

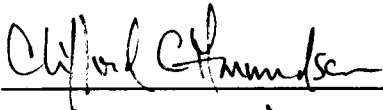
To the Graduate Council:

I am presenting herewith a dissertation written by Eric Frank Pauley entitled "The Influence of Episodic Reproduction by Red Spruce on Long-term Forest Dynamics in the Cranberry Wilderness, West Virginia." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology.

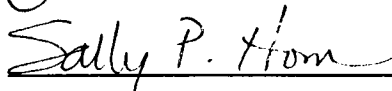


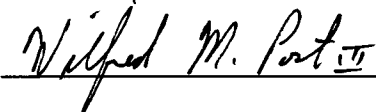
Edward E. C. Clebsch, Major Professor

We have read this dissertation
and recommend its acceptance:









Accepted for the Council:



Associate Vice Chancellor
and Dean of The Graduate School

The Influence of Episodic Reproduction by Red Spruce on Long-term Forest
Dynamics in the Cranberry Wilderness, West Virginia

A Dissertation

Presented for the
Doctor of Philosophy
Degree

The University of Tennessee, Knoxville

Eric Frank Pauley

May, 1993

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ABSTRACT

Episodic reproduction ("masting") by shade-tolerant tree species could be a significant influence on long-term forest dynamics. A recent episode of high seed production by red spruce (Picea rubens Sarg.) in second-growth (64-71 yr old) forests of the Cranberry Wilderness, West Virginia provided an opportunity to examine seedling mortality, the development of seedling spatial patterns, and possible effects of reproductive episodes on long-term forest dynamics.

Canopy conditions in the spruce forests were quantified to infer their future influences on regeneration. Spruce comprised 81% of the live basal area and 65% of live stems. Most live spruce were in codominant crown positions, while dead spruce were mostly small, suppressed trees. One third of live spruce, mostly intermediate or suppressed trees, showed >10% needle loss and had below-average crown ratios. Over half of live spruce showed some loss of recent needles, and 64% showed narrowed or one-sided crowns. Little evidence of fungal or insect pathogens was found. These data suggest typical post-logging stand development. Continued dominance by spruce in the canopy should favor shade-tolerant spruce seedlings.

A large seed crop by spruce in Cranberry generated 2,944,000 new seedlings per hectare by August 1990. Changes in $\log_e(\text{density})$ of this cohort were adequately explained by linear and negative exponential survivorship curves. A power function fit the data less well. These models gave widely differing predictions of seedling density after 5 yr. The linear function suggested little effect of this cohort on seedling

pool size, the negative exponential model suggested that pool size would triple, and the power function predicted that pool size would increase 8-fold. First-year mortality was inversely correlated with initial density, indicating that conditions favoring germination also favored early survival. Seedling associations with rooting substrates changed erratically, perhaps because of the shallow rooting of seedlings. A strong association of seedlings with bryophyte-covered surfaces developed early and persisted. Declining seedling mortality, implicit in the negative exponential and power models, should allow this cohort to dominate the seedling pool for several years.

The long-term effects of such episodic recruitment were assessed with a forest gap model. An existing model was modified to simulate semi-periodic recruitment of spruce in West Virginia forests under several scenarios: logging, varying available soil nitrogen, a 50% spruce growth decline, and varying nitrogen combined with spruce decline. Episodic recruitment reduced the importance of yellow birch (Betula alleghaniensis Britton), even after logging. Varying soil nitrogen reduced birch importance with or without spruce masting. A spruce growth decline allowed birch to become more important, but masting moderated decline effects. Varying nitrogen combined with spruce decline resulted in low spruce and birch basal areas and high densities of spruce and red maple (Acer rubrum L.). The addition of masting to this scenario nearly eliminated birch. Masting appeared to act as a stabilizing influence on spruce dominance by reducing recruitment of its competitors. Highly variable seedling recruitment may noticeably influence long-term forest dynamics.

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CHAPTER 1

INTRODUCTION

"Who can put the boundary between perturbations in systems too small to matter and long-term patterns of appropriate generality?"

(Gould 1989, p. 22)

The structure of an ecological community at any point in time is the result of a sequence of events. The importance of particular events in shaping that structure is occasionally obvious. For example, the species composition and age structure of some forests in Puerto Rico are affected by hurricanes passing near the island about every 60 years (Scatena and Larsen 1991). The vegetation of Yellowstone National Park reflects a long history of natural fires (Romme and Despain 1989). Nearly all forests in eastern North America have been cleared for farmland, burned intentionally or unintentionally, logged, or otherwise disturbed by humans. Events like these leave lasting impressions on community composition and structure.

Changes in community structure occur over a wide range of spatial and temporal scales. Climatic changes over the last 20,000 years have produced major changes in the composition and distribution of temperate zone vegetation (Huntley and Birks 1983; Delcourt and Delcourt 1987; Liu 1988). Regional climates, interacting with geology, topography, and species dispersal capabilities, have defined the broad limits of terrestrial communities and the ranges of their component species.

Within a region, variations in topography, weather patterns, substrates, and species dispersal all constrain habitat availability for those species. At the scale of the "stand" or other concrete example of a community, interactions among organisms become important in determining the abundance, distribution, and population structure of species. Individuals appear, grow, use resources, reproduce, and die, all while interacting with other organisms engaged in similar activities.

Clearly, large-scale ecological processes constrain smaller-scale processes. However, the reverse is not so clear. To what extent do small-scale, short-term processes affect or even constrain larger-scale processes? How do properties of individuals and populations affect the structure and dynamics of whole communities and ecosystems? Small-scale processes determine what is available to be acted upon by processes operating at larger scales. For example, all trees in a forest must first be seedlings; therefore, the small-scale processes controlling the seedling survival will influence large-scale forest dynamics. The broad goal of this study was to investigate the long-term consequences of small-scale processes in a forest community. More specifically, this study aimed to determine the role that episodic reproduction plays in the population dynamics of a dominant tree species.

Many temperate tree species produce seeds every year, but seed crop size can be extremely variable. A whole population of trees can produce major seed crops synchronously at intervals of two or more years, with little seed production by most trees in the intervening years. In taxa whose large seeds are important wildlife food (e.g., Quercus, Fagus), such episodic reproduction is called "masting." The

causes of masting in trees are not fully understood but certainly involve a number of factors. The synchrony in seed production may be effected by regional climatic conditions. The initiation of flower bud production is often cued by temperature and moisture combinations in the year preceding flowering and fruiting (Burns and Honkala 1990). The timing between successive seed crops is influenced by the physiological status of each tree. Several years may be required for a tree to regain stored energy and nutrients used to produce a large seed crop (e.g., Eis et al. 1965). Seed predation may be partially responsible for the maintenance and timing of synchronous reproduction. Masting may satiate the appetites of seed predators, thereby ensuring that at least some seeds escape to germinate (Janzen 1971; Silvertown 1980, 1982). The trees may satiate seed predators one year while starving them for several years thereafter, preventing predators from surviving long enough to reproduce. Thus, heavy seed predation may favor trees showing masting (Silvertown 1980).

Once dispersed, a seed can die, germinate, or become dormant as part of a reserve or "pool" of seeds stored in the soil. Dormancy may last months, years, or even decades, and is broken by environmental cues such as light, temperature, and/or moisture. If there is little variation in the response of seeds to environmental cues and these cues are widespread (e.g., warm spring temperatures), then large numbers of seeds may germinate simultaneously.

Maintaining a seed pool is one of two general strategies used by tree species to maintain their populations. Another strategy is to maintain a pool of established seedlings. Tree species differ in the

ability of juveniles to survive in shade, and shade tolerance is a major factor controlling forest composition and dynamics. Seedlings of shade-intolerant species (e.g., Liriodendron tulipifera L., Prunus pensylvanica L.f.) require high light levels to survive, and such species are most successful in large forest openings. Shade-tolerant species (e.g., Acer saccharum Marsh., Picea rubens Sarg., Tsuga canadensis (L.) Carr.) can persist as seedlings for decades in deep shade at low growth rates, and such species can successfully exploit small gaps in a forest canopy. Shade-intolerant species tend to maintain seed pools, while shade-tolerant species tend to maintain pools of established seedlings (Canham and Marks 1985).

The outcome of either strategy is the acquisition of canopy status by individual trees. Because only one seedling need survive to replace a canopy tree, the number of seedlings involved in canopy replacement may seem unimportant to the extent that it is sufficient. However, the high fecundity typical of forest trees can enable seeds to colonize a wide range of microsites, allowing them to capture canopy positions not occupied by conspecifics. In shade-tolerant tree species (e.g., Picea rubens), episodes of high fecundity and seedling establishment could allow such a species to saturate the seedling pool and exclude other species. Thus, a short-term reproductive event may have lasting effects on the size, age structure, and spatial patterns of a tree population.

Most studies of spatial distribution in plants find pattern at some scale, but it is often difficult to determine the processes by which spatial patterns are generated. Initial patterns are imposed by dispersal mechanisms, but later patterns are superimposed by factors

allowing survival. Microhabitats suitable for plant establishment have been termed "safe sites" (Harper et al. 1965; Harper 1977). For example, a number of studies have found that tree seedlings can be unexpectedly abundant on certain rooting substrates, such as fallen logs. Once established, a plant cannot move by itself (except by directional growth), and the development of spatial patterns different from those of seeds must occur by site-specific mortality. The mortality processes producing spatial patterns in trees have rarely been documented. Large, discrete cohorts of seedlings provide convenient opportunities to quantify these processes.

Red spruce (Picea rubens) in the Cranberry Wilderness, West Virginia produced a heavy seed crop in 1989, resulting in the appearance of nearly 3×10^6 newly germinated seedlings per hectare by August 1990. Can such a large pulse of germination in this shade-tolerant species build up the seedling pool to the extent that spruce will continue to dominate the forest after the current even-aged canopy dies? Or do those seedlings suffer such heavy mortality that the long-term effect of a reproductive episode is negligible and other species dominate the next stand? Because seedling mortality may not be uniform across the forest floor mosaic, pulses of seedling establishment may allow dominance on the most favorable microsites to affect the future spatial pattern of trees. The central objective of this study was to determine how episodic reproduction in red spruce affects the size and spatial distribution of the seedling pool and, ultimately, the composition of the forest canopy. The seed crop of 1989 and its resulting seedlings provided an unusually clear and simple case with which to pursue this

objective. That cohort was monitored for three years, and the field data provide insights into the dynamics of the seedling pool (see Chapter 4). The longer-term influences of reproductive pulses were explored using an individual-based forest gap model (see Chapter 5).

In studying seedling pool dynamics and spatial patterning in a forest, data on the forest canopy are essential. The canopy influences what happens below it. Trees produce seeds and shade the resulting seedlings. Trees moderate temperature and moisture variations, they deposit litter and coarse woody debris, and their roots create and modify soil. The structure of the canopy also provides evidence of the history of the site. Forests in the eastern United States are often highly even-aged stands resulting from logging and fire. In such stands, tree growth, reproduction, and senescence can become synchronized, predisposing them to relatively sudden mortality events triggered by chronic, low-level stresses (Sprugel 1976; Mueller-Dombois *et al.* 1983; Skipworth 1983; Mueller-Dombois 1987). An initial objective of this study, therefore, was to determine the composition, structure, and various canopy conditions in second-growth red spruce forest whose history is simple and known (see Chapter 3). Accomplishment of this objective is requisite to an assessment of possible future dynamics of canopy trees and the seedlings that will replace them.

CHAPTER 2

THE APPALACHIAN RED SPRUCE FOREST

A. The Current Distribution of Red Spruce and Its Associates

Red spruce is widespread in the Maritime region of Nova Scotia, New Brunswick, Quebec, and New England. Total annual precipitation in the region exceeds 100 cm. Minimum January temperatures reach -18°C , and maximum July temperatures reach 27°C . Red spruce occurs on acid soils along the coasts, in wetlands, in old fields, and on well-drained uplands. Frequent associates of red spruce in this region include black spruce (Picea mariana (Mill.) B.S.P.), balsam fir (Abies balsamea (L.) Mill.), and paper birch (Betula papyrifera Marsh.) (Blum 1990).

A similarly cool, moist climate occurs in the high elevations of the White Mountains of New Hampshire and Maine, the Green Mountains of Vermont, and the Adirondack and Catskill Mountains of New York. Red spruce forests in these mountains are herein called the Northern Appalachian spruce forests. In the White, Green, and Adirondack Mountains, red spruce is important at elevations of 700-1200 m, above which balsam fir dominates up to the climatic timberline at about 1500 m (Bliss 1963; Leak and Graber 1974; Siccama 1974; Foster and Reiners 1983; Battles et al. 1992). Yellow birch (Betula alleghaniensis Britton) occurs with red spruce below 900 m, while paper birch is more abundant above 900 m (Leak and Graber 1974; Siccama 1974; Foster and Reiners 1983). Spruce-fir forests of the Catskill Mountains reach

"maximum development" at 1000-1200 m (McIntosh and Hurley 1964).

Red spruce forests of the Allegheny Mountains of Pennsylvania/West Virginia and the Valley and Ridge Province of west-central Virginia (sensu Fenneman 1938) are herein called the Central Appalachian spruce forests. In Pennsylvania, red spruce occurs mostly in the Pocono Mountains (Wherry et al. 1979). Apparently, no detailed studies of red spruce forest in Pennsylvania have been published. Oosting and Billings (1951) state that "the spruce-fir type is absent or poorly developed through the relatively low Allegheny Mountains of Pennsylvania, West Virginia, and Virginia" (p. 84). However, West Virginia includes extensive forests at 1000-1480 m elevation of which red spruce is a component (Bones 1978; Mielke et al. 1986; DiGiovanni 1990). Associates of spruce there are yellow birch and red maple (Acer rubrum L.) (Stephenson and Clovis 1983; Adams and Stephenson 1989; Pauley 1989). Balsam fir occurs naturally at only four wetland sites in the state, all at 900-1100 m elevation (Stephenson and Adams 1986). Red spruce occurs primarily on uplands in West Virginia but occurs also in ravines, swamps, and bogs (Allard and Leonard 1952; Gibson 1970; Edens 1973; Stephenson and Adams 1986). Red spruce is scarce in west-central Virginia. In Highland County, Virginia, red maple and sweet birch (Betula lenta L.) are associates of red spruce on ridges and in swamps, respectively (Bailey and Ware 1990). Yellow birch is uncommon in those stands.

Red spruce forests in southwestern Virginia, eastern Tennessee, and western North Carolina are herein called the Southern Appalachian spruce forests. Red spruce forms small stands at Salt Pond Mountain,

Whitetop Mountain, and Mount Rogers in Virginia, extensive stands in the Great Smoky Mountains of North Carolina/Tennessee and the Black, Plott Balsam, and Balsam Mountains of North Carolina, and small stands on Grandfather Mountain, North Carolina and Roan Mountain, North Carolina/Tennessee (Adams and Stephenson 1989; Ramseur 1960). In those areas, spruce occurs at 1300-2037 m, with peak dominance at 1700-1800 m (Whittaker 1956; Crandall 1958). Above 1800 m, Fraser fir (Abies fraseri (Pursh) Poir.), a Southern Appalachian endemic, becomes increasingly dominant. Yellow birch is a frequent associate except at the highest elevations. Eastern hemlock (Tsuga canadensis (L.) Carr.) dominates with spruce at Salt Pond Mountain (Adams and Stephenson 1989). Red maple is scarce in the Southern Appalachian spruce-fir forests (Stephenson and Adams 1984; Adams and Stephenson 1989; Nicholas et al. 1992b).

B. Quaternary History of Spruce

Analyses of pollen-containing sediments from lakes, ponds, and wetlands in eastern North America show distributional shifts of tree taxa over the last 20,000 years (Delcourt and Delcourt 1987). At the peak of the Pleistocene glaciation 20,000 years ago, Picea comprised 20-60% of the trees across large areas of east-central North America. Climatic warming beginning 12,000-14,000 years ago allowed Picea to follow the retreating Laurentide ice sheet northward. By 10,000 years ago, population centers of Picea clustered in present-day Wisconsin, Michigan, New York, and Maine. Some populations persisted in the

Central and Southern Appalachian regions, migrating upward in elevation instead of northward. This Appalachian extension of the Picea population was well established by 6000 years ago with the occurrence of the Hypsithermal temperature peak. The Central and Southern Appalachian populations became disjunct from the main region of Picea dominance by 2000 years ago (Delcourt and Delcourt 1987).

This disjunction, occurring in present-day Pennsylvania, may explain the current scarcity of red spruce there. Pielke (1981) suggested that spruce failed to regenerate in west-central Virginia after early 20th-century logging and fire. However, Bailey and Ware (1990) cited published pollen data showing reductions in spruce abundance in Virginia 9000 years ago. They conclude that climatic warming eliminated spruce from that area and that spruce was unable to recolonize the discontinuous high-elevation topography after the Hypsithermal period. The more continuous high-elevation topography in West Virginia allowed spruce to migrate more freely there. The Southern Appalachian region includes large contiguous areas 1500-2000 m in elevation, and spruce was able to persist there despite warming. All Central and Southern Appalachian spruce forests are quite fragmented at a regional scale due to the island-like nature of the higher elevations (White and Cogbill 1992).

C. Natural Disturbance in Appalachian Red Spruce Forests

The high elevations of the Appalachian Mountains are cool, wet, windy, and often steeply sloping. Climatic stresses and shallow, stony

soils subject spruce forests to several types of natural disturbances. Frost, winter dessication, and ice storms affect red spruce throughout the Appalachians (Friedland et al. 1984; Nicholas and Zedaker 1989; DeHayes et al. 1990; W. A. Jackson, personal communication). Low temperatures, high rainfall, and evergreen canopies make red spruce forests resistant to fire. Korstian (1937) states that undisturbed stands of red spruce have stopped fires that burned upslope into them. Fahey and Reiners (1981) estimate fire rotation periods (total area of a vegetation type divided by mean area burned per year) for spruce-fir forests in Maine and New Hampshire of 760-5740 years, the longest such periods of all vegetation types in those states. White et al. (1985) calculate that only $10^{-5}\%$ of the area in Great Smoky Mountains spruce-fir forests shows evidence of fire. Burned areas are associated with historical logging (see History of Human Impact below).

The Northern Appalachian region experiences some of the highest windspeeds on Earth. U. S. Weather Bureau records from Mt. Washington, New Hampshire (cited in Bliss 1963) indicate a monthly mean windspeed of 58 km/hr, with a maximum recorded speed of 372 km/hr. Foster and Reiners (1983) suggested that windthrow of mature trees was the major cause of canopy gap formation at Crawford Notch, New Hampshire. Harrington (1986) and Rizzo and Harrington (1988) found radial growth reductions, needle loss, and root damage of red spruce exposed to high winds in New Hampshire. Hurricanes struck the northeastern United States in 1938 and 1957 and damaged large areas of forest (McIntosh and Hurley 1964; Henry and Swan 1974; Reiners and Lang 1979). Reiners and Lang (1979) recognized numerous "hurricane patches" (even-aged stands

35-40 years old) on Mt. Moosilauke, New Hampshire and speculated that these patches may be "the single most important disturbance on an area basis" (p. 412).

Wind apparently causes less damage in Central and Southern Appalachian spruce forests. In some high-elevation areas, strong "flagging" (mortality of windward branches) is evident on red spruce (personal observation). Most other sites in West Virginia, however, show little evidence of flagging (W. A. Jackson, personal communication). Apparently no estimates of the areal extent of wind damage are available. In the Great Smoky Mountains spruce-fir forest, windthrow patches of $>200 \text{ m}^2$ occupy only about 0.1% of the forest area (White et al. 1985). Smaller patches, many from windthrow of 1-3 trees, occupy 5-20% of the area (White et al. 1985).

In steep topography, landslides can be common disturbances. Slides and talus areas cover about 15% of the area from 1200 m to treeline in the White Mountains of New Hampshire (Reiners and Lang 1979). In the Great Smoky Mountains spruce-fir forest, slide headwalls and scour channels each cover about 1% of the forest area (White et al. 1985). Slides are apparently uncommon in the Central Appalachians (Clark 1987), perhaps because of more gentle topography.

Biotic disturbance agents are also important. Red spruce hosts several important insect pests. The spruce budworm (Lepidoptera, Tortricidae: Choristoneura fumiferana (Clemens)), a defoliant, and the four-eyed spruce beetle (Coleoptera, Scolytidae: Polygraphus rufipennis (Kirby)), a wood borer, are among the most damaging insects of red spruce (Blum 1990). While spruce is not the preferred host of the

spruce budworm, significant damage to spruce does occur in stands dominated by balsam fir, the preferred host (Frank and Bjorkbom 1973; Blum 1990). Souto and McCreery (1988) stated that the four-eyed spruce beetle is "a significant mortality factor" (p. 344) in spruce-fir forests of the Adirondack Mountains but is rare elsewhere in the Northern Appalachians. However, Worrall and Harrington (1988) found the four-eyed spruce beetle to be a major cause of spruce mortality up to 1000 m elevation at Crawford Notch, New Hampshire. Hopkins (1891, 1899) noted extensive insect damage to "black spruce" in the Central Appalachian region. (Hopkins' statement actually refers to red spruce, but he regarded red and black spruce as indistinguishable.) He reported that "thousands upon thousands of acres" of spruce died during 1880-1893 in West Virginia. He found four-eyed spruce beetles infesting both live and dead spruce and concluded that these beetles contributed to spruce death. He reported that the pine bark beetle (Dendroctonus frontalis Zimm.) appeared to be the primary cause of spruce mortality at some sites. Mielke et al. (1986), in an extensive survey of red spruce pathology and mortality in West Virginia, did not mention the spruce budworm or the pine bark beetle. They did report, however, that all dead spruce, and some live spruce in poor condition, showed evidence of the four-eyed spruce beetle. In Southern Appalachian spruce-fir forests, Bruck (1989) did not find the spruce budworm, the four-eyed spruce beetle, or the pine bark beetle.

The balsam woolly adelgid (Adelges piceae Ratz.), an insect pest on species of fir, has had indirect effects on red spruce. The balsam woolly adelgid was introduced from Europe into New England prior to 1908

(Kotinsky 1916). By 1957, it was found in the Southern Appalachian spruce-fir forests (Speers 1958), and the insect has since killed most mature Fraser fir (Hay *et al.* 1978; Eagar 1984; Busing and Clebsch 1988; Busing *et al.* 1988; Dull *et al.* 1988; Nicholas *et al.* 1992b). Death of fir has altered the natural gap dynamics of the forest (White *et al.* 1985). Nicholas *et al.* (1992b) suggested that fir death exposes spruce to increased wind damage.

Several species of fungi cause significant damage to red spruce. Worrall and Harrington (1988) found Armillaria ostoyae (Romagn.) Herink (which causes root and heart rot) to be a major cause of spruce mortality at Crawford Notch, New Hampshire. In West Virginia, Valsa kunzei Fr. (which causes reddening and loss of needles) is widespread, while Armillaria mellea Vahl. ex Fr. is confined to spruce growing in poorly drained soils (Mielke *et al.* 1986). Bruck (1989) found 15 species of fungi infecting red spruce in the Southern Appalachians, but none occurred on >13% of trees.

Without large-scale disturbances, the primary disturbance in a forest becomes the occasional deaths of one to several trees. Tree death creates canopy gaps and initiates competition among seedlings and saplings for those gaps. Several studies have estimated the extent and rates of formation of canopy gaps in red spruce forests. Foster and Reiners (1983) estimated that gaps occupied 24% of the area at Crawford Notch, New Hampshire. Most gaps at Crawford Notch were <200 m² in area (Foster and Reiners 1986). By aging saplings in gaps, Foster and Reiners (1986) estimated that about 0.33% of the total canopy area becomes new gaps each year. Estimates of gap characteristics are

apparently lacking for Central Appalachian spruce forests. In the Great Smoky Mountains, White et al. (1985) found that gaps $<200 \text{ m}^2$ occupy 5-20% of the canopy area of old-growth spruce-fir forest and estimated that 0.6-1.7% of the total canopy area becomes new gaps each year.

Large- and small-scale disturbances ensure that nearly all forests contain dead trees. Several studies have estimated the abundance of standing dead trees in red spruce forests. Tritton and Siccama (1990) summarized data on the proportions of standing dead trees in the northeastern United States. Among trees $\geq 10 \text{ cm}$ in diameter in red spruce-balsam fir forests of Maine, Vermont, and New York, standing dead trees comprised 14-36% of the total; the fraction of total basal area (the cross-sectional area of all trees) of dead trees was 5-17%. These values were among the highest of all forest types included by Tritton and Siccama (1990). Foster and Reiners (1983) and Battles et al. (1992) both found that density and basal area of dead trees increased with elevation in spruce forests at Crawford Notch and on Whiteface Mountain, New York, respectively. None of these studies reported the fraction of red spruce that was dead. In West Virginia stands (mostly second-growth) composed of $>50\%$ red spruce, Mielke et al. (1986) found that 11-34% of standing spruce trees $\geq 12.7 \text{ cm}$ diameter were dead; dead spruce basal area comprised 9-28% of all spruce basal area. In three old-growth red spruce stands in West Virginia, Adams and Stephenson (1989) found that, among spruce trees $\geq 2.5 \text{ cm}$ diameter, 15-43% of those trees and 32-58% of their basal area were dead. Among standing red spruce $\geq 5.0 \text{ cm}$ diameter in the Black Mountains (some old-growth and some second-growth stands), Nicholas et al. (1992b) found 10-100% of trees

and 4-61% of their basal to be dead. In the mostly old-growth forests of the Great Smoky Mountains, Nicholas et al. (1992b) found only 7-16% of spruce trees and only 6-9% of their basal area to be dead. At Mount Rogers (mostly second-growth), 10-23% of spruce trees and 8-25% of their basal area were dead (Nicholas et al. 1992b). Comparisons among these studies are difficult because they included stands of various ages and different minimum sizes of trees. Younger stands should have more dead trees (Oliver and Larson 1990), and detailed comparisons require similar size-class distributions.

Because of interest in the health of red spruce forests (see History of Human Impact below), some of the above studies have attempted to evaluate "mortality" by enumerating dead trees. However, the abundance of standing dead trees is a pattern that integrates several processes, including mortality, decay and fall of dead trees, and recruitment of new individuals (Peart et al. 1992). Only repeated censuses can directly yield mortality rates. Few estimates of mortality rates of red spruce are available. Miller-Weeks and Cooke (unpublished data cited in Peart et al. 1992) found mean annual mortality rates for red spruce of 0.4-1.4% in Vermont, New Hampshire, and New York over the period 1985-1989. These are apparently the only mortality rates available for red spruce in the Northern Appalachian forests. No such data seem to exist for Central Appalachian red spruce. From 1985 to 1988, annual mortality rates of spruce in the Black Mountains of North Carolina averaged 2.4-8.1% (Nicholas and Zedaker 1989). Between 1964 and 1986, Busing and Wu (1990) found average annual mortality of old-growth spruce to be 1.1% in the Great Smoky Mountains. While mortality

rates appear high in the Black Mountains, ice storms there have killed many trees (Nicholas and Zedaker 1989). Also, many stands there are second-growth (Pyle and Schafale 1988; Nicholas et al. 1992b) and may not be comparable to Busing and Wu's (1990) study site. Peart et al. (1992) do not state whether Miller-Weeks and Cooke's study sites are second-growth or old-growth.

D. History of Human Impact

Most Appalachian spruce forests have been logged (Ayers and Ashe 1902; Chittenden 1904; Brooks 1910; Core 1929; Westveld 1931; Korstian 1937; Minckler 1945; Clarkson 1964; Stephenson and Clovis 1983; Pyle 1988; Pyle and Schafale 1988; Weiss and Millers 1988). Red spruce has been used for house construction, interior and exterior finishings, furniture, food containers, musical instruments, airplanes, boats and ships, railroad ties, pulp for paper, and even chewing gum (Brooks 1910; Murphy 1917; Blum 1990). The advent of the steam locomotive and an influx of immigrant workers to the Appalachian region in the late 1800s (Clarkson 1964) allowed widespread timbering in remote areas. Large tracts were clearcut, and residual trees were often damaged (Korstian 1937). In some areas, dense second-growth spruce stands regenerated. In other areas, firs and hardwoods replaced spruce (Westveld 1931; Korstian 1937; Oosting and Reed 1944). Highly flammable slash (stumps, branches, and tops) left after logging fueled numerous fires (Korstian 1937; Minckler 1945; Pyle and Schafale 1988). Damage to the forest floor left many burned sites nearly devoid of soil or vegetation (Brooks

1910; Coile 1938; Diebold 1941; Minckler 1945). Some sites are still in this condition (personal observation) despite reforestation efforts (Minckler 1940a,b, 1945; Wahlenberg 1951; Speers 1975).

These disturbances have reduced the range of red spruce (Chittenden 1904; Brooks 1910; Core 1929; Westveld 1931; Korstian 1937; Oosting and Reed 1944; Minckler 1945; Clarkson 1964; Pyle and Schafale 1988). How much reduction occurred is difficult to determine, because estimates of original spruce abundance are vague. For example, Millspaugh (1891) estimated the "extent of . . . distribution" of "black" (red) spruce in West Virginia at about 191,000 ha. This distribution does not necessarily reflect the forest area dominated by spruce. However, the impact of logging is apparent in later estimates of spruce distribution. For example, Brooks (1910) stated that, in 1895, the "area of standing spruce" in West Virginia was estimated at only 91,000 ha. As of Brooks' writing, the distribution of spruce covered 77,000 ha. Bones (1978) estimated that the "spruce-fir" forest type in West Virginia covered 24,000 ha. Mielke et al. (1986) used aerial photographs to delimit 16,700 ha of forest with >50% conifers (mostly spruce) in the overstory in West Virginia; forests with >25% but ≤50% conifers covered another 27,000 ha. DiGiovanni (1990) used aerial photography and plot data to estimate that the "spruce-fir" type covered only 17,500 ha in West Virginia.

Red spruce forests are now believed to be affected by exposure to atmospheric pollutants. These forests receive high precipitation and fog moisture. Soils are usually acid, unbuffered, and nutrient-poor. The high surface area of evergreen foliage collects airborne substances

efficiently. Thus, red spruce forests are likely to be sensitive indicators of air pollution.

Numerous studies have found apparently unusual trends and patterns in Appalachian spruce forests. Siccama et al. (1982) reported that, between 1964 and 1979, density of live spruce declined by 41-93% at several sites in the Green Mountains of Vermont; live basal area declined by 40-87%. Scott et al. (1984) reported 61-69% declines in red spruce basal area between 1964-1966 and 1982 on Whiteface Mountain in the Adirondack Mountains of New York. Vogelmann et al. (1985) found a 49% decline in spruce density and a 69% decline in spruce basal area on Camels Hump in the Green Mountains between 1965 and 1983. These declines continued through 1986 (Vogelmann et al. 1988). Silver et al. (1991) found significant increases in the percentages of dead spruce at several Northern Appalachian sites between 1982 and 1987. Reduced radial growth has been observed at many sites throughout the range of red spruce (Adams et al. 1985; Hornbeck and Smith 1985; McLaughlin et al. 1987; Adams and Stephenson 1989). Loss of foliage also has been documented at many sites (Friedland et al. 1984; Mielke et al. 1986; DeHayes et al. 1990; Peart et al. 1992).

These "spruce decline" characteristics show considerable geographic variation. High mortality has not been found in the Central or Southern Appalachians (Busing et al. 1988; Busing and Wu 1990; Silver et al. 1991; Peart et al. 1992). Radial growth declined in the Northern Appalachians somewhat earlier than in the Southern Appalachians (McLaughlin et al. 1987). Silver et al. (1991) found substantial foliage loss at some Northern Appalachian sites but not in the Southern

Appalachians. Loss of younger needles has been noted in the Northern Appalachians (Friedland et al. 1984; DeHayes et al. 1990), while loss of older needles has been observed in the Southern Appalachians (N. S. Nicholas, personal communication). Both types of needle loss have been observed in West Virginia (Mielke et al. 1986; W. A. Jackson, unpublished data).

Possible contributors to spruce decline include weather extremes or climate trends (Friedland et al. 1984; Harrington 1986; Hamburg and Cogbill 1988; Rizzo and Harrington 1988; Cook and Johnson 1989; DeHayes et al. 1990), insect/fungal pathogens (Mielke et al. 1986; Worrall and Harrington 1988; Bruck 1989), low genetic variability of red spruce (DeHayes and Hawley 1988), post-logging stand maturation (Federer and Hornbeck 1987; Zedaker et al. 1987; Van Deusen 1987, 1990; Van Deusen et al. 1991), natural soil nutrient dynamics (Pastor et al. 1987), and air pollution (Johnson and Siccama 1983; McLaughlin 1985; Bruck and Robarge 1988; Shortle and Smith 1988; Johnson et al. 1991).

Disagreements persist as to the relative importance of these factors. The variations in nature, extent, and timing of decline characteristics preclude explanations applicable to all sites. In a review of the spruce decline problem, however, Johnson et al. (1992) concluded that "regional scale air pollution has played a significant role in the decline of red spruce" (p. 406). However, this conclusion stems from studies mostly spanning only a few years. Moreover, numerous sites within the Appalachian red spruce forest remain unstudied. A major task remains detailing forest conditions at particular sites so that natural or expected patterns can be determined.

E. Regeneration Patterns and Future Forest Dynamics

Assessment of long-term human impacts on red spruce forests requires an understanding of tree reproduction and seedling establishment. Although red spruce reportedly produces major seed crops irregularly every 3-8 yr (Murphy 1917; Fowells 1965; Safford 1974; Blum 1990), few quantitative estimates of seed production are available. Agmata and Bonner (1988) collected red spruce seeds from high-elevation stands in New Hampshire, Virginia, Tennessee, and North Carolina. They collected seeds during poor seed years, and no estimates of seedfall density were made. Germination percentages of collected seeds ranged from <25% to >90%. Nicholas et al. (1992a) monitored seedfall and seed viability from 1986 to 1990 in the Great Smoky Mountains. Seedfall density varied from 95,000 seeds/ha to 35,343,000 seeds/ha and was substantially higher in 1987 than in other years. Seed viabilities were comparatively low, ranging from 0% to 41%. Data from Nicholas et al. (1992a) indicate that few seeds ever result in a seedling (0.4% in a non-mast year up to 2.3% in a mast year).

Most germination is believed to occur within one year after dispersal (Fowells 1965; Frank and Safford 1970; Blum 1990). Pavlovic (1981) found no red spruce seeds in the soil seed bank of a spruce forest in the Great Smoky Mountains. Large seedling cohorts follow a year of high seed production; few seedlings appear in other years (Nicholas et al. 1992a; Pauley and Clebsch, submitted). Nicholas et al. (1992a) found densities of germinal spruce of up to 189,000 stems/ha one year after the 1987 seed crop in the Great Smoky Mountains.

Early mortality among spruce seedlings can be very high. Westveld (1931) found 71% mortality over the first winter in New Hampshire. Pauley and Clebsch (submitted) found 94% first-year mortality among spruce seedlings of the 1987 cohort in the Great Smoky Mountains. Annual mortality rates of older seedlings, however, can be much lower (ca. 5%--Pauley and Clebsch, submitted).

Seedling appearance and survival can vary substantially across substrates. Westveld (1931) found that, after a seed year in New Hampshire, more red spruce seedlings appeared on exposed mineral soil (11,600 stems/ha) than on an undisturbed forest floor (4200 stems/ha). Studies by Place (1955) in New Brunswick indicate that moisture is critical to red spruce germination, especially during summer. In a dry summer, a conifer canopy may favor germination of red spruce by moderating temperature and moisture. With adequate rainfall, germination may be less site-specific. Seedling survival is apparently quite variable under a conifer canopy during a dry season and seems to be favored by disturbed soil or exposed mineral horizons (Place 1955). Hardwood leaf litter or heavy moss cover may not allow penetration of slow-growing roots into moisture-retaining mineral soil (Fuller 1977; Harmon and Franklin 1989).

For seedlings to become established on favorable substrates, seeds must reach those substrates while they are available. Establishment may occur continuously or, in the case of red spruce, in pulses. The long-term effects of reproductive pulses are unclear. High tolerance for shade causes significant variation in the age/size relationship of red spruce (Oosting and Billings 1951; Busing 1985; Nicholas and Zedaker

1992), and age may be a poor indicator of survivorship trends.

Presumably, as seedlings in one cohort become more variable in size, age *per se* becomes less significant than size. Establishment pulses would then be obscured. However, Nicholas *et al.* (1992b) found surprisingly even-aged populations of red spruce in old-growth forests of the Great Smoky Mountains and suggested that establishment of large cohorts is highly irregular even in supposedly stable populations.

Such observations challenge prevailing notions of forest dynamics. The concept that forests recover from disturbances and develop stable states bears close scrutiny when gaps are found in the age distributions of apparently undisturbed populations. Could episodes of seedling establishment, or the lack thereof, be important to a species whose individuals can live for 400 years? Do forests ever stabilize, even in the absence of large-scale disturbance? Red spruce forests provide suitable contexts in which to address such questions.

CHAPTER 3

AN ASSESSMENT OF CANOPY CONDITIONS IN RED SPRUCE
FORESTS OF THE CRANBERRY WILDERNESS, WEST VIRGINIA

A. Introduction

Analyses of regeneration processes in a forest require data on canopy conditions because trees influence seedling establishment. Concern for human impacts on red spruce makes an assessment of canopy structure necessary in anticipating future changes in forest composition.

Unexplained mortality, growth declines, and foliage loss prompted efforts to determine the presence and causes of unusual conditions in high-elevation red spruce forests (Carey et al. 1988; Eagar and Adams 1992). However, normal conditions must first be determined. Most Appalachian spruce forests have histories of human disturbance (especially logging) upon which recent stresses may be superimposed. Many studies of "spruce decline" do not describe the disturbance history of their study sites. Detailed assessments of stands with known histories will help forest ecologists detect unexpected conditions and understand future changes (Zedaker et al. 1988; Van Deusen et al. 1991; Peart et al. 1992).

Relatively few quantitative studies of Central Appalachian spruce forests have been published (Stephenson and Clovis 1983; Adams et al. 1985; Mielke et al. 1986; Miller-Weeks et al. 1988; Adams and Stephenson

1989; Pauley 1989; Bailey and Ware 1990). Not all of these studies have addressed decline characteristics. This chapter presents an assessment of canopy conditions in three second-growth red spruce stands in West Virginia. The objectives are (1) to quantify stand composition and structure, (2) to determine associations among different crown characteristics, (3) to decide if unexpected patterns exist, and (4) to allow prediction of future stand dynamics.

B. Study Area

The Cranberry Wilderness (38°15' N, 80°15' W) is a 14,500 ha preserve on the Monongahela National Forest, West Virginia (Figure 1). The Wilderness contains some of the largest contiguous areas of spruce forest in the state (Mielke *et al.* 1986). The area is a dissected plateau of level-bedded Pennsylvanian-aged sediments capped by a resistant sandstone conglomerate (Meissner *et al.* 1981). The mountains have broad, gently rolling summits reaching elevations of 1402 m. Relief is typically <500 m and maximum slopes are <20°. Weather data from Snowshoe Mountain, 29 km northeast of the Wilderness at an elevation of 1453 m, show mean monthly temperatures of 17.7° C in July and -7.3° C in January for the period 1976-1991 (National Oceanic and Atmospheric Administration 1976-1991). The highest temperature recorded at that station was 30° C, and the lowest was -38° C. Mean annual precipitation was 147 cm. July was typically the wettest month with about 50% more precipitation than September, the driest month. The mean frost-free period (minimum temperatures >0° C) was 131 days. Little

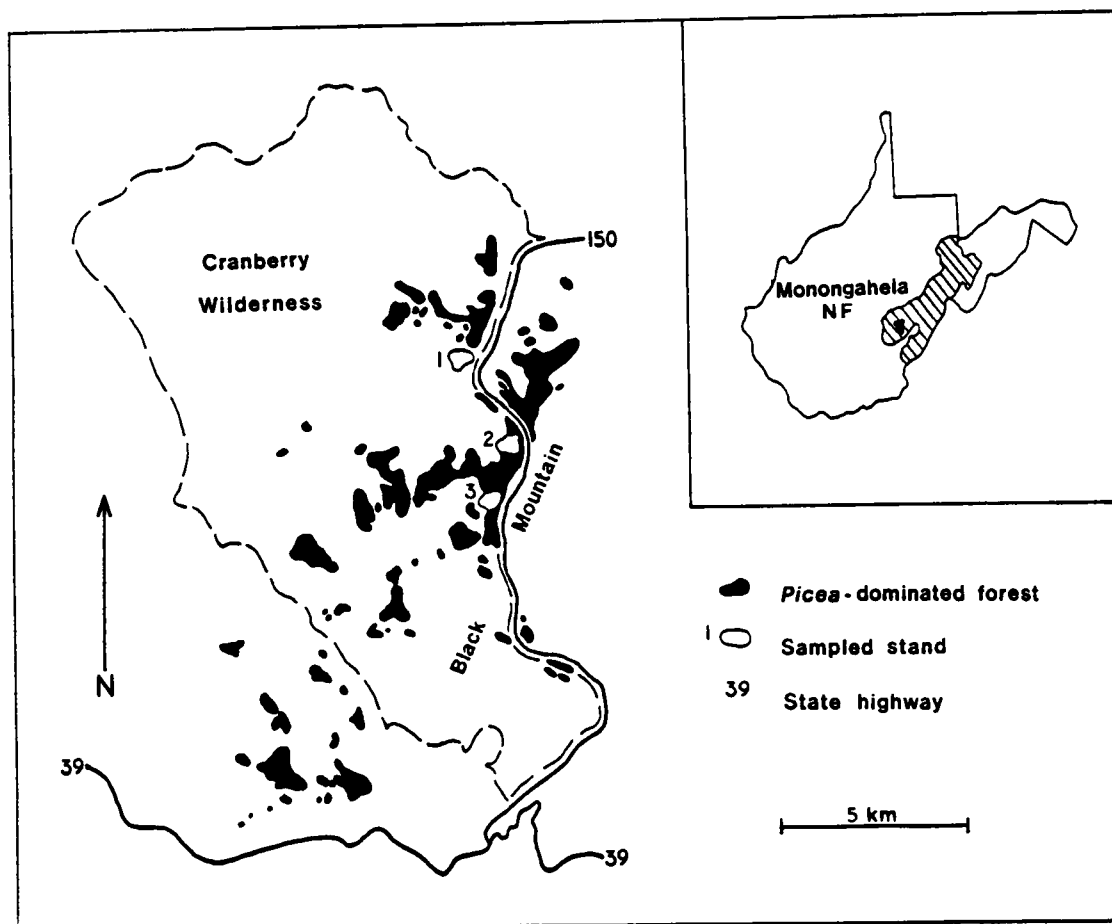


Figure 1. The distribution of red spruce-dominated forest in the Cranberry Wilderness, Monongahela National Forest, West Virginia. Areas of *Picea*-dominated forest were interpreted from black-and-white aerial photographs taken in April 1981.

chronic wind damage to tree crowns (e.g., flagging) is evident in the Cranberry Wilderness (personal observation). Soils under red spruce forest in the Wilderness are extremely stony sandy loams of the Gauley Series (Spodosols), 50-100 cm deep, with pH ranging from <4.5 to 5.5 (D. Flegel, personal communication).

According to a map of lands owned by the Cherry River Boom and Lumber Company (Allen and Roberts 1931; on file at the Gauley Ranger Station, Monongahela National Forest, Richwood, West Virginia), nearly all of the Cranberry Wilderness was logged in the early 1900s. The high elevations of Black Mountain, where most spruce forest in the Wilderness occurs, were logged in the 1920's. Photographs taken earlier this century (Brooks 1910; Clarkson 1964) indicate that red spruce dominated the original high-elevation forest. Species of fir do not occur naturally in the Wilderness, although a small plantation of Fraser fir was established on Black Mountain about 1940 (Minckler 1945). In 1936, a fire burned an estimated 485 ha of logged forest in one contiguous area on Black Mountain (USDA Forest Service 1978). Red spruce regenerated poorly on the burned area, but at least 500 ha of logged, unburned forest are now dominated by maturing, second-growth red spruce. Few other post-logging disturbances have occurred in the Wilderness.

C. Methods

Aerial photographs taken in 1981 were used to select three visually homogeneous, accessible stands of unburned, closed-canopy spruce forest for sampling (Figure 1). Those stands were logged between

1920 and 1926 (Allen and Roberts 1931), probably by clearcutting (L. S. Minckler, personal communication). All three stands are 1200-1400 m in elevation, 21-33 ha in area, and similar in topography (shoulder slopes and broad ridgetops). Stands 1 and 2 were sampled in summer 1990, and Stand 3 was sampled in summer 1991. In each stand, six 20 x 20 m quadrats were established at random locations. Mean slope of all 18 quadrats was 9.6° ($\pm 4.7^{\circ}$ S.D.). Aspects of all quadrats were 213° - 350° , and mean aspect was 277° ($\pm 50^{\circ}$ S.D.) azimuth. Within each quadrat, the diameters of all standing stems ≥ 5.0 cm diameter at 1.30 m height, both live and dead, were measured. Spruce trees were visually assessed for (1) crown position (dominant, codominant, intermediate, or suppressed), (2) needle loss (1-10%, 11-50%, and 51-99%, and dead), (3) crown ratio (percentage of total tree height with live branches), and (4) frequency of qualitative characteristics of a tree's form or health. (See Appendix A, Table 10, p. 127 for a list of characteristics used.) Loss of younger or older needles affected the needle loss estimates. Crown assessments similar to these have been used elsewhere in Appalachian spruce-fir forests in efforts to detect unusual forest patterns (Mielke *et al.* 1986; Bruck and Robarge 1988; Miller-Weeks *et al.* 1988; Nicholas *et al.* 1990; Silver *et al.* 1991; Peart *et al.* 1992).

The sapling/shrub layer was sampled to obtain information on potential canopy successor species. Within each 20 x 20 m quadrat, three 2 x 2 m plots were established at random locations. In each plot, all live woody stems >1.30 m tall and <5.0 cm diameter at 1.30 m height were counted by species. Species nomenclature for vascular plants in the Cranberry Wilderness followed Strausbaugh and Core (1970-1977).

D. Results

Few significant compositional differences were evident among the three stands sampled. Live basal area and density of red spruce did not differ significantly among stands ($P > 0.05$, Wilcoxon rank-sums test (SAS Institute 1987)). Most among-stand differences were due to patchy distributions of less abundant taxa. Thus, data for all stands were pooled (Table 1). Red spruce comprised 81% of the total live basal area and 65% of live stems. Most remaining basal area and density were composed of yellow birch (Betula alleghaniensis) and red maple (Acer rubrum). Most live spruce were 15-30 cm in diameter, while birch and maple were mostly ≤ 20 cm in diameter (Figure 2). Only 20% of the total standing basal area was dead, while 40% of total stems were dead (Table 1), indicating that dead trees were typically small. The small size of dead trees was also shown by diameter-class distributions for the dominant species (Figure 2). Although 43% of spruce were dead, 50% of dead spruce were ≤ 10 cm in diameter.

Crown position, needle loss, and live crown ratio were all associated to some degree. Of the 580 live spruce trees tallied, most were codominants (i.e. trees forming the general canopy level) (Figure 3). The great majority of dead spruce were in a suppressed (overtopped) crown position. Most dominant and codominant spruce showed $\leq 10\%$ needle loss; more severe needle loss was most frequent among intermediate and suppressed spruce (Figure 3). Premature loss of older needles was not generally apparent. "Needle loss" therefore refers primarily to loss of recently produced foliage. Overall, 66% of live spruce showed 1-10%

Table 1. Canopy composition of red spruce forest in the Cranberry Wilderness, West Virginia. All stems ≥ 5.0 cm diameter at 1.30 m height in 18 20 x 20 m quadrats are included.

Taxon	Basal Area				Density			
	(m ² /ha $\pm$ 1 S.E.)				(stems/ha $\pm$ 1 S.E.)			
	Live		Dead		Live		Dead	
	Stems		Stems		Stems		Stems	
<u>Picea rubens</u>	29.8	(2.6)	6.8	(1.0)	806	(95)	610	(109)
<u>Betula alleghaniensis</u>	3.7	(1.1)	1.3	(0.7)	242	(49)	104	(23)
<u>Acer rubrum</u>	1.9	(0.6)	0.1	(<0.1)	61	(17)	8	(5)
<u>Fagus grandifolia</u>	0.7	(0.4)	0.2	(0.2)	71	(51)	46	(35)
<u>Prunus serotina</u>	0.3	(0.3)	0		3	(3)	0	
<u>Pyrus americana</u>	0.2	(0.1)	0.3	(0.2)	14	(6)	22	(12)
<u>Ilex montana</u>	0.1	(0.1)	<0.1	(<0.1)	32	(13)	14	(6)
<u>Acer pensylvanicum</u>	<0.1	(<0.1)	<0.1	(<0.1)	3	(3)	1	(1)
<u>Acer spicatum</u>	<0.1	(<0.1)	0		3	(2)	0	
<u>Amelanchier</u> spp.	<0.1	(<0.1)	<0.1	(<0.1)	4	(3)	3	(3)
<u>Tsuga canadensis</u>	<0.1	(<0.1)	<0.1	(<0.1)	4	(2)	3	(2)
<u>Prunus pensylvanica</u>	0		0.3	(0.1)	0		17	(8)
Unidentifiable	0		0.1	(0.1)	0		10	(5)
Total	36.8	(1.4)	9.2	(1.1)	1242	(72)	834	(93)

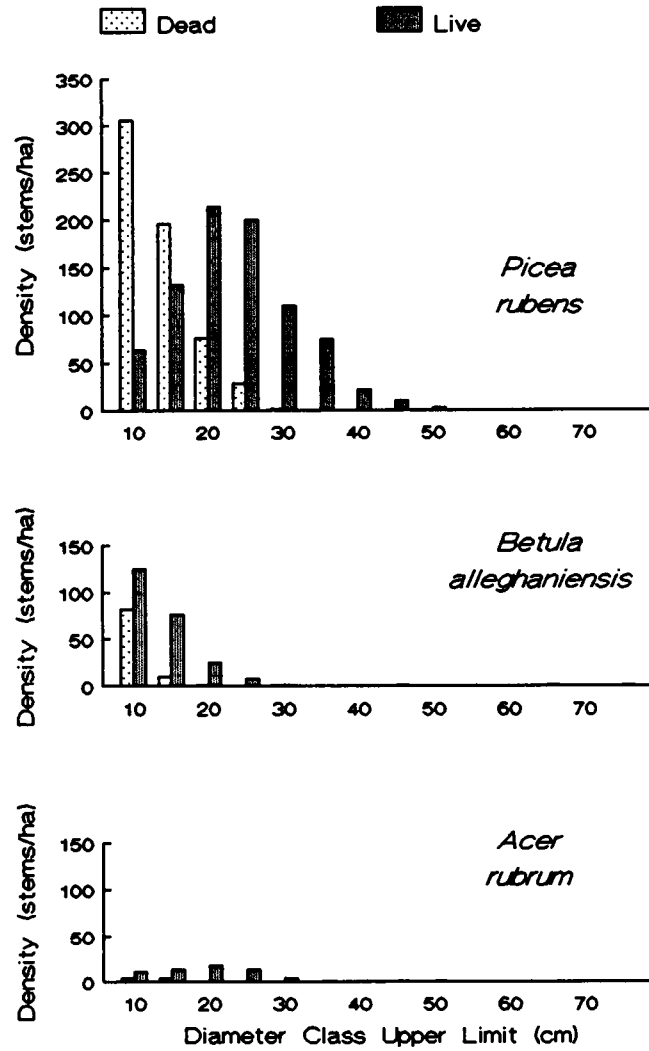


Figure 2. Diameter distributions of dominant tree species in red spruce forest. All stems ≥ 5.0 cm diameter at 1.30 m height in 18 20 x 20 m quadrats are included.

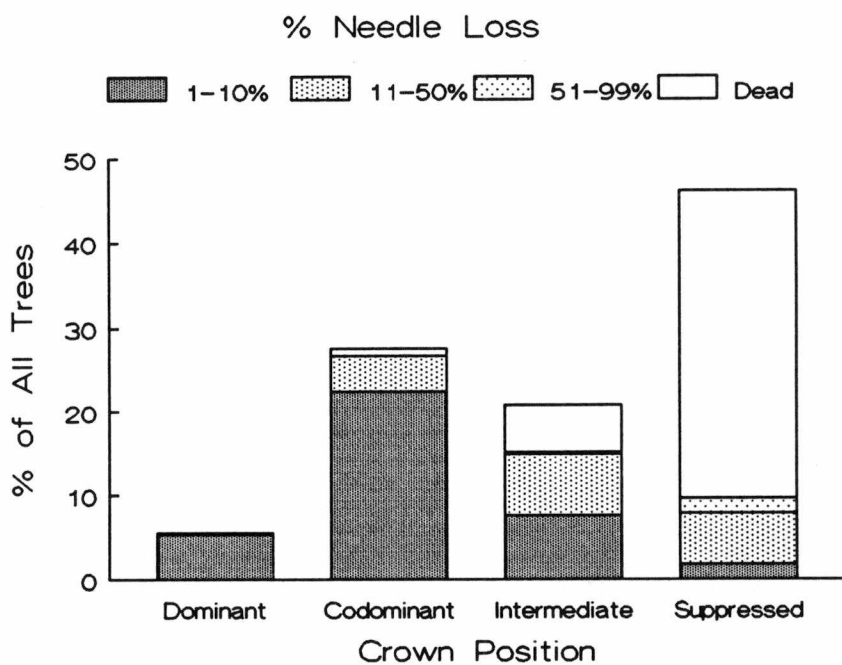


Figure 3. Frequencies of red spruce among crown positions, stratified by percent needle loss. A dead tree was one having no green needles.

needle loss, 31% showed 11-50% needle loss, and only 3% showed >50% needle loss. Mean crown ratio of spruce was only 36%. Intermediate and suppressed trees generally had below-average crown ratios (Figure 4), as did trees with >10% needle loss (Figure 5). The most frequent indications of tree form or health in live spruce were "lateral competition" (64%) and "loss of recent needles" (59%) (Table 2). Lateral competition refers to a narrowed or one-sided tree crown due to the nearness of neighboring trees. Lateral competition and loss of recent needles were particularly frequent among codominant and intermediate trees and among trees showing >10% needle loss. Most trees with crown ratios $\leq 25\%$ were in intermediate or suppressed positions and showed >10% needle loss. Fungal fruiting structures were not evident on the lower boles of any live trees. A single tree (in Stand 3) showed evidence of damaging insects (Polygraphus rufipennis (Kirby)).

Mountain holly (Ilex montana) made up 67% of stems in the sapling/shrub layer (Table 3). Great laurel (Rhododendron maximum) was rather uncommon (13% of stems) and patchy. There were notably few tree saplings, especially those of shade intolerant yellow birch (5% of stems). Red maple was not found in the sapling/shrub layer.

E. Discussion

The composition and size structure of the Black Mountain spruce forest reflect its logging history. Spruce is shade-tolerant (Blum 1990), and its seedlings and saplings can be abundant beneath an existing canopy. Spruce can also become established in large numbers

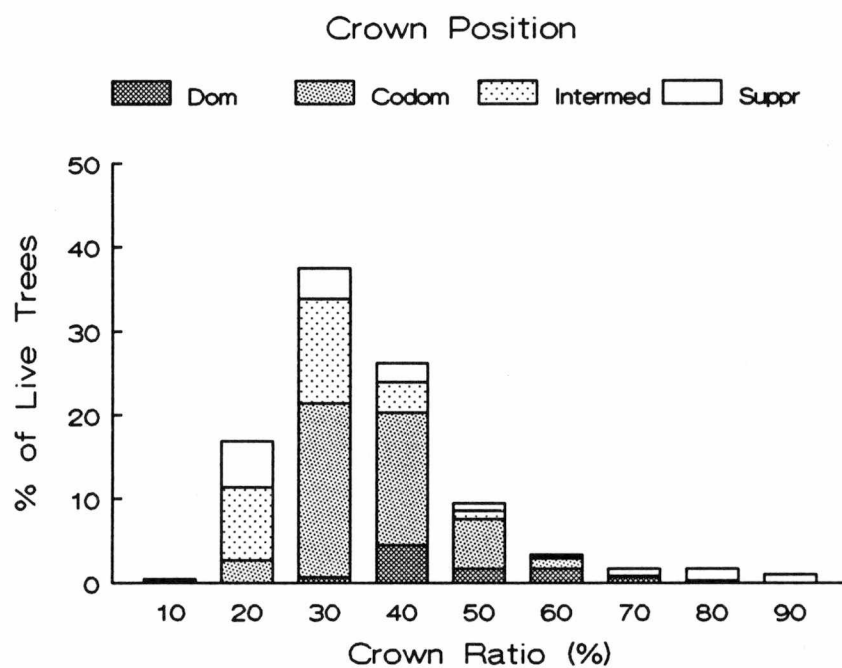


Figure 4. Frequencies of red spruce among crown ratios, stratified by crown position. Crown ratio is the percentage of tree height with live branches. "Dom" = dominant; "Codom" = codominant; "Intermed" = intermediate; "Suppr" = suppressed.

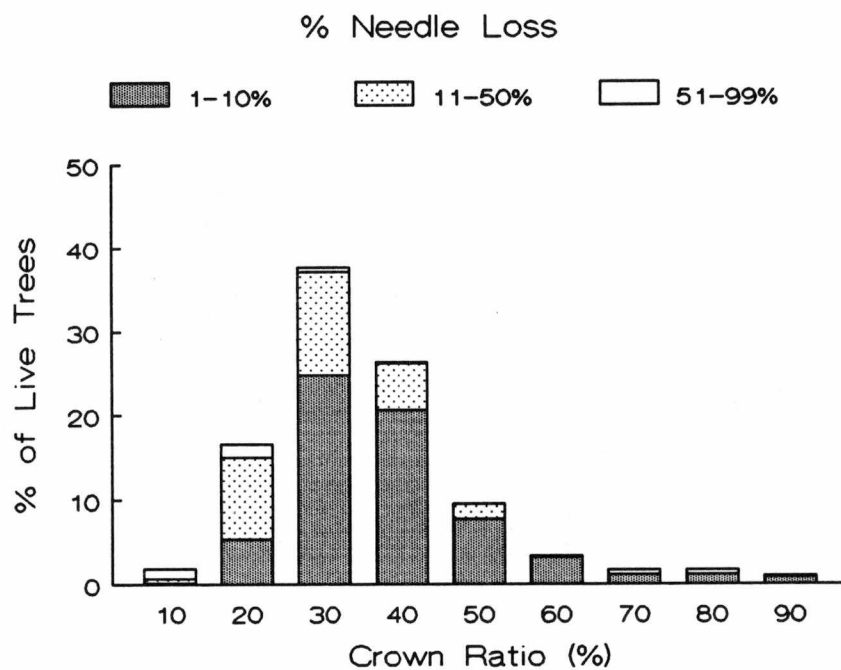


Figure 5. Frequencies of red spruce among crown ratios, stratified by percent needle loss. Crown ratio is the percentage of total tree height occupied by live branches. Only live trees are included.

Table 2. Frequency of qualitative characteristics among live red spruce, stratified by crown position and percent needle loss. D = dominant; C = codominant; I = intermediate; S = suppressed. Frequencies do not sum to 100 because many trees received more than one comment.

Characteristic	Crown Position				% Needle Loss			Total
					1-	11-	51-	
	D	C	I	S	10	50	99	
Number of trees	56	272	154	98	380	180	20	580
Lateral competition ^a	27%	67%	80%	53%	59%	72%	55%	64%
Loss of recent needles	34	54	71	66	43	90	65	59
Crown ratio $\leq 25\%$	0	6	31	40	8	31	80	18
Stilt-rooted	9	11	13	3	10	11	5	10
Stem crook/sweep	7	6	8	6	6	8	5	7
Non-continuous crown	4	4	5	4	3	7	0	4
Terminal replacement ^b	0	<1	5	9	1	7	5	3
Dieback/dead top	2	0	2	12	<1	6	25	3
Witch's broom ^c	2	3	3	2	2	4	0	3
Forked below 1.30 m	0	2	2	3	2	2	10	2
Multiple leaders ^d	5	1	2	3	2	1	10	2
Common rootstock ^e	2	1	3	1	2	1	0	2
Miscellaneous								
mechanical injury	0	1	1	3	1	2	5	2

Table 2. Continued.

Characteristic	Crown Position				% Needle Loss			Total
					1-	11-	51-	
	D	C	I	S	10	50	99	
Number of trees	56	272	154	98	380	180	20	580
Stem crack	4%	2%	1%	0%	2%	1%	0%	1%
Stem disease/ lesions/burls	2	1	1	1	1	1	0	1
Top missing	0	0	1	4	1	1	5	1
Recently released	0	0	1	1	1	1	0	1
Insect feeding/ defoliation	0	0	1	0	0	0	5	<1
Uprooted but alive	0	0	0	1	<1	0	0	<1

^anarrowed or one-sided crown due to the presence of neighboring trees

^breplacement of terminal stem by lateral branch in upper 1/3 of tree

^cdense sprouting near end of branch

^dtwo or more terminal stems, not all necessarily living

^etwo or more stems obviously sharing roots

Table 3. Densities of live woody stems in the sapling/shrub layer of red spruce forest of the Cranberry Wilderness. Included are all live stems >1.30 m tall and <5.0 diameter at 1.30 m height in 54 2 x 2 m plots.

Species	Density (stems/ha $\pm$ 1 S.E.)	
<u>Ilex montana</u>	1204	(540)
<u>Rhododendron maximum</u>	232	(152)
<u>Picea rubens</u>	139	(79)
<u>Betula alleghaniensis</u>	93	(65)
<u>Fagus grandifolia</u>	93	(93)
<u>Acer pensylvanicum</u>	46	(46)
Total	1807	(551)

after canopy removal. After Black Mountain was logged, sufficient spruce regeneration must have been already present and/or subsequently established in the stands examined here to exclude most shade-intolerant trees (e. g., birch and maple). That few spruce saplings occur is probably due to the young age of the canopy trees; insufficient time has elapsed for their offspring to reach sapling size (>1.30 m tall). The many small, suppressed, dead spruce probably reflect competition during stand regeneration. Larger trees gained dominance and smaller trees became suppressed and eventually died. This process has been termed "differentiation" (Oliver and Larson 1990) and is expected in even-aged, monospecific stands.

Low crown ratios also reflect competition among closely-spaced trees (Oliver and Larson 1990). In old-growth forest of the Great Smoky Mountains, where total density of live trees is about two-thirds that on Black Mountain (Nicholas et al. 1992b), red spruce shows a mean crown ratio of 49% (data courtesy of N. S. Nicholas), as compared to 36% on Black Mountain. Mielke et al. (1986), in a large-scale survey of spruce decline in West Virginia, defined "declining" trees as those with a crown ratio of $<40\%$. By this criterion, 56% of live spruce on Black Mountain would be declining. However, Mielke et al. (1986) noted that most declining spruce trees <14 cm diameter were suppressed. Crown ratio is thus associated with both stand density and tree stature and does not in itself indicate an anomalous "decline."

Needle loss in red spruce has been widely used as an indicator of tree vigor (Friedland et al. 1984; Mielke et al. 1986; Bruck and Robarge 1988; Miller-Weeks et al. 1988; DeHayes et al. 1990; Silver et al. 1991;

Peart et al. 1992). However, needle loss is difficult to quantify on a large scale and to interpret. It requires a subjective concept of how a tree crown should appear if the tree were healthy. On Black Mountain, most spruce showed $\leq 10\%$ needle loss and were in codominant crown positions; trees showing more severe needle loss were generally in subdominant crown positions and had low crown ratios. Such characteristics could be expected in dense, even-aged forests, but these assessments have at least three limitations. First, needle loss was judged by only one observer; the direction and degree of bias are unknown. Second, the greater needle loss indicated for suppressed trees may be exaggerated. The number of needles per shoot length and their thicknesses are often less on shaded spruce, giving a visual impression of needle loss. Third, estimates of needle loss on Black Mountain cannot always be compared with similar data from more mature forests. Small, young trees growing in dense stands require a different concept of expected crown appearance from that appropriate for trees in older stands. The needle loss estimates in the present study (and probably other studies as well) are therefore useful only for within-site and among-year comparisons when observer bias is constant and/or known.

Lateral competition and loss of recent needles are most common among trees in subdominant canopy positions. One factor probably contributing to both characteristics is mechanical abrasion when closely-spaced trees contact each other on windy days. Winter injury, indicated by red-brown foliage in early spring, was noted in some West Virginia spruce forests in 1991, although it was not severe (W. A. Jackson, personal communication). The fungus Valsa kunzei Fr. has also

been determined to be very frequent on red spruce in West Virginia and may also be responsible for some needle loss (Mielke *et al.* 1986; W. A. Jackson, personal communication). The present study did not examine the occurrences of Valsa or winter injury. Insect infestations are apparently unimportant in the stands studied here.

In conclusion, there are no external characteristics apparent in the present study that require explanations other than those involved with post-logging stand development. These stands resemble a late stage of the "stem exclusion" (Oliver 1981) or "thinning" (Peet and Christensen 1987) phase of post-disturbance regeneration, where small trees are suppressed and die and few plants have yet become established in the understory. A likely future scenario would be continued but decelerating tree growth, the occasional death of individual canopy trees, the reappearance of tree species in the sapling/shrub layer, and a gradual transition to an all-aged (old-growth) forest. The maximum age of red spruce is about 400 years (Blum 1990). Since the stands examined here are only 64-71 years old, any abrupt, large-scale canopy deterioration within the next few decades would be unexpected. Such conditions should favor the regeneration of shade-tolerant red spruce seedlings. If widespread canopy mortality occurs (for whatever reason), shade-intolerant birch and maple may gain dominance.

CHAPTER 4

EPISODIC REPRODUCTION BY RED SPRUCE
IN THE CRANBERRY WILDERNESS, WEST VIRGINIA

A. Introduction

Forest communities are widely recognized as being affected by climate, soils, topography, geology, and natural and anthropogenic disturbances (Whittaker 1956; Heinselman 1973; White 1979; Harmon et al. 1983; Pickett and White 1985; Delcourt and Delcourt 1988; Oliver and Larson 1990). The effects of these mostly large-scale factors are usually quite persistent. However, trees show individual- and population-level behaviors that could influence community structure and dynamics in more subtle ways. For example, populations of some tree taxa (e.g., Abies, Fagus, Picea, Quercus) produce large seed crops at intervals of two or more years, with little seed production in the intervening years (Burns and Honkala 1990). Such episodic reproduction is often called "masting." The causes of masting include climatic conditions that synchronize flowering, the time each tree requires to regain energy and nutrients used to produce seeds, and, over evolutionary time, natural selection for trees that can alternately satiate and starve seed predators, thereby ensuring that some seeds escape (Silvertown 1980, 1982).

Whatever the causes, episodic reproduction could have significant effects not only on seed predators but also on the structure of the tree

population. Shade-tolerant species can accumulate a "pool" of seedlings that persist at low growth rates and respond rapidly to canopy gap formation (Whitmore 1989). Seedling pools are composed of many successive cohorts. Presumably, density-dependent mortality buffers the periodic input of large cohorts, so that the seedling pool develops an all-aged distribution (e.g., sugar maple, Acer saccharum Marsh.; Hett 1971). Thus, a reproductive pulse would be damped out and have no lasting effect on population age structure or stand composition. Although reasonable, this presumption has not been widely tested. Mortality can be expected to decline with age as seedlings become better established (Hett 1971; Oliver and Larson 1990). Shade-tolerant species that also reproduce episodically (e.g., red spruce) may establish large cohorts of seedlings despite high initial mortality. Several large cohorts could generate a multi-aged seedling pool, pre-empt many favorable microsites, and thereby increase the representation of that species in the canopy.

The microsite distribution of seedlings is rarely uniform. Dispersal by wind, water, and animals may produce non-random distributions of seeds. Survival of resulting seedlings is not strictly density-dependent. A forest floor is usually very heterogeneous, and seedling mortality may vary across microsites. Many studies have found tree seedlings to be non-randomly distributed across the forest floor mosaic (Marquis 1982; Huenneke and Sharitz 1986; Collins and Good 1987; Gibson and Good 1987; Palmer 1987; Pauley and Clebsch 1990; Titus 1990). Such static evaluations show patterns but not the processes causing those patterns. Other studies have monitored tree seedling survivorship

across microsites through time (Christy and Mack 1984; Antos and Zobel 1986; Harmon and Franklin 1989; Collins 1990; Huenneke and Sharitz 1990). Such studies show more conclusively how spatial patterns develop.

In 1989, red spruce in the Cranberry Wilderness, West Virginia (see Chapter 3), produced a heavy seed crop as shown by abundant fresh cones on most canopy trees. Seedfall density and viability are unknown, but mean density of the resulting seedlings reached 2,944,000 stems/ha the following summer. Such a large, discrete cohort of seedlings provided a simple context in which to examine the effects of episodic reproduction on the structure of the seedling pool. The objectives of this chapter are (1) to determine if a single large cohort of tree seedlings remains a conspicuous feature of the seedling pool after the first few years and (2) to evaluate temporal changes in seedling distribution produced by microsite-specific mortality.

B. Methods

Three 1 x 1 m plots were established at random locations within each of the quadrats described in Chapter 3. All 54 plots were evaluated in early May and early August from 1990 through 1992. Within each plot, percent coverages of six substrate types and three surface types were visually estimated at each date. A "substrate" was a microtopographic feature that could provide mechanical support for plant roots: forest floor, dead log, dead root, live root, rock, and stump (<1.30 m tall). A "surface" was the visible covering of a substrate:

bryophytes, litter (including twigs and branches <5 cm diameter), and bare (*i.e.*, uncovered substrate). Pit-and-mound microtopography produced by windthrown trees was uncommon because damaging winds are very local on Black Mountain. No plots included such pits or mounds.

Percent cover of each herbaceous taxon in the plots was visually estimated at each date. Live woody stems <1.30 m tall were also counted. Nomenclature for vascular plants in the study site followed Strausbaugh and Core (1970-1977).

Red spruce seedlings in the 1 x 1 m plots were classified by height (<25, 25-49, and 50-129 cm), age since germination (<1, 1, 2, 3, 4, and ≥ 5 years), and the substrate and surface on which they occurred. The large number of newly germinated spruce seedlings encountered in the 54 plots (15,897) and their small size (<2 cm tall) precluded marking of individuals. Calculations of mortality rates were possible because age of individuals in the 1990 cohort could be determined at all dates by counting bud scale scars. Mortality rates were calculated as (initial number - final number)/initial number, expressed in percent.

Distributions of seedlings among substrate and surface types were tested for non-randomness with the chi-square (χ^2) test (Sokal and Rohlf 1981). Expected numbers of seedlings on a particular substrate or surface were derived from the mean cover of that substrate/surface. For example, if dead logs covered 10% of the ground, then 10% of all seedlings were expected to occur on dead logs if seedling occurrence was independent of that substrate.

C. Results

Total cover of herbaceous taxa (Figure 6) varied cyclically. Seasonal growth of fern taxa (Dennstaedtia punctilobula, Dryopteris spp., and Osmunda cinnamomea) accounted for most variations. Oxalis montana (white wood sorrel) also showed some seasonal increases. A slight between-year increase (from 10 to 13%) in total cover was evident, but no one taxon contributed consistently to this increase.

Woody taxa other than red spruce (Figure 7) showed more variable behavior. Two major changes occurred during 1990: a large increase in the density of yellow birch (Betula alleghaniensis) and a decline in the density of "unknown" seedlings. "Unknown" seedlings were those too small and undeveloped to identify. The increase in birch was nearly the same as the original density of "unknowns," and many of the latter may have been small birch seedlings. Birch density declined through 1991. Minor changes included a small increase of mountainash (Pyrus americana) in 1990 due to germination, the decline of mountainash in 1991, and a slight increase in yellow birch in 1992. Most other taxa showed relatively constant densities.

By August 1990, density of small (<25 cm tall) spruce seedlings had increased greatly (Table 4). Newly germinated (<1 yr old) seedlings accounted for nearly all small seedlings. Their densities declined quickly. By the time the 1990 cohort was two years old (August 1992), nearly 97% had disappeared (Table 4), but mortality rate did not decline monotonically. Mortality from August 1990 to May 1991 (the first winter) was about 56%, while mortality of remaining seedlings between

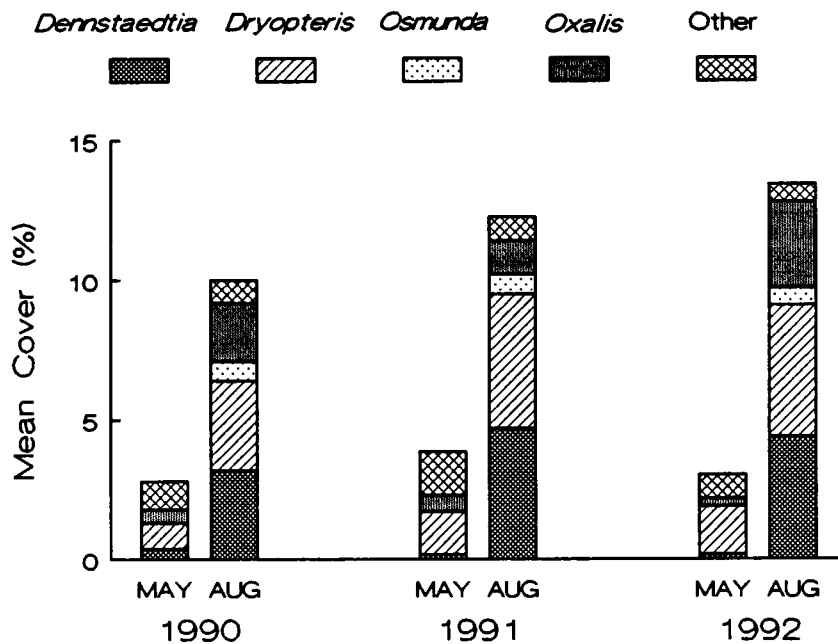


Figure 6. Mean coverages of herbaceous taxa in 54 1 x 1 m plots in red spruce forest. Taxa shown are: *Dennstaedtia punctilobula*, *Dryopteris* spp., *Osmunda cinnamomea*, and *Oxalis montana*. "Other" taxa are: *Clintonia borealis*, *Carex* spp., *Erythronium* spp., *Lycopodium* spp., *Maianthemum canadense*, *Medeola virginiana*, *Mitchella repens*, *Monotropa uniflora*, *Polypodium virginianum*, and *Trillium undulatum*.

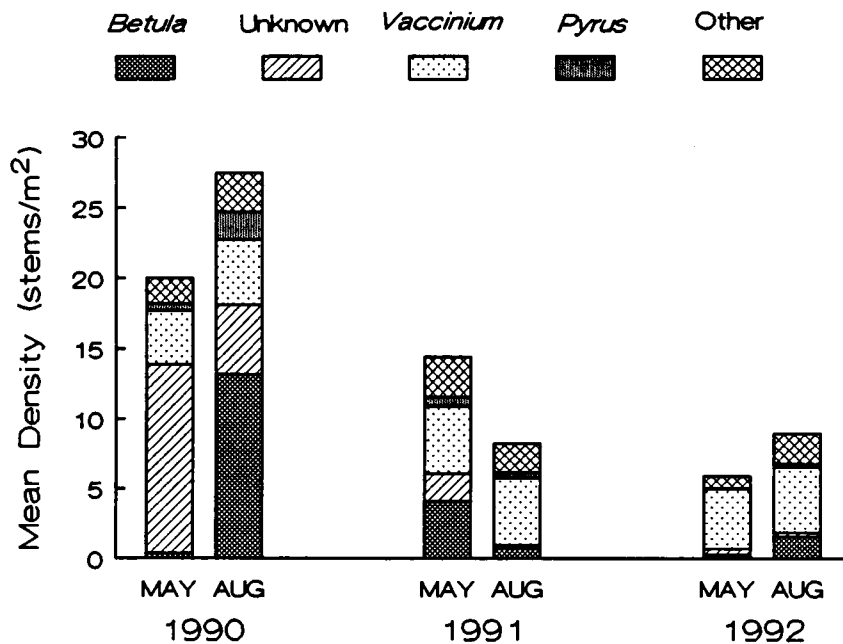


Figure 7. Mean densities of woody taxa <1.30 m tall, other than red spruce, in 54 1 x 1 m plots in red spruce forest. Taxa shown are: Betula alleghaniensis, "unknown" (woody seedlings too small to be identified), Vaccinium erythrocarpum, and Pyrus americana. "Other" taxa are: Acer pensylvanicum, Acer rubrum, Fagus grandifolia, Kalmia latifolia, Menziesia pilosa, Rubus spp., Rhododendron maximum, and Tsuga canadensis.

Table 4. Mean densities of red spruce seedlings (<1.30 m tall) in 54 1 x 1 m plots in the Cranberry Wilderness, stratified by height and age classes. Age is time since germination, as determined by counting bud scale scars.

Class	Evaluation Date (mo/yr)					
	5/90	8/90	5/91	8/91	5/92	8/92
Height (cm)	Mean Density (stems/m ²)					
<25	23.2	295.0	131.1	18.2	10.7	18.8
25-49	0.2	0.3	0.2	0.2	0.2	0.1
50-129	<0.1	<0.1	<0.1	<0.1	0.1	0.1
Age (yr)						
<1	22.4	294.4	0	0.2	0	8.7
1	<0.1	0	130.5	17.6	<0.1	<0.1
2	<0.1	<0.1	0	0	10.2	9.5
3	0.1	<0.1	0	0	<0.1	0
4	0.1	0.1	<0.1	<0.1	0	0
≥5	0.7	0.8	0.8	0.6	0.6	0.7

May and August 1991 was nearly 87%. Seedlings surviving their first entire year (only 6% of the original number) suffered an additional 42% mortality during their second winter. Less than 7% of second-winter survivors died during summer 1992. Almost no germination occurred in 1991, while a small amount occurred in 1992 (Table 4).

Three different survivorship curves fit these data to varying degrees. A linear and a negative exponential model of $\log_e(\text{density})$ over time explained about equal amounts of the variation (Figure 8a,b). A linear model of $\log_e(\text{density})$ over $\log_e(\text{time})$, which is a power function (Hett 1971; Hett and Loucks 1971, 1976), fit the data less well (Figure 8c). Projection of the linear function, which assumes a constant mortality rate, over 60 months indicated that seedling density from this cohort would be only 0.03 stems/m². Projection of the negative exponential function, which assumes declining mortality, indicated a density of 1.6 stems/m². The power function, which also assumes declining mortality, indicated that 5.0 stems/m² would remain from this cohort after 60 months.

The data also permit an evaluation of the dependency of mortality on initial density. To avoid spurious percentages, this relationship was tested only with plots having ≥ 100 seedlings in August 1990 ($n = 43$). Mortality over the first winter showed a moderate negative relationship with initial density (Figure 9a). This relationship weakened after a full year (Figure 9b) and became non-significant thereafter (Figure 9c,d).

At no time were red spruce seedlings in the 1990 cohort distributed independently of substrate type (Table 5). The squared

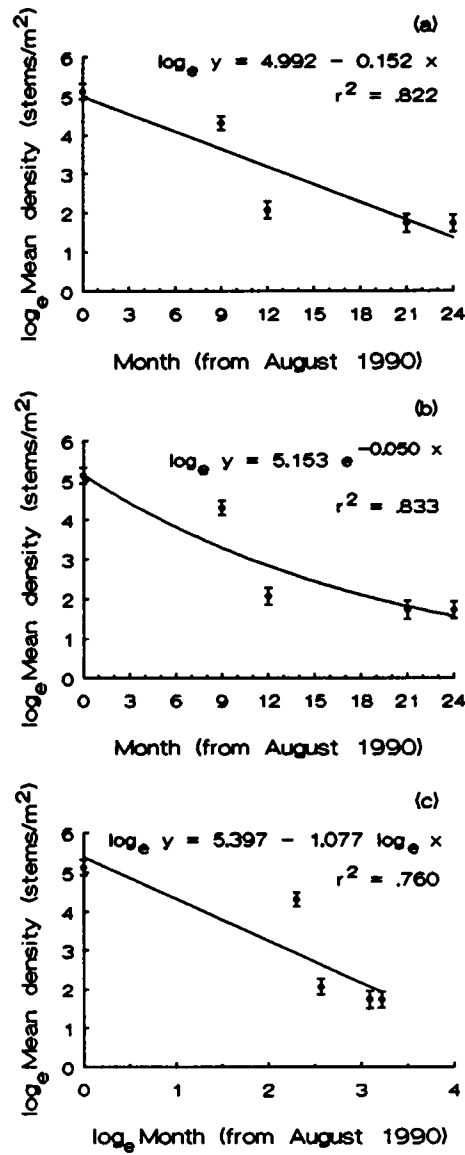


Figure 8. Survivorship curves of red spruce seedlings appearing by August 1990, through August 1992. Densities are means (± 1 standard error) of 54 1 x 1 m plots.

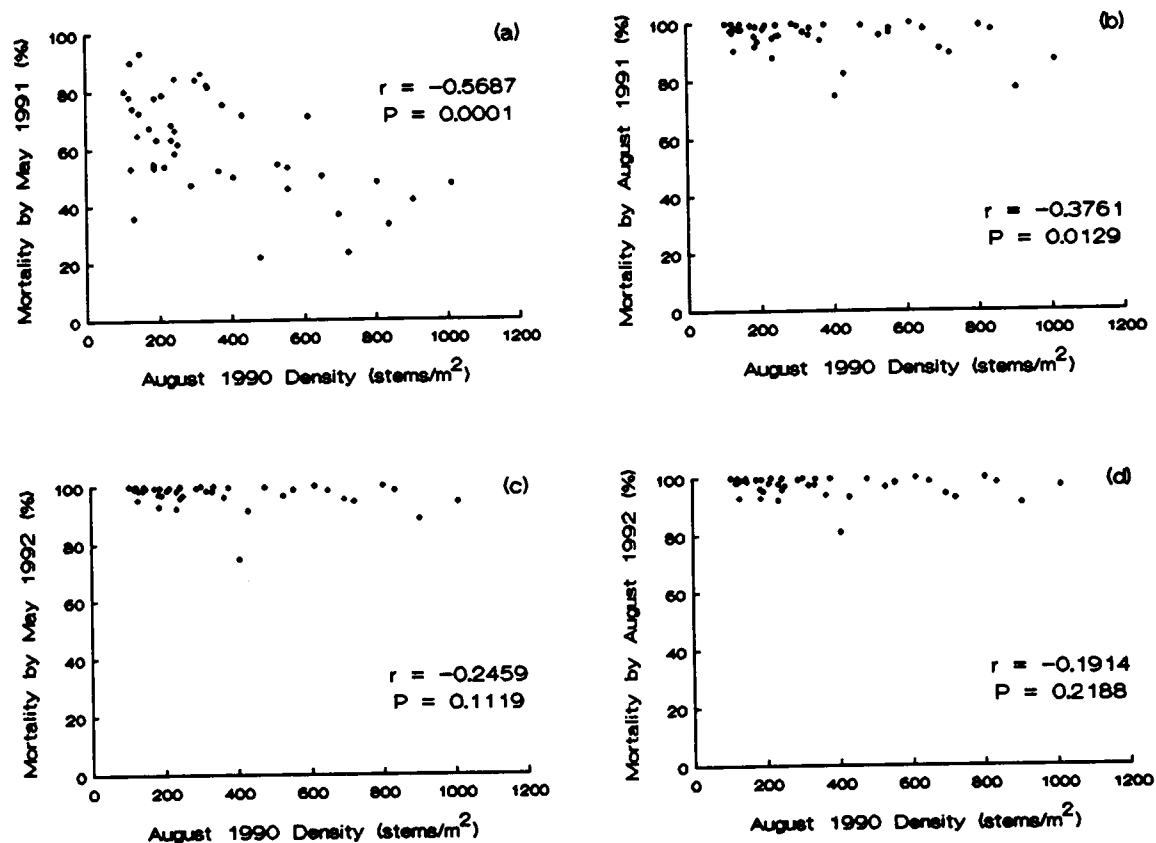


Figure 9. Relationships between initial (August 1990) densities and total mortality at each date of red spruce seedlings. "r" is the Pearson correlation coefficient. Only plots with initial densities ≥ 100 stems/m² are shown (n = 43 plots in all cases).

Table 5. Associations between expected and observed numbers of 1990-origin red spruce seedlings occurring on substrate types. Expected numbers were calculated as: (mean % cover of a substrate) x (total number of seedlings on all substrates) / 100. A "*" indicates an observed value where the squared difference: $[(\text{observed number}) - (\text{expected number})]^2 / (\text{expected number})$ is >10. These squared differences contribute the most to the overall value of chi-square (X^2).

Substrate Type	Evaluation Date (mo/yr)					
	5/90	8/90	5/91	8/91	5/92	8/92
Number of Seedlings	1209	15,897	7045	948	553	514
FOREST FLOOR (% Cover)	76.9	80.4	77.6	78.2	79.4	82.8
Expected (#)	930	12,781	5467	741	439	426
Observed (#)	906	13,257*	5475	735	385	366
DEAD LOG (% Cover)	2.4	4.9	5.7	5.3	5.4	4.1
Expected (#)	29	779	402	50	30	21
Observed (#)	12	422*	168*	24*	30	23
DEAD ROOT (% Cover)	5.7	2.0	2.4	2.2	1.9	2.5
Expected (#)	69	318	169	21	11	13
Observed (#)	33*	627*	465*	24	7	10
LIVE ROOT (% Cover)	5.7	5.2	7.0	6.0	5.7	4.8
Expected (#)	69	827	493	57	32	25
Observed (#)	80	748	406*	30*	36	42*

Table 5. Continued.

Substrate Type	Evaluation Date (mo/yr)					
	5/90	8/90	5/91	8/91	5/92	8/92
Number of Seedlings	1209	15,897	7045	948	553	514
ROCK (% Cover)	9.3	7.5	7.1	8.1	7.5	5.8
Expected (#)	112	1192	500	77	42	30
Observed (#)	178*	838*	489	132*	91*	69*
STUMP (% Cover)	<0.1	<0.1	0.2	0.2	0.1	<0.1
Expected (#)	1	3	14	2	1	<1
Observed (#)	0	5	42*	3	4*	4*
Overall X^2	69.85	595.63	724.55	67.22	92.02	145.05
d.f.	5	5	5	5	5	5
P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

difference of observed and expected percentages of seedlings (used in computing X^2) identified seedling-substrate/surface associations contributing the most to non-random distributions. Squared differences greater than 10 are indicated (*) in Tables 5 and 6. Few consistent trends were evident among seedling-substrate associations. Initially, seedlings were less frequent than expected on dead logs but, by 1992, became about as frequent as expected. Early-germinating seedlings in 1990 were infrequent on dead roots, then became more frequent than expected, and finally became mostly independent of that substrate. Live roots, initially unimportant, were unfavorable substrates in 1991 yet became favorable by August 1992. Rocks were favorable to early 1990 germinal seedlings, unfavorable by August 1990, and favorable for later survivors. Stumps were rare microsites, and the distinction between "dead root" and "stump" was often arbitrary in the field. Small variations in cover estimates of stumps generated illogical trends (e.g., negative mortality from August 1990 to May 1991--Table 5). Similar effects are apparent for other substrates, particularly at later dates when the absolute number of seedlings becomes small.

Seedling distributions among surface types showed simpler trends (Table 6). Although early spruce germination in 1990 tended to occur on litter more often than on bryophytes, this tendency reversed by the time the remainder of the cohort appeared (August 1990). By August 1992, 80% of seedlings occupied bryophytes, even though bryophytes (predominantly the liverwort Bazzania trilobata [L.] S.F. Gray) covered only about half of all surfaces. Few seedlings became established on surfaces devoid of bryophytes or litter.

Table 6. Associations between expected and observed numbers of 1990-origin red spruce seedlings occurring on surface types. Expected numbers were calculated as: (mean % cover of a surface) x (total number of seedlings on all surfaces) / 100. A "*" indicates an observed value where the squared difference: $[(\text{observed number}) - (\text{expected number})]^2 / (\text{expected number})$ is >10 . These squared differences contribute the most to the overall value of chi-square (X^2).

Surface Type	Evaluation Date (mo/yr)					
	5/90	8/90	5/91	8/91	5/92	8/92
Number of Seedlings	1209	15,897	7045	948	553	514
BRYOPHYTES (% Cover)	48.6	48.9	52.1	48.7	46.7	48.2
Expected (#)	588	7774	3670	462	258	248
Observed (#)	431*	10,593*	5494*	758*	436*	414*
LITTER (% Cover)	49.3	48.8	45.1	48.8	50.6	48.8
Expected (#)	596	7758	3177	463	280	251
Observed (#)	778*	5296*	1548*	189*	116*	100*
BARE (% Cover)	2.1	2.3	2.8	2.5	2.7	3.0
Expected (#)	25	366	197	24	15	15
Observed (#)	0*	8*	3*	1*	1*	0*

Table 6. Continued.

Surface Type	Evaluation Date (mo/yr)					
	5/90	8/90	5/91	8/91	5/92	8/92
Number of Seedlings	1209	15,897	7045	948	553	514
Overall χ^2	122.71	2153.50	1932.88	373.71	231.11	217.72
d.f.	2	2	2	2	2	2
P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

D. Discussion

Although herbaceous taxa showed seasonal fluctuations, (mostly in response to growth of ferns), total herbaceous cover was low. This may reduce competition of woody seedlings with herbs. Densities of woody seedlings fluctuated by orders of magnitude over periods of months. Both red spruce and yellow birch can show major germination pulses. However, yellow birch is less shade-tolerant and is unlikely to establish in large numbers until major gaps form in the forest canopy.

Fowells (1965) and Blum (1990) both state that most red spruce seeds germinate the spring following dispersal. Nicholas et al. (1992a), in a survey of spruce forest of the Great Smoky Mountains from 1985 through 1990, found mean densities of newly germinated spruce of up to 18.9 stems/m² after a major seed crop in 1987. (This density was exceeded >15-fold in Cranberry in 1990, probably because Nicholas et al. (1992a) sampled a much wider range of stand conditions.) These data suggest that most seedlings emerging in 1990 in the Cranberry Wilderness originated from 1989 seed production. Trees produced notably fewer cones in 1990 and 1991 (personal observation), and few new seedlings appeared in 1991 and 1992 (Table 4). Most seedlings established prior to 1990 were ≥ 5 yr old. Appearance of red spruce seedlings seems closely coupled to the previous year's seed production.

First-winter mortality (56%) appears to have been moderate. Westveld (1931) found first-winter mortality of red spruce seedlings to be 70% in a New Hampshire spruce-hardwoods forest, both in plots cleared of vegetation and litter and in undisturbed plots. Moore (1926) sowed

200 red spruce seeds onto mineral soil beneath a forest canopy and a "small opening" in Maine. Under the canopy, 75 seedlings appeared and 46 (61%) of those died by June 1923. In the opening, only 50 appeared but only 6 (12%) of those died by June 1923. In a cohort of red spruce in the Great Smoky Mountains, first-winter mortality (1988-1989) was about 92% (Pauley and Clebsch, submitted). By comparison, mortality among first-winter survivors in the Cranberry Wilderness during summer 1991 was quite high (87%). One reason for high summer mortality may have been drought, to which young red spruce are very susceptible (Place 1955; Fowells 1965; Blum 1990). Total precipitation at nearby Snowshoe Mountain, West Virginia, during May, June, and July of 1991 was 41% less than the mean total for the same months over the previous 15 years. Later seedling mortality, however, is considerably lower.

Both a linear and a negative exponential model adequately describe changes in $\log_e(\text{density})$ of spruce seedlings in the Cranberry Wilderness from 1990 to 1992. The negative exponential model fits the data better than the a power function model and may be more biologically reasonable than the linear model. As a seedling becomes better established, its probability of mortality should decline. The seedling develops more foliage, its roots penetrate further into its substrate, and it becomes less susceptible to environmental extremes. If mortality of the 1990 cohort remains relatively constant (Figure 3a), its addition to seedling pool size after five years will be very small. However, if survivorship approximates the exponential model (Figure 8b), the 1990 cohort would more than triple seedling pool size. Survivorship approximating the power function model (Figure 8c) would increase pool size 8-fold.

Factors favoring seedling appearance also seemed to favor early survival. Later seedling mortality became more influenced by factors other than initial density. Because final seedling density was only about 3% its initial value and most seedlings were still very small (generally <5 cm tall), intra-specific competition is unlikely. Microsite variables are probably more important.

Several studies in North American forests have found that conifer seedlings can be unexpectedly abundant on fallen logs (Christy and Mack 1984; Harmon and Franklin 1989; Pauley and Clebsch 1990). In some cases, these associations developed within the first few years after germination because of lower mortality rates on logs. However, spruce seedlings in the Cranberry Wilderness have not yet become more abundant than expected on dead logs. Seedlings have survived better on rocks, particularly from August 1991 onward. This association may be coincidental because most rocks were covered with bryophytes and seedlings were strongly associated with bryophyte cover (see below). The irregularities of other associations suggest that substrate properties have not yet begun to affect seedling survival in persistent ways. Because 1990-origin seedlings are still very small, their roots may not have penetrated deeply enough for subsurface features to significantly influence their survival.

Clear trends in seedling-surface associations are evident. Certainly some type of surface covering is necessary for seedling appearance simply because surfaces devoid of litter or bryophytes do not retain seeds efficiently (Harmon 1989). Early seedling appearance occurred mainly on litter. Forest litter (leaves and twigs) can show

large temperature fluctuations in spring (Fuller 1977), possibly warming up faster than bryophytes and stimulating germination. However, bryophytes clearly and consistently supported more seedlings than expected throughout the remaining study period and are favorable places for seedling survival. Bryophytes may retain moisture, moderate temperature changes, and alter nutrient concentrations in the soil water film, thus favoring high survival of spruce seedlings.

The numerical effect of the 1990 cohort on seedling pool size appears to be very sensitive to mortality rate trends. Constant mortality will dampen episodic reproduction, while declining mortality will permit a reproductive pulse to persist for many years. A large pulse of seedling production coupled with a declining mortality rate may allow red spruce to dominate the seedling pool in spruce forests of the Cranberry Wilderness. Meanwhile, canopy trees will continue to reproduce in an episodic fashion, and the seedling pool will continue to receive inputs of new cohorts. Although seedlings may begin competing with each other as they grow, by that time red spruce may occupy many of the most favorable microsites in the understory. If spruce can saturate a forest understory with seedlings, canopy trees are more likely to be replaced by spruce. Thus, short-term reproductive pulses may become persistent influences on forest structure and composition.

CHAPTER 5

MODELING EPISODIC REPRODUCTION BY RED SPRUCE
IN THE CRANBERRY WILDERNESS, WEST VIRGINIA

A. Introduction

Many "gap" models have been constructed that track the birth, growth, and death of individual trees on simulated plots 0.01-0.08 ha in area (Botkin et al. 1972; Shugart and West 1977, 1979, 1981; Doyle 1980, 1981; Solomon et al. 1980, 1984; Shugart 1984; Busing 1985; Davis and Botkin 1985; Pastor and Post 1985, 1986; Busing and Clebsch 1987; Pastor et al. 1987). Such models are useful for investigating aspects of forest dynamics occurring on timescales not amenable to field studies. However, the models use data from published sources (e.g., Fowells 1965) to develop parameters and algorithms that are often generalized and simplistic. For example, the JABOWA model of Botkin et al. (1972), one of the first such models, recruits new trees into a simulated plot by selecting the species and the number of seedlings to plant almost at random. Although this method is suitable for some purposes, seedlings can be recruited into a tree population in more complex ways, as shown in Chapter 4. Improved models should account for such processes.

The survivorship data for red spruce in Chapter 4 suggest that, for shade-tolerant species with declining seedling mortality, establishment of large cohorts could allow such species to suddenly dominate the seedling pool. Whether occasional large cohorts of

seedlings alter long-term forest dynamics cannot readily be determined in the field. The use of simulation models may provide insights into this question. The objectives of this chapter are (1) to simulate the effects of episodic recruitment of red spruce seedlings on stand-level attributes and (2) to compare the results with simulations where spruce showed more continuous recruitment.

B. Model Structure, Parameterization, and Modification

Most gap models are fashioned after the JABOWA model (Botkin et al. 1972) written in the FORTRAN programming language. The FORTRAN code is usually divided into subroutines called in sequence by a main program. For example, JABOWA first calls a PLOTIN subroutine, which initializes conditions on simulated plots 10 x 10 m in size. The plots can either be bare or contain actual field data. A BIRTH subroutine randomly selects shade-tolerant species from a list of available species and randomly chooses the number of stems (0-2) to enter the plot. Shade-intolerant species are recruited in larger numbers but only when the weight of foliage in the plot drops below a threshold value. Subroutine KILL removes selected trees from the simulated plot according to (1) an assumption that $\leq 2\%$ of recruits will reach maximum known age of that species and (2) whether or not each tree shows an annual diameter increment below a threshold value. Slow-growing trees have a higher chance of mortality. Subroutine GROW uses an equation with species-specific parameters to calculate the annual growth of a tree on an optimum site with no competition. Growth is sigmoid in form (i.e.

slow at first, then rapid, and finally slow at tree maturity) and is based on an assumption that a tree will attain $2/3$ of its maximum diameter at $1/2$ its maximum age. In a given year, this maximum possible growth is reduced according to light availability, accumulated growing degree-days, and a measure of soil quality. In JABOWA, soil quality is indicated by the maximum basal area of a stand under ideal conditions. The resulting data are then recorded by an OUTPUT subroutine, and the whole program is repeated for replicate plots over many simulated years.

Most of JABOWA's successors use this same basic programming structure. One modification of the BIRTH subroutine that has been made is in the selection of the number of seedlings to be recruited. Instead of nearly random recruitment as in JABOWA, Pastor and Post's (1985) LINKAGES model reduces a maximum number of seedlings of each species by plot-wide light, soil moisture, and temperature constraints. The maximum numbers of seedlings used are "reasonable approximations taken from the literature" (Pastor and Post 1985, p. 54). This modification accounts for large among-species differences in potential recruitment rates observed in nature. Busing and Clebsch's (1987) FORANAK model uses maximum numbers of seedlings but reduces them according to the "canopy influence" of trees only within 5 m of each seedling. Some models have additional subroutines. For example, the LINKAGES model has a DECOMP subroutine that calculates nitrogen availability in decomposing litter as influenced by moisture, litter chemistry, and soil temperature. This subroutine is thus a significant extension of conventional gap models that do not explicitly simulate soil nutrient dynamics. One intriguing consequence of varying nitrogen availability

can be a long-term alternation in dominance by coniferous and deciduous trees. Pastor et al. (1987) have found this behavior when simulating boreal forests composed of spruce and birch, and they suggested that such endogenous nutrient cycles may contribute to spruce declines (see Chapter 2, History of Human Impact, p. 17). The main objective of this chapter is to test the long-term effects of episodic reproduction as it affects long-term forest composition, especially with the possibility of red spruce decline. Because LINKAGES has shown spruce decline behavior, this model was selected for adaptation to West Virginia red spruce forests.

Although mast seeding is episodic production of seeds, the LINKAGES model, like most JABOWA-type models, recruits individuals into the population when they are 1.0-1.4 cm diameter at breast height (ca. 1.4 m). Computational difficulties would arise if smaller individuals were included. For example, in LINKAGES, each plot may contain up to 1500 trees, and a 1000-year run of 20 replicate plots requires about three minutes of processing time on the University of Tennessee VAX mainframe computer. Tracking thousands or millions of seeds and seedlings on a simulated plot becomes impractical. Furthermore, the functions used to model growth and mortality rely on parameters that exist almost exclusively for trees above 1.4 m height. For these reasons, mast seeding in red spruce was simulated by episodic seedling recruitment rather than episodic seed production.

Important parameters used in this version of LINKAGES are listed in Tables 7 and 8. Climatic data are from Snowshoe Mountain Resort, 29 km northeast of the Cranberry Wilderness at an elevation of 1453 m

Table 7. Climatic parameters used in the LINKAGES model. "S.D." is standard deviation. Data are from Snowshoe Mountain Resort, 29 km northeast of the Cranberry Wilderness, elevation 1453 m (National Oceanic and Atmospheric Administration 1976-1991).

Month	Parameter			
	Mean	S.D.	Mean	S.D.
	Temperature (°C)		Precipitation (cm)	
January	-7.0	2.2	13.5	6.2
February	-4.2	2.5	11.5	3.4
March	0.5	2.1	14.5	3.9
April	5.2	1.8	11.7	5.8
May	11.5	2.2	11.0	4.2
June	15.4	1.1	11.6	6.1
July	17.7	1.0	15.4	5.0
August	17.2	1.3	12.9	7.0
September	13.5	1.0	9.7	6.1
October	6.7	2.0	11.8	7.0
November	2.9	1.9	12.2	5.7
December	-3.4	3.2	12.0	5.1

Table 8. Species parameters used in the LINKAGES model. Species nomenclature follows Strausbaugh and Core (1970-1977).

Species	Parameter ^a							
	DD _{max}	DD _{min}	b ₃	b ₂	ITOL	AGEMAX	G	MPLANT
<u>Acer rubrum</u>	3400	1100	0.51	76.4	2	150	180	100
<u>Betula alleghaniensis</u>	2300	1000	0.24	47.3	1	250	100	120
<u>Fagus grandifolia</u>	5537	1326	0.23	56.1	1	350	72	40
<u>Picea rubens</u>	2000	1000	0.29	57.3	1	300	120	40
<u>Prunus pensylvanica</u>	2500	560	1.51	90.9	2	30	250	600
<u>Prunus serotina</u>	5993	1932	0.29	57.3	2	200	66	20
<u>Tsuga canadensis</u>	3800	1200	0.15	44.8	1	650	50	8

^aParameters are: DD_{max} and DD_{min}, maximum and minimum growing degree-day tolerance (days)

b₃ and b₂, parameters relating maximum height and maximum diameter (Pastor and Post 1985, p. 56)

ITOL, shade tolerance class (1 = tolerant, 2 = intolerant)

AGEMAX, maximum reported age of species (yr)

G, growth parameter such that diameter is 2/3 maximum at 1/2 maximum age (Botkin et al. 1972, p. 872)

MPLANT, maximum number of seedlings planted/year on a 1/12 ha plot (Pastor and Post 1985, p. 54)

(National Oceanic and Atmospheric Administration 1976-1991). These data are used by LINKAGES to calculate growing degree-days and evapotranspiration as well as to compare species frost tolerances with stochastically varying climate. Soil field capacity (18.0 cm) and wilting point (7.5 cm) used in the model are rather low because of the coarse texture of soils in Cranberry (sandy loams--D. Flegel, personal communication). However, this rarely produces moisture stress in the model because precipitation is moderately high and consistent (Table 7). Although LINKAGES draws on a list of 72 tree species, those species not actually occurring in Cranberry were deleted from the data set. Several of the degree-day maxima and minima (Table 8) were adjusted because they did not permit important species to grow well or even at all (e.g., Acer rubrum).

One of the most important parameters in JABOWA-type models is G, a growth scaling parameter that determines each species' growth rate. The value of G will vary across a species' range and must be adjusted to the optimum growth expected at a particular site. One way to estimate G involves using maximum age, diameter, and height of a species from published sources (e.g., Blum 1990) in a FORTRAN program called GEST (Urban 1990). GEST uses an equation from Botkin et al. (1972, p. 872) to determine diameter increment of a tree growing under optimum conditions. An initial G value is entered and adjusted until reasonable tree size and growth are obtained. Red spruce in second-growth forest of the Cranberry Wilderness can attain 40-50 cm diameter 60-70 years after logging (see Figure 2, p. 31), and increment cores (E. F. Pauley, in preparation) show annual radial increments of up to 0.6 cm. These

parameters gave a rather high estimate of G for red spruce (120) as compared to that in JABOWA (50--Botkin et al. 1972), LINKAGES (89--Pastor and Post 1985), and FORANAK (50--Busing and Clebsch 1987). However, lower values resulted in stands with very low total basal areas (10-15 m²/ha). The values of MPLANT were, for the most part, unmodified from Pastor and Post (1985). Red spruce had a low MPLANT value (8), but adjustment to 40 produced more reasonable basal areas and densities.

The major modification made to the LINKAGES model was the addition of a mastling routine for red spruce. The timing between successive mast crops in forest trees is partly determined by the build-up of energy reserves (Silvertown 1980). The mastling routine simulated this behavior by multiplying a random number between 0 and 1 by a variable called ENERGY (initially 0, indicating the amount of energy reserves) and assigning the product to a variable called MAST. MAST was then compared with a constant value (3.0, the minimum number of years believed to elapse between successive mast crops in red spruce--Fowells 1965; Blum 1990). If MAST was less than 3.0, the value of MAST was stored, ENERGY was increased by 1, and the foregoing process was repeated for the next year. If MAST was equal to or greater than 3.0, that year was a mast year, the value of MAST was stored, and ENERGY was set back to 0 (indicating a depletion of energy reserves). Thus, mast years could not occur in two successive years. As ENERGY accumulated, MAST became more likely to exceed 3.0. The result was an array of multipliers, typically 0, often 1, sometimes 2, and occasionally 3 or more. Only rarely did the value of MAST exceed 8. The array containing the values of MAST was then used to multiply recruitment normally simulated by LINKAGES to

obtain the number of recruits for that year. This routine produced recruitment episodes about every 4-6 years. The same values of MAST were used over replicate plots, thus simulating stand-wide synchrony in masting behavior. The masting routine was applied only to red spruce.

In the non-masting version, recruitment was determined in the conventional way, *i.e.* by changing a maximum number (MPLANT in Table 8) of spruce seedlings (40 stems/plot) by multipliers sensitive to growing-degree-day accumulation, light level, and soil moisture for each year. A random number factor made recruitment stochastic. Figure 10a shows a typical pattern of annual seedling recruitment where the masting routine was bypassed. Recruitment was high in a young stand with no canopy but was gradually reduced to a low and fairly constant level. Use of the masting routine caused highly variable recruitment (Figure 10b). Seedling crops in a mast year could be many times the size of those in non-mast years, and frequently no new recruits entered the population at all.

Simulations were made, with and without the use of this masting routine, under several different scenarios. Beginning with bare plots, the stand was first allowed to develop under stable conditions with available nitrogen set at a constant 100 kg/ha/yr, a level well above that required for all species in these simulations. (Excess nitrogen has no effect in LINKAGES.) The effects of logging this forest were also simulated by removing all trees >15 cm diameter at year 500. Available nitrogen was also allowed to vary according to leaf litter quality, the major innovation of the LINKAGES model. In another simulation, a decline in red spruce annual diameter growth was

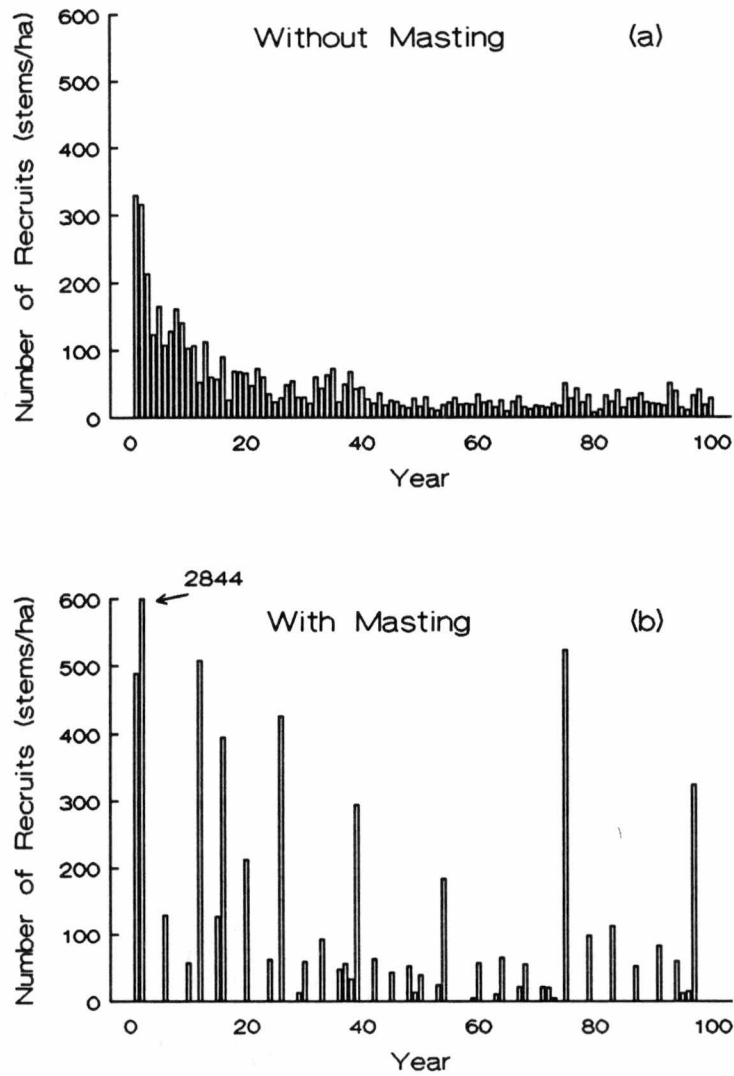


Figure 10. Red spruce annual recruitment in LINKAGES without (a) and with (b) a masting routine.

introduced. Beginning at year 300, growth was decreased by 25% in all spruce trees, and after year 320, growth was decreased by 50%. Finally, a growth decline was combined with varying nitrogen availability. These scenarios stressed the forest in several different ways, and the effect of masting was examined under these different scenarios.

C. Results

Table 9 shows compositional data for actual stands in West Virginia (Clovis 1979; Stephenson and Clovis 1983; Adams and Stephenson 1989; Pauley 1989) and for a simulated stand. In the actual stands, age was based on increment cores (e.g., the mean age of dominant and codominant trees--Adams and Stephenson 1989) or general historical information (Pauley 1989). Mielke *et al.* (1986) also presented summaries of red spruce basal area and density data for a large number of forests in West Virginia, but they did not report stand ages or data for other species. In those forests, red spruce basal areas ranged from 17.7 to 27.4 m²/ha, and densities ranged from 495 to 946 stems/ha.

In the actual stands, spruce basal area appears to increase and then decrease with stand age. Spruce density appears to be high in some young stands, decline, and then rise somewhat (with the exception of the 201 yr old stand). Overall spruce importance thus increases and then declines with stand age (Table 9). Basal areas and densities of hardwoods (yellow birch, red maple, and beech) in older stands could not be determined from Adams and Stephenson's (1989) data. However, hardwoods appear to be important in young stands, decline with age

Table 9. Composition of actual spruce stands in West Virginia reported by published studies compared with that of a simulated stand. In all studies, Picea is P. rubens, Betula is B. alleghaniensis, Acer is A. rubrum, and Fagus is F. grandifolia. Except where noted, the minimum diameter of trees included in all studies is 2.5 cm.

Stand Attribute	Stand Age (yr)	Species				NOTE
		<u>Picea</u>	<u>Betula</u>	<u>Acer</u>	<u>Fagus</u>	
Basal Area						
(m ² /ha)						
ACTUAL	39-84	12.0	5.7	7.0	7.3	1
	60-80	33.4	2.7	1.6	0.1	2
	164	27.9	-	-	-	3
	200	18.3	-	-	-	3
	201	11.8	-	-	-	3
SIMULATED	40	13.5	4.4	3.8	<1	
	60	19.8	3.5	4.3	<1	
	80	22.1	3.2	3.6	<1	
	160	20.9	2.9	0.9	<1	
	200	22.7	1.0	0.4	<1	

Table 9. Continued.

		Species				
Stand	Stand					
Attribute	Age (yr)	<u>Picea</u>	<u>Betula</u>	<u>Acer</u>	<u>Fagus</u>	NOTE
Density						
(stems/ha)						
ACTUAL	39-84	492	439	216	128	1
	60-80	1215	205	55	5	2
	164	285	-	-	-	3
	200	525	-	-	-	3
	201	230	-	-	-	3
SIMULATED	40	755	494	206	24	
	60	404	145	99	1	
	80	284	103	50	8	
	160	565	145	78	93	
	200	545	79	38	76	

Table 9. Continued.

Stand	Stand	Species				NOTE
		<u>Picea</u>	<u>Betula</u>	<u>Acer</u>	<u>Fagus</u>	
Attribute	Age (yr)					
Importance						
Value (%) ^a						
ACTUAL	39-84	31	25	18	6	1
	60-80	78	9	4	<1	2
	164	69	14	1	0	3
	200	38	22	6	18	3
	201	34	22	0	0	1
SIMULATED	40	57	27	16	1	
	60	67	18	15	<1	
	80	70	17	12	1	
	160	74	14	6	5	
	200	79	12	4	5	

^aImportance value is: (% total basal area + % total density) / 2.

NOTES:

1. Clovis (1979); Stephenson and Clovis (1983). Means of eight stands above 1000 m elevation. Basal area and importance value data for trees >10 cm diameter only.

Table 9. Continued.

Notes: (continued)

2. Pauley (1989). One stand 1270-1380 m elevation.
3. Adams and Stephenson (1989). One stand each, all stands 1110-1200 m elevation. Importance value data are for trees >10 cm diameter only. The 201 yr-old stand had a dense Rhododendron maximum understory.

as spruce dominates, and then reestablish as spruce becomes less important.

The simulated stand shows somewhat different behavior (Table 9). Over the first 200 yr (beginning from bare plots), red spruce basal area increases asymptotically. Spruce density is initially high, then declines, and finally rises again and stabilizes. Overall importance of spruce also increases somewhat over 200 yr. Deciduous species tend to be important early and then decline, with the exception of beech, which increases slightly in the older stand.

The actual data come from a range of sites varying not only in age but also in such attributes as aspect, elevation, and reason for study. Most of the young stands (Clovis 1979; Stephenson and Clovis 1983) occurred on north-facing slopes below 1200 m elevation and were chosen primarily for a study of habitats of the Cheat Mountain salamander (Plethodon nettingi nettingi Green). In many of those stands, red spruce was a minor component. Pauley's (1989) stand was higher in elevation (>1270 m), on very gentle slopes, and studied specifically as an example of closed-canopy spruce forest. The three older stands are the only significant old-growth spruce forests known in West Virginia (Adams and Stephenson 1989). All are 1110-1200 m elevation and vary widely in aspect (0°-215° azimuth). One (the 201 yr old stand) has a dense Rhododendron maximum understory that may reduce tree regeneration (Adams and Stephenson 1989). The variation in stand attributes makes their use to approximate a chronological sequence questionable.

For this reason, model parameters were adjusted only to produce attributes within the range of actual stands. The comparable basal

areas and densities in the older simulated and actual stands suggests that the model is a reasonably valid representation (sensu Shugart 1984) of red spruce-yellow birch-red maple forests in West Virginia.

In simulations showing continuous spruce recruitment, spruce comprised most of the basal area and density (Figure 11a,b). The young stand had high proportions of yellow birch (Betula alleghaniensis) and red maple (Acer rubrum); maple basal area subsequently declined. Pin cherry (Prunus pensylvanica L.) was also a major component of the young stand, as is typical for the species (Marks 1974). (For clarity, pin cherry is not shown.) Where red spruce was allowed to mast, birch showed slightly reduced basal area and density (Figure 12a,b), especially in the early stages of stand development. Logging of the stand slightly increased the basal area of birch where spruce did not mast (Figures 13a), but where spruce showed masting, birch basal area and density were both low even after logging (Figure 14a,b). Permitting available nitrogen to vary as a function of leaf litter quality greatly reduced yellow birch basal area (Figure 15a), although many small stems appeared briefly in the young stand (Figure 15b). In all simulations where nitrogen was allowed to vary, nitrogen availabilities dropped from 65 kg/ha/yr to about 29-33 kg/ha/yr by year 300 and were quite constant thereafter. Where red spruce showed masting, yellow birch was almost completely eliminated (Figure 16a,b). A red spruce growth decline dramatically reduced spruce basal area, increased birch and maple basal area, and increased the densities of all species (Figure 17a,b). Red spruce masting tended to moderate these changes, making spruce basal area decline more gradually and reducing the final basal area of yellow

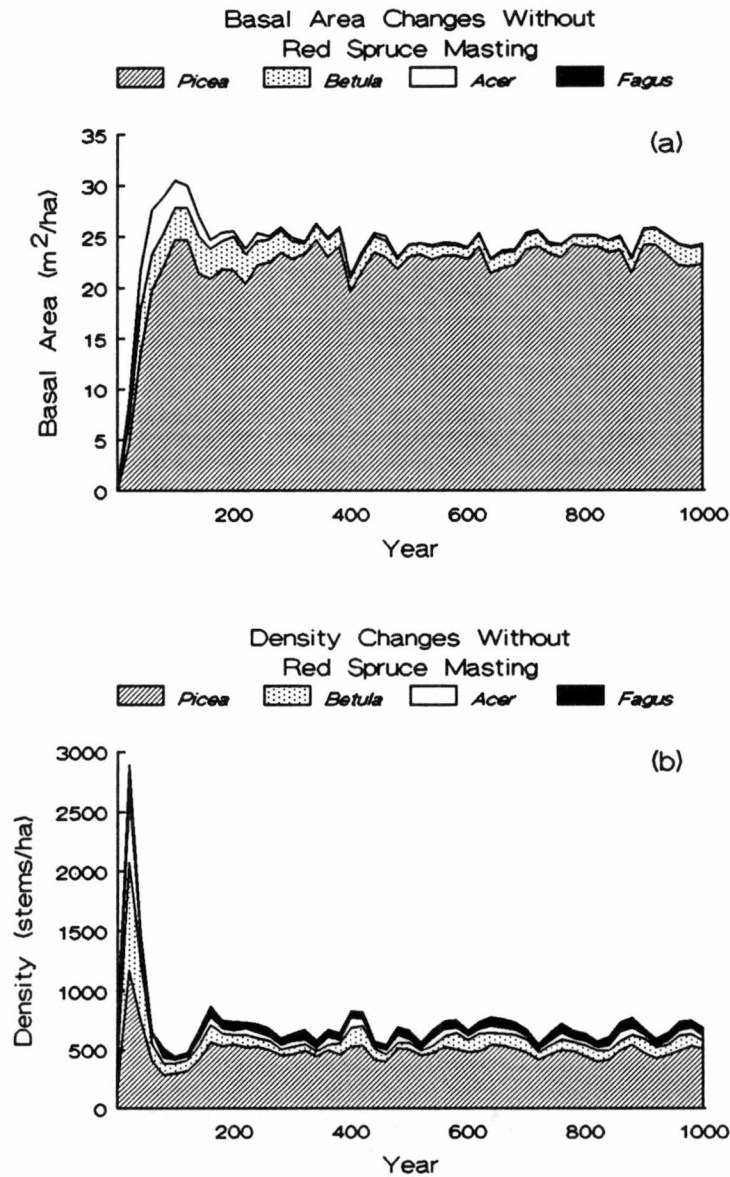


Figure 11. Changes in basal areas (a) and densities (b) in simulated plots without red spruce masting. Values are means of 20 replicate plots.

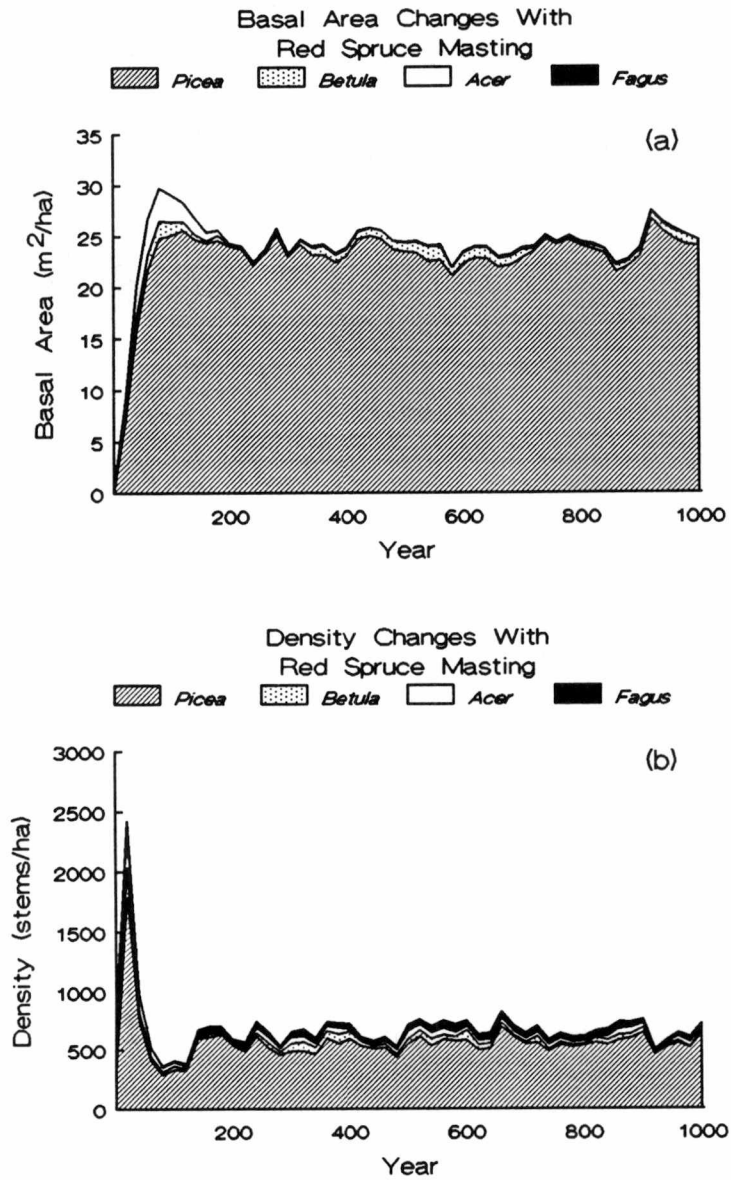


Figure 12. Changes in basal areas (a) and densities (b) in simulated plots with red spruce masting. Values are means of 20 replicate plots.

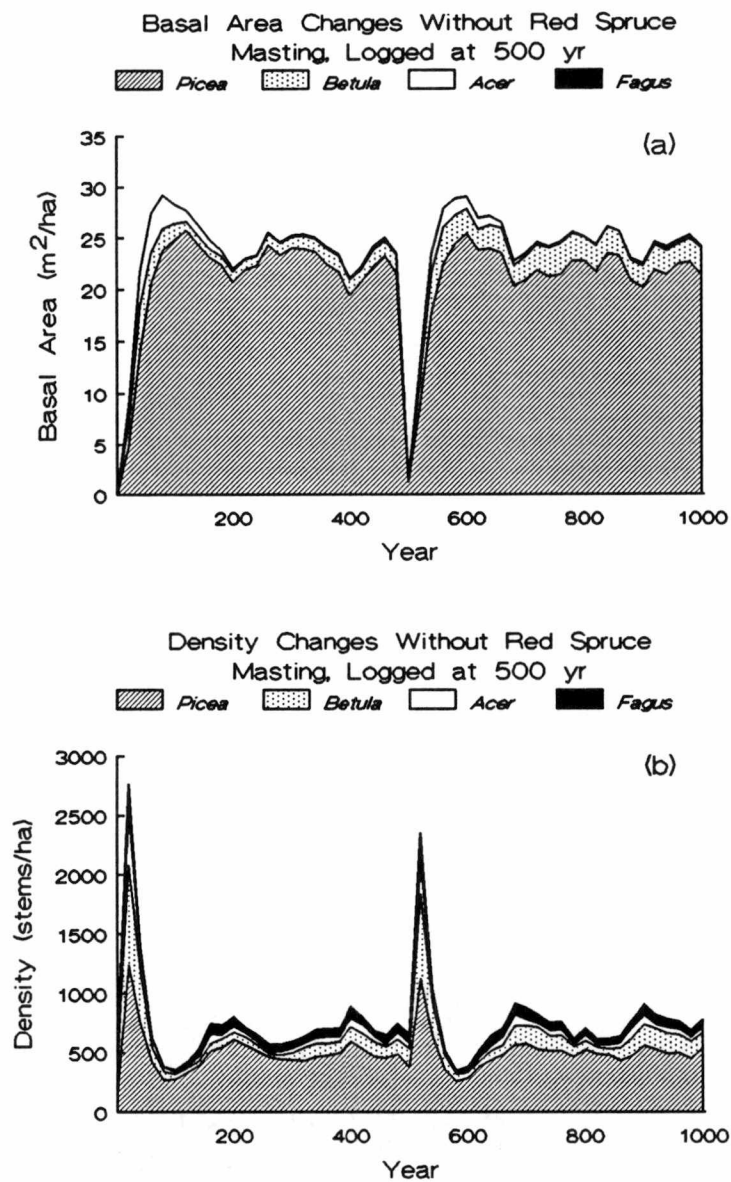


Figure 13. Changes in basal areas (a) and densities (b) in simulated plots without red spruce masting, with all trees >15 cm diameter removed at 500 yr. Values are means of 20 replicate plots.

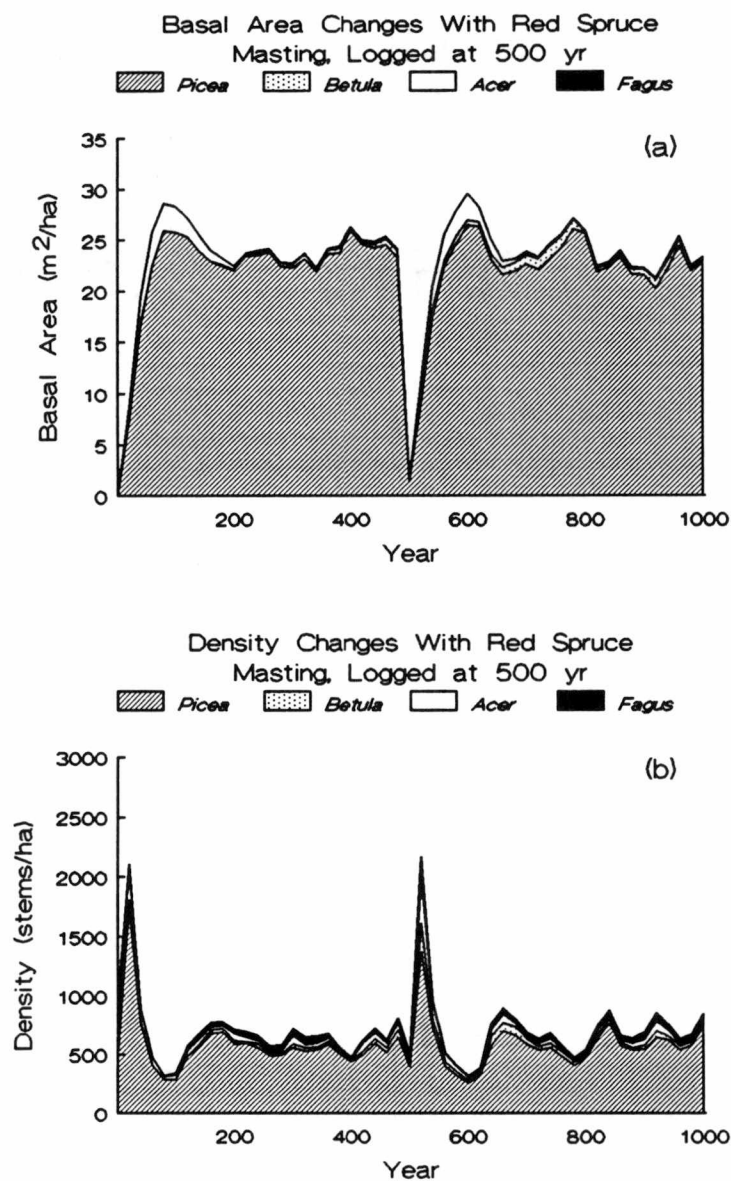


Figure 14. Changes in basal areas (a) and densities (b) in simulated plots with red spruce masting, with all trees >15 cm diameter removed at 500 yr. Values are means of 20 replicate plots.

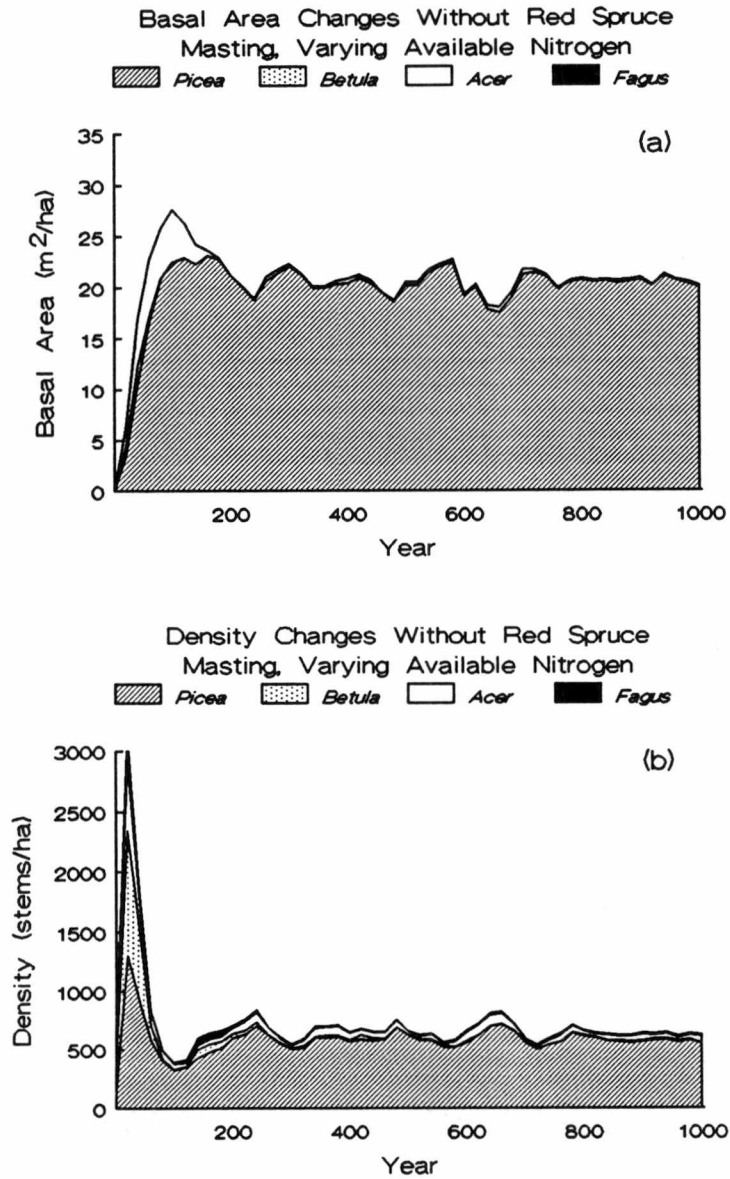


Figure 15. Changes in basal areas (a) and densities (b) in simulated plots without red spruce masting, with varying available soil nitrogen. Values are means of 20 replicate plots.

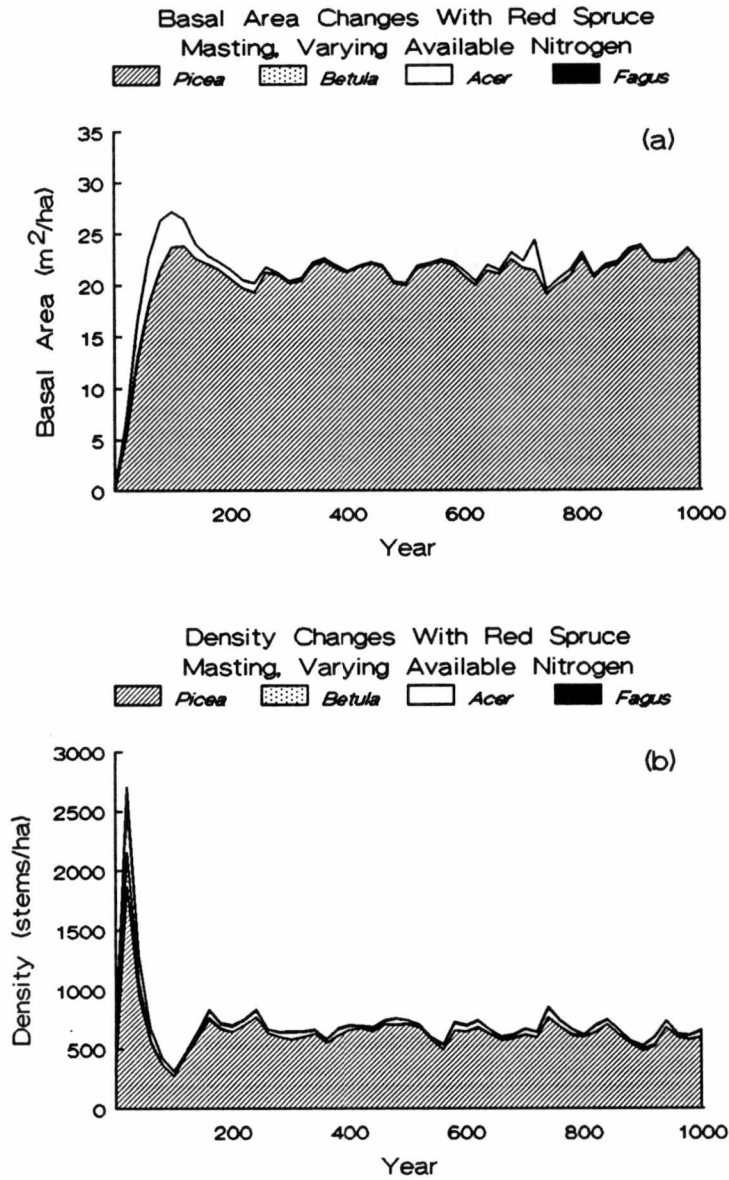


Figure 16. Changes in basal areas (a) and densities (b) in simulated plots with red spruce masting, with varying available soil nitrogen. Values are means of 20 replicate plots.

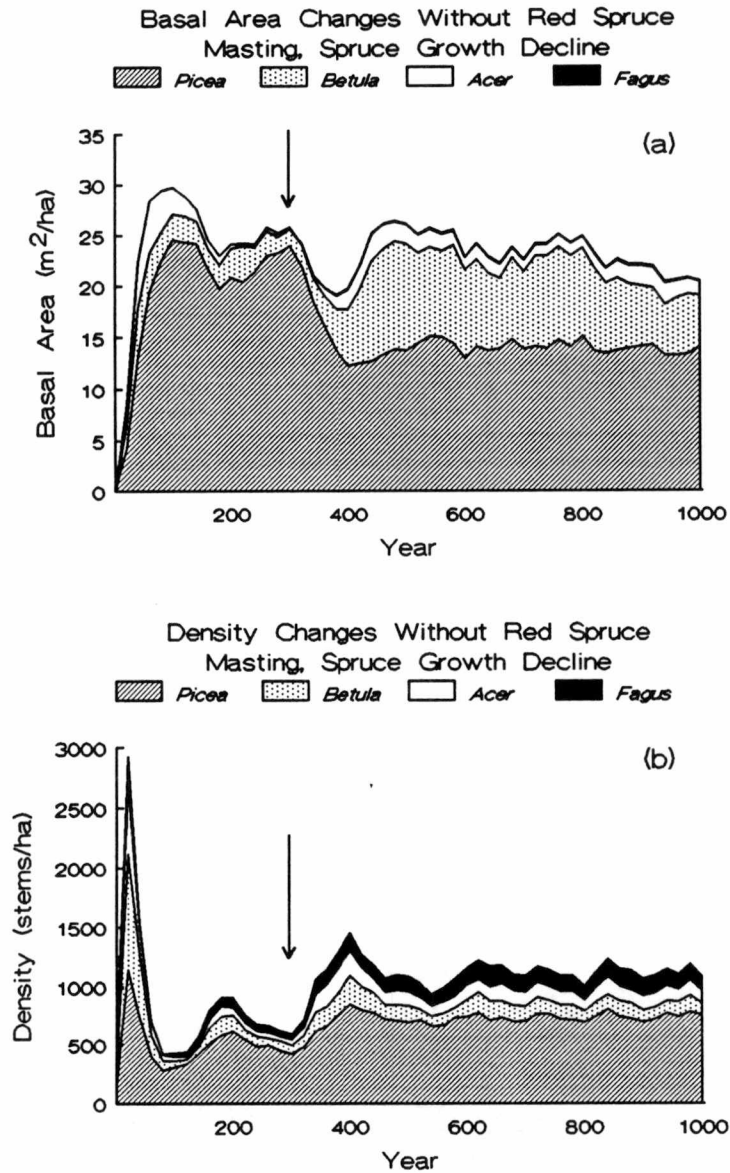


Figure 17. Changes in basal areas (a) and densities (b) in simulated plots without red spruce masting, with a red spruce growth decline. Spruce diameter increment is reduced, beginning at year 300 (arrow), by 25% and, after year 320, by 50%. Values are means of 20 replicate plots.

birch (Figure 18a,b). Combining a spruce growth decline with varying nitrogen availability produced a very low diversity stand composed almost solely of red spruce and red maple (Figure 19a,b). Yellow birch density was initially high but decreased to near zero. Red spruce masting reduced birch density even in the early stages of stand development (Figure 20b). With or without spruce masting, overall stand basal areas were about half of previous values, and overall densities nearly doubled.

D. Discussion

The present version of LINKAGES produces a red spruce-yellow birch-red maple forest whose composition is similar to that of other such forests in West Virginia. The model is probably most applicable to spruce-dominated forests like those studied in the Cranberry Wilderness. One feature of the forests in Cranberry the model was unable to produce was the combination of spruce basal area and density found there. The forests in Cranberry are 64-71 yr old and have a live spruce basal area of 29.8 m²/ha and a live density of 806 stems/ha (Table 1, p. 30). The model produced similar basal areas at this stand age, but spruce density was about half the actual value. Adjustments of parameters to give higher spruce density produced lower spruce basal area. Apparently, high basal area and high density are incompatible in the model. The model data and the actual data of Stephenson and Clovis (1983) (Table 9) and Mielke et al. (1986) suggest the forests of Cranberry are unusual in this respect. The reasons for this are unclear at present.

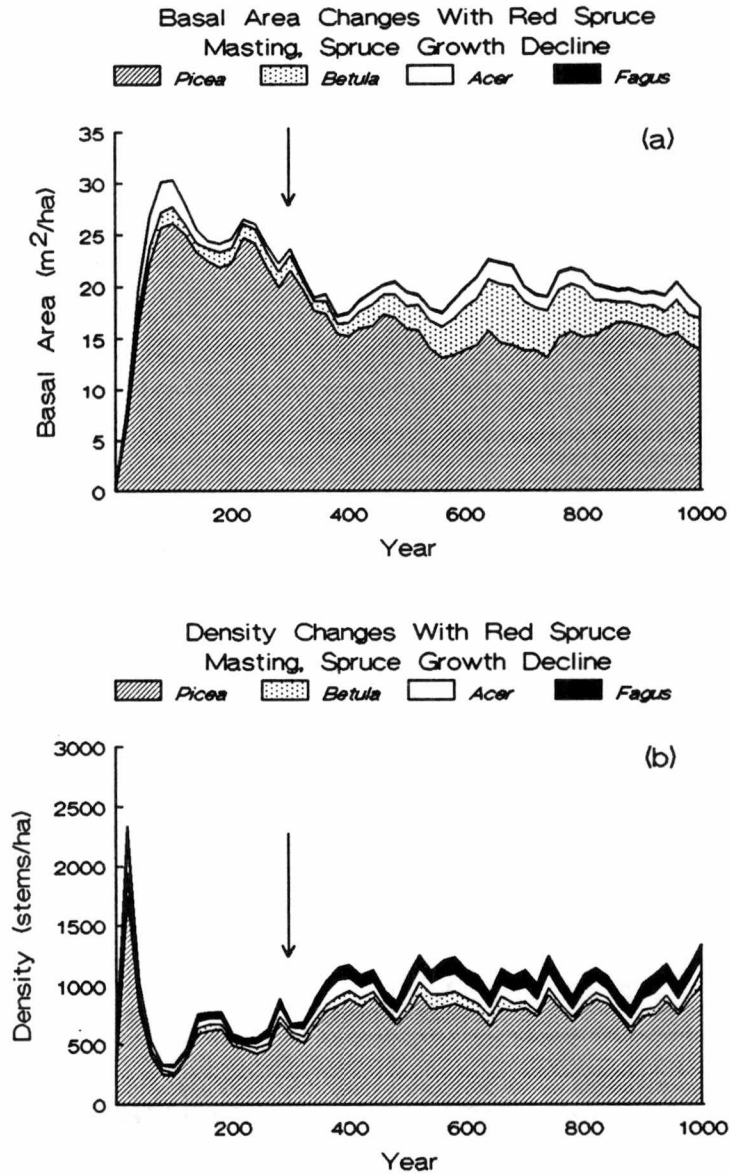


Figure 18. Changes in basal areas (a) and densities (b) in simulated plots with red spruce masting, with a red spruce growth decline. Spruce diameter increment is reduced, beginning at year 300 (arrow), by 25% and, after year 320, by 50%. Values are means of 20 replicate plots.

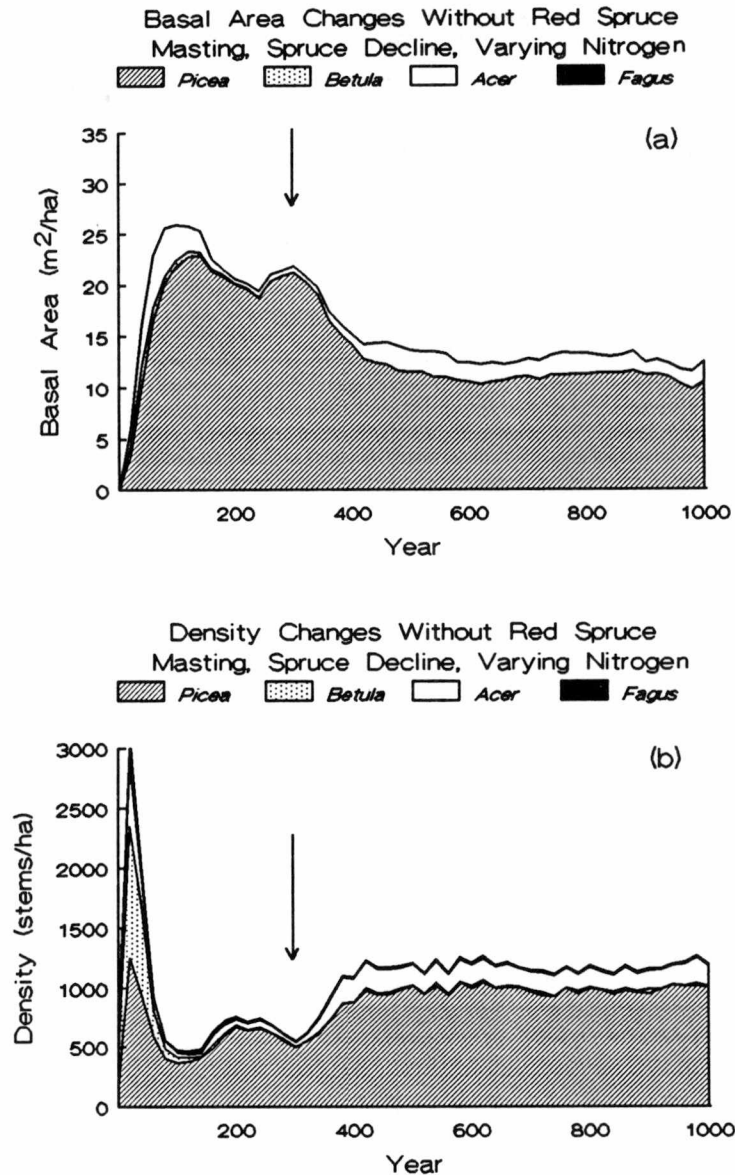


Figure 19. Changes in basal areas (a) and densities (b) in simulated plots without red spruce masting, with a red spruce growth decline and varying available soil nitrogen. Spruce diameter increment is reduced, beginning at year 300 (arrow), by 25% and, after year 320, by 50%. Values are means of 20 replicate plots.

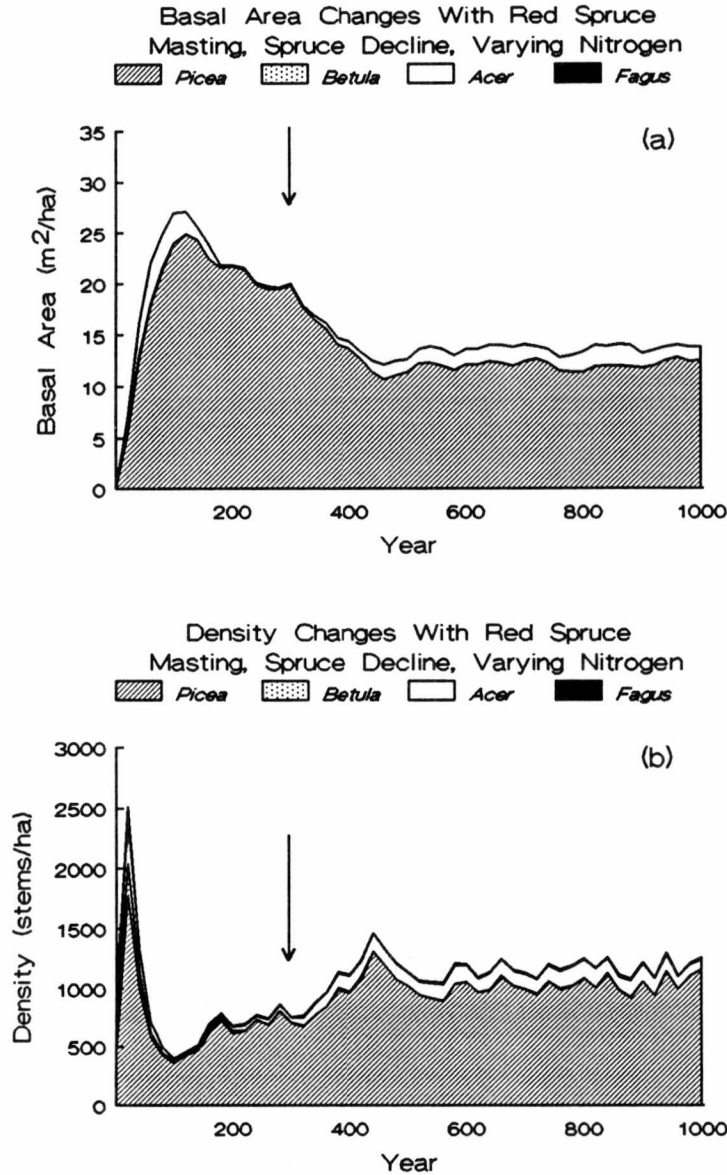


Figure 20. Changes in basal areas (a) and densities (b) in simulated plots with red spruce masting, with a red spruce growth decline and varying available soil nitrogen. Spruce diameter increment is reduced, beginning at year 300 (arrow), by 25% and, after year 320, by 50%. Values are means of 20 replicate plots.

Masting by red spruce had an adverse effect on yellow birch, especially in the first 100 yr of stand development. Yellow birch is considered intermediate in shade tolerance but does not regenerate well in shade and requires mineral soil for seedling establishment (Fowells 1965; Erdmann 1990). The loss of birch in simulated stands where red spruce showed masting suggests that masting can allow spruce to gain early dominance and prevent birch establishment, even after logging. Red maple is similarly affected but its ability to sprout may enable it to persist and replace birch in the simulations where spruce showed masting.

In contrast to the findings of Pastor et al. (1987), these simulations did not show alternation between spruce and birch dominance with varying nitrogen availability. In fact, varying nitrogen nearly eliminated yellow birch. Apparently, yellow birch does not compete well under nitrogen stress induced by slowly decomposing spruce litter. Initially high nitrogen values (65 kg/ha/yr) declined and stabilized at about 30 kg/ha/yr, with or without red spruce masting. The high growth parameter (G) and maximum recruitment value (MPLANT) of spruce used here may have maintained spruce dominance even with strong nitrogen immobilization. A comparison of model parameters might show if this is the case. However, Pastor et al. (1987) did not list the parameters used in their simulations.

Another factor may be that Pastor et al. (1987) simulated stands composed of tree species different from those in West Virginia spruce forests. One of their simulations was of a forest composed of red spruce, aspen (Populus sp.), and paper birch. Bigtooth aspen (Populus

grandidentata Michx.), although present in the Cranberry Wilderness, is confined to roadsides and burned areas (personal observation); paper birch is rare in West Virginia (Strausbaugh and Core 1970-1977). Paper birch and most Populus species grow rapidly, are short-lived, and are very intolerant of shade (Burns and Honkala 1990; Safford et al. 1990). Yellow birch and red maple, however, are longer-lived and persist into later stages of stand development. The greater longevity of these two species, combined with high spruce recruitment and growth, may moderate nitrogen dynamics in the forest simulated here.

A 50% red spruce growth decline, instituted over a 20-year period, produced the most dramatic changes of any simulations. Yellow birch became a major component where spruce did not show masting. Red maple responded positively as well, and numerous beech stems became established (although their low basal area indicated that few beech trees became large). Red spruce masting, however, made these changes more gradual. Yellow birch, again, showed reduced basal area and density with spruce masting. The post-decline peak in total density shown without masting was less noticeable with masting. Low spruce basal area and high spruce density after the onset of the decline suggest a high turnover rate of small stems, with or without masting. Spruce trees were probably not reaching maximum size or age under suppressed growth.

Masting had little long-term effect where a spruce decline was combined with varying nitrogen. With or without masting, total basal area declined and total density increased. Yellow birch basal area was very small in both scenarios, while birch density was reduced by masting

from its normally high level in the young stand. This highly stressed forest had very low diversity.

These results suggest significant effects of episodic seedling recruitment by red spruce. The importance of spruce's main competitor in these forests (yellow birch) is adversely affected by masting, although nitrogen immobilization by slowly-decomposing spruce litter is important as well. The high growth and seedling input levels used in the model may prevent an endogenous, nutrient-driven spruce decline and subsequent alternation with deciduous species. The overall effect of episodic recruitment by red spruce in these forests seems to be a moderation of rapid changes in forest composition in response to stress. In these simulations, masting appears to stabilize the red spruce population, allowing it to maintain dominance in the presence of more shade-intolerant species.

CHAPTER 6

SYNTHESIS

Although few ecologists would today openly embrace Clements' (1936) paradigm of the "climax" community, the idea is implicit in modern concepts of forest succession. Goff and West (1975) suggest that young forest stands undergo a transition from being even-aged to all-aged. Oliver (1981) suggests a general trend of forest stand development after disturbance: stand initiation (recolonization), stem exclusion (closed-canopy, no new colonization), understory reinitiation (appearance of shade-tolerants in the understory), and old-growth ("uneven mosaic pattern" of gap dynamics). Peet and Christensen (1987) describe similar stages: establishment, thinning, transition, and steady state.

Whether a community ever actually attained the "climax" status was not really Clements' point. His point was that a community tends toward equilibrium (=all-aged, old-growth, steady state). Inherent in this view is that, over a particular scale, finer-scale variations tend to "average out" in the climax stage. While it is easy to dismiss the equilibrium concept simply because it assumes unrealistically stable environments, it is more difficult to accept or reject the idea that small-scale fluctuations balance each other. The dynamic nature of ecological systems at all scales should prompt examination of how processes at one scale affect those at smaller and larger scales. The present research began with the notion that seedling pool dynamics must

ultimately affect forest canopy dynamics in some fashion, and it has attempted to determine if short-term fluctuations in seedling establishment can alter long-term stand composition and dynamics. The answer to this question is a guarded "yes."

The fate of a seedling is related to the fate of canopy trees above it. Trees in the stands studied in the Cranberry Wilderness are even-aged and show patterns apparently typical of the "stem exclusion" or "thinning" stage of forest development. There is some variation in tree size and condition, so how synchronous growth and mortality processes will remain is unclear. The expected future trend is a transition to a patchy, all-aged, old-growth state. However, some studies indicate that even-aged stands can show cohort senescence, where stand-wide growth reductions and mortality occur even without major exogenous disturbances. A sudden dieback of the canopy from cohort senescence, a catastrophic disturbance, or some chronic low-level stress would initiate a scramble for dominance among existing and subsequently established seedlings. This has happened before in Cranberry with historical logging; red spruce was the "winner" that time. Now the forest is maturing, and large cohorts of spruce seedlings are beginning to become established.

Although early survival among 1990-origin spruce seedlings is low, the survivorship data indicate declining mortality as seedlings become better established. A large cohort showing declining mortality could saturate the seedling pool, pre-empt the most favorable microsites ("safe sites"--Harper et al. 1965; Harper 1977) before the onset of density-dependent mortality, and thus allow spruce to dominate the

seedling pool for many years. The most notable feature of the survivorship data is that different models fitted to the data suggested substantially different numerical impacts of the cohort on overall seedling pool size. Constant mortality rates would dampen episodic reproduction, while declining mortality rates could increase pool size up to 8-fold. Similar sensitivities of overall population size to juvenile mortality rates may occur in cactus (Parker 1987), starfish (Birkeland 1989), and fish (Trebitz 1989).

Large, irregular recruitment episodes in a dominant species could be expected to create erratic variations in abundances of all species. The long-term effects of episodic recruitment by red spruce were tested by modifying an existing forest gap model. Episodic recruitment consistently decreased the abundance of a major associate of spruce (yellow birch) and moderated changes in spruce abundance under stress. Decreases in birch were particularly noticeable in the early stages of stand development, when birch is typically a major forest component. Apparently, dense thickets of young spruce, originating from large recruitment episodes, prevented birch recruitment even though spruce may not have regenerated at all for several years thereafter. Episodic recruitment of spruce does indeed appear to affect some overall aspects of forest dynamics.

The reasons this conclusion is "guarded," however, are (1) the parameters chosen for the model produced a spruce-dominated forest anyway, and (2) the model recruited individuals of fairly large size. First, a forest greatly dominated by one species may cause the behaviors of other species to be susceptible to even minor changes in the dominant

species. Simulations of stands where spruce grows slower and shows lower maximum reproductive output may produce less noticeable changes. Second, a major assumption in the model is that episodic appearance of seedlings <5 cm tall in the field plots leads to episodic recruitment of what are essentially saplings (stems ≥ 1.4 m tall) in the model. This assumption is a serious one for red spruce. The ability of spruce to tolerate shade can produce great variation in size among seedlings of the same age. Red spruce can reach 1.4 m height in as few as 10-15 years where open-grown or as many as 50 years beneath a forest canopy (Fowells 1965). The longer a cohort of spruce must persist beneath a forest canopy, the less likely that cohort is to remain a significant fraction of the seedling pool. Even a very large cohort could conceivably be lost to attrition if many decades pass before its constituents reach sapling size. How well this assumption holds in the second-growth spruce forests of Cranberry will require longer-term monitoring of both seedlings and canopy trees in the field.

The present study is certainly not the last word on the influence of episodic reproduction. Continued field studies will yield data relevant to this issue. Forest gap models have much room for refinement. If such models are taken to represent the state of knowledge about forests, more study of forest dynamics is required to understand the scale-dependence of forest processes. A rich variety of processes occurs on small spatial and temporal scales, and how those processes propagate into broader system behaviors appears to be largely unknown. The answer to Gould's (1989) question (p. 1) may simply be "anyone who cares to look hard enough."

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APPENDICES

APPENDIX A

STUDY SITE LOCATIONS, FIELD TECHNIQUES, AND DATA SETS

1. Introduction

During summer of 1990, an array of plots was established in the red spruce (Picea rubens Sarg.) forest of the Cranberry Wilderness, Monongahela National Forest, Pocahontas County, West Virginia. This appendix describes the design of this study, and gives on-the-ground directions to the plots, the field techniques used, and details of the resulting data sets. These descriptions should allow relocation and reevaluation of these plots in the future.

2. Sampling Design and History

Forest stands were chosen arbitrarily but quadrats were established at random locations within each stand. Black-and-white aerial photographs (approximate scale 1:16,700) taken in spring 1981 were used to select three stands dominated by closed-canopy, second-growth red spruce forest that were visually homogeneous, representative in general appearance, and accessible (Figure 1, p. 26). Within each stand, six quadrats, each 20 x 20 m, were established at random locations, and three 1 x 1 m plots were established at random locations within each quadrat. All stands are second-growth. According to Allen and Roberts (1931), Stand 1 was logged during 1924 and 1926,

Stand 2 was logged in 1924, and Stand 3 was logged during 1920-1921. Since few large (>40 cm diameter) trees are present in these stands, clearcutting appears to have been the method used. The stands have probably not been significantly disturbed since then. Data on the original composition of any of these stands apparently do not exist, but old photographs taken in the region suggest a spruce-dominated forest. Well-decomposed stumps to medium size (60 cm diameter) still occur in the stands. No evidence of fire is apparent in the stands.

3. How to Get There (and Back)

This section provides detailed information on site selection and plot locations. All study sites are accessible from the Highland Scenic Highway (WV 150) running north from the Cranberry Mountain Visitor Center 22 miles east on WV 39 from Richwood, West Virginia (Figure 21). All stands are on the Cranberry Wilderness side (west/northwest side) of the Scenic Highway.

Locations of quadrats within a stand were determined by overlaying an aerial photograph with semi-transparent graph paper, delineating the approximate boundary of the stand, and randomly selecting X and Y coordinates within the boundary. The distances and directions to these coordinates on paper were determined and the distances were used "as is" for surveying quadrat centers from known points in the field (e.g. a sign at a trailhead). Although horizontal distances are affected by slope, no attempt was made to correct for slope in surveying quadrat locations. Thus, all distances from one point to another are distances

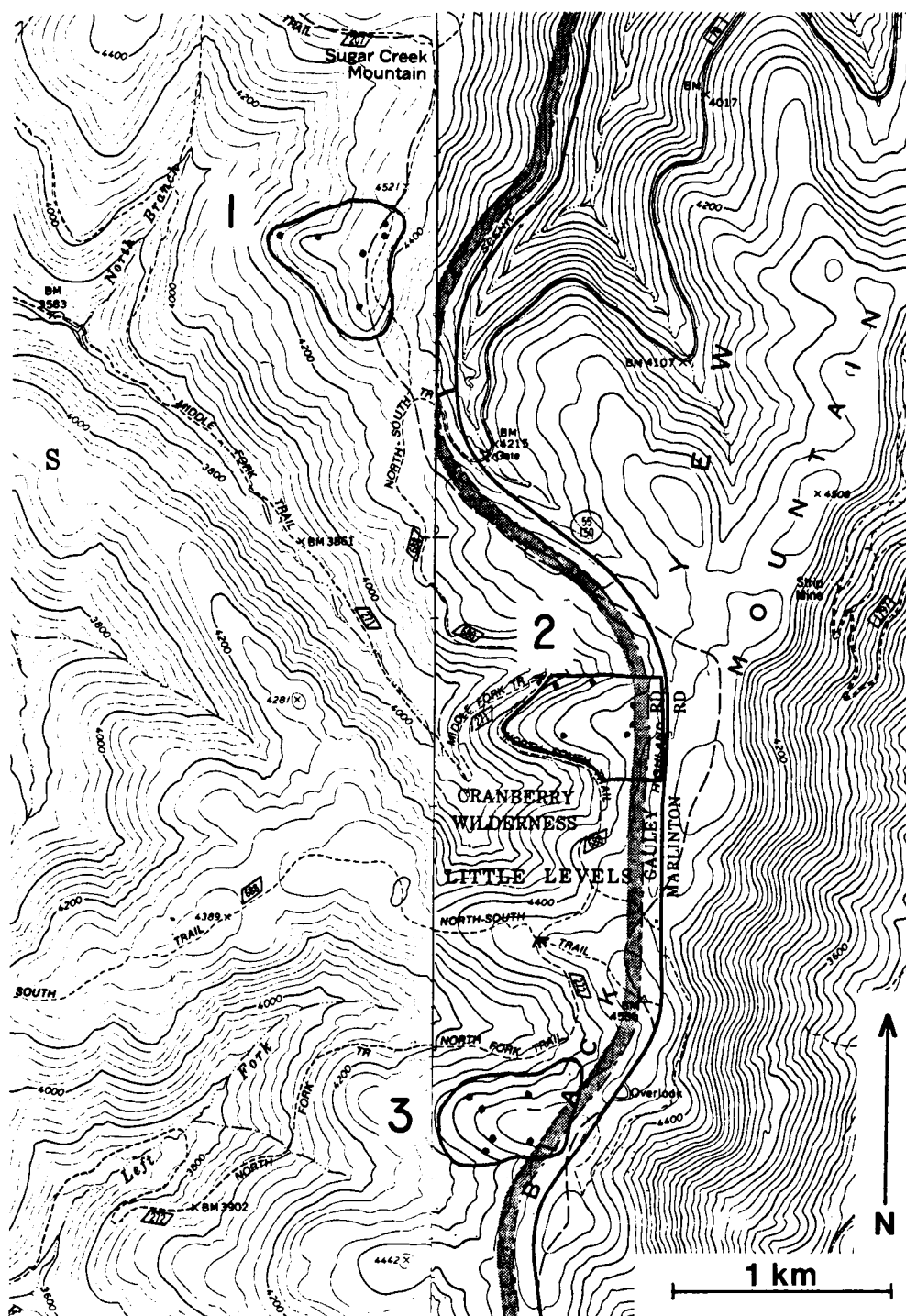


Figure 21. Topographic map (from United States Geological Survey 7.5' Webster Springs SE and Woodrow Quadrangles, 1:24,000 scale) of Black Mountain, Pocahontas County, West Virginia, with red spruce stands outlined and approximate locations of quadrats (dots). Elevations are in feet.

along the ground surface, not horizontal distances corrected for slope. As a result, the locations of quadrats in Figure 21 may vary slightly from their actual locations on the ground.

To reach the centers of these quadrats, the required materials are a hand compass with a mirror (such as a Silva Ranger) and a metric distance tape (at least 50 m). Precise distances and directions to each quadrat in each stand are given below. In the original survey, compass azimuth was not corrected for magnetic declination in surveying to the centers of each quadrat. According to USGS 7.5' topographic quadrangles of the area, 1977 magnetic declination was 5° to the west, and a later 7.5' map series showed declination to be 7° to the west. Until declination changes significantly, the easiest way to relocate these quadrats will be to set compass declination to 0° and follow the uncorrected azimuths given. Because of difficulties with slope distances and uncorrected azimuths, these quadrats should be relocated in the order given below. This becomes especially important in locating points where survey lines change direction.

Stand

Directions and Distances to Quadrats

-
- | | |
|---|---|
| 1 | From the Cranberry Mountain Visitor Center, go north on the Highland Scenic Highway (WV 150) past the first Williams River Road intersection, the Big Spruce Overlook, the Little Spruce Overlook, the North-South Trail parking area, and a small pull-off on the east side of the road marked "No Camping Here." The Scenic Highway then starts down the mountain. Shortly thereafter, Forest Service Road 76 intersects the Scenic Highway. Turn left on this road and park at the dirt/rock pile forming a roadblock. Follow this road on foot until a large field is seen on the right. Just before the field is a part of the North-South |
|---|---|

Trail, designated by a wooden post reading "688." From this post, tape 550 m north along the North-South Trail. Follow all curves in the trail. Closed-canopy Picea forest will be entered. At 550 m, a stone cairn will be noted about 1 m off the west edge of the trail.

- To Q1: From cairn, 100 m at azimuth 270° through Rhododendron.
- To Q2: From Q1, 66 m at 90° and 349 m at 0°. Rhododendron ends along the way.
- To Q3: From Q2, 66 m at 0° and 149 m at 90°.
- To Q4: From Q3, 50 m at 0° and 17 m at 90°.
- To Q5: From Q4, return to Q3, then 365 m at 270°.
- To Q6: From Q5, 33 m at 0° and 199 m at 270°. Pass through an area of mainly deciduous canopy with dense Picea saplings beneath.

When finished, travel east back to the North-South Trail, then turn right to reach Forest Service Road 76 again.

Stand

Directions and Distances to Quadrats

-
- 2 Park at the pull-off marked "No Camping Here." Walk back towards the Visitor Center about 50-100 m and enter the forest on the Wilderness (west) side of the Scenic Highway. Find a small streambed. There are numerous streambeds here, but they all converge. Go downstream 400-500 m until an old road is encountered. This is Forest Service Road 76 (same as above). Nearby will be the intersection of this road and the Middle Fork Trail. On the east side of this intersection will be found an old campfire ring in front of a clump of 8-10 Picea saplings. Behind this clump, in the forest, will be found a stone cairn.
- To Q1: From cairn, 33 m at 180° and 66 m at 90°.
- To Q2: From Q1, 166 m at 90°.
- To Q3: From Q2, 249 m at 180° and 133 m at 270°
- To Q4: From Q3, 282 m at 90°

- To Q5: From Q4, 33 m at 90° and 33 m at 0°.
- To Q6: From Q5, 33 m at 90° and 116 m at 0°.

When finished, travel east back to the Highland Scenic Highway.

Stand	Directions and Distances to Quadrats
3	Go to the Little Spruce Overlook and park. At the southwest entrance (towards the Visitor Center) will be several groups of wooden posts. Find the southwestern-most group. Directly across the Scenic Highway, on the Wilderness (east) side, will be a pile of three rocks.
To Q1:	From rock pile, 515 m at 270°. Pass across a large field. Once in the forest, some <u>Rhododendron</u> will be encountered along the way, but it thins out.
To Q2:	From Q1, 50 m at 90° and 232 m at 180°.
To Q3:	From Q2, 249 m at 270°. Pass several small streams. This quadrat is in a dense patch of <u>Rhododendron</u> .
To Q4:	From Q3, 66 m at 90° and 50 m at 0°.
To Q5:	From Q4, 50 m at 270° and 116 m at 0°.
To Q6:	From Q5, 66 m at 270° and 50 m at 0°.
	When finished, travel east back to the Highland Scenic Highway. Pass through a dense, extensive stand of <u>Rhododendron</u> and other shrubs in a burned area adjacent to the field.

Relocating quadrats should not usually be physically difficult. Rhododendron maximum is abundant in only a few locations, and very little other understory is generally found. The major difficulty is being in the quadrat unknowingly. These quadrats were originally marked with wire survey stakes with orange flags, and these were highly visible. This visibility presented two problems, however. First, two

of the quadrats were close to trails, and the Forest Service objected to the use of such highly visible markers in a Wilderness as being visually intrusive. Second, deer often mistook flags for something edible and regularly plucked them from the ground. Therefore, all flags were replaced with short wooden dowel rods. The two previous problems were resolved, but visibility is now a major problem. Quadrat center stakes, even though they may be 20 cm tall, are still very difficult to see, as the wood fades and will eventually decompose. However, careful surveying should allow relocation of almost all wooden stakes.

Each of these 20 x 20 m quadrats were used to evaluate the overstory (see Field Techniques below). Within each quadrat, three (3) "plots," each 1 x 1 m, were established at random locations. Distances and directions from quadrat center to the plots were determined using ground distances and uncorrected azimuths, and they may be relocated using Figure 22. Their locations were originally surveyed from quadrat center to the southwestern corner stake of each plot. These 1 x 1 m plots were then used to evaluate the understory (see 1 x 1 m Plots below). To evaluate the shrub layer (see below), the southwestern corner of each 1 x 1 m plot was used as the southwestern corner of a 2 x 2 m plot in which the 1 x 1 m plot was nested (see 2 x 2 m Plots below). No additional stakes were used for delimiting the 2 x 2 m plots, since the 1 x 1 m plots defined their locations.

Leaving a stand is accomplished by simply traveling due east. The Highland Scenic Highway or a major trail will eventually be encountered in all cases. Leaving Stand 3 can be difficult, because going due east from Quadrat 6 will traverse a burned area, now densely covered with

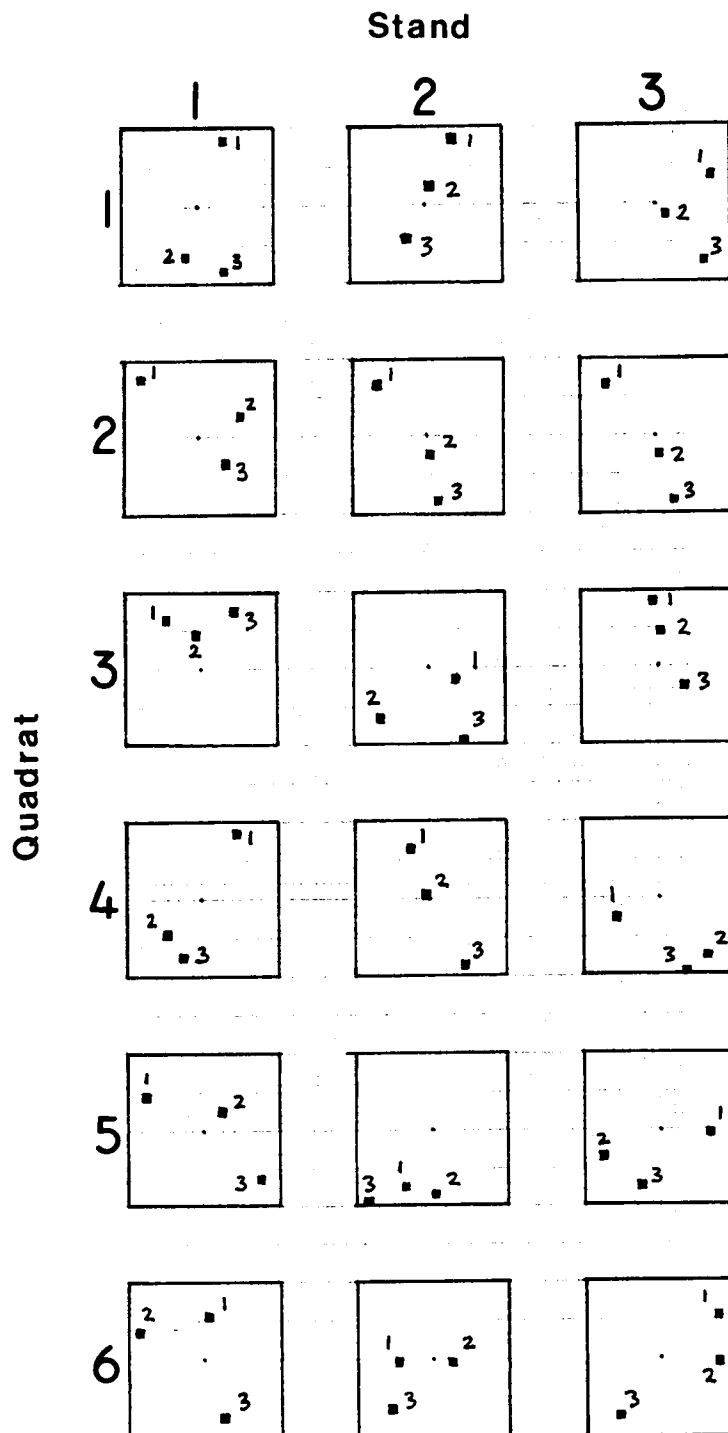


Figure 22. Locations of 1 x 1 m plots within the 20 x 20 m quadrats.

Rhododendron and other woody shrubs. Although physically exerting, this route is the surest. The gentle topography in these stands can be deceiving, and circling around the burned area is often more time-consuming than simply going through it.

4. Field Techniques

This section describes the methods used to delimit quadrats and plots and to take measurements in each. These techniques have been used by other investigators, and many of them are simply standard forest inventory measurements.

20 x 20 m Quadrats. The quadrats were used to evaluate the overstory in each stand. Once a center stake was established, a staff compass, set to 5° West declination (from the most recent map in possession at the time), was used to survey the four corners of the quadrat, this time using slope-corrected distances. First a NW stake was surveyed, then a NE stake, then a SE stake, and finally a SW stake. The "half-diagonal" distance (the horizontal distance from quadrat center to a corner), was 14.14 m in all cases, corrected for slope along that half-diagonal alone. Thus, slope correction varied among half-diagonals. Slopes were generally shallow, with half-diagonals rarely exceeding 15 m ground distance. Once all four corners were established, overstory trees were tallied in 5 x 20 strips (see tree maps in Appendix B). These strips were not surveyed precisely, as they only facilitated keeping track of which trees had been measured during the tally process.

In addition, the location of each tree was mapped visually to enable relocation of individual trees (and quadrat boundaries, where necessary). These maps (see Appendix B) should help reduce "in/out" errors upon future reevaluation.

In these quadrats, a "tree" was defined as any standing stem, dead or alive, that was at least 5.0 cm in diameter at a height of 1.30 m above the ground surface on the uphill side of the tree. Live trees were identified to species (except Amelanchier, where two nearly indistinguishable species may co-occur) and their diameters were measured at 1.30 m height. Highly decomposed dead stems were occasionally unidentifiable; their species designation was thus "Unknown." Species nomenclature followed Strausbaugh and Core (1970-1977). On trees with branches or deformities at 1.30 m height that prevented diameter measurement, diameter was measured immediately above the obstruction. If the diameter tape could be inserted between the forks of a tree at 1.30 m height, each fork was considered to be a separate tree and mapped and measured as such. Snags (dead stems with most of the upper bole missing) were measured as any other tree. If the snag had broken off somewhere around 1.30 m height, the diameter taken was the measurement resulting from wrapping the tape around whatever exists at 1.30 m height. Trees decomposed to such an extent that they were hollowed out on one side were measured by simply wrapping the diameter tape around whatever was there. This method overestimates their true basal area, but no other satisfactory field technique exists.

In addition to identifying, measuring, and mapping the trees, several other characteristics of individual trees were recorded. These

were characteristics of the crowns, and it was often necessary to stand one tree height or more away from the tree to adequately assess these characteristics. First, the relative position of a tree in relation to the "general level of the canopy" (the "crown position") was noted. (In even-sized forests such as these, the general level of the canopy is relatively easily judged. In uneven-aged forests, this judgement becomes more difficult--see Nicholas et al. (1990).) "Dominant" trees were those whose crowns projected well above the general level of the canopy; these trees were typically larger than average. "Codominant" trees were those whose crowns helped form the general level of the canopy; these were the average canopy-sized trees in the stand. "Intermediate" trees were those whose crowns were mostly below the general level of the canopy but still received direct light from above. "Suppressed" trees were well below the canopy and completely shaded from above ("overtopped"). Using these criteria, even rather small trees could be dominant or codominant if the canopy was low, and large trees could be suppressed if they were completely overtopped. Second, the "crown ratio" was estimated. Crown ratio was the percentage of total tree height showing live branches. In this study, crown ratio was estimated to the nearest 10%. Trees with non-continuous crowns were subjected to a "mental rearrangement" of branches; that is, crown ratio was estimated as if all branches formed a vertically continuous crown. Trees with continuous but one-sided tree crowns were not "mentally rearranged". Third, trees were classified according to their "crown condition." For deciduous trees, condition was merely whether they were alive or dead. For conifers (primarily red spruce), however, condition

referred to the degree of apparently unusual needle loss. This highly subjective assessment must be used with caution and is discussed at length below. Finally, each tree was assigned up to four qualitative comments, if necessary, that provided additional descriptions of that tree's form or health. The list of comments drawn upon is given in Table 10. All of these subjective characteristics, or ones analogous to these, have been used by other researchers elsewhere in the Appalachian spruce forests in attempts to determine the existence of unusual forest conditions.

On a healthy red spruce tree, individual needles remain attached to the shoot for 4-8 years. Premature loss of needles (say, after 2 or 3 years) on many branches can produce a visually apparent thinning of the crown from the "inside out." Alternatively, needles may be lost soon after they are formed, giving a visual impression of thinning from the "outside in." Both kinds of needle loss are considered a symptom of stress and have been of much interest in assessment of "spruce decline." The causes of each type of needle loss are numerous and not fully understood. Thinning from the inside out may be related to drought stress, while thinning from the outside in may indicate frost damage, mechanical abrasion, or insect/fungal damage. Branches that are shaded could be expected to show fewer needles. In addition to multiple causation, another problem in understanding needle loss is simply quantification. Other than climbing a tree, removing branch samples, and counting the needles at leisure, there is no way to precisely estimate the number of needles on a single tree. This approach has been used at some sites, but it is labor-intensive, obviously hazardous, and

Table 10. List of comments used to describe canopy trees in the Cranberry Wilderness. These comments were drawn from a study by the Eastern Spruce-fir Research Cooperative of the USDA/EPA Forest Response Program carried out in the Southern Appalachian spruce-fir forest. Some comments used in that study are not applicable (NA) to the present study. Comments 32 and 33 were added to the list for the present study.

Code	Comment	Explanation
1	BWA occurrence	NA ("BWA" = balsam woolly adelgid)
2	Lightning damage	Missing strip of bark or cracked stem usually apparent
3	Dieback/dead top	Uppermost branches dead but present (live trees only)
4	Insect feeding	Eaten foliage, beetle holes in bark or galleries beneath bark (live trees only)
5	Stem disease/ lesions/burls	Sap evident, stem canker, and/or swelling of main stem
6	Top missing	$\geq 1/3$ of crown height missing
7	Lean $>45^\circ$	Tree leans $>45^\circ$ from vertical
8	Wind shearing/ krummholtz	One-sided crown due to windward branch death
9	Terminal replacement	Replacement of terminal leader stem by lateral branch in upper $1/3$ of tree

Table 10. Continued.

Code	Comment	Explanation
10	Root rot/fruiting bodies	Presence of mushrooms or other fungal structures on stems or roots (live trees only)
11	Fire scar	Burned tissue apparent
12	not used	
13	Animal damage	Chewing, holes, claw marks, missing tissue from vertebrates
14	Miscellaneous mechanical injury	Physical damage such as broken branches, scuffed bark, etc., usually from other fallen trees
15	Stem crack	Vertical split in bark and underlying wood not obviously due to lightning damage
16	Crown ratio $\leq 25\%$	$\leq 25\%$ of total tree height occupied by live branches (live trees only)
17	Recently released	Previously suppressed but now receiving light from above, due to fallen canopy tree (live trees only)

Table 10. Continued.

Code	Comment	Explanation
18	Open crown	Branches widely but uniformly spaced on the stem
19	Super-dominant	Crown projecting greatly above the general canopy level
20	Lateral competition	Narrowed or one-sided crown due to the presence of neighboring trees
21	Loss of recent needles	Bare first- or second-year twigs (live trees only)
22	Stem crook/sweep	Bent or curved stem in lower 2/3 of tree
23	Stilt-rooted	Space beneath roots indicating tree establishment on elevated substrate
24	Forked below 1.30 m	Multiple stems joined below 1.30 m height but above the roots
25	Ice breakage	Loss/damage of branches or foliage to ice accumulation
26	Witch's broom	Dense sprouting near end of branch (live trees only)
27	Special comment	

Table 10. Continued.

Code	Comment	Explanation
28	Uprooted but alive	Roots exposed by tree falling but tree is still alive
29	Non-continuous crown	Major gaps in vertical distribution of live branches
30	Common rootstock	Two or more stems (dead and/or live) obviously sharing roots
31	Multiple leaders	Two or more terminal stems, not all necessarily alive
32	Dead and hung up	Dead tree fallen but leaning into and held up by another tree
33	Broken but alive	Main stem snapped completely or nearly so but tree still alive

cannot readily be used for a large number of trees. Therefore, numerous studies (including this one) have attempted to visually estimate the "percent needle loss" from the ground, normally by placing the tree in one of a number of needle loss categories (e.g. 0-10%, 11-50%, 51-99%, dead). The categories are necessarily broad and theoretically could detect major patterns of needle loss. However, this technique presupposes knowledge of how many needles each and every tree "should" have. There are no objective criteria for determining the expected overall appearance of a red spruce crown. For this reason, some scientists who have used the on-the-ground technique have subsequently rejected it. While acknowledging these difficulties, visual estimations of needle loss can be useful. In this study, needle loss estimates were compared across crown positions, crown ratios, and comment classes, and interesting patterns were found that could be explained (see Chapter 3).

In this study, causes of needle loss was not determined. Each red spruce tree was placed in a needle loss category without regard to cause. Normally, crowns were viewed from about one full tree height and from two or three different angles, preferably from uphill. Because the spruce trees in the Cranberry Wilderness are rather small and their crowns are quite compact, thinning from the inside out was not readily apparent. The most evident form of needle loss was from loss of recently produced needles, as shown by branches with bare fine (first- and second-year) twigs. Occasionally these bare twigs would be in localized patches on the crown, but sometimes there were a few bare twigs at many locations all over the crown. Such patterns were not distinguished. To determine what the tree "ought" to look like, such

bare twigs were mentally "filled in" with an appropriate density of foliage. Needle loss categories were: 0-10%, 11-50%, 51-99%, recent dead (no green needles and many fine twigs still present), and old dead (most fine twigs gone, some bark usually missing).

While this method of estimating needle loss may seem reasonable, its value when applied by other workers even to the same stands is questionable. Different people will look at the same tree in different ways. Moreover, different stands necessitate different approaches. For example, other studies have used visual estimation of needle loss in old-growth spruce-fir forests of the Great Smoky Mountains. In those forests, spruce trees are often much taller and more widely spaced, their crown ratios are higher (ca. 50% versus <40% in Cranberry), and their crowns are often much more open. In such different stands, different concepts of how much foliage a tree should have must be adopted. Spruce growing in the Smokies are not so closely spaced and so do not shade each other or abrade each other on windy days. The climate in the Smokies is slightly warmer and wetter than in Cranberry, possibly making frost or drought damage less likely. The greater maximum age of the trees in the Smokies may cause trees to look worse. In short, the subjective concepts necessary to judge needle loss are vague, and their application is recommended only for within-stand comparisons where observer bias is constant and/or known.

1 x 1 m Plots. These small plots were used to estimate cover of microhabitat features and herbaceous taxa and to census live woody stems ≤ 1.30 m tall. Since "micro-" literally means only "small," the term

"microhabitat" connotes different spatial scales to different workers. In this study, microhabitats were viewed as regions on the spatial scale of the individual plant. The microhabitat of a plant was thus a volume with a radius of about the height of that plant. A mature tree would thus have a larger microhabitat than a seedling.

To delimit a 1 x 1 m plot, a frame made from polyvinyl chloride (PVC) tubing ($\frac{1}{2}$ " inside diameter) was used and constructed so that, when assembled (without glue, for portability), the inside dimensions would be 1 x 1 m. No attempt was made to correct plot size for slope; the frame was merely laid on the ground. Wooden dowels, smaller than those used for the quadrat corners, were then pushed into the soil inside the frame at each corner. Occasionally, these small dowels became covered with leaf litter, but relocation was almost always possible. Even if one was missing/invisible, the other three corners indicated the position of the plot. Special care should be taken upon finding a single 1 x 1 m plot stake when others are not immediately visible, so as to avoid stepping in the plots.

Once the plot frame was in position, percent cover of microhabitat features was visually estimated using the following scale: 1, 5, 10, 20, 30, 40, 50, 60, 70, 80, 90, 100%. Two groups of features were recognized:

1. **Substrates** Visible microtopographic features that potentially provide mechanical support for plant roots, including:

- a. dead log (≥ 5 cm diameter at any point)
- b. dead root (visible portion only)
- c. live root (visible portion only)
- d. rock
- e. stump (< 1.30 m tall)
- f. forest floor (the rest of the plot area up to 100%)

2. Surfaces Visible covering of substrates, including:

- a. bryophytes (live mosses, liverworts)
- b. litter (twigs, branches < 5 cm diameter)
- c. bare (uncovered substrate)

Percent cover of each herb taxon was then estimated with the same scale as microhabitat features. Herb cover was estimated only in terms of the percent of the plot covered by each taxon, live material only, not accounting for overlapping foliage within a taxon. Because each herb taxon was assigned its own cover value, independent from other taxa, total herb cover could exceed 100%. Identification of the species of most herb taxa was possible; however, Carex, Dryopteris, Lycopodium, and a few others were recognized only to genus. At least two species of Dryopteris occur (D. campyloptera and D. intermedia), but consistent distinctions could not be made in the field. (D. spinulosa, which is similar to the other two species, may also occur in the area.)

Likewise, Lycopodium annotinum, L. lucidulum, and L. obscurum occur. However, L. annotinum and L. clavatum (which occurs in burned areas nearby) could not be distinguished with certainty in their vegetative states, and the decision was made to group all Lycopodium together. Future evaluations of these plots should separate these species.

Live woody stems (≤ 1.30 m tall) in the plots were then counted by species. Species identifications were not always possible with very small, newly germinated stems. Unidentifiable stems were placed in an "Unknown Germinal" category.

Picea seedlings were counted on a separate data sheet. For each and every live seedling (*i.e.* one with any green tissue) in the plots, its height class, age class, the substrate in which it appeared to be rooted, and the surface covering that substrate immediately surrounding the stem were recorded. Height classes were: ≤ 25 cm, >25 to ≤ 50 cm, and >50 to <130 cm. Age classes were: germinal (<1 yr), 1 yr, 2 yr, 3 yr, 4 yr, and 5+ yr. After a large seed year, there may be hundreds of newly germinated spruce in a 1 x 1 m plot. This was the case in 1990, and a system was developed to tally all these with reasonable accuracy without attempting the impossible task of keeping track of each one. Sticks were used to temporarily partition off the plot, and within each partition germinal spruces on each substrate/surface combination were counted. For example, all germinals were counted on a particular patch of "dead log/bryophyte" and the total recorded on one line of the data sheet. Then, germinals on "forest floor/litter" were counted, and so forth. This complicated the data analysis, but speeded up field work enormously.

The age of a red spruce seedling can be determined nondestructively for the first several years of its life. When a red spruce seed germinates, the first leaves to be produced are arranged in a whorl of 4-8 (usually 5-7). These "cotyledons" are not true leaves. (Indeed, they are not even cotyledons, because cotyledons are features of angiosperms, not gymnosperms.) Then, during the seedling's first summer, it may or may not produce a small vertical shoot with true leaves before it sets bud for its first winter. The first year's growth (*i.e.* that produced the year in which the seedling emerged from the soil) is the foliage below the youngest bud scales. First-winter buds may be formed immediately above the whorl of "cotyledons" or at the tip of a small first-summer shoot. The following spring, the bud swells and breaks, and it then produces another shoot of true leaves. Occasionally, one year's shoot growth may consist of two fairly distinct flushes. These may be ascribed to the same year's growth when no bud scales are found between them. Age designations in this study reflect the number of sets of bud scales apparent on a seedling. If a seedling has not set any buds, it must therefore be <1 yr old (*i.e.* it is a "germinal" seedling). The presence of one set of bud scales with a shoot above them indicates the 1 yr old category. Two sets indicate the 2 yr old category, etc. Another study (Nicholas *et al.* 1992a) used broader age/size categories such as: germinal, 1-4 yr, 4 yr- $\frac{1}{2}$ m tall, etc. In that study, the 4 yr old seedlings were taken to be those with branches (C. Eagar--personal communication). In the present study, branching was found to be an invalid age criterion. Side branches may develop on seedlings only 2 yr old, or branches may not develop on a

seedling until it is 8-10 yr old. Bud scales provide a much more accurate (if more tedious) aging technique. The only difficulty involved in using bud scales is that it may be impossible to age a seedling if a terminal bud aborts and the seedling does not grow at all for a year or two. In this case, age may be underestimated. Side branches cannot be relied upon to provide substitute bud scales because a seedling may abort a terminal bud, not grow for a year, and then produce a side branch.

2 x 2 m Plots. The western and southern boundaries of each 1 x 1 m plot were extended out to 2 m to tally live woody stems >1.30 m tall and <5.0 cm diameter at 1.30 m height. In essence, each 1 x 1 m plot was nested at the southwest corner of a 2 x 2 m plot. The boundaries of the 2 x 2 m plots were not marked because their boundaries were fixed by the 1 x 1 m plots. The sparse shrub layer in closed-canopy spruce forest made these plots much less time-consuming than the 1 x 1 m plots.

5. The Data Sets

The original field sheets are in the possession of the author. Most data have been computerized, however, and the data sets are available by request on IBM-compatible disks. The data are in ASCII format, constructed using Wordstar 3.31 (an easy-to-use old version) as "non-document" files (*i.e.* with no page breaks or other formatting codes).

There are three basic data sets: the 20 x 20 m quadrat data, the 1 x 1 m plot data, and the 2 x 2 m plot data. The quadrat data set is constructed so that each data record represents an individual tree. Each line has stand, quadrat, date, and species designations and alpha-numerical data for each tree (tree number, diameter, crown position, crown ratio, needle loss category, and comment codes). Numerous individual-based analyses are possible with these data. The 1 x 1 m and 2 x 2 m plot data sets are not individual-based. Instead, each record represents a plot, with stand, plot, and date designations and numerical data (stem numbers and percent coverages) for each species in that plot at that date. Because of the large amount of data on individual red spruce seedlings (height, age, substrate, surface, etc.), a separate file was not created for these data. Analyses of these data were made by hand from the original data sheets. All other data sets were analyzed with the Statistical Analysis System (SAS) Version 6.02 (SAS Institute 1987) on an IBM PC at the University of Tennessee. SAS programs for reading the data are supplied on IBM-compatible discs with the data files.

APPENDIX B

QUADRAT MAPS

This appendix reproduces the maps of trees in each 20 x 20 m quadrat, generated in the field as described in Appendix A (Field Techniques, p. 123). These maps are useful for relocating and resurveying the quadrats as well as for recensusing them. Figure 23 shows the tree taxa encountered and the symbols used to represent them on the maps. Figures 24-41 show the approximate positions of all live and dead trees in the quadrats with those symbols. The size of the symbol used indicates the approximate diameter of the tree. Dead trees are indicated by darkened symbols.

Live	Dead		
		<i>Picea rubens</i>	 Quadrat Center
		<i>Betula alleghaniensis</i>	
		<i>Acer rubrum</i>	snag  Dead Tree with Top Missing
		<i>Pyrus americana</i>	
		<i>Ilex montana</i>	
		<i>Fagus grandifolia</i>	
		<i>Amelanchier</i> spp.	
		<i>Tsuga canadensis</i>	
		<i>Prunus pensylvanica</i>	
		<i>Prunus serotina</i>	
		<i>Acer spicatum</i>	
		<i>Acer pensylvanicum</i>	
		Unknown (dead)	

Figure 23. Tree species occurring in the 20 x 20 m quadrats and the symbols used to designate them on the quadrat maps. Darkened symbols indicate dead trees. Nomenclature follows Strausbaugh and Core (1970-1977).

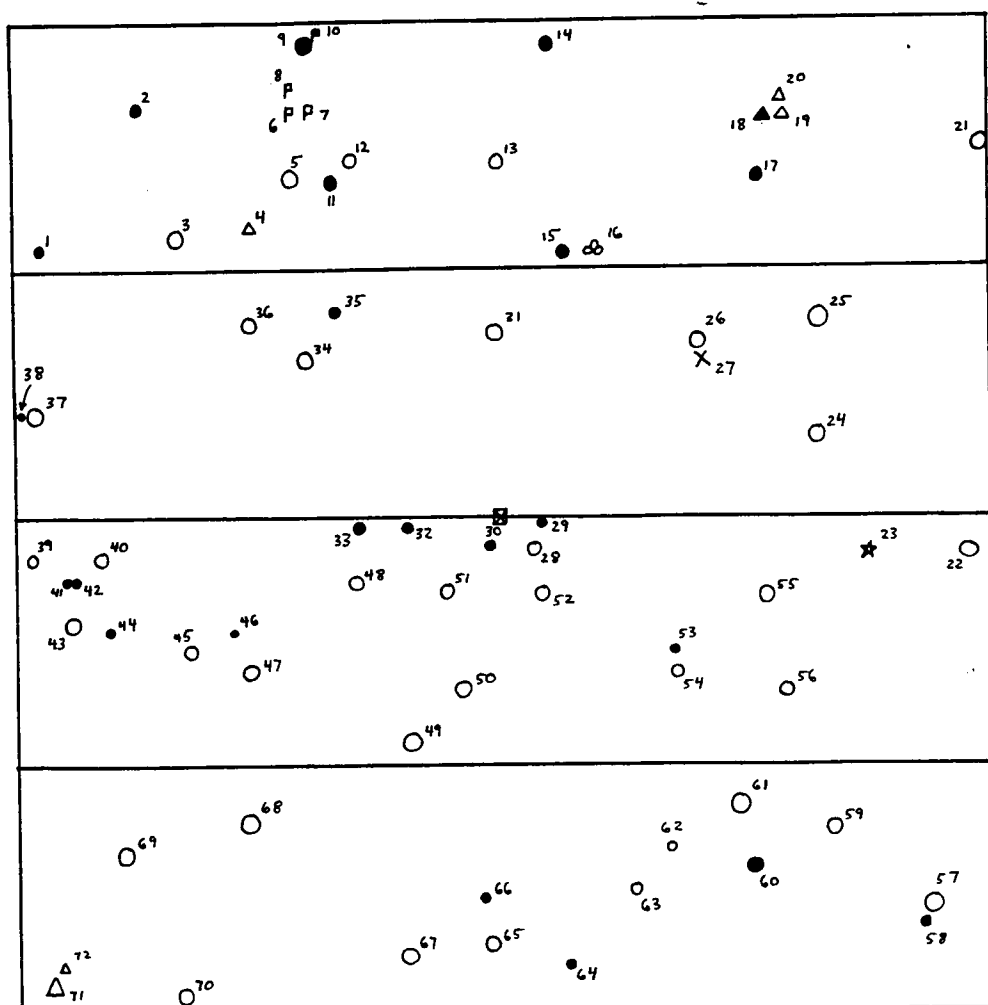


Figure 24. Stand 1, Quadrat 1 tree map.

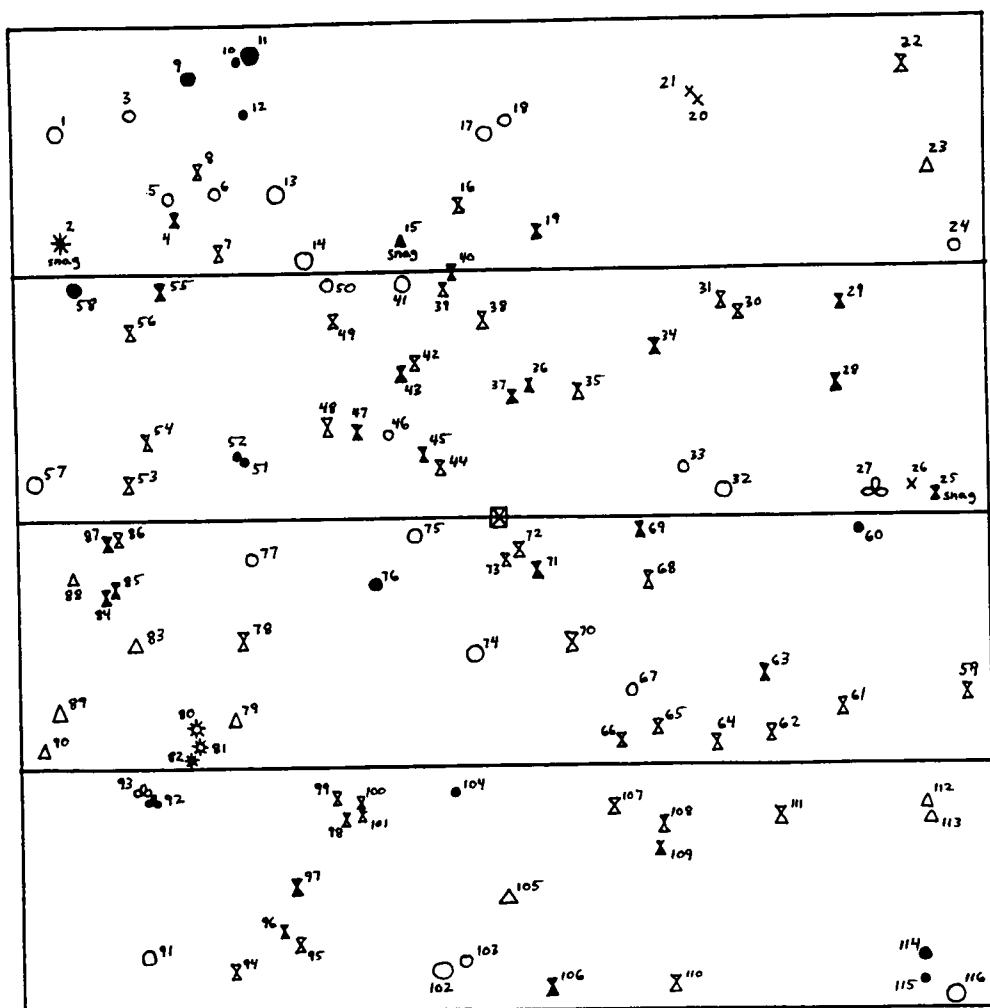


Figure 25. Stand 1, Quadrat 2 tree map.

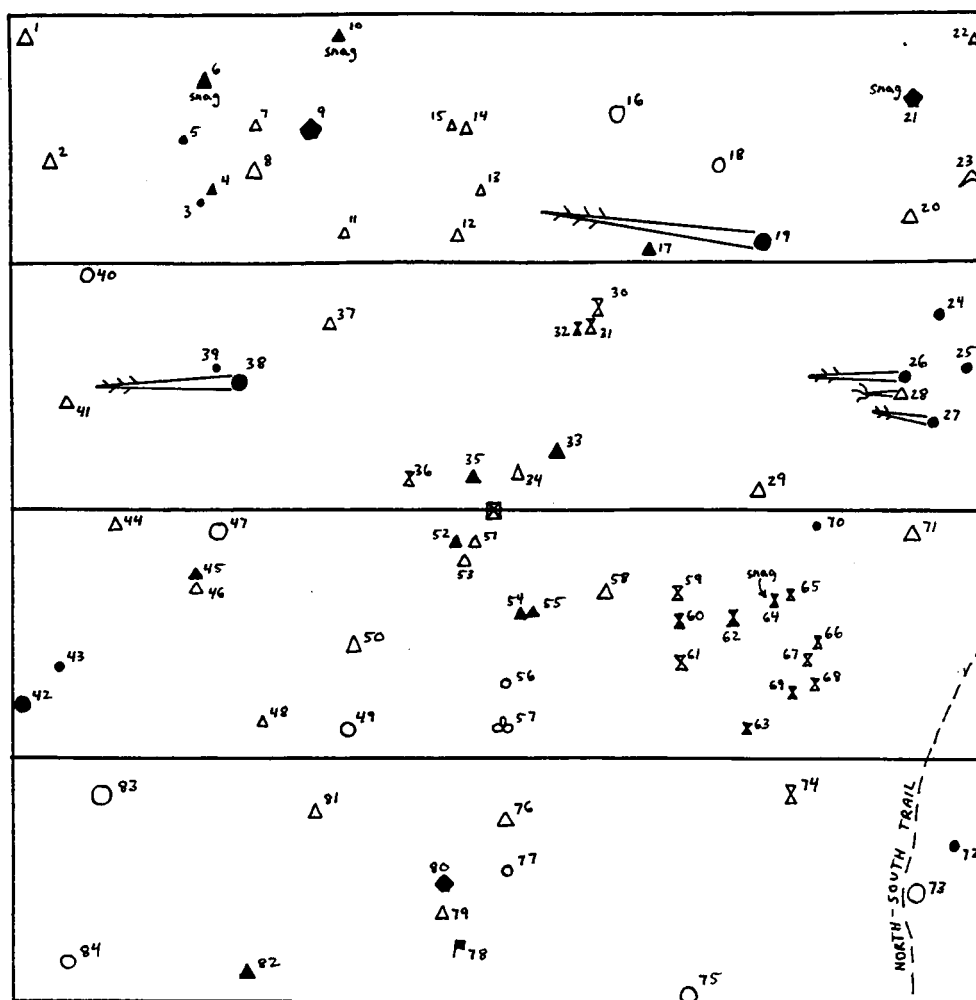


Figure 26. Stand 1, Quadrat 3 tree map.

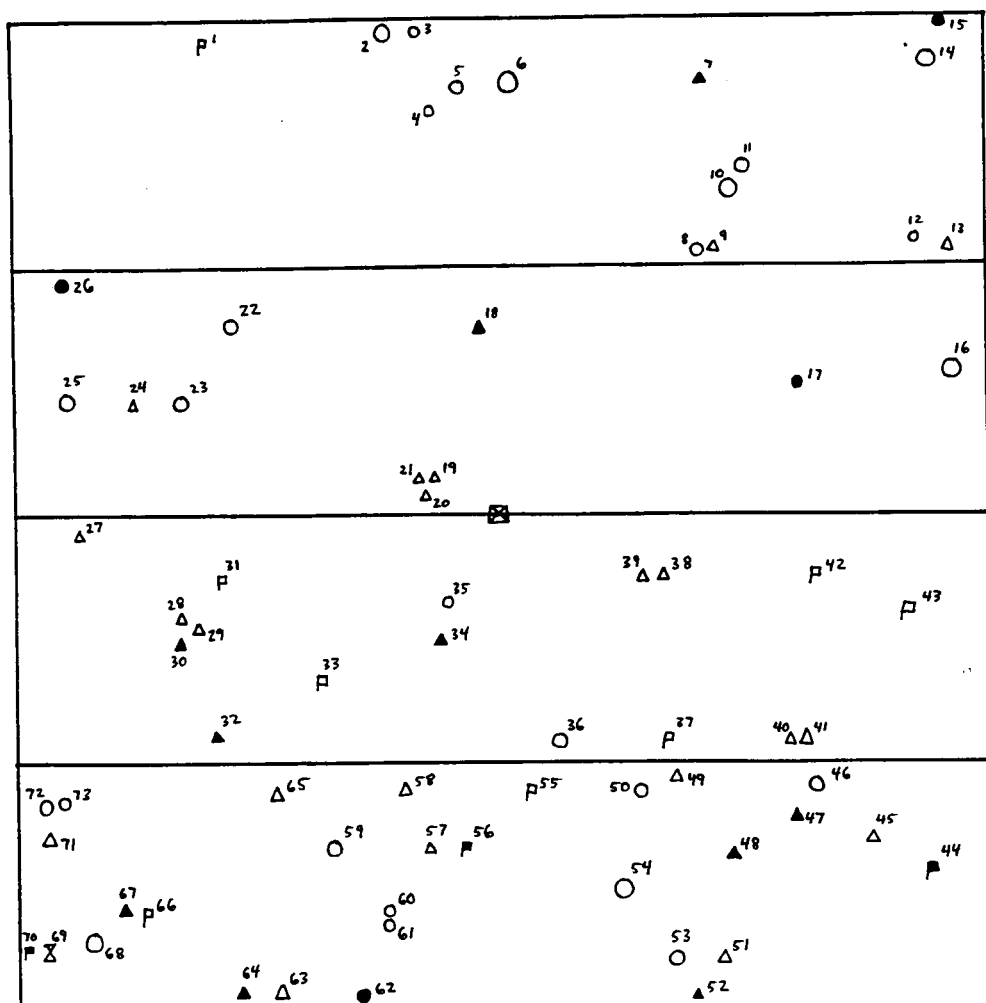


Figure 27. Stand 1, Quadrat 4 tree map.

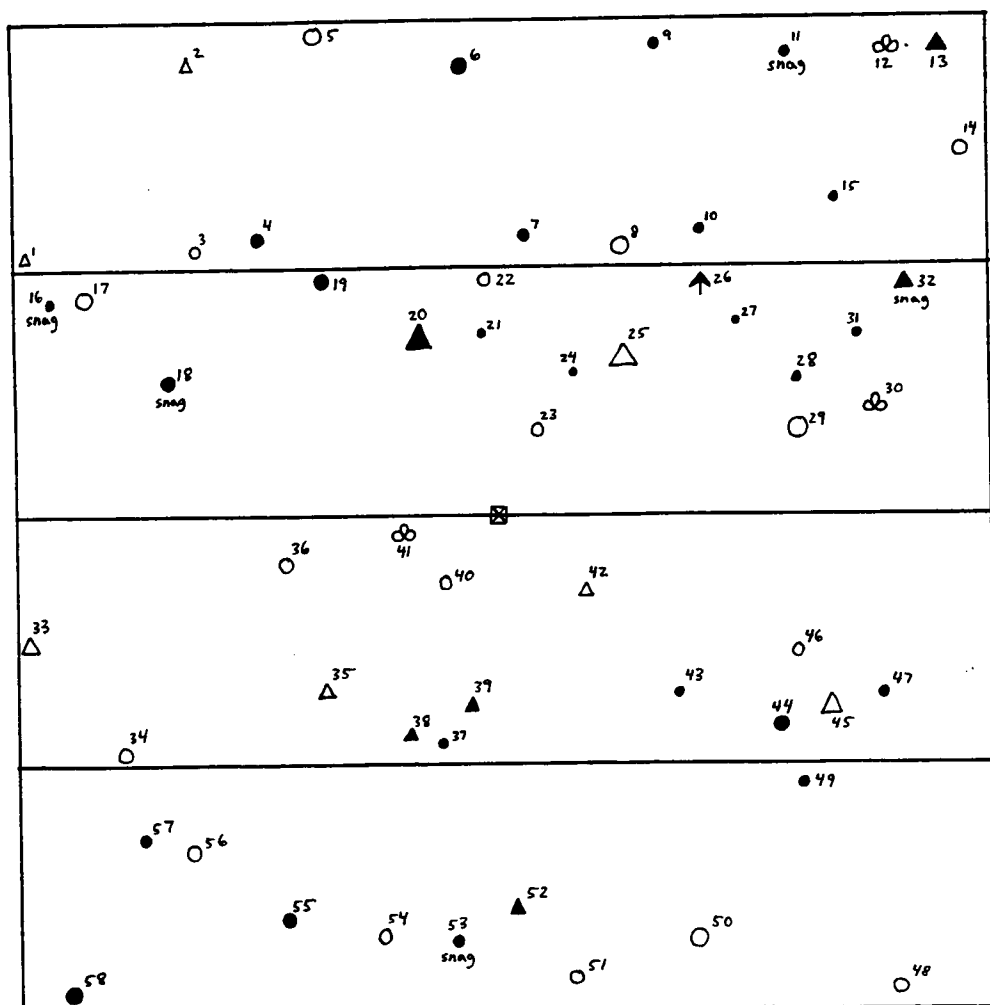


Figure 28. Stand 1, Quadrat 5 tree map.

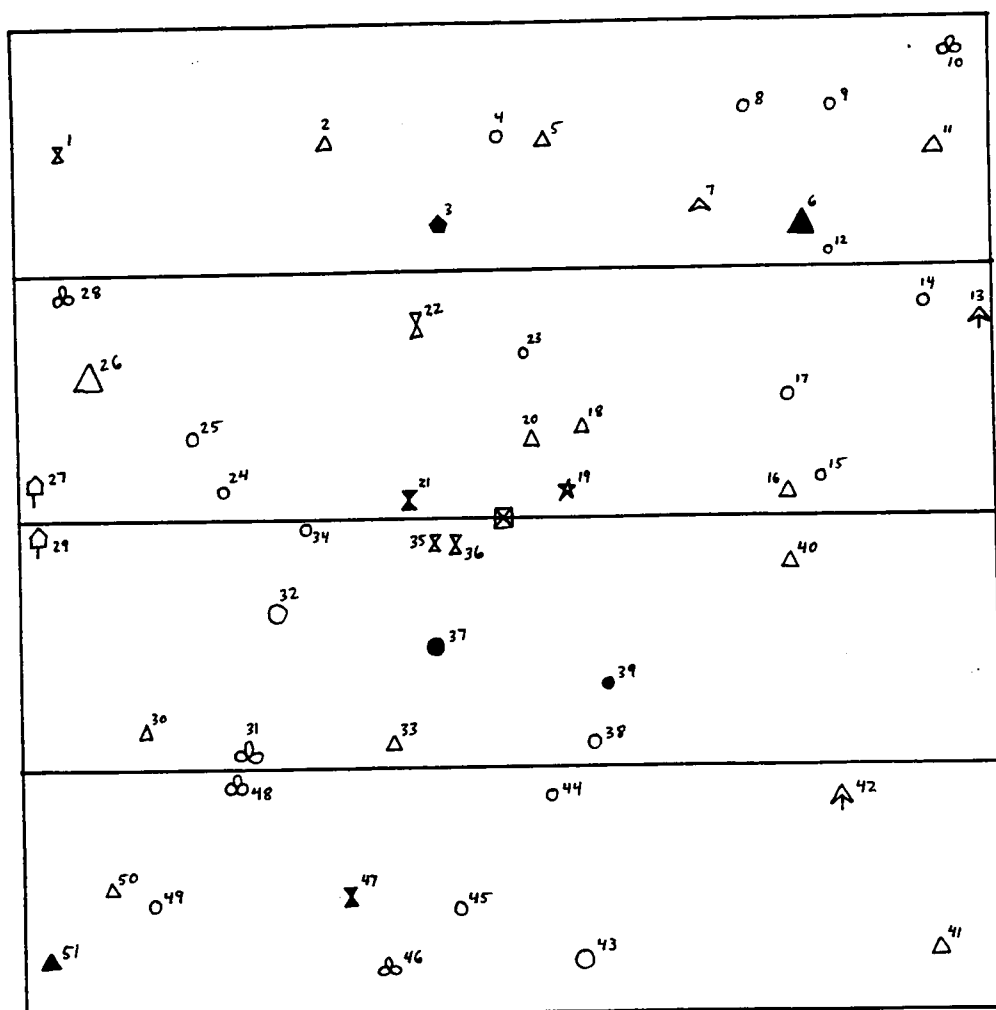


Figure 29. Stand 1, Quadrat 6 tree map.

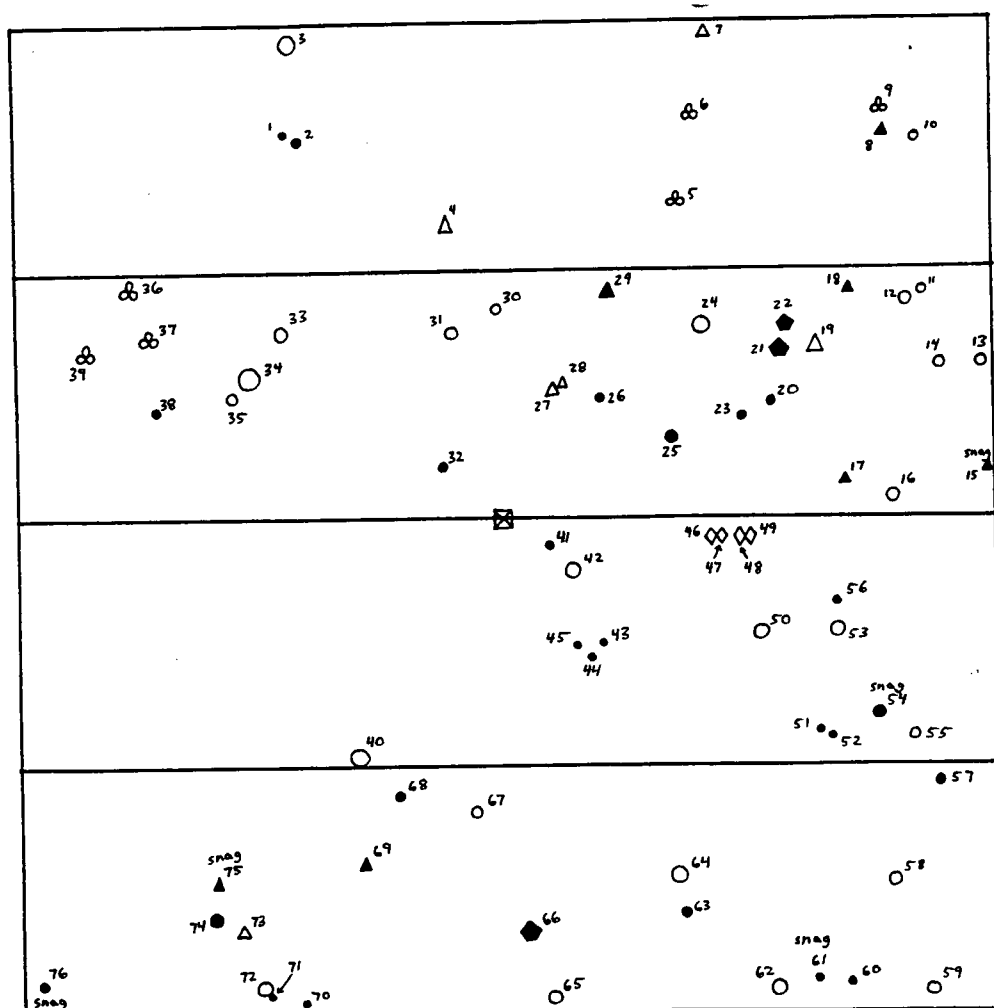


Figure 30. Stand 2, Quadrat 1 tree map.

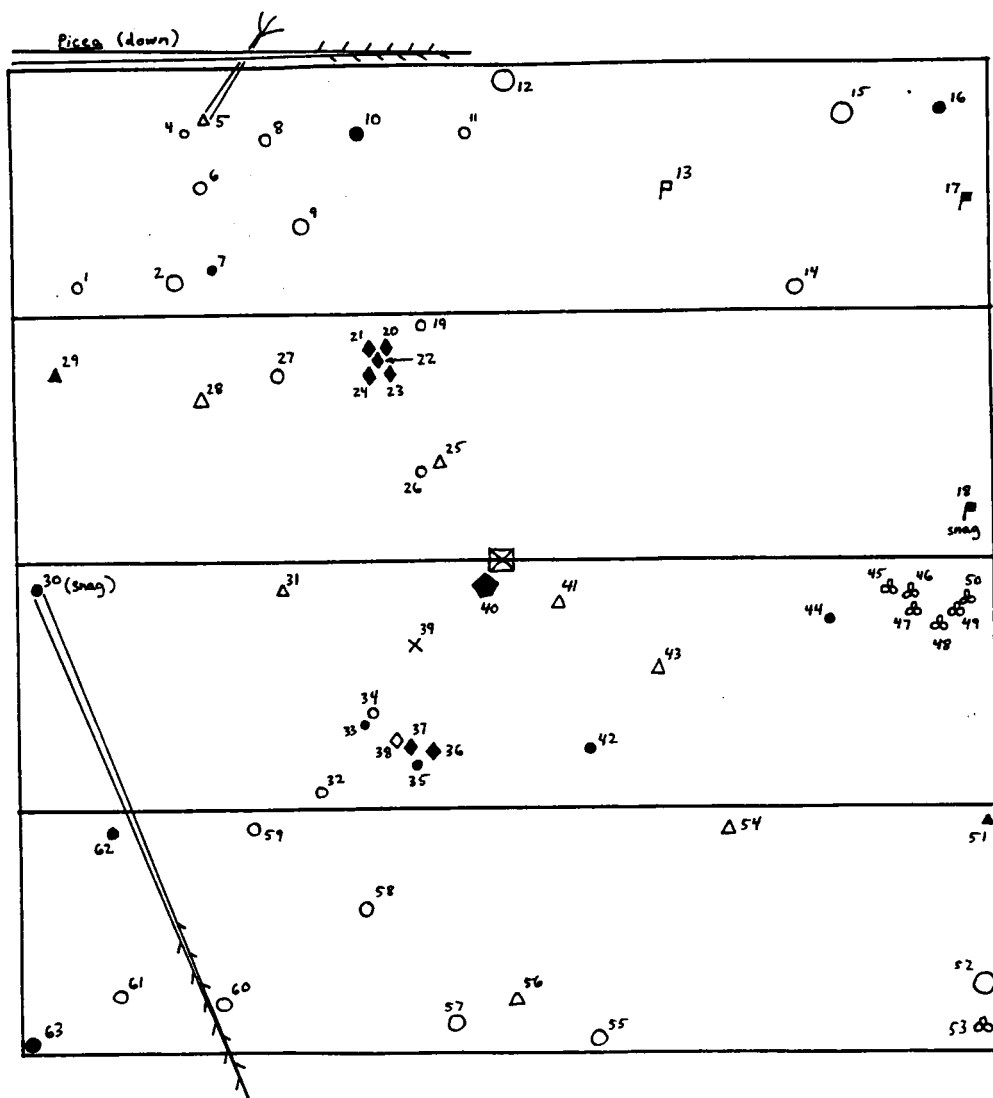


Figure 31. Stand 2, Quadrat 2 tree map.

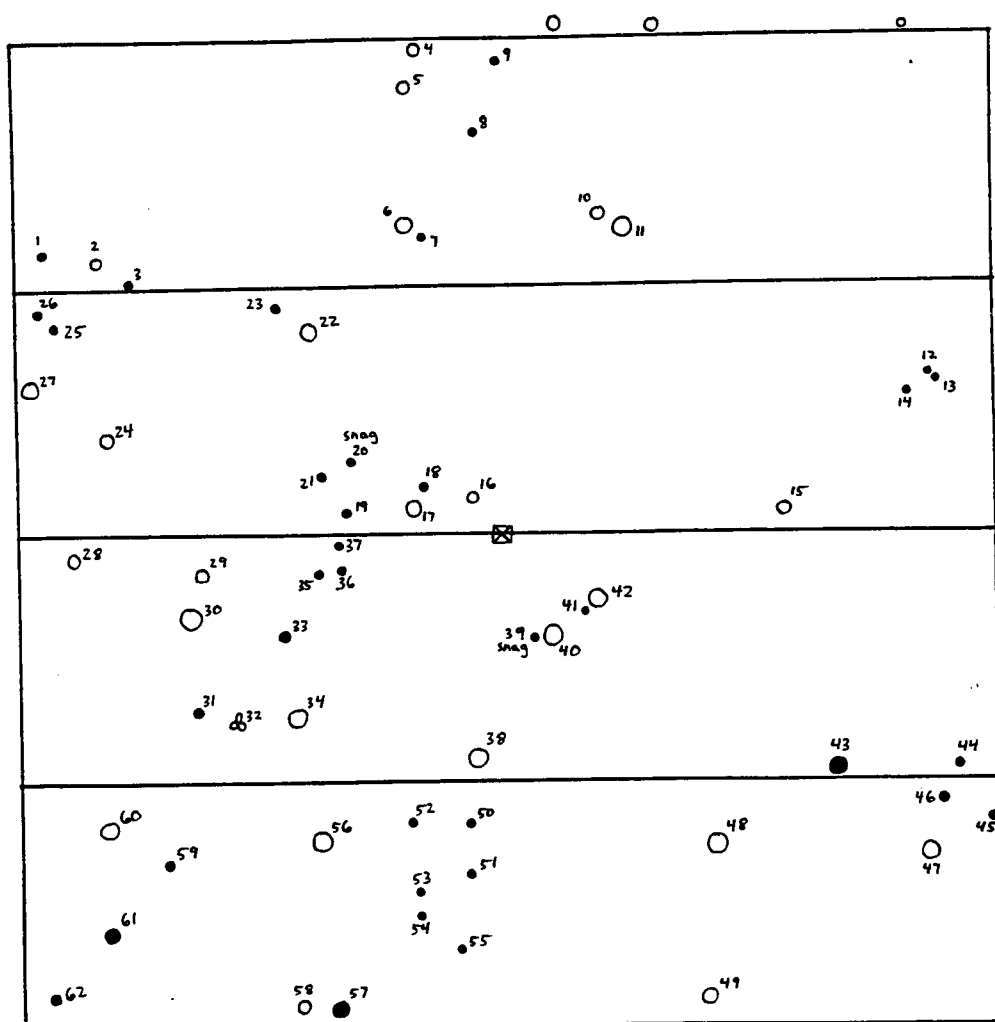


Figure 32. Stand 2, Quadrat 3 tree map.

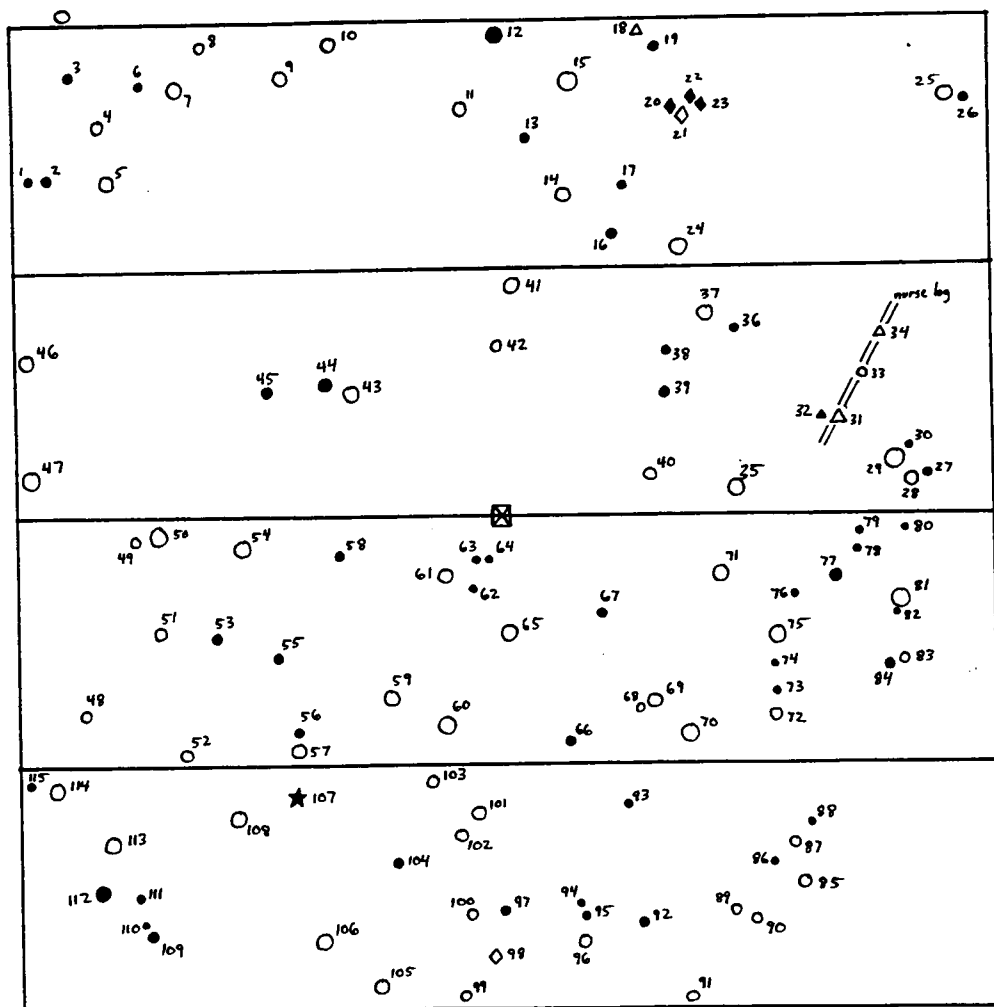


Figure 33. Stand 2, Quadrat 4 tree map.

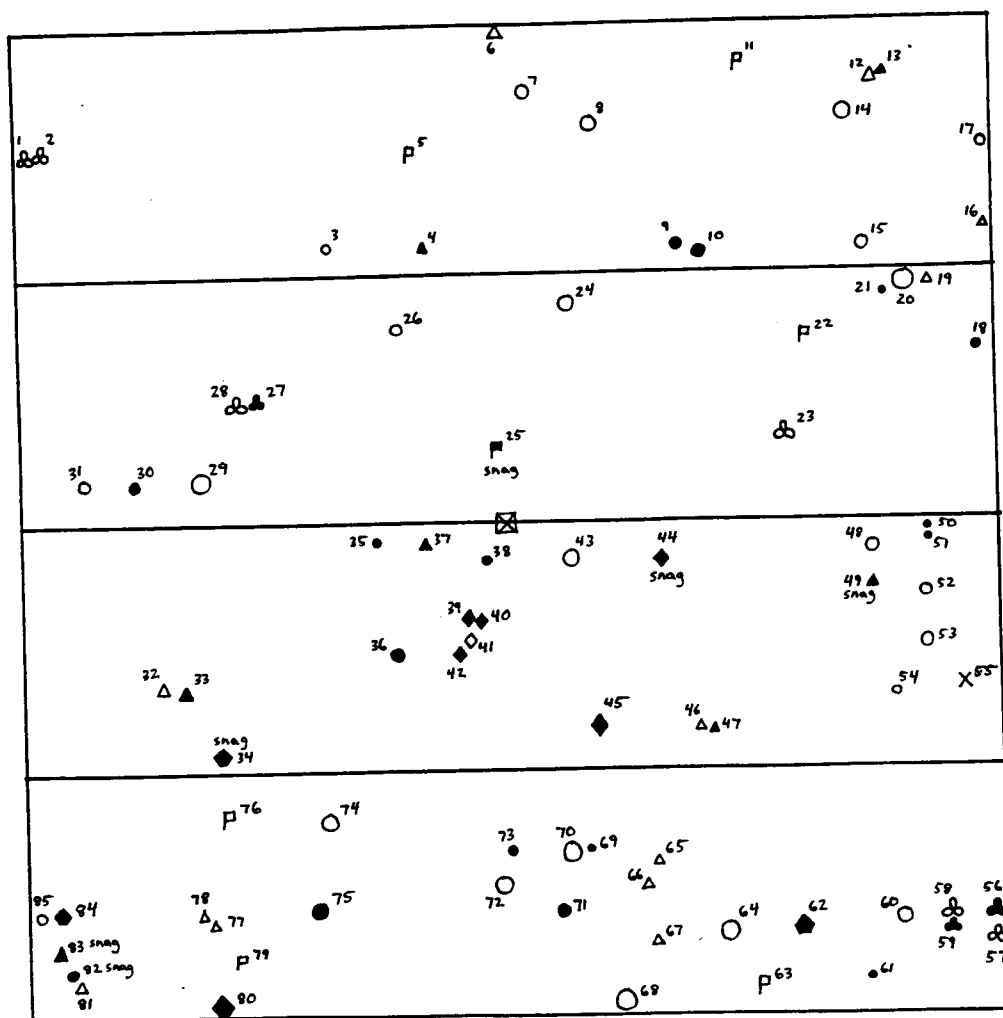


Figure 34. Stand 2, Quadrat 5 tree map.

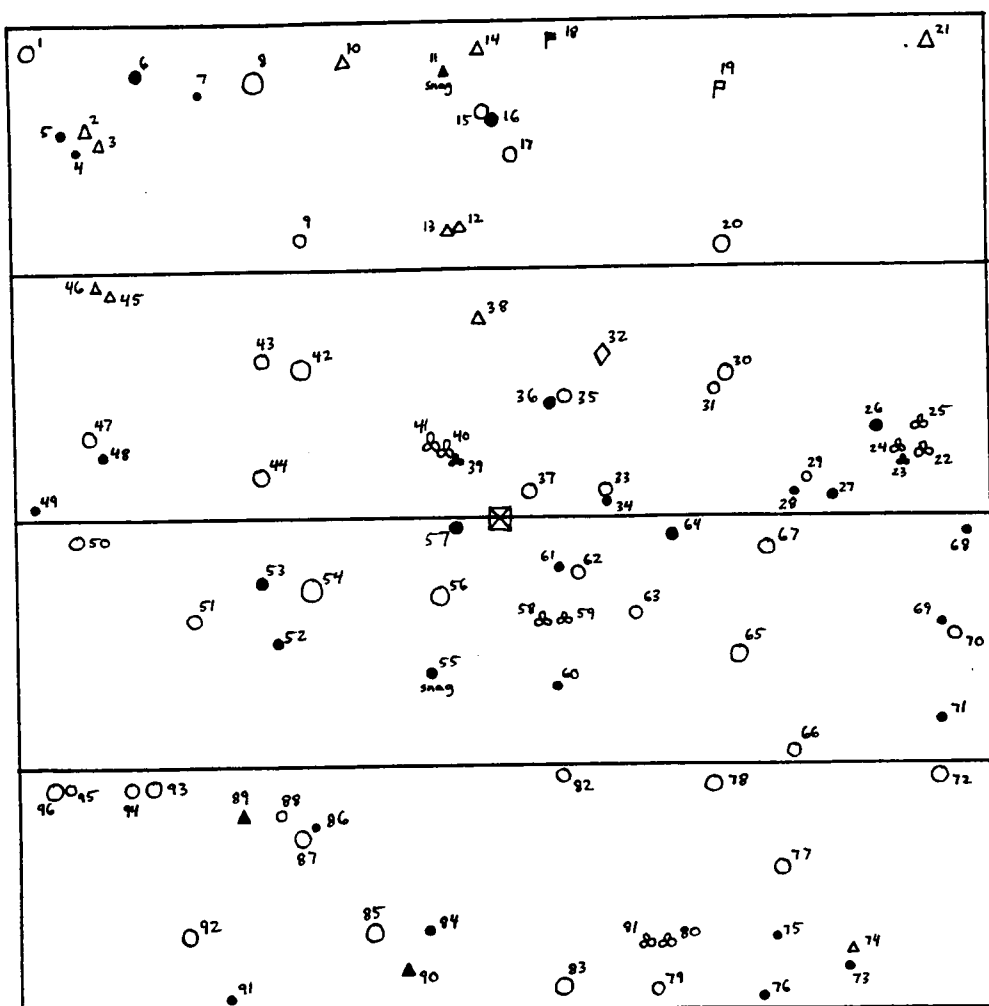


Figure 35. Stand 2, Quadrat 6 tree map.

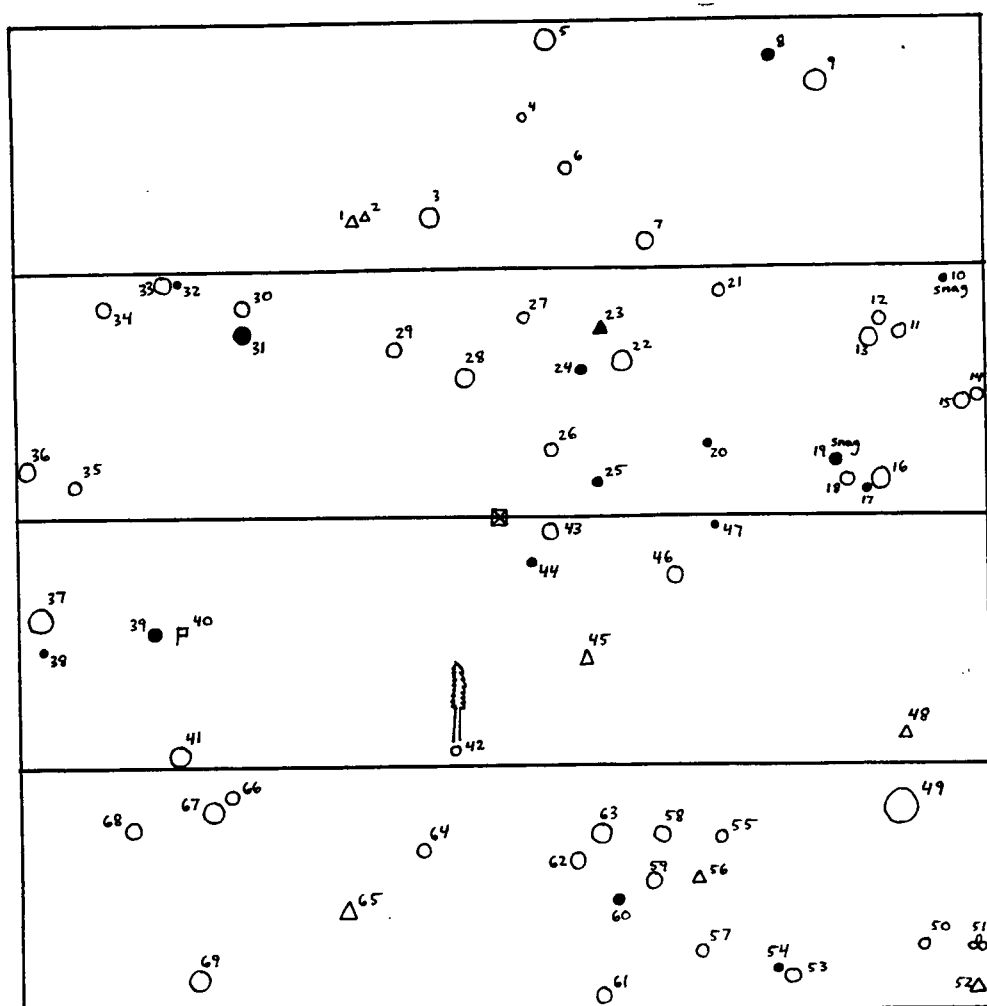


Figure 36. Stand 3, Quadrat 1 tree map.

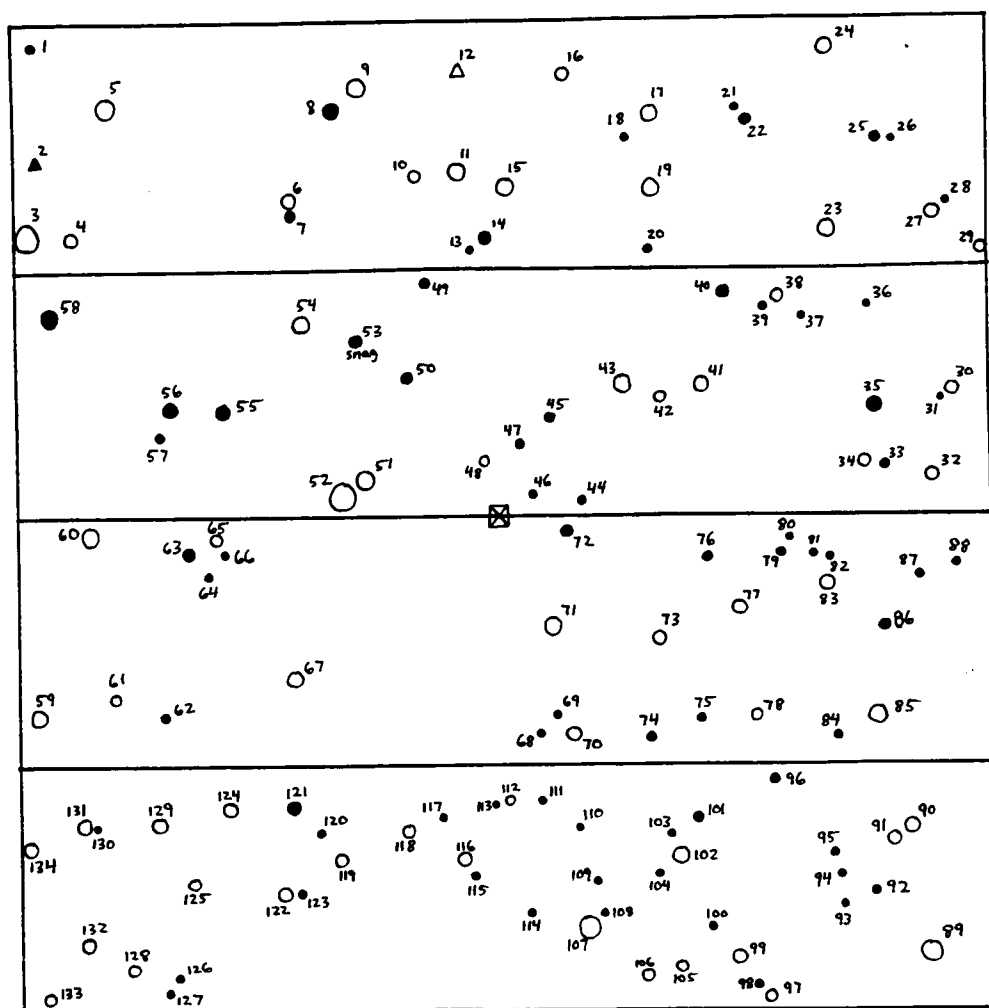


Figure 37. Stand 3, Quadrat 2 tree map.

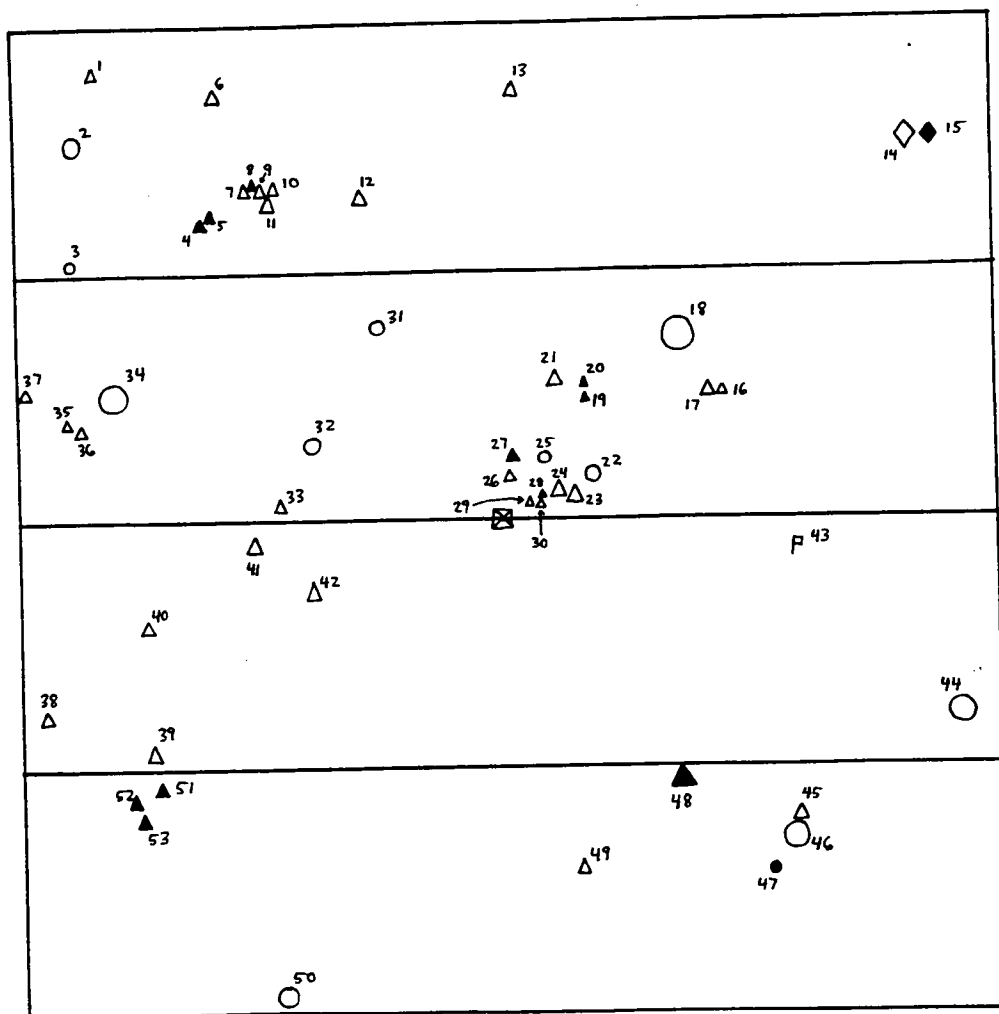


Figure 38. Stand 3, Quadrat 3 tree map.

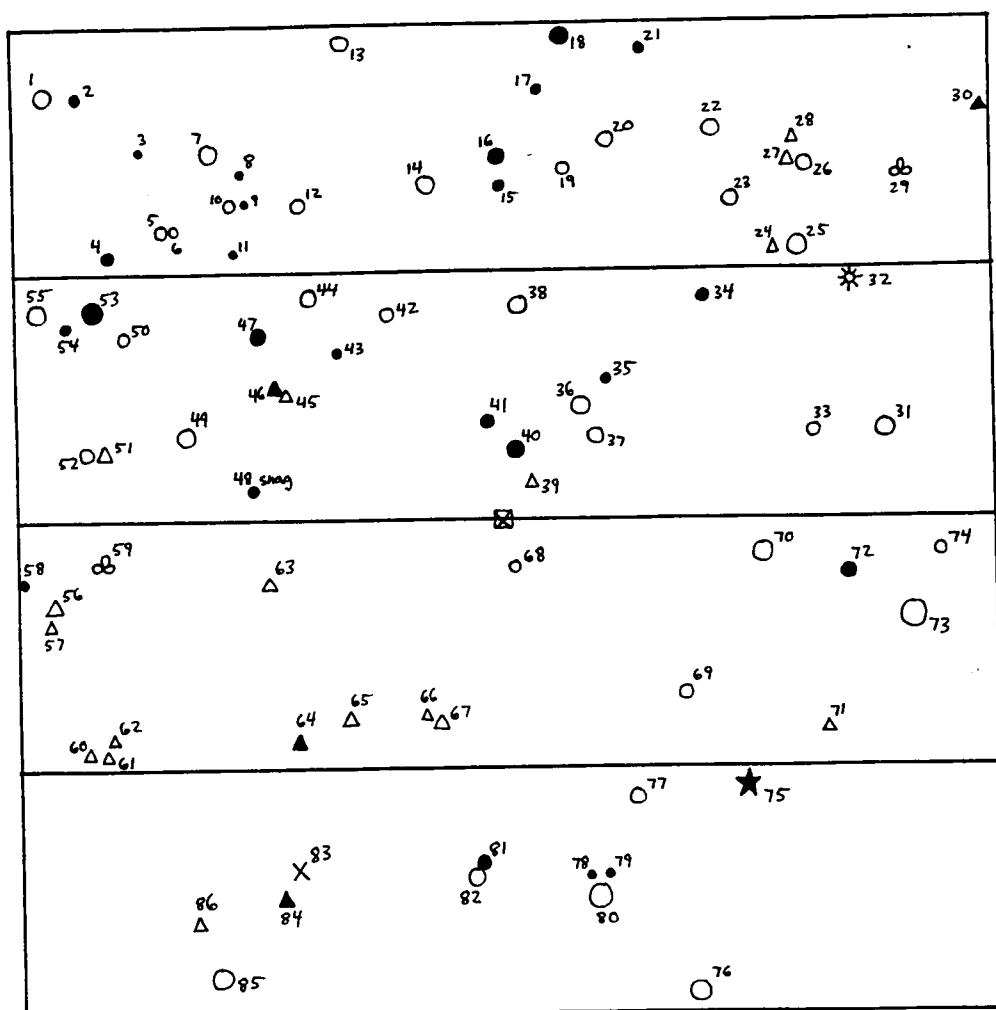


Figure 39. Stand 3, Quadrat 4 tree map.

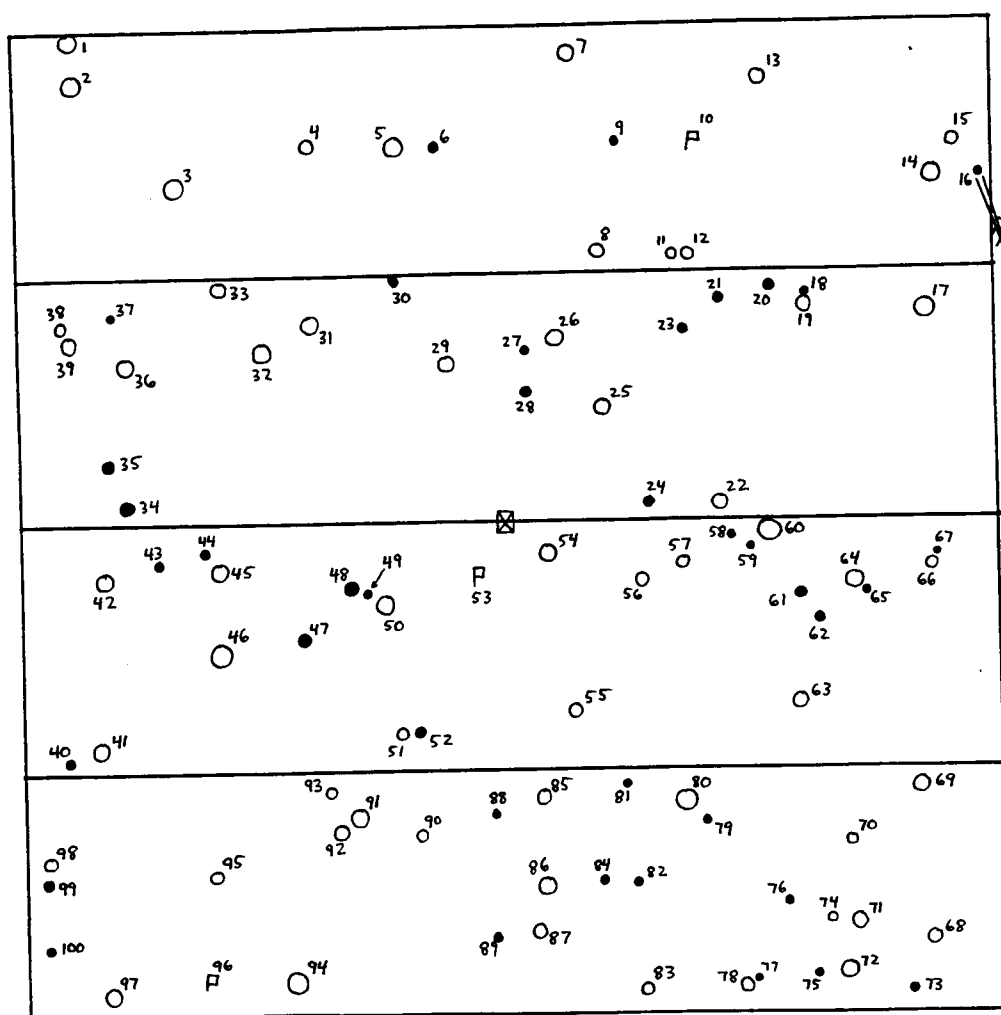


Figure 40. Stand 3, Quadrat 5 tree map.

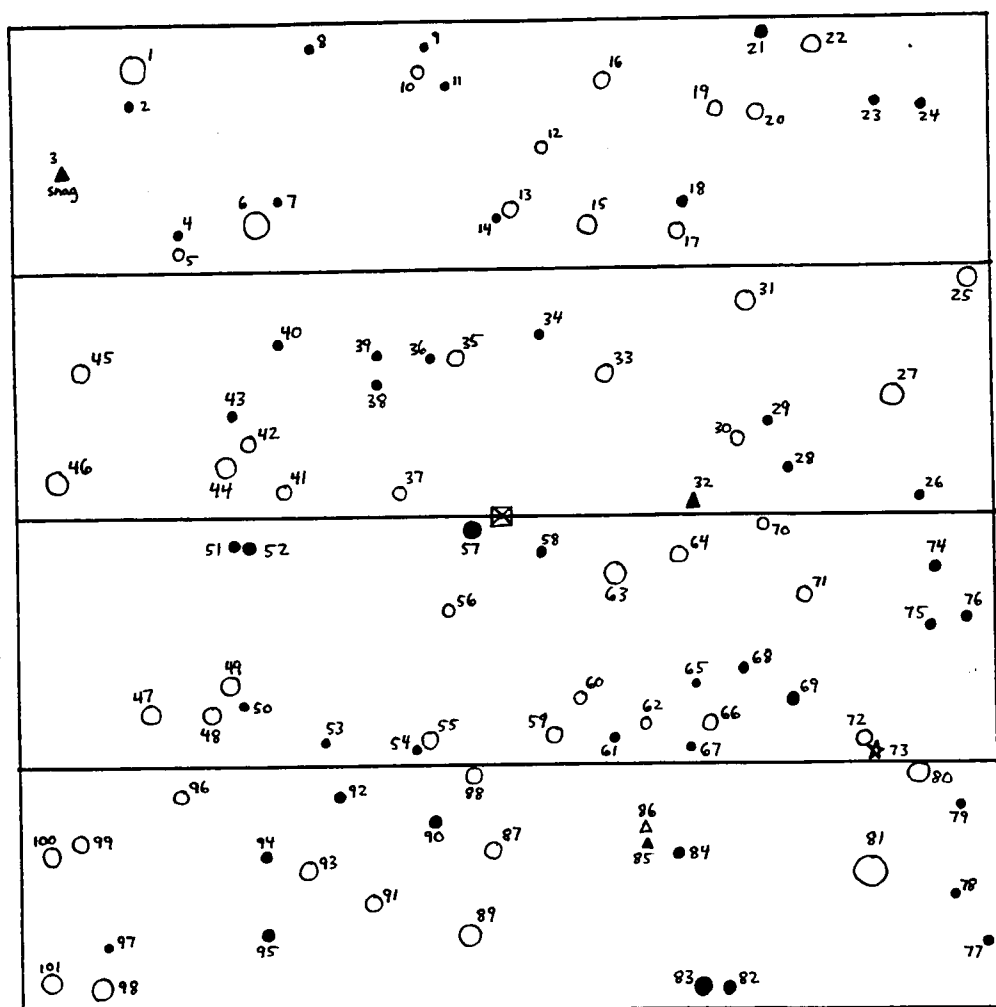


Figure 41. Stand 3, Quadrat 6 tree map.

APPENDIX C

ADDITIONAL DATA

1. Introduction

This appendix provides additional data that may be of value to workers interested in the floristics and plant ecology of the Cranberry Wilderness. Included are presence lists of vascular and bryophyte taxa found in the spruce forests of the Wilderness during this study. Vascular plant taxa are also assigned subjective ratings of their frequency of occurrence.

2. Vascular Taxa Presence

Table 11 lists all woody and herbaceous vascular plant taxa encountered during this study within closed-canopy red spruce forest in the Cranberry Wilderness. Stands were not searched systematically for the purpose of detecting species presence. Each taxon is subjectively rated as to its frequency of occurrence within the forest type as judged during routine sampling procedures described in Appendix A. The rating scale, in order of decreasing frequency of occurrence, is: common (C), frequent (F), infrequent (I), and rare (R). These ratings are not associated with numerical data, and "rare" does not represent any legal designation. No collections of vascular plant taxa were made.

Table 11. Vascular plant taxa found in closed-canopy Picea rubens forest of the Cranberry Wilderness, Monongahela National Forest, Pocahontas County, West Virginia. The frequency scale, in order of decreasing frequency of occurrence, is: common (C), frequent (F), infrequent (I), and rare (R). Nomenclature follows Strausbaugh and Core (1970-1977).

Taxon	Frequency of Occurrence
<u>WOODY TAXA</u>	
<u>Acer pensylvanicum</u>	I
<u>Acer rubrum</u>	C
<u>Acer spicatum</u>	I
<u>Amelanchier</u> spp.	F
<u>Betula alleghaniensis</u>	C
<u>Crataegus</u> spp.	R
<u>Fagus grandifolia</u>	F
<u>Ilex montana</u>	C
<u>Kalmia latifolia</u>	I
<u>Menzesia pilosa</u>	I
<u>Picea rubens</u>	C
<u>Prunus pensylvanica</u>	I (dead stems only)
<u>Prunus serotina</u>	I
<u>Pyrus americana</u>	F
<u>Rhododendron maximum</u>	C
<u>Rubus</u> spp.	R
<u>Sambucus pubens</u>	R
<u>Tsuga canadensis</u>	I

Table 11. Continued.

Taxon	Frequency of Occurrence
WOODY TAXA (Continued)	
<u>Vaccinium erythrocarpum</u>	C
<u>Viburnum alnifolium</u>	I
HERBACEOUS TAXA	
<u>Aster acuminatus</u>	I
<u>Carex</u> spp.	I
<u>Clintonia borealis</u>	F
<u>Cypripedium acaule</u>	R
<u>Dennstaedtia punctilobula</u>	F
<u>Dryopteris campyloptera</u>	C
<u>Dryopteris intermedia</u>	C
<u>Erythronium</u> spp.	I (spring ephemeral)
Poaceae	I
<u>Lycopodium annotinum</u>	R
<u>Lycopodium lucidulum</u>	C
<u>Lycopodium obscurum</u>	I
<u>Maianthemum canadense</u>	C
<u>Medeola virginiana</u>	F
<u>Mitchella repens</u>	I
<u>Monotropa uniflora</u>	I
<u>Osmunda cinnamomea</u>	C

Table 11. Continued.

Taxon	Frequency of Occurrence
HERBACEOUS TAXA (Continued)	
<u>Oxalis montana</u>	C
<u>Polypodium virginianum</u>	R
<u>Thelypteris novaboracensis</u>	I
<u>Trillium undulatum</u>	F
Total Woody Taxa	20
Total Herbaceous Taxa	21
TOTAL VASCULAR TAXA	41

3. Bryophyte Taxa Presence

Bryophytes (mosses and liverworts) are conspicuous features of the spruce forests of the Cranberry Wilderness. Other studies (Cain and Sharp 1938; Oosting and Billings 1951; Calise 1978; Smith *et al.* 1991) have found quite diverse bryophyte floras in Appalachian spruce and spruce-fir forests. A modest effort was made to collect a representative sample of bryophytes in the three stands studied here. More intensive efforts are likely to be more productive. Table 12 lists all bryophyte taxa encountered during this study within closed-canopy red spruce forest in the Wilderness. Also listed are the substrates from which specimens were collected. No attempt was made to rate frequency of occurrence. Taxa were identified by D. Smith, P. Davison, and A. Risk at the University of Tennessee, Knoxville. Specimens are in the possession of the author.

Table 12. Continued.

Taxon	Substrate
LIVERWORTS	
<u>Anastrophyllum</u> <u>michauxii</u>	unrecorded
<u>Bazzania</u> <u>trilobata</u>	forest floor, dead roots, live and dead roots of red spruce, logs, stumps, rocks on forest floor
<u>Calypogeia</u> sp.	rocks in seep
<u>Cepholozia</u> <u>lunulifolia</u>	stumps
<u>Frullania</u> <u>asagrayana</u>	bark of live yellow birch
<u>Jamesoniella</u> <u>autumnalis</u>	bark of live red maple
<u>Lejeunea</u> <u>ulicina</u>	bark of live yellow birch
<u>Lepidozia</u> <u>reptans</u>	forest floor, stumps
<u>Lophozia</u> <u>incisa</u>	stumps
<u>Odontoschisma</u> sp.	stumps
<u>Ptilidium</u> <u>pulcherrimum</u>	bark of live and dead red spruce, bark of dead yellow birch, bark of live red maple, bark of live mountainash, logs of red spruce
<u>Scapania</u> <u>nemorosa</u>	rocks in seep
<u>Tritomaria</u> <u>exsecta</u>	unrecorded

Table 12. Continued.

Taxon	
Total Moss Taxa	16
Total Liverwort Taxa	13
TOTAL BRYOPHYTE TAXA	29

VITA

Eric Frank Pauley was born in Charleston, West Virginia on April 23, 1963. He attended public schools in Charleston, graduating from George Washington High School in May 1981. He entered West Virginia State College, Institute in August 1981 and received his Bachelor of Science degree in Biology in December 1985. After treating gas well wastewater, repairing gas pipelines, and dispatching cement trucks for a summer, he enrolled in the Graduate Program in Ecology at the University of Tennessee, Knoxville in September 1986. During the summer of 1987, he worked at Uplands Field Research Laboratory and counted trees in the spruce-fir forest of the Great Smoky Mountains as part of the Eastern Spruce-fir Research Cooperative of the joint USDA/EPA Forest Response Program, often in the rain. He received the Master of Science degree from UTK in May 1989 by measuring the effect of blackberry on Fraser fir seedlings in the Smokies, often in the rain. He then counted more trees in nearly constant rain of the Smokies for the summer of 1989, again as part of the Spruce-fir Research Cooperative. In August 1989, he again entered the Ecology Program at UTK. After three more summers of working in the rain in spruce forests of West Virginia, he received his Doctor of Philosophy degree in Ecology in August 1993 by generating the foregoing document.