction of these two factors is of particular interest since summer drought may be a significant cause of mortality in young age classes of P. pungens (Barden 1988), particularly newly emerged seedlings (Chapter IV).

The main questions addressed by this study are: 1) does litter influence early establishment of P. pungens seedlings and if so, does

this influence vary with litter type?; 2) what are the effects of different water regimes on early establishment of *P. pungens* seedlings?; and 3) does the interaction of litter and water enhance *P. pungens* seedling establishment at low water regimes?

V.2. MATERIALS AND METHODS

This study was conducted in a greenhouse on the VPI & SU campus from mid-July to mid-September 1988. A completely randomized 3 X 3 factorial design consisting of three litter treatments (pine litter, hardwood litter, no litter) and three water regimes (1, 8, 15 day watering intervals) was employed. Each treatment combination was replicated six times with 25 *P. pungens* seeds per replicate (150 seeds/treatment combination). Maximum and minimum temperatures were recorded daily from a thermometer placed near the experiment.

Litter and soil were collected from pine-oak forest adjacent to study site 3 on Brush Mountain during early July 1988 (see Chapter II). Soil and litter substrates were reconstructed in 36 X 13 cm plastic nursery flats placed on a greenhouse bench. Soil depth in flats averaged 4 cm and total litter depth averaged 2 cm for all treatments containing litter. The litter depth selected for this study was similar to the mean litter depth in which newly emerged *P. pungens* seedlings occur in the field (Chapter IV). Hardwood litter was dominated by leaves of chestnut oak (*Quercus prinus*), scarlet oak (*Q. coccinea*) and black gum (*Nyssa sylvatica*). Needles of *P. pungens* dominated pine litter collections.

Seeds of *P. pungens* were collected from Brush Mountain trees during the early summer of 1988 (seed lot germinability = 86%, n = 100 seeds). Only seeds from cones of two to three years in age were used, as seed viability declines with increasing cone age in *P. pungens* (Barden 1979). Seeds were lightly worked into each flat by hand to simulate natural settling of the seed into the substrate.

Water was applied to flats until soils were saturated. All flats were watered to saturation on the first day of the study and according to treatment regime (1, 8, 15 days) thereafter. An additional three replicates of each litter treatment (hereafter called monitoring flats) were established to monitor soil moisture of treatments during the study. Monitoring flats were watered at 15 day intervals.

Soil moisture content of monitoring flats was determined gravimetrically from soil samples collected at two day intervals (beginning day 1 post-watering) throughout the study. Soil samples were placed in metal cans, weighed, and then dried in an oven at 80°C for 48 hours. Percent soil moisture on a dry weight basis was calculated for each substrate using the formula (Pritchett 1979):

$$((\text{wet wt. of soil} - \text{dry wt.}) / (\text{dry wt.})) * 100.$$

Mean percent soil moisture of each litter treatment for all dates was calculated from three samples.

Seedling emergence, survival and mortality were recorded daily throughout the study. A colored plastic toothpick was placed next to each newly emerged seedling. The color indicated the date of emergence

of each seedling and facilitated accurate determination of the fates of all seedlings.

Surviving seedlings were harvested 61 days after seeds were sown. Root and shoot lengths of all seedlings were determined and seedlings were dried to a constant weight in an oven at 80°C for 4 days. Total seedling dry weight was determined by flat, and mean seedling dry weight per treatment was calculated by dividing total dry weight by the number of seedlings harvested from each flat.

Data were analyzed by two-way ANOVA, with litter, water regime and interaction (litter X water regime) as treatment effects. Traditional multiple comparison procedures are invalid on multifactor experiments if interaction effects are significant (Mize and Schultz 1985) thus graphical means were used to indicate the source of the interaction when significant. When interactions were not significant, data were analyzed by single-factor ANOVA, and Duncan's Multiple Range Test was used to identify individual differences in treatment means. Percentage data were arcsin-transformed and other continuous data were log-transformed before analysis to ensure normality (Sokal and Rohlf 1981).

V.3 RESULTS

V.3.1 Influence of leaf litter on soil moisture

The rate of loss of soil moisture from monitoring flats differed among litter treatments (Fig. 5.1). Loss of soil moisture from litter-free flats exhibited a steep decline over each 15 day watering

interval. Soil moisture in litter-free flats generally stabilized between 1 and 3% at approximately seven days after watering except during the last watering interval when soil moisture stabilized at 10 days post-watering. Lower air temperatures at the latter part of the experiment (Fig. 5.2) may have slowed the rate of moisture during that period.

Loss of soil moisture from both pine and hardwood litter flats was similar and less rapid than that observed in litter-free flats. The decline in soil moisture in pine and hardwood litter flats was generally linear to curvilinear and exhibited far less tendency for rapid stabilization at low soil moistures than did litter-free flats. One-way ANOVA of mean soil moisture by treatment for the study was significant ($P = 0.0001$). Mean soil moisture of samples did not differ between pine (23.7%) and hardwood litter (25.2%) treatments but soil moisture was significantly less in samples from the litter-free treatment (9.0%) (Duncan's Multiple Range Test, $P \leq 0.05$).

Extrapolating from the results obtained from soil moisture monitoring flats, seedlings in 8 and 15 day water treatments would have been exposed to consistently greater soil moistures in pine and hardwood litter treatments than in litter-free treatments. Moreover, the rate of loss of soil moisture from pine and hardwood litter treatments would have been less abrupt than that observed in litter-free treatments.

V.3.2 Seedling emergence

Litter, water, and their interaction had significant impact on the emergence of *P. pungens* seedlings (Tables 5.1, 5.2; Fig. 5.3). Mean seedling emergence in litter-free (83.3%) and pine litter (80.0%) treatments was not significantly different under daily watering (Fig. 5.3) and graphs of cumulative emergence show comparable rates of emergence for both treatments (Fig. 5.6). In contrast, mean seedling emergence in daily water/hardwood litter treatments was significantly lower (56.0%) than either pine litter or litter-free treatments (Figs. 5.3, 5.6).

Mean seedling emergence did not differ significantly in litter-free (54.7%) or pine litter (65.3%) treatments receiving water every 8 days but emergence in hardwood litter (37.3%) was significantly lower (Fig. 5.3). Seedling emergence in both pine and hardwood litter peaked at an earlier date than emergence in the litter-free treatment (Fig 5.7).

The greatest differences in seedling emergence occurred among treatments receiving water at 15 day intervals (Figs. 5.3, 5.8). Mean seedling emergence was highest in pine litter (60.7%), significantly lower in hardwood litter (30.0%), and negligible in the litter-free treatment (0.02%).

V.3.3 Seedling mortality and survival

Two-way ANOVA results indicate that litter, water regime, and the interaction of these factors had a significant effect upon seedling mortality and survival (Table 5.2; Figs. 5.4, 5.5). Mean

seedling mortality was low and did not differ significantly among litter types for daily water treatments (Fig. 5.5), but differences in seedling mortality among treatments became strongly evident at 8 and 15 day watering intervals. Mean seedling mortality in pine (14.0%) and hardwood litters (3.6%) watered at 8 days did not differ significantly but mortality reached 100% in the litter-free treatment for this watering regime (Fig. 5.5). Complete seedling mortality also occurred in the litter-free treatment at 15 day watering intervals but in treatments containing leaf litter, seedling mortality was significantly lower in hardwood litter (82.2%) than in pine litter (98.9%). Graphs of cumulative seedling deaths indicate that peak seedling mortality in both 8 and 15 day water regimes for almost all litter treatments occurred between 29 and 31 days post-planting (Figs. 5.9, 5.10).

V.3.4 Seedling growth

Water regime significantly affected root lengths of *P. pungens* seedlings but the effects of litter and the interaction of litter and water was not significant (Table 5.3). Single-factor ANOVA of root length by water regime was strongly significant ($P = 0.004$). Mean root length of seedlings did not differ significantly between 1 and 8 day water regimes but was significantly less in litter treatments watered at 15 day intervals (Table 5.4).

Both litter and water regime significantly affected shoot growth of seedlings (two-way ANOVA, $P = 0.0001$; Table 5.3). The interaction

of these two factors was not significant. Mean shoot lengths of seedlings grown in pine and hardwood litter did not differ significantly and were greater than that recorded from litter-free treatments. Single-factor ANOVA found a significant effect of water on shoot growth of seedlings ($P = 0.037$) however there were no significant differences among individual treatment means (Duncan's Multiple Range Test, $P > 0.05$). These anomalous results may be due to large sample size differences among water regimes; few seedlings survived in 15 day treatments compared to the other water regimes (8 seedlings emerged in 15 day treatments but measurements from only 7 could be used).

Seedling dry weight differed significantly among water regimes but litter and the interaction of litter and water had no effect on seedling dry weight accumulation (Table 5.3). Mean seedling dry weight did not differ significantly between daily and 8 day water regimes but both were significantly greater than the mean dry weight of seedlings watered at 15 days. Seedling dry weight averaged 0.061 gm/seedling for both 1 and 8 day water treatments and 0.050 gm/seedling in 15 day treatments.

V.4 DISCUSSION

V.4.1 Effects of leaf litter on seedling emergence

Leaf litter had a substantial impact on emergence of *P. pungens* seedlings. Moreover, this impact varied with litter type. In virtually all cases, pine litter treatments exhibited significantly greater

seedling emergence than litter-free or hardwood litter treatments. Only under daily watering did emergence in the litter-free treatment approach that observed in pine litter. Hardwood litter, in all but the 15 day water regime, depressed seedling emergence relative to that recorded from pine litter and litter-free treatments. Given that soil moisture apparently did not differ between pine and hardwood litter treatments, evidence thus suggests a direct, negative effect of hardwood litter itself on emergence of *P. pungens* seedlings.

Most studies attribute the negative influence of dead, fallen hardwood leaves on seed germination and seedling emergence to physical rather than chemical properties (McPherson and Thompson 1972; Sydes and Grime 1981b). The lowered seedling emergence observed in hardwood litter treatments in this study also appears to be due in part to mechanical effects. Three lines of evidence support this conclusion.

First, seedlings that had established in hardwood litter treatments were usually clumped into areas where contact with soil could be made. In contrast, seedlings in pine litter treatments were rarely aggregated and were scattered across the flats. This observation suggests that broad hardwood leaves may provide more of a barrier both to the settling of seeds into the substrate and the penetration of seedling roots into the soil than do the linear needles of pine. Pine litter provides numerous interstices in which seeds may settle and roots can reach soil. In hardwood litter there are

comparatively fewer areas where moist soil may be reached and thus seedlings are aggregated into those sites.

Second, a number of germinated but dessicated *P. pungens* seeds were recovered from hardwood litter treatments during the harvest of seedlings. Radical elongation in dead germinants was typically less than 1 cm and most were found within leaf litter above the soil surface. Seeds that germinate in hardwood litter may be at a distinct disadvantage when moisture levels drop, particularly if hardwood litter is a barrier to penetration of roots into the soil. Germinants whose radicals are unable to reach moist soil would be prone to dessication as hardwood litter dries. Decreased seedling emergence in hardwood litter treatments may therefore largely be a result of the trapping of germinants in the litter layer, their isolation from moist soil, and their subsequent death by dessication.

Third, there were no differences in seedling growth between pine and hardwood litter treatments. Assuming that chemical factors affect seed germination and seedling growth similarly (e.g., DeBell 1971; Lodhi and Rice 1971), there appears to have been little or no allelopathic effects of leaf litter on either seedling emergence or growth. Other studies also conclude that the chemical inhibition of seed germination and seedling growth by hardwood leaf litter is relatively unimportant (McPherson and Thompson 1972; Sydes and Grime 1981b) although effects may vary with litter age (McPherson and Thompson 1972). The possible influence of chemical factors cannot be

wholly ruled out however, and further studies are needed to fully define the potential allelopathic effects of hardwood leaf litter on establishment of *P. pungens*.

V.4.2 Leaf litter, soil moisture, and the growth and survival of seedlings

Leaf litter exerted a strong influence on soil moisture and the interaction of these two factors generally had a significant effect on the growth and survival of *P. pungens* seedlings during this study. Seedling mortality was highest at the less frequent water regimes, particularly in litter-free treatments where mortality reached 100%. However, the presence of leaf litter substantially slowed the loss of moisture from soil and resulted in significantly lower mortalities at low water regimes.

In field situations, soil moisture regimes should be more favorable for seedlings growing in leaf litter than in microsites lacking litter. Establishment of pine seedlings is generally reported to be greatest in exposed mineral soil (e.g., Bramble and Goddard 1942; Fowells 1965) but little information is available concerning the differential survival of newly emerged pine seedlings in alternate substrates, particularly during drought. Although not considered in the present study, leaf litter depth may be an important determinant of *P. pungens* seedling habitat (Chapter IV). Whereas low amounts of leaf litter may enhance establishment and survival by reducing evaporation from soil (Blow 1955), deep leaf litter may be a major

barrier to seedling establishment (Koroleff 1954; Fowler 1986). Thus, litter depth and type are important variables when considering the influence of leaf litter on seedling establishment and survival.

Barden (1988) has shown that the length of rain-free intervals during the growing season is positively correlated with survival of young age classes of *P. pungens*. The results of this study show the same trend. In all cases, survival of *P. pungens* seedlings was lowest with decreased watering intervals. Although litter can mitigate the effects of infrequent water through decreased soil moisture loss, soil moisture must be replenished periodically so that moisture does not fall below a critical level. Rain-free intervals often exceed two weeks in the field [Barden (1988) implicates a 29 day drought in the low survival of *P. pungens* in his study site], and if the results of the present study may be extrapolated to the field, seedling mortality under such moisture conditions may approach 100% regardless of substrate. Thus prolonged drought, in conjunction with substrate conditions, may strongly limit recruitment and ultimately affect maintenance of *P. pungens* populations on a given site.

Table 5.1. Pinus pungens early establishment study data summary (mort. = seedling mortality, surv. = survival).

<u>No litter</u>						
<u>Water</u>	<u># Emerge</u>	<u>% Emerge</u>	<u># Dead</u>	<u>% Mort.</u>	<u># Surv.</u>	<u>% Surv.</u>
1	125	83.3	1	0.01	124	99.2
8	82	54.7	82	100.0	0	0.0
15	3	0.02	3	100.0	0	0.0

<u>Pine litter</u>						
<u>Water</u>	<u># Emerge</u>	<u>% Emerge</u>	<u># Dead</u>	<u>% Mort.</u>	<u># Surv.</u>	<u>% Surv.</u>
1	120	80.0	2	1.7	118	98.3
8	98	65.3	12	14.0	86	87.8
15	91	60.7	90	98.9	1	1.1

<u>Oak litter</u>						
<u>Water</u>	<u># Emerge</u>	<u>% Emerge</u>	<u># Dead</u>	<u>% Mort.</u>	<u># Surv.</u>	<u>% Surv.</u>
1	84	56.0	3	3.7	81	96.4
8	56	37.3	2	3.6	54	96.4
15	45	30.0	37	82.2	8	17.8

Table 5.2. Analysis of variance of percent germination, mortality, and survival of *Pinus pungens* seedlings by litter type, water regime and interaction.

<u>% Germination</u>				
Source of variation	df	ms	F	P
Litter	2	1707.2520	31.13	0.0001
Water	2	4045.9422	73.77	0.0001
Litter X water	4	1298.3712	23.67	0.0001
Error (flats)	45	2467.9299	--	--

<u>% Mortality</u>				
Source of variation	df	ms	F	P
Litter	2	7561.4276	27.81	0.0001
Water	2	40632.8804	149.47	0.0001
Litter X water	4	15627.2367	28.74	0.0001
Error (flats)	45	135.9249	--	--

<u>% Survival</u>				
Source of variation	df	ms	F	P
Litter	2	5366.3283	43.36	0.0001
Water	2	27302.2918	220.63	0.0001
Litter X water	4	4126.5165	33.35	0.0001
Error (flats)	45	123.7496	--	--

Table 5.3. Analysis of variance of growth variables for *Pinus pungens* seedlings by litter type, water regime, and interaction.

<u>Root length</u>				
Source of variation	df	ss	F	P
Litter	2	6750.3956	2.06	0.1289
Water	2	24003.7861	7.32	0.0007
Litter X water	2	7337.0248	2.24	0.1079
Error (seedlings)	466	1639.9816	--	--

<u>Shoot length</u>				
Source of variation	df	ss	F	P
Litter	2	9038.6514	72.52	0.0001
Water	2	569.3686	4.57	0.0108
Litter X water	2	99.1796	0.80	0.4518
Error (seedlings)	464	62.3147	--	--

<u>Seedling dry weight</u>				
Source of variation	df	ss	F	P
Litter	2	0.0001	1.78	0.1880
Water	2	0.0022	32.17	0.0001
Litter X water	2	0.0002	2.65	0.0889
Error (flats)	27	0.0009	--	--

Table 5.4. Mean root and shoot lengths of *Pinus pungens* seedlings by litter type and water regime. The interaction of these two factors was not significant. Means bearing the same letter do not differ statistically (Duncan's Multiple Range Test, $P > 0.05$). Sample sizes for means are contained in parentheses.

<u>\bar{X} Length (mm)</u>		
<u>Litter type</u>	<u>Root</u>	<u>Shoot</u>
No litter	140.9 (n = 121)	48.8a (n = 124)
Pine litter	137.8 (n = 204)	59.3b (n = 204)
Oak litter	131.1 (n = 142)	58.3b (n = 143)

<u>\bar{X} Length (mm)</u>		
<u>Water regime</u>	<u>Root</u>	<u>Shoot</u>
1	133.8a (n = 318)	55.6a (n = 322)
8	144.4a (n = 142)	57.6a (n = 142)
15	104.7b (n = 7)	52.6a (n = 7)

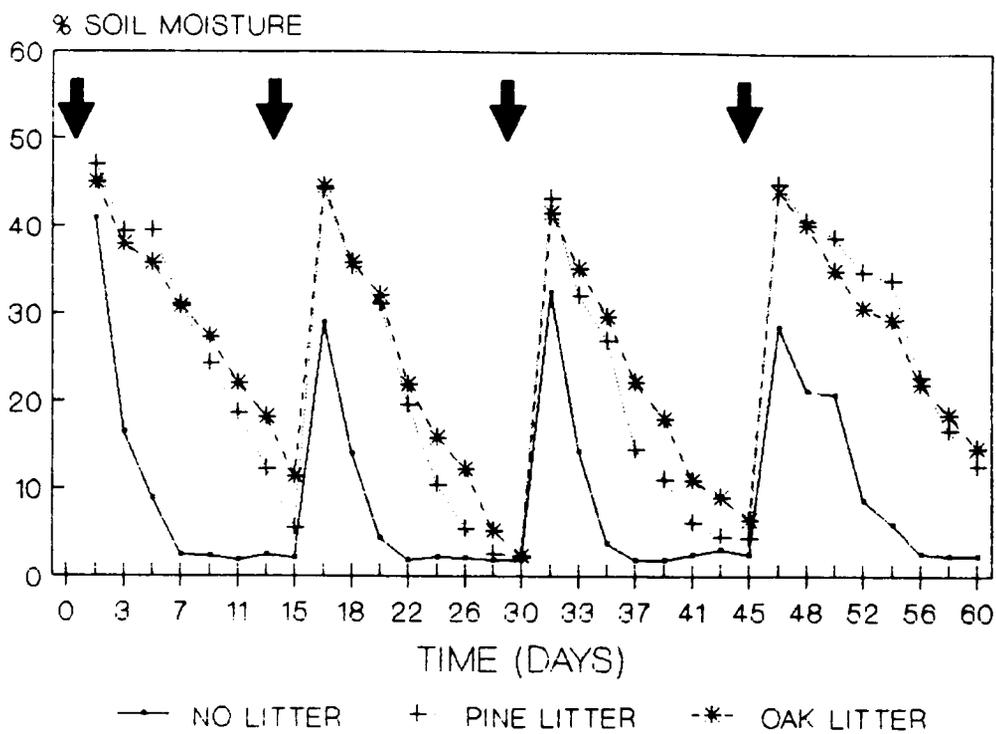


Figure 5.1. Mean percent soil moisture recorded from monitoring flats with different types. Arrows indicate dates when flats were watered.

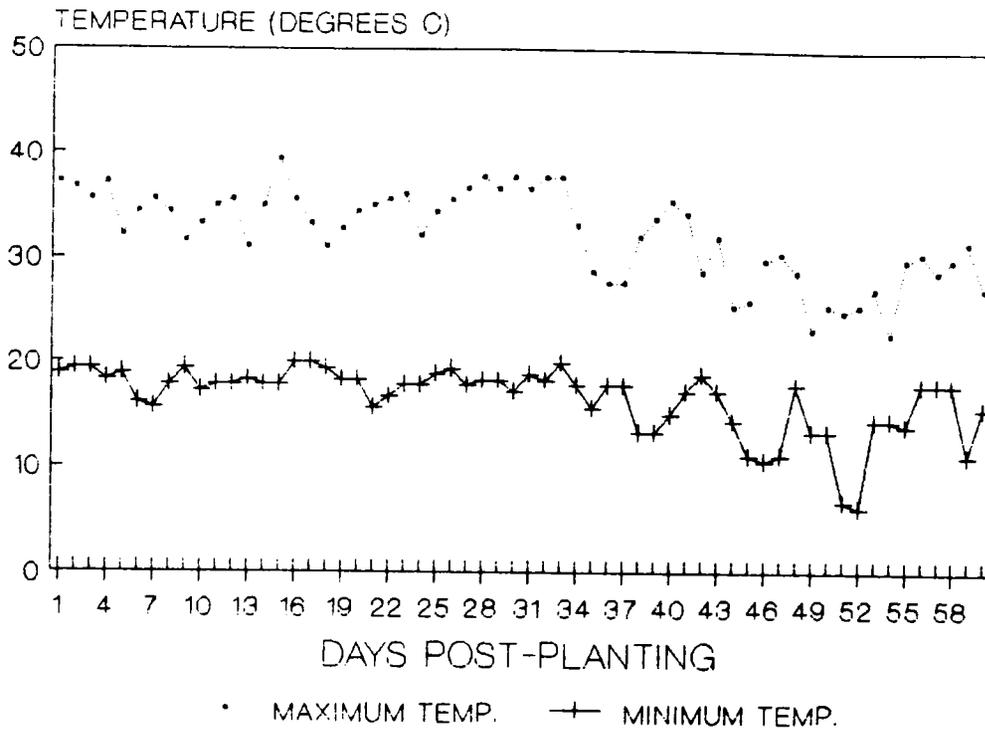
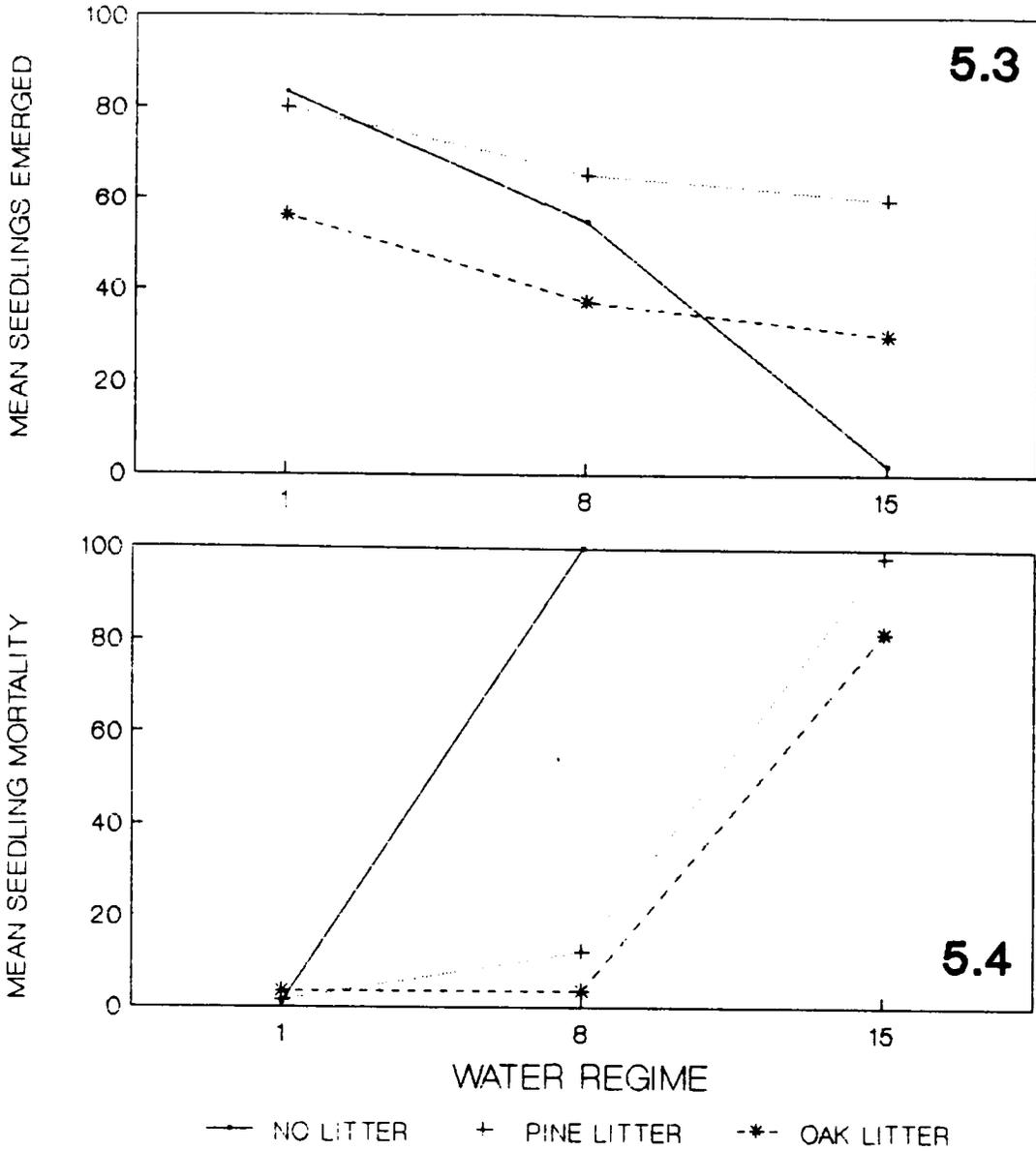
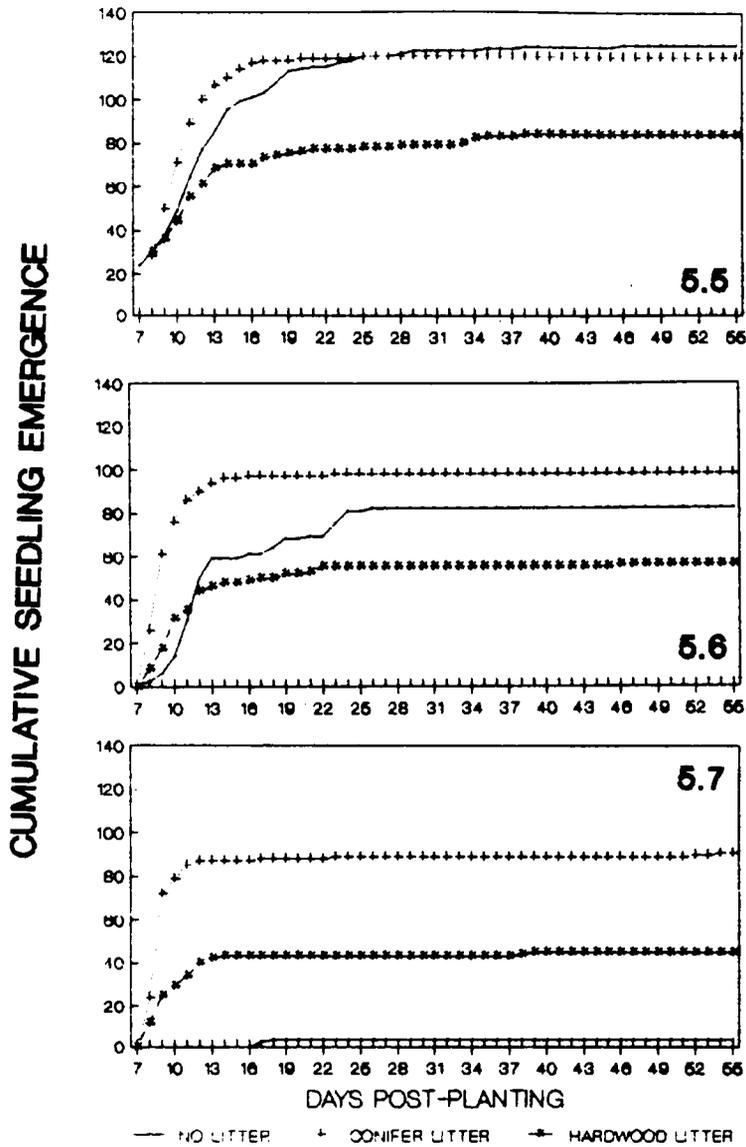


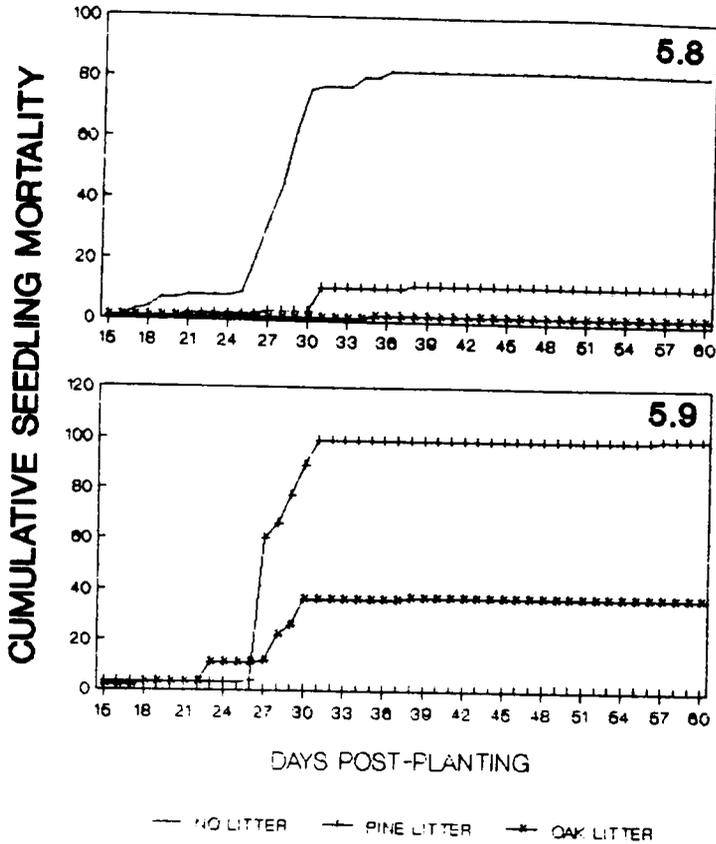
Figure 5.2. Maximum and minimum greenhouse temperatures ($^{\circ}\text{C}$) recorded during the study.



Figures 5.3 - 5.4. Cell means for treatment combinations. Fig. 5.3 - Mean emergence of *Pinus pungens* seedlings. Fig. 5.4 - Mean mortality of *P. pungens* seedlings.



Figures 5.5 - 5.7. Cumulative emergence of *Pinus pungens* seedlings by litter type and water regime. Fig. 5.5 - Emergence of seedlings watered daily. Fig. 5.6 - Emergence of seedlings watered at 8 day intervals. Fig. 5.7 - Emergence of seedlings watered at 15 day intervals.



Figures 5.8 - 5.9. Cumulative mortality of *Pinus pungens* seedlings by litter type and water regime. Mortality of seedlings watered daily was low and is not presented here. Fig. 5.8 - Mortality of seedlings watered at 8 day intervals by litter type. Fig. 5.9 - Mortality of seedlings watered at 15 day intervals by litter type. Mortality of litter-free treatments under this regime are not shown because of low emergence.

VI. CONCLUSIONS

The results of this study indicate that in the absence of fire, maintenance of *P. pungens* populations in pine-oak forest is unlikely. Whittaker's (1956) hypothesis that maintenance of *P. pungens* in pine-oak forest occurs by gap replacement processes is unsubstantiated. Lack of suitable seedling habitat in conjunction with low seed rain, suppressed seedling, sapling and understory age classes, and the prevalence of gap-exploiting woody species indicate that gap replacement would not contribute to *P. pungens* maintenance in the pine-oak forests of Brush Mountain.

Competition for space and resources with shade-tolerant hardwoods and the degradation of seedling habitat through hardwood litter accumulation are major obstacles for pine regeneration in pine-oak forest. Hardwood litter is a barrier to *P. pungens* seedling establishment and as oaks increase in importance, litter inputs and accumulations also increase. Hardwood litter enhances the germination and survival of oak seedlings (Barrett 1931; Wood 1938) and hardwood litter accumulations would favor oak advance regeneration over pines. Thus site modification by hardwoods leads to conditions detrimental to pine recruitment but favorable for establishment of hardwood seedlings, particularly oaks.

Dry, exposed ridges and outcrops are likely sites where populations of *P. pungens* might be maintained in the absence of fire (Barden 1977, 1988). Regeneration of *P. pungens* on sites favorable for

the growth of hardwoods would be possible only if sites were modified by fire. Non-fire disturbance, such as canopy removal by ice storms, would not destroy competing hardwoods or provide seedbed conditions suitable for pine establishment but instead would release hardwood advance regeneration. A pulse-reset disturbance regime (Reiners 1979), incorporating fire at frequent intervals, would be optimal for the maintenance of P. pungens on sites favorable for the growth of hardwoods.

VII. LITERATURE CITED

- Abbott, H. G. 1961. White pine seed consumption by small mammals. *J. For.* 59:197-201.
- Abbott, H. G. and T. F. Quink. 1970. Ecology of eastern white pine seed caches made by small forest mammals. *Ecology* 51:271-278.
- Adams, H. S. and S. L. Stephenson. 1983. A description of the vegetation on the south slopes of Peters Mountain, southwestern Virginia. *Bull. Torrey Bot. Club* 110:18-22.
- Ahlgren, C. E. 1959. Some effects of fire on forest reproduction in northeastern Minnesota. *J. For.* 57:194-200.
- Ahlgren, C. E. 1966. Small mammals and reforestation following prescribed burning. *J. For.* 64:614-618.
- Al-Naib, F. A. and E. L. Rice. 1971. Allelopathic effects of Platanus occidentalis. *Bull. Torrey Bot. Club* 98:75-82.
- Arno, S. F. and K. M. Sneek. 1977. A method for determining fire history in coniferous forests of the mountain west. USDA Forest Service Gen. Tech. Rep. INT-42.
- Auclair, A. N. and G. Cottam. 1971. Dynamics of black cherry (Prunus serotina Ehrh.) in southern Wisconsin oak forests. *Ecol. Monogr.* 41:153-177.
- Barden, L. S. 1977. Self-maintaining populations of Pinus pungens Lam. in the southern Appalachian Mountains. *Castanea* 42:316-323.
- Barden, L. S. 1979. Serotiny and seed viability of Pinus pungens in the southern Appalachian Mountains. *Castanea* 44:44-47.
- Barden, L. S. 1988. Drought and survival in a self-perpetuating Pinus pungens population: equilibrium or nonequilibrium? *Am. Midl. Nat.* 119:253-257.
- Barden, L. S. and F. W. Woods. 1973. Characteristics of lightning fires in southern Appalachian forests. *Proc. Annual Tall Timbers Fire Ecol. Conf.* 13:345-361.
- Barden, L. S. and F. W. Woods. 1976. Effects of fire on pine and pine-hardwood forests in the southern Appalachians. *For. Sci.* 22:399-403.

- Barrett, L. I. 1931. Influence of forest litter on the germination and early survival of chestnut oak, Quercus montana Willd. Ecology 12:476-484.
- Beatty, S. W. and O. D. V. Sholes. 1988. Leaf litter effect on plant species composition of deciduous forest treefall pits. Can. J. For. Res. 18:553-559.
- Bergeron, Y. and D. Gagnon. 1987. Age structure of red pine (Pinus resinosa Ait.) at its northern limit in Quebec. Can. J. For. Res. 17:129-137.
- Blow, F. E. 1955. Quantity and hydrologic characteristics of litter under upland oak forests in eastern Tennessee. J. For. 53:190-195.
- Boerner, R. E. J., S. D. Runge, D. Cho and J. G. Kooser. 1988. Localized ice storm damage in an Appalachian Plateau watershed. Am. Midl. Nat. 119:199-208.
- Bramble, W. C. and M. K. Goddard. 1942. Effect of animal coaction and seedbed condition on regeneration of pitch pine in the barrens of central Pennsylvania. Ecology 23:330-335.
- Buchholz, K. 1983. Initial responses of pine and oak to wildfire in the New Jersey Pine Barren Plains. Bull. Torrey Bot. Club 110:91-96.
- Burns, R. M. 1983. Silvicultural systems for the major forest types of the United States. USDA Forest Service Agriculture Handbook 445.
- Christiansen, N. L. 1985. Shrubland fire regimes and their evolutionary consequences. pp. 85-100. In S. T. A. Pickett and P. S. White (eds.), The ecology of natural disturbance and patch dynamics. Academic Press. New York.
- Christiansen, N. L. and R. K. Peet. 1984. Convergence during secondary forest succession. J. Ecol. 72:25-26.
- Chrosiewicz, Z. 1974. Evaluation of fire-produced seedbeds for jack pine regeneration in central Ontario. Can. J. For. Res. 4:455-457.
- Clark, J. S. 1986. Coastal forest tree populations in a changing environment, southeastern Long Island, New York. Ecol. Monogr. 56:259-277.
- Collins, S. L. and R. E. Good. 1987. The seedling regeneration niche: habitat structure of tree seedlings in oak-pine forest. Oikos 48:89-98.

- Conner, R. N., J. W. Via and I. D. Prather. 1979. Effects of pine-oak clearcutting on winter and breeding birds in southwestern Virginia. *Wilson Bull.* 91:301-316.
- Cregar, W. H., H. C. Hudson and H. C. Porter. 1985. Soil survey of Montgomery County, Virginia. USDA Soil Conservation Service.
- Crutchfield, D. M. and I. F. Trew. 1961. Investigation of natural regeneration of pond pine. *J. For.* 59:264-266.
- Curtis, J. T. and R. P. McIntosh. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. *Ecology* 32:476-496.
- DeBell, D. S. 1971. Phytotoxic effects of cherrybark oak. *For. Sci.* 17:180-185.
- Despain, D. G. 1983. Nonpyrogenous climax lodgepole pine communities in Yellowstone National Park. *Ecology* 64:231-234.
- Feret, P. P. 1974. Genetic differences among three small stands of Pinus pungens. *Theoret. and Appl. Genetics* 44:173-174.
- Feret, P. P., D. Wm. Smith and H. M. Rauscher. 1979. Dry matter accumulation in twenty wind-pollinated Pinus pungens families from southwest Virginia. *Silvae Genetica* 28:194-196.
- Fowells, H. A. (compiler). 1965. Silvics of forest trees of the United States. USDA Forest Service Agriculture Handbook 271.
- Fowler, N. L. 1986. Microsite requirements for germination and establishment of three grass species. *Am. Midl. Nat.* 115:131-145.
- Frothingham, E. H. 1931. Timber growing and logging practice in the southern Appalachian region. USDA Tech. Bull. 250.
- Gashwiler, J. S. 1967. Conifer seed survival in a western Oregon clearcut. *Ecology* 48:431-438.
- Gashwiler, J. S. 1970. Further study of conifer seed survival in a western Oregon clearcut. *Ecology* 51:849-854.
- Geritz, S. A. H., T. J. DeJong and P. G. L. Kirkhamer. 1984. The efficacy of dispersal in relation to safe site area and seed production. *Oecologia* 62:219-221.
- Gibson, D. J. and R. E. Good. 1987. The seedling habitat of

Pinus echinata and Melampyrum lineare in oak-pine forest of the New Jersey Pinelands. *Oikos* 49:91-100.

Grubb, P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* 52:107-145.

Harcombe, P. A. and P. L. Marks. 1978. Tree diameter distributions and replacement processes in southeast Texas forests. *For. Sci.* 24:153-166.

Harmon, M. 1982. Fire history of the westernmost portion of Great Smoky Mountains National Park. *Bull. Torrey Bot. Club* 109:74-79.

Harper, J. L. 1977. Population biology of plants. Academic Press. New York.

Hedlin, A. F., H. O. Yates, III, D. C. Tovar, B. H. Ebel, T. W. Koerber and E. P. Merkel. 1981. Cone and seed insects of North American conifers. USDA Forest Service Coop. Publ.

Hett, J. M. 1971. A dynamic analysis of age in sugar maple seedlings. *Ecology* 52:1071-1074.

Hewlette, C. S. 1977. Relationships between forest cutting and understory vegetation: an overview of eastern hardwood stands. USDA Forest Service Res. Note SE-349.

Hoffman, R. L. 1977. The biotic regions of Virginia. The Insects of Virginia 1:23-67. Virginia Polytechnic Institute and State University Research Publication Series.

Holla, T. A. and P. Knowles. 1988. Age structure analysis of a virgin white pine, Pinus strobus, population. *Can. Field-Nat.* 102:221-226.

Hough, A. F. 1937. A study of natural tree reproduction in the beech-birch-maple-hemlock type. *J. For.* 35:376-378.

Hughes, J. W., T. J. Fahey and F. H. Bormann. 1988. Population persistence and reproductive ecology of a forest herb: Aster acuminatus. *Amer. J. Bot.* 75:1057-1064.

Johnson, W. C., D. M. Sharpe, D. L. DeAngelis, D. E. Fields, and R. J. Olson. 1981. Modeling seed dispersal and forest island dynamics. pp. 215-239. In R. L. Burgess and D. M. Sharpe (eds.), *Forest island dynamics in man-dominated landscapes*. Springer-Verlag. New York.

- Johnson, W. C. and T. Webb, III. 1989. The role of blue jays (*Cyanocitta cristata* L.) in postglacial dispersal of fagaceous trees in eastern North America. *J. Biogeogr.* In press.
- Kleinbaum, D. G. and L. L. Kupper. 1978. *Applied regression analysis and other multivariable methods.* Duxbury Press. Boston, MA.
- Koroleff, A. 1954. Leaf litter as a killer. *J. For.* 52:178-187.
- Kramer, P. J., H. J. Oosting and C. F. Korstian. 1952. Survival of pine and hardwood seedlings in forest and open. *Ecology* 33:427-430.
- Kuchler, A. W. 1964. *Manual to accompany the map of potential natural vegetation of the conterminous United States.* Amer. Geogr. Soc. Special Publ. No. 36.
- Leak, W. B. 1975. Age distribution in virgin red spruce and northern hardwoods. *Ecology* 56:1451-1454.
- Lee, R. 1978. *Forest microclimatology.* Columbia University Press. New York.
- Lenmon, P. E. 1956. A spherical densiometer for estimating forest overstory density. *For. Sci.* 2:314-320.
- Lenmon, P. E. 1957. A new instrument for measuring forest overstory density. *J. For.* 55:667-668.
- Lipscomb, M. V. 1986. The influence of water and light on the physiology and spatial distributions of three shrubs in the southern Appalachian Mountains. Thesis. Virginia Polytechnic Institute and State University, Blacksburg, VA.
- Lipscomb, M. V. and E. T. Nilsen. Environmental and physiological factors influencing the natural distributions of evergreen and deciduous ericaceous shrubs on north and south slopes of the southern Appalachian Mountains. I. Microhabitat and vegetation. Unpublished manuscript.
- Little, E. L., Jr. and W. B. Critchfield. 1969. Subdivisions of the genus *Pinus* (pines). USDA Forest Service Misc. Publ. No. 1144.
- Little, S. 1979. Fire and plant succession in the New Jersey Pine Barrens. pp. 297-314. In R. T. T. Forman (ed.), *Pine Barrens: ecosystem and landscape.* Academic Press. New York.
- Little, S. and E. B. Moore. 1949. The ecological role of

prescribed burns in the pine-oak forests of southern New Jersey. *Ecology* 30:223-233.

Little, S. and H. A. Somes. 1964. Releasing pitch pine sprouts from old stools ineffective. *J. For.* 62:23-26.

Lodhi, M. A. K. 1978. Allelopathic effects of decaying litter of dominant trees and their associated soil in a lowland forest community. *Amer. J. Bot.* 65:340-344.

Lodhi, M. A. K. and E. L. Rice. 1971. Allelopathic effects of Celtis laevigata. *Bull. Torrey Bot. Club* 98:83-89.

McClanahan, T. R. 1986. The effect of a seed source on primary succession in a forest ecosystem. *Vegetatio* 65:175-178.

McCune, B. 1988. Ecological diversity in North American pines. *Amer. J. Bot.* 75:353-368.

McIntyre, A. C. 1929. A cone and seed study of the mountain pine (Pinus pungens Lambert). *Amer. J. Bot.* 16:402-406.

McMaster, G. S. and P. H. Zedler. 1981. Delayed seed dispersal in Pinus torreyana. *Oecologia* 51:62-66.

McPherson, J. K. and G. L. Thompson. 1972. Competitive and allelopathic suppression of understory by Oklahoma oak forests. *Bull. Torrey Bot. Club* 99:293-300.

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

Milne, B. T. 1985. Upland vegetational gradients and post-fire succession in the Albany Pine Bush, New York. *Bull. Torrey Bot. Club* 112:21-34.

Mittlebach, G. G. and K. L. Gross. 1984. Experimental studies of seed predation in old fields. *Oecologia* 65:7-13.

Mize, C. W. and R. C. Schultz. 1985. Comparing treatment means correctly and appropriately. *Can. J. For. Res.* 15:1142-1148.

Mollenhauer, W., Jr. 1939. Table mountain pine - squirrel food or timber tree? *J. For.* 37:420-421.

Mood, A. M. 1950. Introduction to the theory of statistics. McGraw-Hill. New York.

Mowbray, T. B. and H. J. Oosting. 1968. Vegetation gradients in relation to environment and phenology in a southern Blue Ridge gorge. *Ecol. Monogr.* 38:309-344.

Myers, R. L. 1985. Fire and the dynamic relationship between Florida sandhill and sand pine scrub vegetation. *Bull. Torrey Bot. Club* 112:241-252.

Nicholas, N. S. and P. S. White. 1984. The effect of the southern pine beetle on fuel loading in yellow pine forests of Great Smoky Mountains National Park. USDI National Park Service. Research/Resources Management Rep. SER-73.

Olson, D. F. and R. G. McAlpine. 1973. Oak-pine. pp. 83-86. In R. M. Burns (compiler), *Silvicultural systems for the major forest types of the United States*. USDA Forest Service Agriculture Handbook 445.

Parker, A. J. 1986. Persistence of lodgepole pine forests in the central Sierra Nevada. *Ecology* 67:1560-1567.

Parker, A. J. and R. K. Peet. 1984. Size and age structure of conifer forests. *Ecology* 65:1685-1689.

Pitelka, L. F., D. S. Stanton and M. O. Peckenham. 1980. Effects of light and density on resource allocation in a forest herb, Aster acuminatus (Compositae). *Amer. J. Bot.* 67:942-948.

Pritchett, W. L. 1979. Properties and management of forest soils. John Wiley and Sons. New York.

Radvanyi, A. 1970. Small mammals and regeneration of white spruce forests in western Alberta. *Ecology* 51:1102-1105.

Reiners, W. A. 1979. Ecological research opportunities in the New Jersey Pine Barrens. pp. 557-567. In R. T. T. Forman (ed.) *Pine barrens: ecosystem and landscape*. Academic Press. New York.

Rosenzweig, M. L. 1973. Habitat selection experiments with a pair of coexisting species. *Ecology* 54:111-117.

Ross, M. S., T. L. Sharik and D. W. Smith. 1982. Age-structure relationships in an Appalachian oak forest in southwest Virginia. *Bull. Torrey Bot. Club* 109:287-298.

Sargent, C. S. 1884. Report on the forests of North America. USDI Census Office. U.S. Govt. Printing Office. Washington, DC.

- Schopmeyer, C. S. (tech. coord.) 1974. Seeds of woody plants in the United States. USDA Forest Service Agriculture Handbook No. 450.
- Selter, C. M., W. D. Pitts and M. G. Barbour. 1986. Site microenvironment and seedling survival of Shasta red fir. *Am. Midl. Nat.* 115:288-300.
- Sharik, T. L., M. S. Ross and A. H. Price. 1983. A micro-borer for extracting increment cores from small stems of woody plants. *For. Sci.* 29:329-331.
- Silvertown, J. W. 1980. The evolutionary ecology of mast seeding in trees. *Biol. J. Linn. Soc.* 14:235-250.
- Smith, C. F. and S. E. Aldous. 1947. The influence of mammals and birds in retarding artificial and natural reseeding of coniferous forests in the United States. *J. For.* 45:361-369.
- Smith, D. Wm. and N. E. Linnartz. 1980. The southern hardwood region. pp. 145-230. In J. W. Barrett (ed.), *Regional silviculture of the United States*. John Wiley and Sons. New York.
- Sokal, R. R. and F. J. Rohlf. 1981. *Biometry*. 2nd edition. W. H. Freeman and Co. New York.
- Stephenson, S. L., H. S. Adams and M. L. Lipford. 1986. Ecological composition of indigenous stands of red pine (*Pinus resinosa*) in West Virginia. *Castanea* 51:31-41.
- Stoneburner, D. L. 1978. Evidence of hurricane influence on barrier island slash pine forest in the northern Gulf of Mexico. *Am. Midl. Nat.* 99:234-237.
- Sydes, C. and J. P. Grime. 1981a. Effects of tree leaf litter on herbaceous vegetation in deciduous woodland. I. Field investigations. *J. of Ecol.* 69:237-248.
- Sydes, C. and J. P. Grime. 1981b. Effects of tree leaf litter on herbaceous vegetation in deciduous woodland. II. An experimental investigation. *J. of Ecol.* 69:249-262.
- Tevis, L., Jr. 1953. Effect of vertebrate animals on seed crop of sugar pine. *J. Wildl. Manage.* 17:128-131.
- Webb, S. L. and M. F. Wilson. 1985. Spatial heterogeneity in post-dispersal predation on *Prunus* and *Uvularia* seeds. *Oecologia* 67:150-153.

- White, P. S. 1987. Natural disturbance, patch dynamics, and landscape pattern in natural areas. *Natural Areas Journal* 7:14-22.
- Whitney, H. E. and W. C. Johnson. 1984. Ice storms and forest succession in southwestern Virginia. *Bull. Torrey Bot. Club* 111:429-437.
- Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. *Ecol. Monogr.* 26:1-80.
- Williamson, G. B. and E. M. Black. 1981. High temperatures of forest fires under pines as a selective advantage over oaks. *Nature* 293:343-344.
- Wilson, J. 1902. A report of the Secretary of Agriculture in relation to the forests, rivers, and mountains of the southern Appalachian region. U.S. Govt. Printing Office. Washington, DC.
- Wood, O. M. 1938. Seedling reproduction of oak in southern New Jersey. *Ecology* 19:276-293.
- Yeaton, R. I. 1983. The effect of predation on the elevational replacement of digger pine by ponderosa pine on the western slopes of the Sierra Nevada. *Bull. Torrey Bot. Club* 110:31-38.
- Zar, J. H. 1984. *Biostatistical analysis*. 2nd edition. Prentice-Hall. Englewood Cliffs, NJ.
- Zobel, D. B. 1969. Factors affecting the distribution of Pinus pungens, an Appalachian endemic. *Ecol. Monogr.* 39:303-333.
- Zobel, D. B. 1970. Morphological characterization of Pinus pungens. *J. Elisha Mitchell Sci. Soc.* 86:214-221.

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