To the Graduate Council:

I am submitting herewith a dissertation written by Richard T. Busing entitled "Gap and Stand Dynamics of a Southern Appalachian Spruce-Fir Forest." 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 Botany.

Edward E. C. Clebsch,
Major Professor

We have read this dissertation
and recommend its acceptance:

Accepted for the Council:

Vice Provost
and Dean of The Graduate School

GAP AND STAND DYNAMICS OF A SOUTHERN APPALACHIAN SPRUCE-FIR FOREST

A Dissertation

Presented for the

Doctor of Philosophy

Degree

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Richard T. Busing

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ABSTRACT

Southern Appalachian spruce-fir forest dynamics were investigated by field studies and computer simulations. Mechanisms of old-growth stand dynamics were determined in a Great Smoky Mountains spruce-fir forest (elev. 1770-1830 m). The possible effects of anthropogenic disturbances on the mature forest were investigated with a gap model adapted to upper spruce-fir zone forests.

An analysis of stand dynamics involved the study of population interactions in the context of gap phase dynamics. Tree population structure and dispersion were quantified. Regeneration requirements and canopy-understory interactions were determined. Canopy turnover was modeled using species-by-species gap phase tree replacement probabilities. Finally, a spatial gap model was developed to simulate compositional and structural dynamics of a forest stand.

The old-growth forest is comprised of stable, all-aged spruce and fir populations. Fir is more abundant than spruce, but spruce dominates the forest because of its relatively long life span and large size. Shade tolerant spruce and fir saplings, regenerated in advance, are highly successful invaders of canopy gaps created by tree fall. Fir captures a large proportion of gaps regardless of gapmaker species. It is successful because of its high regeneration and growth rates. The canopy residence time of fir, however, is relatively short. Birch and other hardwoods are maintained by gap phase regeneration resulting in occasional gap capture.

Simulated balsam woolly aphid infestation results in a spruce dominated forest. In the absence of fir, stand biomass recovery is slow and total stand density is reduced. A moderately severe spruce growth decline in the presence of an undisturbed fir population results in a fir-birch forest. In association with a fir population decline the effects of spruce growth stress are diminished. The contemporaneous decline of spruce and fir populations results in a hardwood dominated forest with low total stand biomass.

The old-growth forest is close to equilibrium composition. As a consequence of small disturbance patch size, forest composition, biomass and structure are relatively constant over a small landscape area. This degree of equilibrium is unique among spruce-fir forests of eastern North America.

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CHAPTER I

INTRODUCTION

Viewing the forested landscape as a mosaic of patches is a useful approach to the study of forest dynamics. When canopy gaps created by tree fall are the mosaic elements, the underlying process is gap phase dynamics. Watt (1947) noted that the canopy gap was the unit of succession in an old-growth beech forest, and more recently this has been shown to be true for a variety of old-growth forests in temperate and tropical regions (Runkle 1984, Shugart 1984). A study of disturbance regimes in southern Appalachian spruce-fir indicates that natural disturbance generally results in small canopy gaps created by the fall of one to three trees (White et al. 1985b). It is therefore appropriate to study the gap phase dynamics of an old-growth southern Appalachian spruce-fir forest to attain an understanding of larger scale stand dynamics.

The spruce-fir forest zone is of particular interest because the two dominant tree species of this zone, red spruce (*Picea rubens*[1]) and Fraser fir (*Abies fraseri*), are threatened by anthropogenic disturbances. A marked decline in the radial growth rate of red spruce in the Great Smoky Mountains has recently been detected by McLaughlin (1983). It is possible that this growth decline will result in high levels of spruce mortality such as those ongoing in New

---

[1]Nomenclature follows Radford et al. (1968) unless noted otherwise.

England (Siccama et al. 1982). Possible causes for the growth decline of red spruce will be discussed later. Fraser fir has been subjected to high mortality over much of its range as a result of balsam woolly aphid (Adelges piceae Ratz.) infestation (Eagar 1984). Both of these declines are recent in origin and have affected some areas of the Great Smoky Mountains over the last two decades.

This study is aimed at understanding and simulating gap dynamics of a spruce-fir forest in the Great Smoky Mountains. The general purposes of the study are two-fold. The first is to obtain a record of the mechanisms involved in the dynamics of the old-growth spruce-fir forest in its natural state. The second is to make predictions of the future forest resulting from potential disturbances. A more specific discussion of objectives is provided below.

Objectives

The first seven objectives are directed at characterizing old-growth fir stand dynamics. They involve the study of population interactions in the context of gap phase dynamics.

1) To determine the present forest stand composition.

2) To determine the size- and age-structure of the spruce-fir forest dominants, and to estimate survivorship of these species.

3) To determine the intra- and interspecific spatial relationships among individual trees. The quantification of dispersion patterns may provide insight into interactions among trees.

4) To determine the regeneration niche components of spruce-fir forest tree species. These components include species-specific

canopy-understory interactions, canopy gap requirements and substrate requirements.

5) To determine species-by-species gap phase tree replacement patterns in the forest, and to test for reciprocal replacement between spruce and fir.

6) To model canopy composition dynamics using species-by-species replacement probabilities in a differential equation model of canopy turnover. This will allow the prediction of equilibrium canopy composition.

7) To simulate forest stand dynamics using a type of forest growth simulator known as a spatial gap model. This model will be adjusted to agree with field observations to attain a high level of accuracy.

The second set of objectives is directed at the prediction of future forest stand composition, structure and dynamics in response to major disturbance. They rely on the spatial gap model.

8) To test the predictive capabilities of the spruce-fir forest spatial gap model. Several field data sets quantifying compositional and structural changes of the forest following disturbance will be used in validation of the model.

9) To predict future forest composition, structure and dynamics in the spruce-fir zone using the spatial gap model. The model will predict the future forest in response to several potential disturbances including: 1) cyclic regeneration of fir, 2) complete loss of fir, 3) retardation of spruce growth, and 4) increased spruce mortality.

CHAPTER II

THE SOUTHERN APPALACHIAN SPRUCE-FIR FOREST

Vegetation

The red spruce-Fraser fir forest is restricted to the high peaks (>1750 m) of Virginia, Tennessee and North Carolina (Fig. 1). Although the range of red spruce extends northeast to Canada, Fraser fir is endemic to the southern Appalachians. The spruce-fir association typically ranges from 1670 to 1890 m in elevation, but on the north slopes of the Great Smoky Mountains it may extend to elevations as low as 1370 m (Fig. 2A). Red spruce dominates drier sites at elevations ranging from 1400 to 1800 m (Fig. 2B). Above 1890 m Fraser fir increases in relative dominance and forms almost pure stands on high peaks and ridges (Fig. 2C).

Five deciduous tree species often occur in the spruce-fir zone. They are yellow birch (Betula lutea), mountain maple (Acer spicatum), mountain ash (Sorbus americana), fire cherry (Prunus pensylvanica) and serviceberry (Amelanchier arborea). The distribution of each of these species except fire cherry and serviceberry along elevation and moisture gradients is shown in Fig. 2D-F. Yellow birch is the most important deciduous species in the forest and it commonly attains canopy tree size. Mountain maple is a small tree that ranges up to 1770 m in elevation. Mountain ash is a small boreal tree occurring from 1520 to 2010 m in elevation. Fire cherry is a disturbance adapted species (Marks 1974) with a distribution extending into the spruce-fir zone. Although serviceberry ranges to elevations of 1960 m

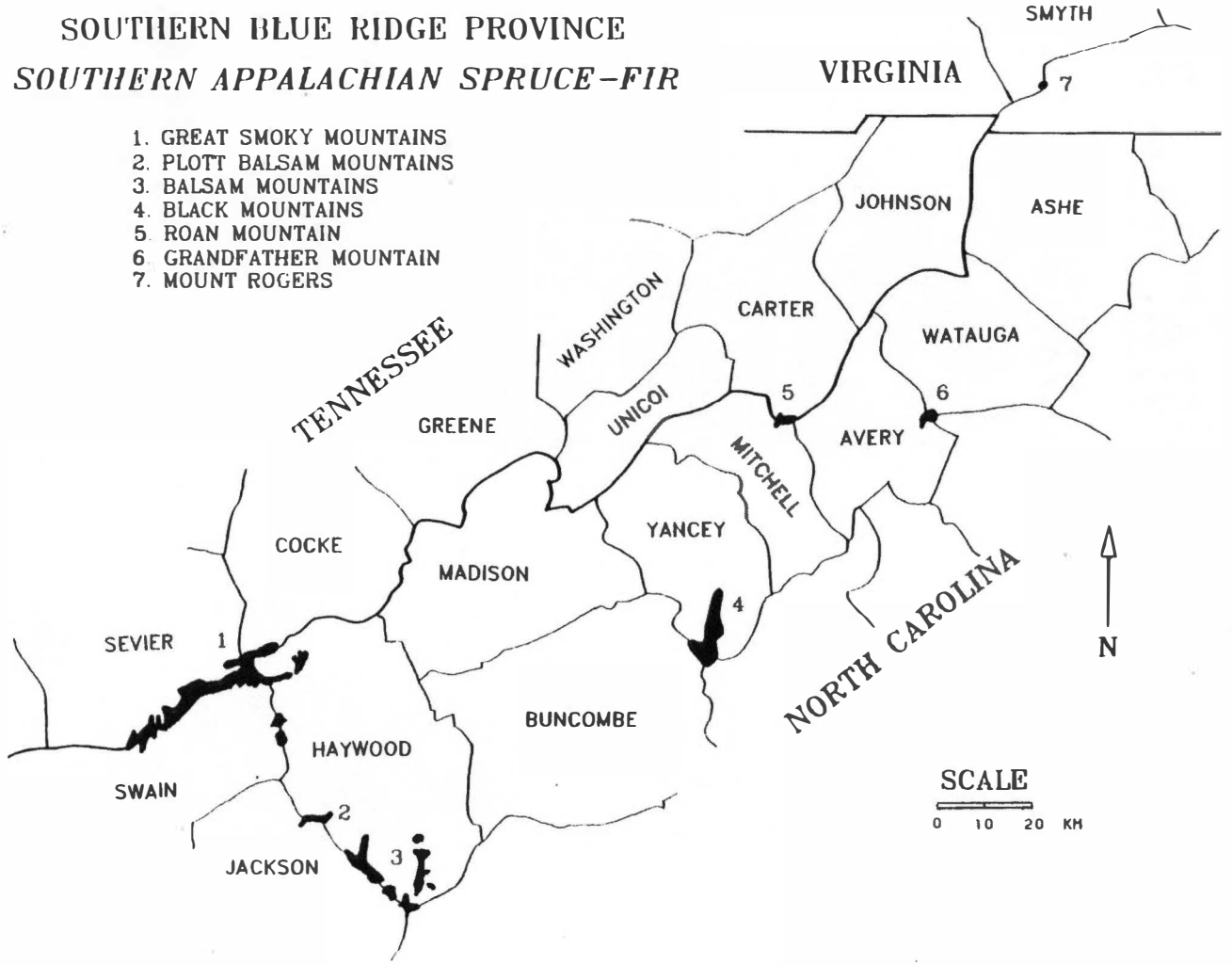


Fig. 1. Map of the present distribution of the southern Appalachian spruce-fir forest. Modified from Saunders (1979).

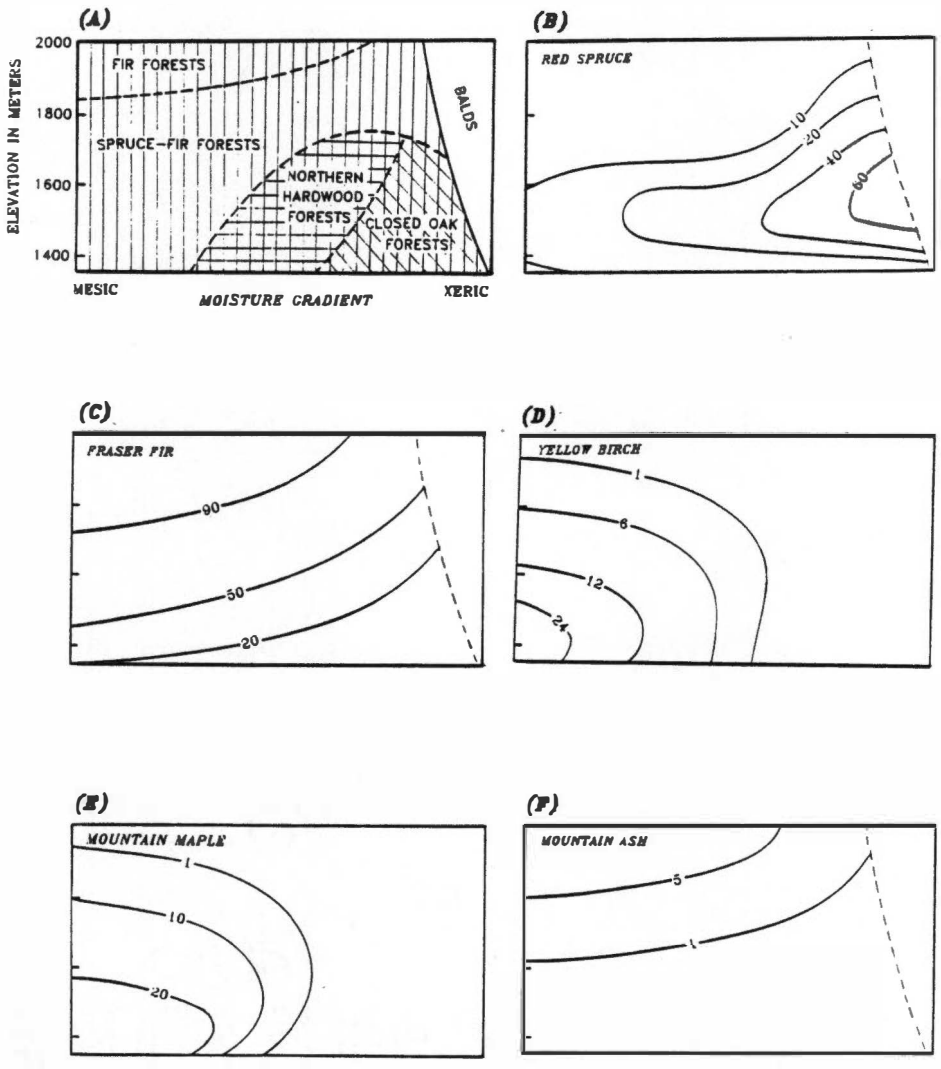


Fig. 2. Population charts for major tree species of the spruce-fir forest. Chart (A) shows the high elevation vegetation pattern along axes of site moisture and elevation. Charts (B)-(F) show the percent relative density of each tree species along these same axes. The charts are adapted from Whittaker (1956).

it is usually a small tree of low relative frequency in the spruce-fir zone. Ramseur (1960) states that serviceberry may attain canopy tree size near the hardwood-conifer ecotone.

Arboreal composition of the spruce-fir association at disjunct locations is summarized in Table 1. Five of the seven arboreal species mentioned above were reported from all five study locations considered. However, Shields (1962) and Castro (1969) did not record mountain maple on Mt. Rogers and Roan Mountain, respectively. Also, Davis (1930) did not record serviceberry in the spruce-fir zone of the Black Mountains. Beech (Fagus grandifolia), winterberry (Ilex ambigua var. montana), paper birch (Betula papyrifera), sugar maple (Acer saccharum), black cherry (Prunus serotina) and hawthorn (Crataegus spp.) were recorded at low frequency in at least one location. Other arboreal species that may occur at very low frequencies above 1650 m include striped maple (Acer pensylvanicum), buckeye (Aesculus octandra), and alternate leaved dogwood (Cornus alternifolia).

Spruce-fir vegetation of the southern Appalachians has been studied extensively. In the Great Smoky Mountains Cain (1935), Oosting and Billings (1951), Shanks (1954a), Whittaker (1956), Crandall (1958), Schofield (1960) and Boner (1979) have provided information on species composition of old-growth stands. The vegetation of the Black Mountains was described by Davis (1930), while the vegetation of Roan Mountain was described by Brown (1941) and Mark (1958). Ramseur (1960) studied the second-growth vegetation of the Balsam and Plott Balsam Mountains. Weaver (1972) also studied the

Table 1. Arboreal species of the spruce-fir zone.[a]

Species	Great Smoky Mtns.[b]	Black Mtns.[c]	Mt. Rogers[d]	Balsam Mtns.[e]	Roan Mtn.[f]
Picea rubens	D	D	D	D	D
Abies fraseri	D	D	D	D	D
Betula lutea	D	D	D	D	D
Sorbus americana	S	S	S	S	S
Prunus pensylvanica	S	S	S	S	I
Acer spicatum	S	S		S	
Amelanchier arborea	I		I	I	I
Fagus grandifolia	I			I	S
Ilex ambigua	I			I	
Betula papyrifera		I			
Acer saccharum					I
Prunus serotina					I
Crataegus spp.					I

[a]Reported from field studies above 1646 m (5400 ft.). D = dominant, S = subdominant and I = infrequent.

[b]Oosting and Billings (1951).

[c]Davis (2930), Ramseur (1960).

[d]Shields (1962).

[e]Pittilo and Smathers (1979).

[f]Castro (1969).

Balsam Mountains spruce-fir. Information on the spruce-fir vegetation of Mt. Rogers has been presented by Shields (1962). Finally, the forests of Grandfather Mountain were described by Reed (1905).

Quantitative vegetation analyses of old-growth and second-growth spruce-fir are summarized in Table 2. Red spruce dominated the old growth stands with a relative basal area of 50.4%. Fraser fir was more abundant, however, with a relative density of 61.9%. Yellow birch had notably lower basal area and density than spruce and fir. Second-growth forests were dominated by fir (relative basal area > 70%). Although spruce accounted for 17-26% of the density, because of their slow growth rate, individuals of this species were small in successional stands. Surprisingly, yellow birch was of less importance in the second-growth communities than in the old-growth communities.

Successional trends in the spruce-fir zone have been outlined by Davis (1930) and Ramseur (1960). Following large-scale disturbances such as logging, the colonizing tree species is usually fire cherry. It typically grows in dense stands, and is often accompanied by yellow birch; both species are capable of rapid growth even on eroded slopes if sufficient moisture is available. Trees of the fire cherry-yellow birch stands attain diameters of 10-15 cm, although a few trees approach diameters of 25 cm (Ramseur 1960). These stands often have mountain maple, mountain ash, Fraser fir and red spruce present at lower densities. In the Black Mountains, paper birch is also a component of this community. The fire cherry-yellow birch community is short in duration (<50 yr) and is eventually replaced by spruce-fir

Table 2. Density and basal area of southern Appalachian spruce-fir forests.

Location and Type	Species	Density (trees/ha)	% Density	Basal Area (m^2/ha)	% Basal Area
Great Smoky Mtns. (Old growth)[a]	*Picea rubens*	510	21.6	31.4	50.4
	Abies fraseri	1210	61.9	19.7	34.4
	Betula lutea	110	5.1	9.5	15.8
Balsam Mtns. (Second growth, 50-70 years)[b]	*Picea rubens*	558	28.4	13.6	26.4
	Abies fraseri	1151	58.6	36.2	70.2
	Betula lutea	89	4.5	1.2	2.3
Mt. Rogers (Second growth, 30-40 years)[c]	*Picea rubens*	232	17.3	8.4	17.6
	Abies fraseri	915	67.5	36.3	74.7
	Betula lutea	59	4.5	1.3	2.4

[a]Average of 7 stands ranging from 1660 to 1920 m (Oosting and Billings 1951).

[b]Average of 5 stands ranging from 1660 to 1900 m (Weaver 1972).

[c]Average of 4 stands ranging from 1660 to 1740 m (Shields 1962).

forest. Davis (1930) designated the spruce-fir forest a climax association.

Natural Disturbance Regimes

Large-scale disturbance is infrequent in the southern Appalachian spruce-fir forest. Fire, debris avalanches and wind are the prime agents of natural disturbance (Table 3). Lightning caused fires are infrequent and small in size because humidity and fuel moisture are high (Barden and Woods 1973, Harmon 1981). Debris avalanches are restricted to steep headwalls and scour channels which constitute a small portion of the spruce-fir landscape. Their frequency is on the order of 100 to 1000 years (Bogucki 1970). Wind is clearly the most important form of disturbance in the spruce-fir zone. Large areas of windfall are infrequent and occur predominantly on exposed ridges and summits. They are often colonized by even-aged fir stands. Small canopy gaps created by the fall of 1 to 3 canopy trees are the most frequent and widespread result of wind disturbance in the spruce-fir forest (White et al. 1985b). Consequently, small canopy gaps play an important role in stand dynamics.

Forest Dynamics

Each tree species of the spruce-fir forest has its own set of life history traits. The species differ in their growth rates, longevities, shade tolerances and roles in gap phase processes (Table 4). Red spruce lies at one end of the *r*- and *K*-continuum (MacArthur and Wilson 1967, Gadgil and Solbrig 1972). Because it is a large, long lived species with a slow growth rate and a tolerance to

Table 3. Great Smoky Mountains spruce-fir forest disturbance regimes.[a]

	Percent of Area	Return Interval (yr)	Recovery Time (yr)	Last Episode
Natural Disturbance				
Fire	0	--	--	--
Debris Avalanches:				
Headwalls	1	$?10^2$	10^2+	1951+
Scour Channels	1	$?10^2$	10^2	1951
Windfall (>200 m^2)	0.1	10^3	10^2	Ongoing
Canopy Gaps (<200 m^2)	1.2	180	50	Ongoing
Fir patches (summits)	10	50	20	Ongoing
Human Disturbance				
Balsam Woolly Aphid	95	Unstable	Unstable	Ongoing
Logging	40	10^3	10^3	1920
Slash Fires	10	10^3-10^4	10^3-10^4	1920

[a]Information from White et al. (1985a).

Table 4. Traits of southern Appalachian spruce-fir forest trees.

Species	Average Growth Rate (cm diam./yr)	Average Life Span	Shade Tolerance	Average Years in Suppression	Role in Gap Phase Processes: Gap Created by Death	Role in Gap Phase Processes: Gap Required for Regeneration
Picea rubens	0.2[a]	225[b]	Tolerant[c]	32[b]	Yes	No
Abies fraseri	0.3[a]	137[b]	Tolerant[c]	24[b]	Yes	No
Betula lutea	0.3	154[b]	Intermediate[c]	3[b]	Yes	Yes
Acer spicatum	0.3	<150	Intermediate	?	No	?
Sorbus americana	0.4	<100	Intolerant	<5	No	Yes
Prunus pensylvanica	0.5	<50	Intolerant	<5	No	Yes

[a]Oosting and Billings (1951).

[b]White et al. (1985a).

[c]Daniel (1979).

competition for light, it can be termed a K-selected species. It is not adapted to frequent disturbance. In fact, it is uncommon on summits and exposed ridges where large-scale windfall occurs. In contrast, Fraser fir, like its northern relative balsam fir (Abies balsamea) (Sprugel 1976), is well adapted to regeneration following windfall. Fire cherry is an r-selected species that depends on disturbance for persistence in the stand. It is a fast growing, short lived, shade intolerant species that is perpetuated by a reservoir of buried dormant seeds (Marks 1974). The remaining tree species lie between fire cherry and red spruce on the r- and K-continuum.

Stand dynamics are greatly affected by gap phase events. All of the deciduous tree species require canopy gaps for regeneration, while red spruce and Fraser fir may attain sapling size in the shaded understory. Fir seedlings are much more abundant than spruce seedlings (>4:1). Yet spruce codominates because of its long life span and high survivorship in the understory (White et al. 1985a). When a canopy gap is available the advanced regeneration of spruce or fir may enable one of these species to capture the gap. Even though fir captures the largest proportion of gaps, the deciduous species are able to compete for gaps because of their high growth rates (White et al. 1985b).

Canopy-understory interactions between certain species may affect regeneration and subsequent gap capture (Woods and Whittaker 1981). This reasoning is based on the fact that each type of canopy creates a characteristic microsite on the forest floor where the conditions for growth of seedlings and saplings of certain species are favorable.

Fox (1977) proposed that spruce regenerates underneath fir and vice versa. To test the hypothesis of reciprocal replacement he made counts of saplings beneath spruce and fir canopies in the Great Smoky Mountains. When analyzed by the chi-square test, his results revealed a highly significant trend of greater regeneration beneath spruce canopies ($X^2 = 12.1$, $P < .001$). Fir saplings were far more abundant beneath spruce canopies, while spruce saplings were slightly higher in abundance beneath spruce canopies. Fox's results are summarized in Table 5 below.

Table 5. Overstory-understory interactions between spruce and fir. Numbers are sapling counts beneath canopy trees.

		Canopy	
		Picea	Abies
Sapling	Picea	15	10
	Abies	82	8

Further counts by Fox concerned replacement predictions of canopy species. A slight but statistically insignificant trend of reciprocal replacement was revealed ($X^2 = 3.12$, $P > .05$). The data are presented in Table 6.

Table 6. Tree replacement in a southern spruce-fir forest. Numbers are potential successor saplings beneath canopy trees, 1 successor per tree.

		Canopy	
		Picea	Abies
Successor	Picea	4	5
	Abies	32	8

Similar counts of saplings by Culver (1981) in the Great Smoky Mountains suggested that fir was largely self-replacing. Further study of the interactions between these two codominants would be valuable to the understanding of stand dynamics. Also, the role of yellow birch and other deciduous species in canopy-understory interactions of this nature is unclear and needs further study.

Physiography and Geology

The southern Appalachians are the loftiest and most massive mountains of the Appalachian range. In the south, forty-six high mountain areas exceed 1676 m (5500 ft) in elevation. The total land area above this elevation is 121 km^2 (Ramseur 1960). Mount Mitchell in the Black Mountains is the highest peak (elev. 2037 m) in eastern North America.

The bedrock of the southern Appalachian mountains was formed in the late Precambrian and early Paleozoic eras from sediments deposited by an inland sea. Faulting and uplift of the Appalachian geosyncline occurred in the late Paleozoic. Erosion exposed metamorphosed sediments which are the primary components of the bedrock (King et al.

1968). Although highly eroded, the southern Appalachians remain unglaciated.

The various summits forested with spruce-fir differ in the composition of their surface rock. The Great Smoky Mountains, Plott Balsam Mountains and the Black Mountains are of the Great Smokies Group, a feldspathic sandstone interbedded with feldspathic quartz-mica schist or phyllite. The Balsam Mountains are muscovite schist and gneiss (Hadley and Nelson 1971). Roan Mountain is Roan gneiss, a hornblende gneiss, while Grandfather Mountain is of the Grandfather Mountain Formation, a graywacke sandstone with minor interbeds of phyllite and siltstone. Mount Rogers is of the Mount Rogers Formation, a rhyolitic lava (Rankin et al. 1972).

Climate

The spruce-fir zone is subject to short, cool growing seasons and cold winters. Mean monthly temperatures range from -3.3°C in January to 16.7°C in July (Grandfather Mtn.). The zone is very moist throughout the year. Mean annual precipitation ranges from 145.9 cm (Roan High Knob) to 208.5 cm (Clingmans Dome, Saunders 1979). At 1920 m in the Great Smoky Mountains the highest monthly average precipitation levels occur in January (30.1 cm) and August (25.8 cm) while the lowest average level occurs in October (12.6 cm) (Stephens 1969). Snow accumulation is usually less than 30.5 cm. Moisture inputs from fog are significant. Condensation on spruce and fir trees is substantial because of their high leaf surface area, and it is an

important mode of moisture input in the forest (unpublished data cited by Hay and Eagar 1981).

Exposed peaks of the southern Appalachians are subject to high wind velocities. On the average, ten days per year have wind velocities in excess of 120.7 km/hr (Grandfather Mtn.). The spruce-fir forest is restricted to less exposed sites where wind velocities are more moderate. February, March and April are the windiest months of the year (Saunders 1979).

Soils and Nutrient Cycling

Soils of the southern Appalachian spruce-fir are Inceptisols or Spodosols, depending on site topography and parent material texture. In general, on stable surfaces at an elevation of 1700 m Spodosols occur on coarse textured parent material, while Inceptisols occur on medium textured parent material. The soils are typically shallow, stoney, acidic and low in mineral nutrients (Springer and DeSelm 1983).

McCracken et al. (1962) studied soil morphology and genesis in the spruce-fir zone of the Great Smoky Mountains. These highly weathered soils were classified in the Sol Brun Acide great soil group (currently classified as a subgroup of the order Inceptisols) in accordance with their low base saturation, high C/N ratio, high exchangeable Al, and the lack of relative accumulation of free iron and of layer silicates. Their thick organic layer contained considerably more bases and N than the mineral A horizon. Nutrient

exchange between vegetation and the forest floor appeared to be restricted almost entirely to the organic layers.

Wolfe (1967) also studied soils under spruce-fir in the Great Smoky Mountains. These soils were classified as Spodosols of the Entic Normothod subgroup. They were low in base saturation and highly acidic. Soil microflora and fauna were low and decay was slow. Frequent uprooting of trees and soil movement downslope appeared to hinder Spodosol development.

High levels of dry-matter accumulation in the soil are characteristic of the spruce-fir ecosystem. Mg, K and P are concentrated in the soil, while Ca is concentrated in the vegetation (Weaver 1972, 1975). N cycling has not been studied in the southern Appalachian spruce-fir even though N is an important nutrient in some coniferous forest ecosystems. The productivity of young spruce-fir stands has been estimated at 816 g/m^2/year on Balsam Mountain (Weaver 1972), while the productivity of old spruce-fir stands has been estimated at 580 g/m^2/year in the Great Smoky Mountains (Shanks et al. 1961). The overstory accounts for a large portion of the vegetation biomass which ranges from 300 to 340 metric tons/ha in old stands (Whittaker 1966).

Prehistory and History

During the full glacial, 18,000 yr bp, the spruce-fir forest was widely distributed across the eastern U.S. As the climate became warmer spruce-fir was restricted to the mountain regions. Maximum constriction of the spruce-fir range occurred during the hypsithermal

interval (ca. 5000 yr bp). Local extinction of spruce-fir on summits above 1740 m may have occurred during this period of maximum warmth (Whittaker 1956). Over the last 5000 years the range of Southern Appalachian spruce-fir has expanded with the cooling climate (Delcourt and Delcourt 1979, 1984).

In historical time the range of the spruce-fir forest has been greatly reduced by logging (Table 7). The original extent of the spruce-fir forest is estimated at over 13,500 ha, while the current extent is only 6831 ha, 49.2% of the original forest. The largest expanses of virgin spruce-fir are in the Great Smoky Mountains and the Black Mountains. The remaining spruce-fir localities are second-growth stands regenerated following logging. The combination of logging and burning has retarded or prevented spruce-fir regeneration in some areas (Korstian 1937, Saunders 1979). Loss of soil by erosion and soil nutrients through leaching may be responsible for slow revegetation of spruce and fir after disturbances of this nature (Weaver 1975).

Two anthropogenic disturbances currently threaten the spruce-fir forest. Fraser fir is threatened by the balsam woolly aphid (Adelges piceae Ratz.), an exotic insect pest introduced into New England and Canada from Europe prior to 1908. The balsam woolly aphid was first discovered in the southern Appalachians in 1957 on Mt. Mitchell of the Black Mountains (Speers 1958). In 1962 it was found on Roan Mountain, and in 1963 it was found on Grandfather Mountain and Mt. Sterling of the Great Smoky Mountains (Amman and Speers 1965). Within the Great Smoky Mountains the infestation spread to the southwest and all fir

Table 7. Areal extent of southern Appalachian spruce-fir forests before and after logging.[a]

Location	Past Extent (ha)	Current Extent (ha)	Percent Remaining	Current Condition
Great Smoky Mountains	6,013	3,665	61.0	Virgin/Second Growth
Plott Balsam Mountains	662	193	29.2	Second Growth
Balsam Mountains (N.C.)	3,127	614	19.6	Second Growth
Black Mountains	2,524	1,457	57.7	Virgin/Second Growth
Roan Mountain	896	355	39.6	Second Growth
Grandfather Mountain	247	220	89.1	Second Growth
Mount Rogers	406	326	80.3	Second Growth
Total	13,875	6,831	49.2	

[a]Information from Saunders (1979).

stands were infested by 1983. The fir stands on Mt. Rogers have shown some resistance to infestation (Hay and Eagar 1981). Eagar (1978), Hay et al. (1978), and Johnson (1977) have provided detailed accounts of the effects of infestation on Fraser fir in the Great Smoky Mountains. It is possible that the infestation will result in the elimination of natural Fraser fir populations (Hay and Eagar 1981). Red spruce has been subject to abnormally high mortality levels in the northern Appalachians over the last decade. In areas of the Green Mountains in Vermont, the Adirondack Mountains in New York and the White Mountains in New Hampshire the density and basal area of red spruce have diminished. The radial growth of the surviving trees in these areas has also declined (Siccama et al. 1982). Recently a decline in the radial growth of red spruce was detected in the southern Appalachians as well (McLaughlin and Braker 1985). Such growth declines may foreshadow increased red spruce mortality in the southern Appalachians. The direct causes of growth decline and mortality are unknown. Some likely agents include acid precipitation, heavy metals, and insect or fungal pests.

The future of the southern Appalachian spruce-fir forest is uncertain. If both dominants are eliminated or greatly reduced in importance the hardwood species may become the forest dominants. It has also been suggested that some areas may become grass and shrub communities. Predictions have been complicated by the fact that the magnitude of anthropogenic disturbance is unknown at this time. Useful predictions should be based on a range of potential levels of disturbance.

CHAPTER III

GAP DYNAMICS OF FORESTS

Introduction

The role of forest canopy gaps in old-growth forest dynamics was first emphasized by Watt (1925, 1947). His observations in a beech community led him to conclude that canopy gaps were important tree regeneration sites. In particular, he noted that beech seedlings survived only in canopy openings. The term "gap phase" was used in reference to the early stage of plant colonization following gap creation by the death of a canopy tree (Watt 1947). Further evidence of gap phase tree regeneration was presented by Bray (1956) for a maple-basswood forest. Basswood (Tilia americana) reproduced by sprouting from the stumps of former canopy trees, while sugar maple (Acer saccharum) reproduced from dense seedling growth in gaps. The rapid growth of maple in gaps enabled it to outcompete slow growing shade tolerant trees of oak and hickory, and thereby codominate the forest. Jones (1945) also mentioned the importance of canopy gaps in the persistence of shade intolerant species in old-growth forests. Examples of temperate forest species dependent on canopy gaps include yellow birch (Godman and Krefting 1960), fire cherry (Marks 1974); black cherry, Prunus serotina (Auclair and Cottam 1971); tulip poplar, Liriodendron tulipifera (Skeen 1976, Wallace and Dunn (1980); and striped maple, Acer pensylvanicum (Hibbs et al. 1980).

Gap dynamics are particularly important in old-growth forests lacking large-scale disturbance. They are least important in forests

subject to large-scale disturbances caused by fire, wind storms and pathogens. Many forests of temperate and tropical regions appear to be strongly affected by gap events. Examples from temperate regions include beech (Watt 1925, 1947; Jones 1945; Nakashizuka 1983, 1984), hemlock-hardwood-white pine (Jones 1945, Woods and Whittaker 1981), maple-basswood (Bray 1956), southern floodplain (Robertson et al. 1978), beech-maple (Woods 1979), mixed mesophytic (Barden 1980, 1981; Runkle 1981, 1982) hemlock-hardwood (Barden 1979, Hibbs 1982), and spruce-fir forests (White et al. 1985b). In tropical regions light gaps are extremely important in tree regeneration because of the typically dense canopy of the forests. Numerous studies of tropical forest gap dynamics have been done. Some examples have been presented by Richards (1952), Poore (1968), Whitmore (1975), Hartshorn (1978, 1980), Denslow (1980) and Brokaw (1982).

Gap Events

The gap phase is initiated by the death of one to several canopy trees. Mortality can occur in several ways including uprooting, snapping or standing death. The form of mortality affects gap characteristics and subsequent regeneration (Putz et al. 1983). Uprooting of trees exposes soil and creates a pit-mound microtopography that can be exploited by certain species (Hutnik 1952, Lyford and Maclean 1966, Falinski 1978). Snapping of trees usually does not result in substantial soil disturbance and the canopy tree may self-regenerate by sprouting. Sprouts are generally faster growing than seedlings, but they appear to have a high frequency of heartrot

(Putz et al. 1983). Gaps created by uprooting and snapping are large in size because the event of tree fall opens the canopy. Large gaps have higher light intensities and, for this reason, they allow the regeneration of shade intolerant species. In contrast, gaps created by standing death are small and favor shade intolerant species. Standing death can result from pathogens or senesence, and gap creation by this means can be relatively slow.

The role of regeneration requirements of species in vegetation composition and dynamics has been stressed by Grubb (1977) and Grime (1979). As defined by Grubb (1977), the "regeneration niche" of a species consists of a unique set of regeneration requirements. Important variables of the tree regeneration niche include the influence of established canopy trees, canopy gap size, gap age, substrates and soil depth. Canopy tree influence refers to the characteristic forest floor microsite created by light conditions and root effects near a canopy tree. It is particularly important in forests with low substrate variability and low frequency of disturbance (Woods and Whittaker 1981). In addition, the availability of propagules is an important consideration. Oliver (1981) recognized several modes of tree propagule dispersal that allow rapid regeneration following disturbance. The strategies include regeneration from newly dispersed seeds, dormant seeds, sprouting, layering and seedling banks.

Regeneration following gap formation is a crucial stage in gap dynamics. Although regeneration prior to gap formation is important in some temperate forests (Woods and Whittaker 1981), the event of gap

creation often triggers tree regeneration by providing a suitable microhabitat. The relatively high light intensity in canopy gaps is a major factor. A large number of arboreal species regenerate only in canopy gaps because of their intolerance to shading. Microhabitat moisture and temperature are also affected by canopy gaps. In large canopy gaps the forest floor receives direct sunlight which raises the temperature and lowers the surficial soil moisture of the site. Increased soil temperature fluctuations trigger germination of certain species (Mayer and Poljakoff-Mayber 1975), but seedlings of species such as red spruce that are unable to tolerate low soil moisture (Fowells 1965) are not favored in large openings (Roller 1942). Gaps with exposed mineral soil are favorable regeneration sites for a variety of species including paper birch, yellow birch, fire cherry and tulip poplar (Hutnik 1952, Marks 1974, Buckner and McCracken 1978).

Regeneration prior to gap formation may also play a significant role in gap colonization. In fact, understory composition has been used with some success to predict future overstory composition (Horn 1971, 1975b). Typically, shade tolerant species slowly attain sapling size beneath the closed canopy and upon release, quickly grow to close the canopy opening. For example, Fraser fir and red spruce may survive for several decades in suppression and grow vigorously upon release (White et al. 1985b). Microhabitat factors affecting regeneration beneath a closed canopy include the type of canopy tree nearby and the substrate. The influence of canopy trees on regeneration has been demonstrated by Woods (1979) in a beech-maple

forest. An analysis of spatial distributions of juveniles in relation to canopy trees revealed that maple regenerates in higher numbers beneath beech canopies and vice versa. Species exhibiting advance regeneration in old-growth forests must be capable of seedling establishment on substrates other than mineral soil (Graham 1941). Such substrates include the litter layer and fallen logs. Provided sufficient moisture, red spruce and Fraser fir are capable of regeneration on a variety of substrates (Fowells 1965). A disadvantage of advance regeneration is the risk of mortality during canopy gap formation; nonetheless, the advance regeneration strategy is highly successful in old-growth forests.

Gap capture and canopy closure involve regeneration and growth of trees within the canopy opening. Gap phase species are typically fast growing and are adapted to efficient photosynthesis under high light intensities (e.g., Wallace and Dunn 1980). They will capture a gap unless outcompeted by species regenerated in advance. Because gap phase species are not shade tolerant they may be shaded out by saplings remaining after tree fall. Gap size affects what types of species will successfully invade. Lateral extension of surrounding canopy trees may quickly close small gaps, excluding shade intolerant species (Hibbs 1982). Small to medium sized gaps favor shade tolerant species because the regeneration and growth rates of shade intolerant species are low in these openings. Large sized gaps allow the regeneration of both shade tolerant and shade intolerant species; the latter are likely to capture the gap because of their high growth rates (Minckler and Woerheide 1965, Marks 1975, Runkle 1982).

The gap event is terminated by the closure of the canopy and the replacement of one to several old canopy trees by new canopy trees. Studies of tree replacement patterns in the final stages of gap capture have been carried out by Fox (1977), Brewer and Merrit (1978), Barden (1979, 1980, 1981, 1983) and White et al. (1985a, 1985b). Some patterns of species-by-species replacement are evident. In a Rocky Mountain Engelmann spruce (Picea Engelmannii [Parry] ex Engelm.)-subalpine fir (Abies lasiocarpa Nutt.) forest, spruce was found to replace fir and vice versa (Fox 1977). In the more diverse southern Appalachian hardwood forests, the replacement patterns were complex. Self-replacement, exhibited only by basswood (Tilia heterophylla), was uncommon. Otherwise the replacement observations did not reveal ordered interactions among species. The randomness of tree replacement in these forests was related to their high species diversity (Barden 1980).

Forest composition and dynamics can be viewed as the result of gap phase tree replacement events (Horn 1981). The magnitude and frequency of disturbance determine the frequency of gap formation in a given area and in turn affect species diversity (Doyle 1981). More specifically, frequency of gap formation is dependent on canopy tree longevities which are a function of species' life histories and disturbance. Under a fixed disturbance regime, nonrandom tree replacement will, in time, produce a forest composition that is near equilibrium and will not change unless replacement patterns become altered. This is analogous to the current forest climax concept of constant vegetational composition within adequate forest area subject

to static disturbance and climatic regimes (Whittaker and Levin 1977, White 1979). For these reasons, tree-by-tree replacement and gap dynamics are processes that lend themselves to mathematical analysis and simulation of larger scale forest dynamics.

Forest Succession Models

Forest succession models that are based on gap dynamics are called gap models. Such models use a gap sized area of land as the unit of simulation. This category of model is intermediate between tree models that consider individual trees as the basic unit of simulation, and forest models that consider larger land areas as the unit of simulation (Shugart and West 1980). Because gap models are best suited to the simulation of gap dynamics they will be discussed in detail. Also, some tree models are capable of predicting the long-term effect of gap dynamics on forest composition. These relatively simple tree models will be considered first.

A class of tree models that has been used to model ecological succession in old-growth forests is the mixed aged, mixed species, nonspatial tree model (Shugart and West 1980). Markov chain models which simulate the long-term outcome of tree-by-tree replacement in forests fall into this category. A Markov model is simple and limited in its applicability. It is based on the assumption that the probability of one species replacing another is fixed and dependent only on the identity of the tree being replaced. The model best applies to long-term dynamics of forests lacking large-scale disturbance. A major weakness in application is the difficulty of

obtaining accurate replacement probabilities (Horn 1981). Horn (1975a, 1975b, 1976) developed and tested Markov models of a mature hardwood forest in New Jersey. Model predictions of canopy composition at equilibrium generally agreed with actual canopy composition. Other successful approximations of mature forest composition using this type of tree model have been made by Barden (1980) for a southern Appalachian cove hardwood forest and Culver (1981) for a southern Appalachian spruce-fir forest.

Gap models can be separated into two classes: nonspatial and spatial (Shugart and West 1980). Nonspatial gap models closely resemble the Markov tree models of Horn (1975a). Waggoner and Stephens' (1970) model of northern hardwood forest dynamics, for example, is based on transition probabilities of gap sized (0.01 ha) areas of land from one vegetation state to another over a 10 year interval. The model was tested for its ability to reproduce actual forest changes over a 40 year period. There was general agreement between predicted and observed forest composition except that the model overestimated the proportion of oaks in the forest. In this case, the overestimation of oak is the result of time invariant transition probabilities that do not account for natural declines and surges of populations. Although Markov models can be modified to account for a variety of changing environmental factors (e.g., Acevedo 1981) they are limited by the difficulty of obtaining accurate transition probabilities and by the fact that they only provide general information on forest composition.

Spatial gap models are relatively complex models of individual tree interactions within a gap sized area (Botkin et al. 1972, Shugart 1984). The spatial considerations of these models are vertical within a small, fixed horizontal area. The relative heights of trees are important because the smaller, shaded trees are grown at slower rates. Annual calculation and tabulation of recruitment, growth and death of individual trees are performed in the simulations. Annual increases in tree diameter are calculated from an optimal growth equation unique to each species. Diameter growth is decreased by a function of leaf area above the individual. Retardation of growth and possible mortality of the supressed individual is dependent on its shade tolerance classification. In addition, the effects of crowding are approximated by a decrease in growth of all individuals within a simulated gap as the total biomass approaches the maximum biomass recorded for the forest. Finally, mortality of unsupressed trees is a probabilistic function of their maximum recorded age. The mathematical relationships used in the first model of this type, JABOWA (Botkin et al. 1972), and most of its predecessors are discussed below.

The fundamental equation of spatial gap models was developed by Botkin et al. (1972) to simulate optimal tree growth:

$$\frac{d(D^2H)}{dt} = rLA\left(1 - \frac{DH}{D_{max}\, H_{max}}\right)$$

where D is diameter at breast height, H is tree height, D_{max} and H_{max} are the respective maxima for the species, r is a growth parameter and

LA is leaf area of the tree. In this equation the annual volume increment is given as a linear function of leaf area and it is reduced as a tree approaches its maximum size.

Height to diameter relations are based on the equation of Ker and Smith (1955):

$$H = 137 + b_2 D - b_3 D^2$$

where b_2 and b_3 are parameters quantifying the relations for a species, and the constant 137 is breast height in cm. Using this relationship the height of individual trees is calculated in the simulation of light limitation of tree growth. Leaf area above individual trees is calculated and the reduction of optimal growth is then determined by an adaptation of Beer's law:

$$AL = PHI \exp(-k \cdot SLA)$$

where AL is the light available to the shaded tree, PHI is the annual insolation, k is a constant and SLA is the shading leaf area above the tree. Optimal tree growth is reduced by the value r(AL) which is calculated by one of two formulas depending on the tree's shade tolerance:

$$r(AL) = 1 - \exp(-4.64(AL - 0.05)), \text{ shade tolerant}$$

$$r(AL) = 2.24\,(1-\exp(-1.136(AL - 0.08))), \text{ shade intolerant}$$

These functions fit measured photosynthesis curves of Kramer and Kozlowski (1960) for shade tolerant and shade intolerant trees.

The effect of crowding on tree growth is modeled by:

$$S(BAR) = 1 - BAR/SOILQ,$$

which is a factor in the growth equation. BAR is the total stand biomass and SOILQ is the maximum biomass recorded for the forest type. In effect, tree growth approaches zero as the stand approaches the maximum potential biomass.

The mortality of trees is simulated using the following relationship:

$$p = 1-(1-E)^n$$

where p is the probability of mortality by year n and E is the annual mortality probability. Intrinsic tree mortality yielding approximately 1% survival at maximum age (AGEMAX) is based on an annual mortality probability of 4.605/AGEMAX (Shugart and West 1977). The mortality of suppressed trees is based on an additional annual mortality probability of 0.368 which results in a 1% chance of surviving 10 years.

Tree recruitment in spatial gap models is usually based on simple stochastic routines which determine the number of seedlings to be input per species annually. More sophisticated models monitor environmental conditions and approximate their effects on the recruitment of certain species. For example, the FORET model is capable of simulating annual temperatures and then preventing the regeneration of certain species during hot years. The simulation of regeneration is relatively difficult and as a result it is a weak

component in these models. Because regeneration is a crucial part of population dynamics and vegetation dynamics, accurate simulation of this event is essential. Possible means of improving the regeneration components of such models will be discussed later.

Two early spatial gap models serve as good examples of model testing and application. These are the JABOWA model of Botkin et al. (1972) and the FORET model of Shugart and West (1977). JABOWA was developed to simulate dynamics in a northern hardwood forest at various elevations in the White Mountains of New Hampshire. The simulated forest composition over a range of elevations agreed well with actual composition patterns. In fact, the elevation of the conifer-hardwood transition was successfully predicted. Some quantitative measures for simulated stands 50 to 60 years old also agreed with actual measures of second-growth forests with similar site characteristics. The average simulated basal area values appeared to be particularly realistic in this case. Long-term forest composition (over 600 yr) produced by the model compared favorably with earlier descriptions of old-growth forests of the region. This model has since been applied to the study of forested landscape dynamics. For example, Botkin (1977) has simulated the effects of carbon dioxide fertilization on the northern hardwood forest. Borman and Likens (1979a,b) used the model to study the biomass dynamics of landscapes in response to disturbance regimes. These investigations have provided insights into forest dynamics that would be difficult to obtain from field data.

The FORET model of Shugart and West (1977) is an adaptation of JABOWA that simulates southern Appalachian deciduous forest dynamics. The model was validated using two species sets for simulation: 1) the forest with American chestnut (Castanea dentata), and 2) the forest without chestnut. Three types of 1000 year simulations were performed: 1) succession with chestnut, 2) succession without chestnut, and 3) succession with the removal of chestnut after 500 years. The simulated forest composition and biomass were similar to those of actual forests with appropriate histories. The FORET model has since been applied to a variety of ecological problems. Forest responses to air pollution stress, for example, have been studied by McLaughlin et al. (1978), West et al. (1980) and Shugart and McLaughlin (1984). Also, the responses to carbon dioxide fertilization have been simulated (Shugart 1984). Patterns of forest landscape dynamics have been investigated in detail by Emanuel et al. (1978) and Shugart et al. (1981). Finally, the FORET model has been used with some success to reconstruct prehistoric climatic conditions and vegetation of eastern North America (Solomon et al. 1980, Solomon and Shugart 1984). In all of these studies the model has been a valuable tool in the assessment of forest dynamics. It has provided insight into ecosystem level responses resulting from interactions within the system. It has also shown that these ecosystem level responses may deviate from simple predictions based on the behavior of isolated components of the system.

CHAPTER IV

FIELD STUDY METHODS

Site Description

Field data were collected from a 60 ha area on the north and east slopes of Mt. Collins in the Great Smoky Mountains National Park (Fig. 3). Elevations of the sampling area range from 1750 to 1830 m. The forest is dominated by red spruce, Fraser fir and yellow birch. Mountain maple, mountain ash, fire cherry and serviceberry are of lesser importance in the area. Hobblebush (*Viburnum alnifolium*), bearberry (*Vaccinium erythrocarpum*), blackberry (*Rubus canadensis*) and elderberry (*Sambucus canadensis*) comprise the typically sparse shrub layer. Dense growth of shrubs is restricted to large canopy openings. The study site has only recently (1982) shown signs of disturbance from the balsam wooly aphid.

In general, the site is subject to short, cool and wet growing seasons, and cold winters. At 1920 m the length of the frost-free season is estimated at 152 days. Mean monthly temperatures range from -1.8°C in February to 13.6°C in July (Stephens 1969). Precipitation is high throughout the year on the crest of the Great Smoky Mountains. The highest average levels of precipitation occur in January (30.1 cm) and August (25.8 cm), while the lowest average level occurs in October (12.6 cm) (Stephens 1969). The average annual precipitation at this elevation is 230.9 cm (Shanks 1954b). Cloud moisture condensation also accounts for moisture input in these high elevation forests. Moderately high wind velocities occur in the spruce-fir zone.

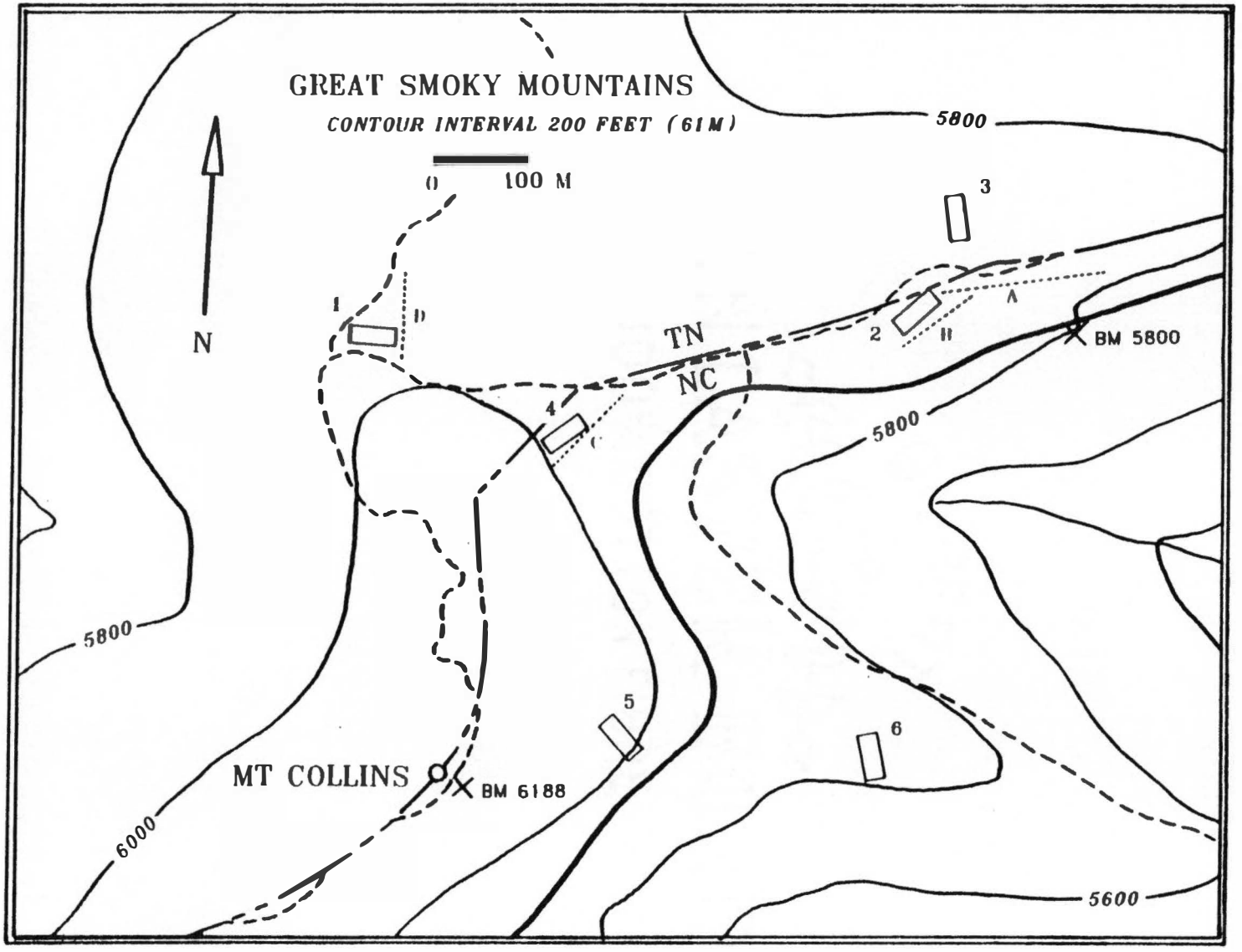


Fig. 3. Map of study area. Transects are labeled A-D, while 0.1 ha quadrats are labeled 1-6.

Soils of the Mt. Collins site have been described by Oosting and Billings (1951). In general, they are shallow podzols, 50 to 60 cm deep, with a thick organic horizon. The mineral horizons are sandy and relatively indistinct. Ecologically important characters include moderate drainage, low pH, low base saturation and high exchangeable aluminum (McCracken et al. 1962, Wolfe 1967).

Gap Phase Tree Replacement

An analysis of gap phase tree replacement involved the methods of Runkle (1981) and Barden (1983). Their studies focused on successor trees invading canopy gaps created by tree-fall. Information on fallen trees, successor trees and gap characters was collected. Runkle sampled all woody stems 1 m or more in height within each gap, while Barden chose one dominant successor tree to fill the gap. The study described herein was an intermediate approach. The 5 tallest trees in each gap were considered. Species, DBH, height, crown diameter, substrate and health were recorded for each invading tree. Successor trees were then ranked as dominant, codominant or subdominant according to their relative height. The tallest tree was ranked as dominant. If two or more trees were approximately equal in height they were ranked as codominant. Other trees were ranked as subdominant. Increment cores were taken from the 2 tallest invading trees to determine gap age, tree age, and growth rates before and after release. Species, DBH, stage of decay and type of fall were recorded for the gapmaking tree(s). Gap size was determined by measuring the short and long axes of the gap and then calculating the

area of an ellipse ($A = \pi LS/4$). Cover of shrub, herb and moss layers was estimated within each gap as well.

The results from 70 gaps selected in random walks through the study area were tallied as follows to determine species-by-species replacement probabilities. For each species of gapmaker (red spruce, Fraser fir, or yellow birch) the number of dominant and codominant successor trees of each species was tallied. Each codominant was given half the weight of a dominant successor tree in the calculation of replacement probabilities.

A differential equation model of tree replacement was constructed using these species-by-species replacement probabilities. The forest was treated as a mosaic of patches, each patch comprised of a single canopy tree. Replacement probabilities and average life spans of each species were used as the basis of the model which has some of the same ecological assumptions as Horn's (1975a,b; 1976) Markov matrix simulations of forest succession. The model was used to predict equilibrium composition of the forest from the observed patterns of gap phase tree replacement.

Given the life spans and replacement probabilities of the three canopy species, differential equations were formulated and solved for steady state relative densities as follows. Let y_s, y_f, and y_b be the fraction of canopy trees of spruce, fir and birch, respectively, such that $y_s + y_f + y_b = 1$. Let L_x be the average life span of species x in years. Assuming that the population of each species is all-aged, the average fraction of canopy trees of species x dying per year is

equal to y_x/L_x. The change in the fraction of spruce canopy trees over time can be determined by the following equation:

$$\frac{dy_s}{dt} = \frac{-y_s}{L_s} + p_{ss}\frac{y_s}{L_s} + p_{sf}\frac{y_f}{L_f} + p_{sb}\frac{y_b}{L_b}$$

where p_{ss} is the probability that spruce replaces spruce, p_{sf} is the probability that spruce replaces fir, and p_{sb} is the probability that spruce replaces birch. Similar equations were written for fir and birch. The three simultaneous equations were then solved for steady state ($dy/dt = 0$) values of y_s, y_f and y_b to estimate mature forest canopy composition.

Canopy Influence on Understory

Canopy influence data was collected following the methods of Woods (1979). Six 0.1 ha (20 X 50 m) quadrats were selected to avoid areas of recent disturbance (Fig. 3). Slope angle and aspect were recorded and each plot was permanently marked. DBH, average crown radius, distance to nearest canopy neighbor, and species and DBH of the nearest neighbor were recorded for all canopy trees (DBH greater than 12 cm). Species, DBH, height, average crown radius, substrate and health were recorded for saplings (greater than 2.5 cm DBH and less than 12 cm DBH). Species, height, average crown radius, substrate and health were recorded for seedlings 0.25 m or more in height. Distance and direction to all canopy trees within 5 m of each tree seedling and sapling as well as the DBH and species of each canopy tree were noted. These canopy influence measurements were made

for all understory individuals over 0.25 m tall except for fir and spruce. Because understory fir trees and spruce seedlings were abundant, the area of sampling was reduced as follows. In quadrats 2-6 fir seedlings within a 1 m wide strip along the long axis of the quadrat were considered. In quadrat 3 fir saplings within a 700 m^2 area were considered, while in quadrats 4-6 they were considered within a 500 m^2 area. Finally, in quadrats 5-6 spruce seedlings within a 500 m^2 area were included (see Appendix).

The analytical techniques of Woods and Whittaker (1981) were used to determine species-specific canopy-understory interactions. A useful index is the canopy influence measure for spruce and fir saplings or seedlings:

$$I = \sum^{s} \frac{dbh}{D} - \sum^{f} \frac{dbh}{D}$$

where s is the number of spruce trees within 5 m of the individual, f is the number of fir trees, dbh is the diameter of the canopy tree and D is the distance to the tree. A positive value of I shows a high spruce canopy influence, while a negative value shows a high fir canopy influence. This index was calculated for each sapling or seedling and the frequency distributions of pairs of understory species were compared using the Wilcoxon rank-sum test. Such comparisons were made for pairwise combinations of the three canopy species spruce, fir and birch.

The following null hypotheses were tested statistically as outlined above.

1) H_o: Spruce, fir and birch saplings are similarly distributed with respect to canopy species.

2) H_o: Spruce, fir and birch seedlings are similarly distributed with respect to canopy species.

The rejection of either null hypothesis indicates that one or more of the species tends to regenerate at higher levels under a certain canopy species or a set of canopy species.

Population Dispersion

The dispersion pattern of individual populations was analyzed using Morisita's index (Vandermeer 1981). The index formula is:

$$I = Q \frac{\sum_{i=1}^{Q} X_i(X_i-1)}{N(N-1)}$$

where Q is the number of quadrats sampled, X_i is the number of individuals in the ith quadrat, and N is the total number of individuals sampled. I is a ratio between the probability of drawing a random pair of individuals from the same quadrat, and the expected value for a randomly dispersed population. An I value greater than 1 indicates a clumped dispersion, a value equal to 1 indicates a random dispersion, and a value less than 1 indicates a uniform dispersion (Vandermeer 1981).

Morisita's index was calculated for populations of red spruce, Fraser fir, yellow birch and mountain maple. All individuals over 2.5 cm DBH were tallied within sixty 10 X 10 m quadrats (only 40 quadrats were included for maple). The dispersion patterns of red spruce,

Fraser fir and yellow birch seedlings (>2.5 m tall, $\leq$ 2.5 cm DBH) were also determined in this manner. Fifty quadrats were used in the seedling dispersion analysis.

Interactions between populations were analyzed using the methods of Pielou (1961). Segregation of species pairs was tested by a nearest neighbor analysis whereby observed and expected nearest neighbor frequencies were compared using the chi-square test with Yate's correction. The pairwise comparisons were made for canopy trees (>12 cm DBH) of red spruce, Fraser fir and yellow birch. A significant chi-square value indicates an interaction between canopy trees of the species pair. Further study of interaction involved correlations between distances to nearest neighbor and tree sizes. A set of sum of trunk circumferences of each base tree and its nearest neighbor was created for each species pair and then correlated with the corresponding set of distances to nearest neighbor. A significant positive correlation indicates that large trees are spatially segregated from small trees. Segregation of this nature may result from inter-tree competition (Pielou 1960, 1961).

Population Structure

Size structure of the red spruce, Fraser fir, yellow birch, mountain maple and mountain ash populations was determined using all individuals over 2.5 cm DBH sampled from six 0.1 ha quadrats. Individuals were grouped into size classes and the numbers per class were used to calculate the percent frequency of each class.

Age structure of the spruce, fir and birch populations was determined using 0.3 m wide strip transects (Fig. 3). Age was determined by counting bud scale scars whenever possible. Other individuals were clipped at the base or cored near the base and their age was determined by counting annual growth rings. The age of cored trees was adjusted using average height to age ratios to estimate age at bore height. In order to increase the sample size of older trees, wider 0.9 m transects were superimposed upon the 0.3 m transects. All trees over 100 yr old were included in the 0.9 m wide transects. Age structure estimates were then made by multiplying the number of individuals in each of the older age classes (>100 yr) by 1/3 to correct for the greater sampling area. Substrate, overlying canopy tree species, tree height, DBH, and age were recorded for each individual surviving through the previous winter. Relationships among these variables were then determined for each species.

Survivorship estimates for each of the dominant species were obtained by using the number of individuals per age class as survivorship information. Assuming stable age distributions for each of the populations, approximate survivorship curves and life tables were generated (Deevey 1947, Hibbs 1979). A power function employed by Hett (1971), Hett and Loucks (1971, 1976), Leak (1975) and Hibbs (1979) for tree populations was used to generate survivorship curves for red spruce and Fraser fir:

$$y = y_o x^{-b'}$$

where y is the number of plants surviving to age x, y_o is the initial

population size and b' is a mortality rate that decreases with age. A straight line was obtained by the following transformation:

$$\ln y = \ln y_o - b' \ln x$$

A linear regression of ln y on ln x was performed on trees grouped in 5 year age classes to obtain b', the slope.

Two sets of life tables were generated. The first set was based on actual age class data for individuals up to 75 years of age. Survivorship was estimated by grouping individuals into 15 year age classes and adjusting the data to fit a standard initial cohort of 1000 individuals. Life table values were then calculated as outlined by Cox (1976). The second set of life tables was based on survivorship curves fitted to the age class data. From these curves, survivorship was determined at 20 year intervals for the entire life span of each species, and life tables were generated for an initial cohort of 1000 individuals.

CHAPTER V

FIELD STUDY RESULTS

Site Vegetation

Table 8 lists density and basal area values for tree species in six 0.1 ha quadrats. Average values generally agree with those of Oosting and Billings (1951) for old-growth spruce-fir forests of the Great Smoky Mountains. Notable differences include a lower average Fraser fir basal area and a higher average yellow birch density for the six quadrats sampled. Quadrats 5 and 6, on south facing slopes, had less fir and more birch than quadrats on other slopes. Also, mountain ash was more abundant in the south facing quadrats. Fire cherry and serviceberry were infrequent on the site. Total tree density ranged from 1450 to 2240 stems/ha with an average of 1779 stems/ha. Total basal area ranged from 42.0 to 59.6 m^2/ha with an average of 49.0 m^2/ha.

A profile of the forest canopy at quadrat 3 is shown in Fig. 4. The canopy is comprised of red spruce, Fraser fir and yellow birch. Subcanopy species include mountain ash, mountain maple and fire cherry. In the old-growth stands studied, these subcanopy species were typically restricted to canopy gaps.

Gap Phase Tree Replacement

The age of canopy gaps studied ranged from 4 to 77 years and gaps were most frequent in the 30 to 40 year class (Fig. 5). Canopy gap areas were less than 160 m^2 (Fig. 6) and gaps 40 to 80 m^2 were most

Table 8. Basal area and density of trees in six 0.1 ha quadrats.[a]

Species	Quadrat 1[b] (NE)		Quadrat 2 (--)		Quadrat 3 (N)		Quadrat 4 (NE)		Quadrat 5 (SE)		Quadrat 6 (S)		Mean Values	
	BA	D	BA	D	BA	D	BA	D	BA	D	BA	D	BA	D
Picea rubens	3.07	65	4.18	40	2.66	32	2.07	25	2.95	46	2.94	39	2.98	41.2
Abies fraseri	1.78	137	1.50	156	1.27	80	1.23	96	0.88	70	0.70	78	1.23	102.8
Betula lutea	0.77	21	0.25	12	0.60	13	1.10	13	0.70	42	0.39	20	0.51	20.2
Acer spicatum	0.00	1	0.03	8	0.09	21	0.04	11	0.02	9	0.04	10	0.04	10.0
Sorbus americana	0	0	0.00	1	0.00	2	0.00	0	0.02	5	0.05	10	0.01	3.0
Prunus pensylvanica	0	0	0	0	0	0	0	0	0	0	0.09	3	0.01	0.5
Amelanchier arborea	0	0	0	0	0	0	0	0	0.00	1	0	0	0.00	0.2
Total	5.62	224	5.96	217	4.62	148	4.45	145	4.57	173	4.20	160	4.90	177.9

[a] Basal area is in m^2/0.1 ha. Density is in trees/0.1 ha.

[b] Slope aspect is given in parentheses.

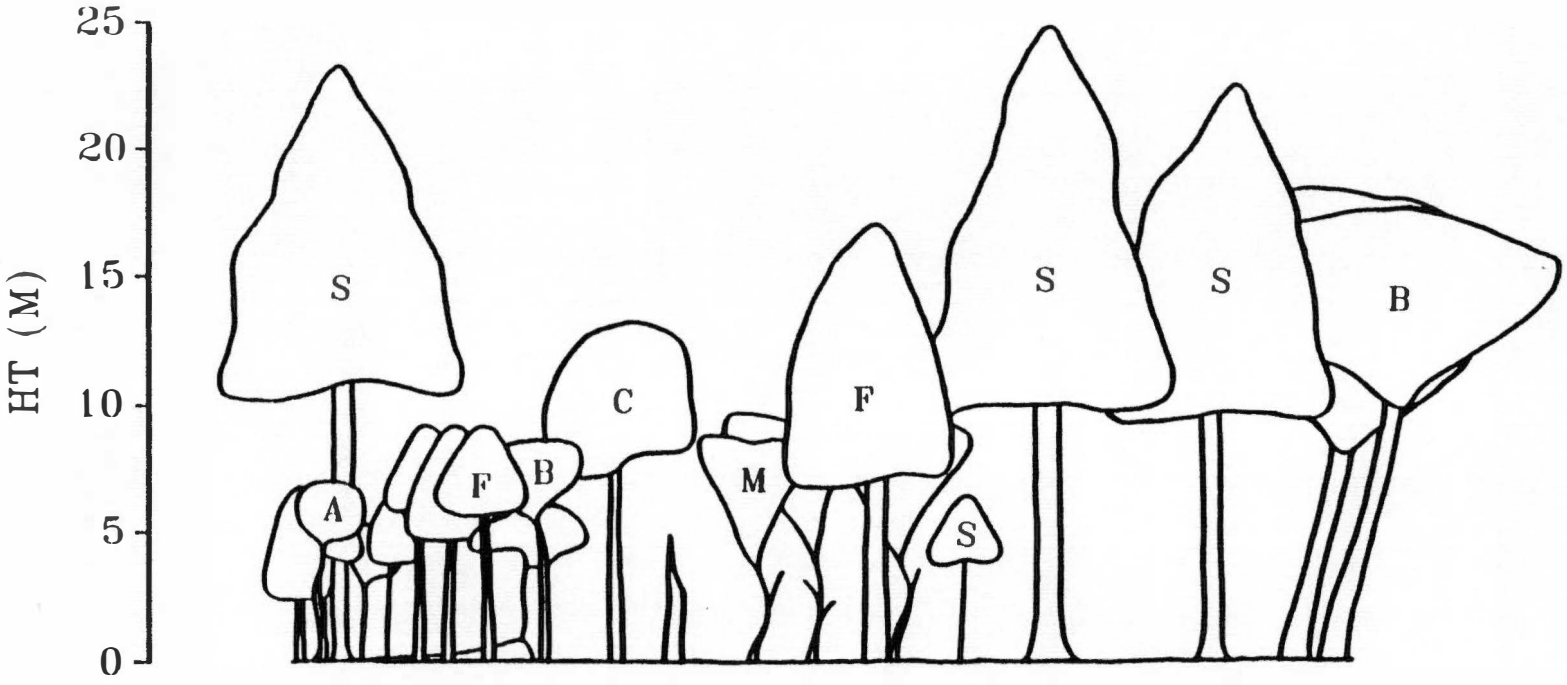


Fig. 4. Tree stratum diagram of an old-growth spruce-fir forest. The diagram is based on a 40 X 5 m transect. All trees under 5 m tall are omitted. S = red spruce, F = Fraser fir, B = yellow birch, M = mountain maple, A = mountain ash and C = fire cherry.

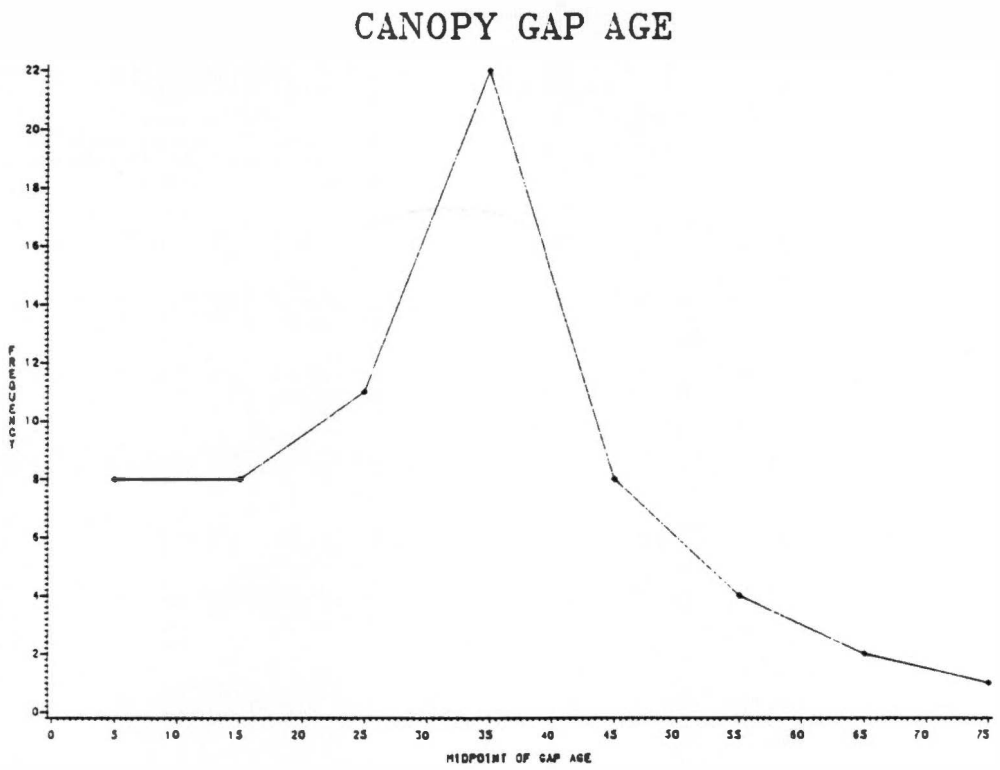


Fig. 5. Graph of canopy gap age distribution.

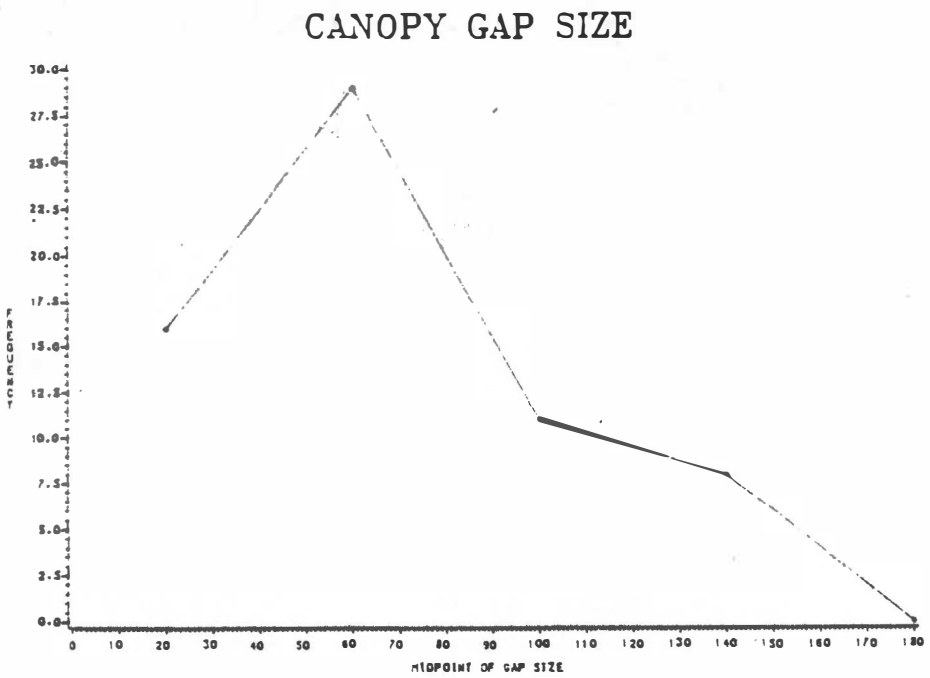


Fig. 6. Graph of canopy gap size distribution. Size is in m^2.

frequent. The area measurements are likely to be underestimates of original gap size because of subsequent lateral extension from surrounding trees. Gap size appeared to affect the species of tree invading the gap (Fig. 7). Red spruce successor trees were most frequent in small gaps (<40 m^2), while Fraser fir was most frequent in slightly larger gaps (40-80 m^2). Yellow birch captured relatively few gaps; the majority of them were less than 80 m^2.

Species-by-species replacement trends are summarized in Table 9. Fraser fir captured 58% of the 70 gaps sampled. It was the most frequent successor tree in gaps regardless of gapmaker species. Red spruce captured 17% of the gaps and it tended to replace fir or birch rather than itself. Yellow birch captured 15% of the gaps and it did not appear to be strongly self-replacing. Of the gaps sampled, less than 10% were captured by a subdominant species such as mountain ash, mountain maple and fire cherry. The canopy residence time of subdominants is brief because of their short life spans and the likelihood of overtopping by the shade tolerant coniferous species.

Species-by-species replacement probabilities generated from the gap capture data are listed in Table 10. In order of decreasing replacement probability, the successors of spruce are fir, birch and spruce. Of these, fir is by far the most likely to replace spruce. For fir the successors in order of decreasing probability are fir, spruce and birch. Again, the probability of replacement by fir is much higher than that of spruce or birch. For birch self-replacement is unlikely, while spruce and fir have almost equal replacement probabilities.

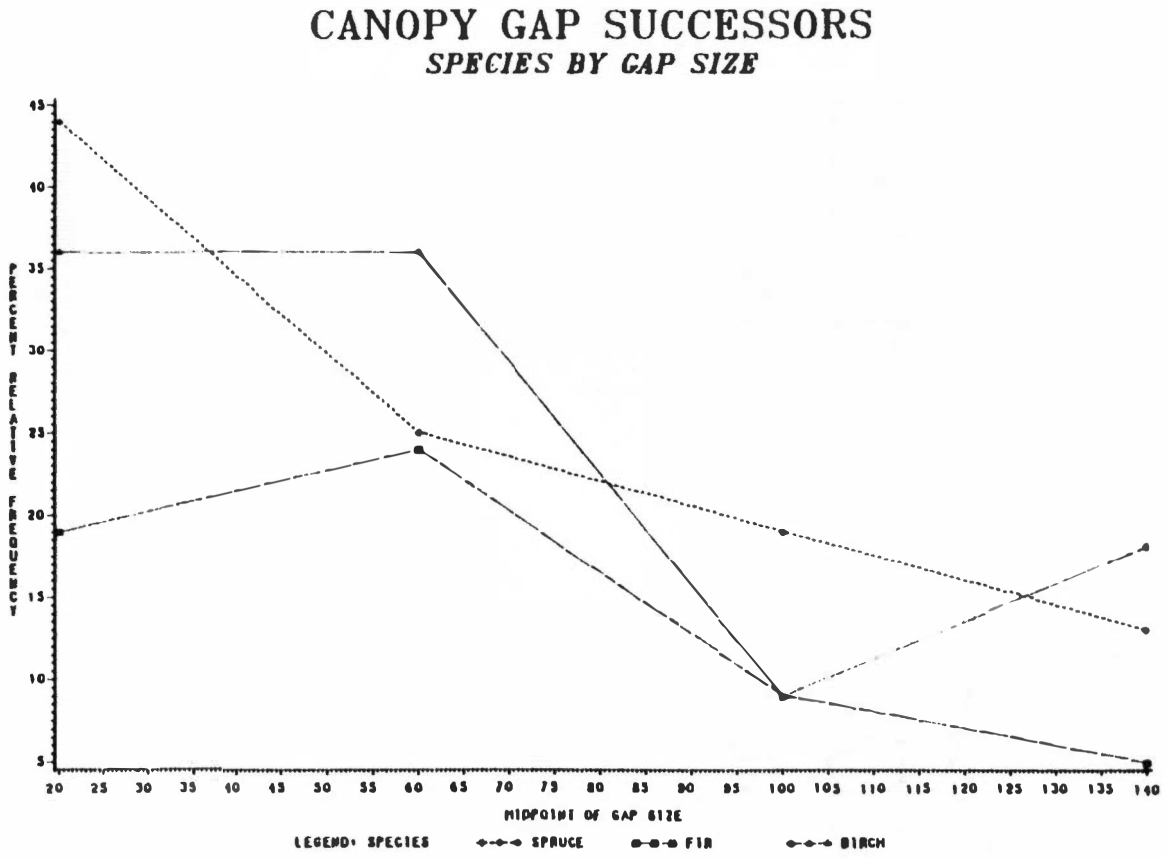


Fig. 7. Graph of gap successor species by gap size. Size is in m^2.

Table 9. Tree replacement in canopy gaps.[a]

Successor	Gapmaker			Totals
	Picea rubens	*Abies fraseri*	*Betula lutea*	
Picea rubens	2.0	5.2	4.5	11.7
Abies fraseri	19.8	16.0	5.0	40.8
Betula lutea	3.7	6.0	1.0	10.7
Sorbus americana	1.0	0.8	0.5	2.3
Acer spicatum	1.5	0	0	1.5
Prunus pensylvanica	1.0	2.0	0	3.0
Totals	29.0	30.0	11.0	70.0

[a]Values indicate number of gaps captured by a successor species.

Table 10. Matrix of species-by-species replacement probabilities.

Successor	Gapmaker		
	Picea rubens	*Abies fraseri*	*Betula lutea*
Picea rubens	0.0785	0.1900	0.4286
Abies fraseri	0.7779	0.5890	0.4762
Betula lutea	0.1436	0.2209	0.0952

Output from a differential equation model of canopy turnover based on these species-by-species replacement probabilities and the average canopy residence times for each species, determined by White et al. (1985a), is presented in Table 11. The predicted equilibrium canopy composition closely resembled that of the mature forest on Mt. Collins. These results strongly support the importance of gap phase tree replacement in overall stand dynamics.

Canopy Influence on Understory

The distributions of spruce minus fir index values for spruce, fir and birch seedlings are shown in Fig. 8. Values were most frequent near zero, indicating spatial segregation of seedlings from large spruce and fir canopy trees. No significant differences among the distributions of these seedling species were revealed by rank-sum tests (Table 12). The spruce minus fir index value distributions for spruce, fir and birch saplings are shown in Fig. 9. Positive values were notably frequent indicating a high level of spruce canopy influence. The distribution of index values for fir saplings is compared to those of spruce saplings and birch saplings in Figs. 10 and 11. In both cases, positive values were more frequent for fir. A significant difference between distributions of fir and birch saplings, and a highly significant difference between distributions of fir and spruce saplings were revealed by rank sum tests (Table 12). It is clear that fir saplings have a relatively strong tendency to occur near large spruce trees rather than large fir trees.

Table 11. A comparison of actual and predicted canopy composition.

Species	Average Canopy Residence (yr)[a]	Percent of Canopy	
		Actual[b]	Predicted
Picea rubens	225	34	30
Abies fraseri	137	54	53
Betula lutea	154	11	18

[a]From White et al. (1985a).

[b]Based on four 0.1 ha quadrats on NE facing slopes. All trees over 12 cm DBH were considered.

CANOPY INFLUENCE INDEX

SEEDLINGS

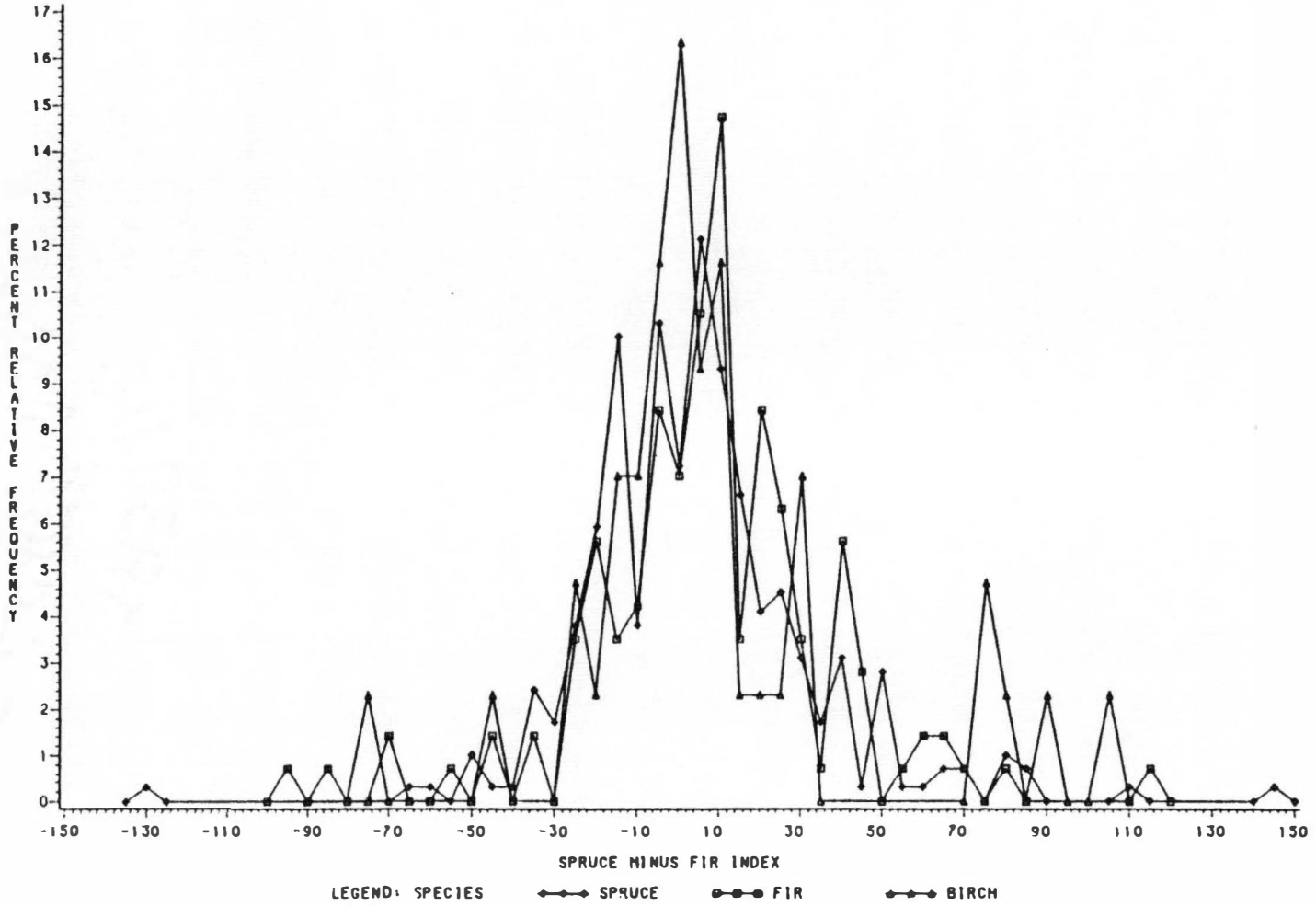


Fig. 8. Distribution of spruce, fir and birch seedlings in relation to spruce and fir canopy trees as quantified by the spruce minus fir index. No significant differences among distributions were revealed by rank-sum tests.

Table 12. Wilcoxon rank-sum results for the spruce minus fir index.

Understory Species Pair	n	Mean Score	z	Prob. >/z/	Significance
Picea-	108	163.9	-3.8110	0.0001	**
Abies (saplings)	291	213.4			
Picea-	108	92.9	0.7338	0.4631	n.s.
Betula (saplings)	82	98.9			
Abies-	291	193.1	-2.0414	0.0412	*
Betula (saplings)	82	165.5			
Picea-	290	209.2	1.8540	0.0637	n.s.
Abies (seedlings)	143	232.9			
Picea-	290	166.7	0.1324	0.8947	n.s.
Betula (seedlings)	43	168.8			
Abies-	143	95.7	-1.0241	0.3058	n.s.
Betula (seedlings)	43	86.1			

**Significant at .01.

*Significant at .05.

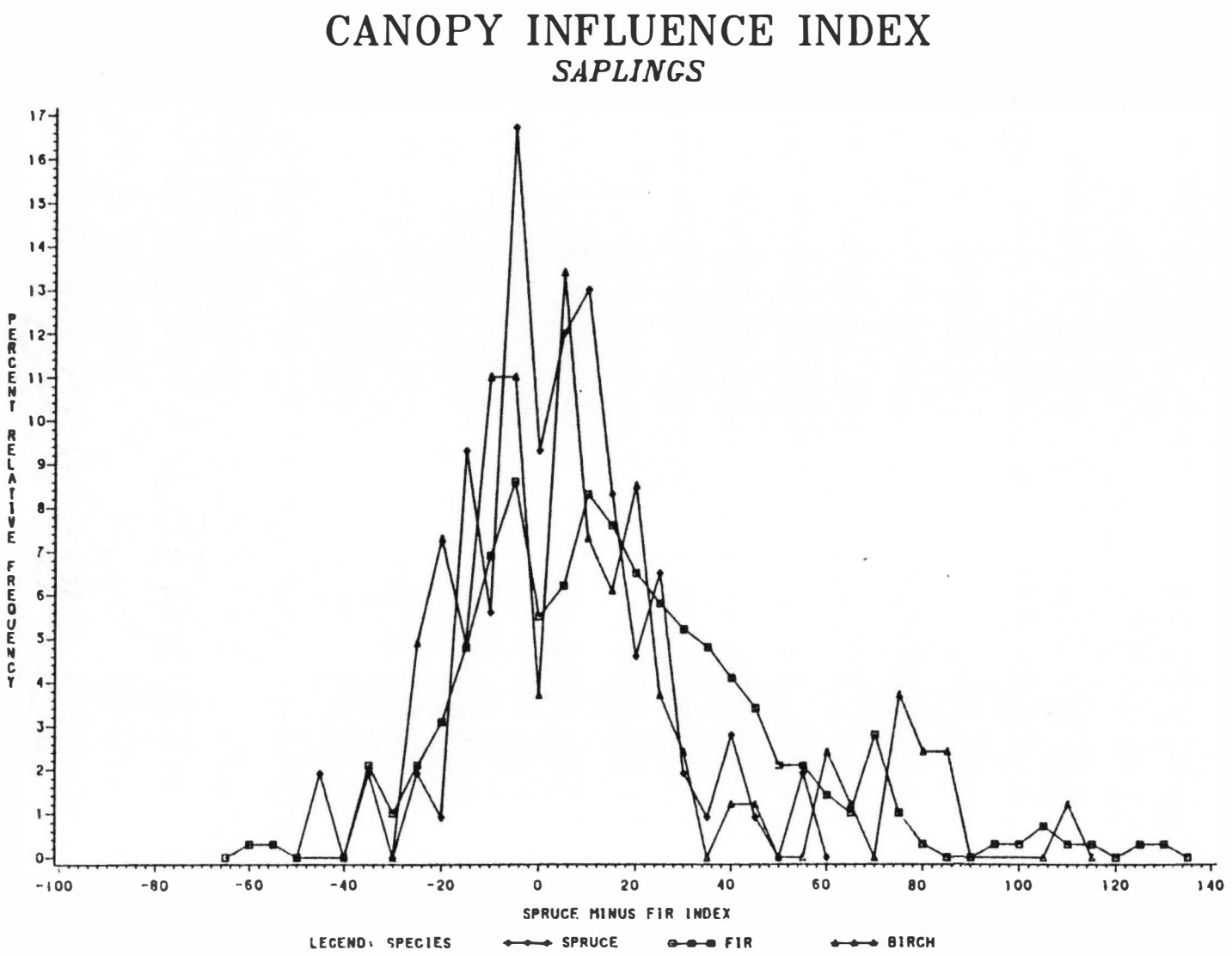


Fig. 9. Distribution of spruce, fir and birch saplings in relation to spruce and fir canopy trees as quantified by the spruce minus fir index.

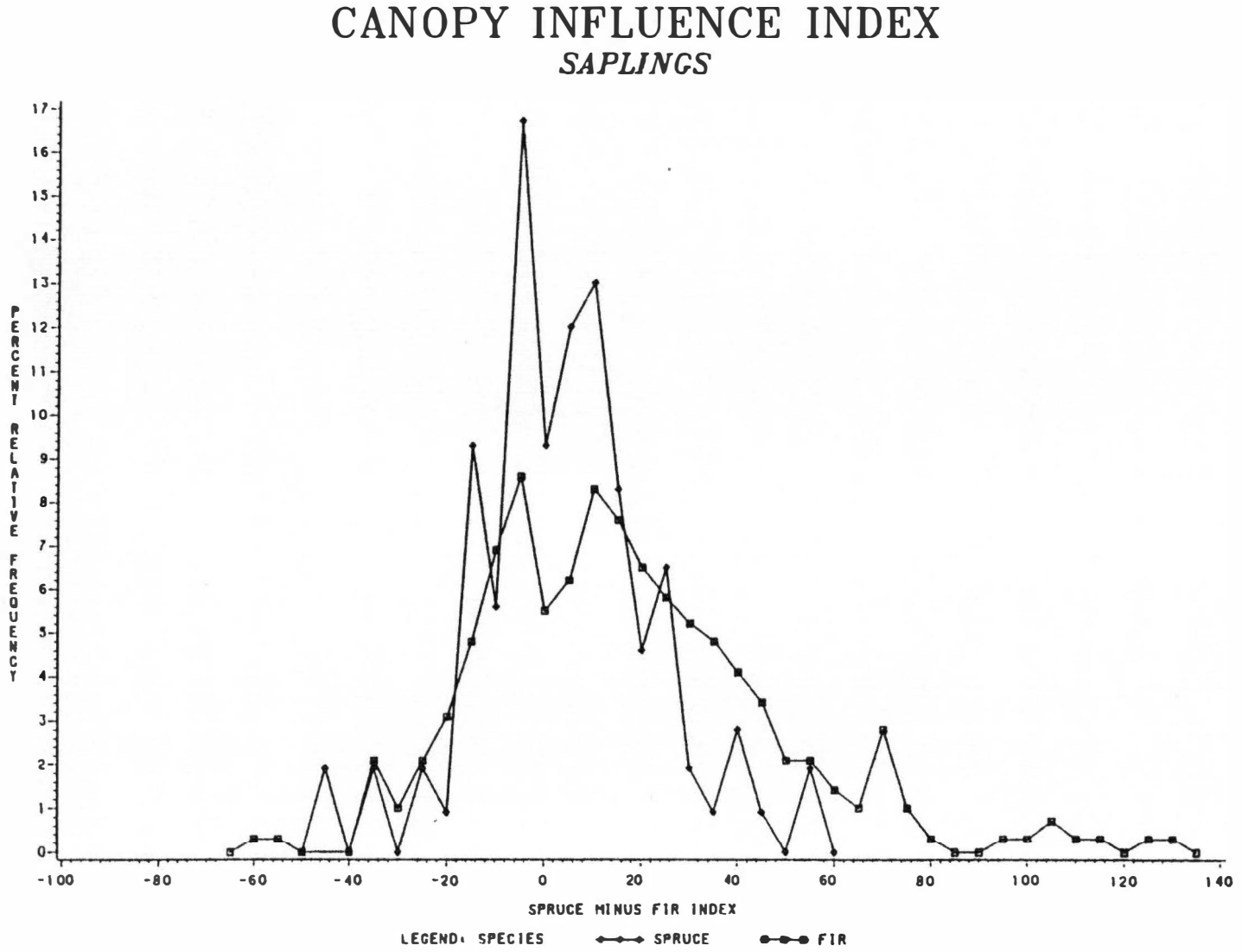


Fig. 10. Distribution of spruce and fir saplings in relation to spruce and fir canopy trees as quantified by the spruce minus fir index. A highly significant difference between distributions was revealed by the rank-sum test ($p<0.01$).

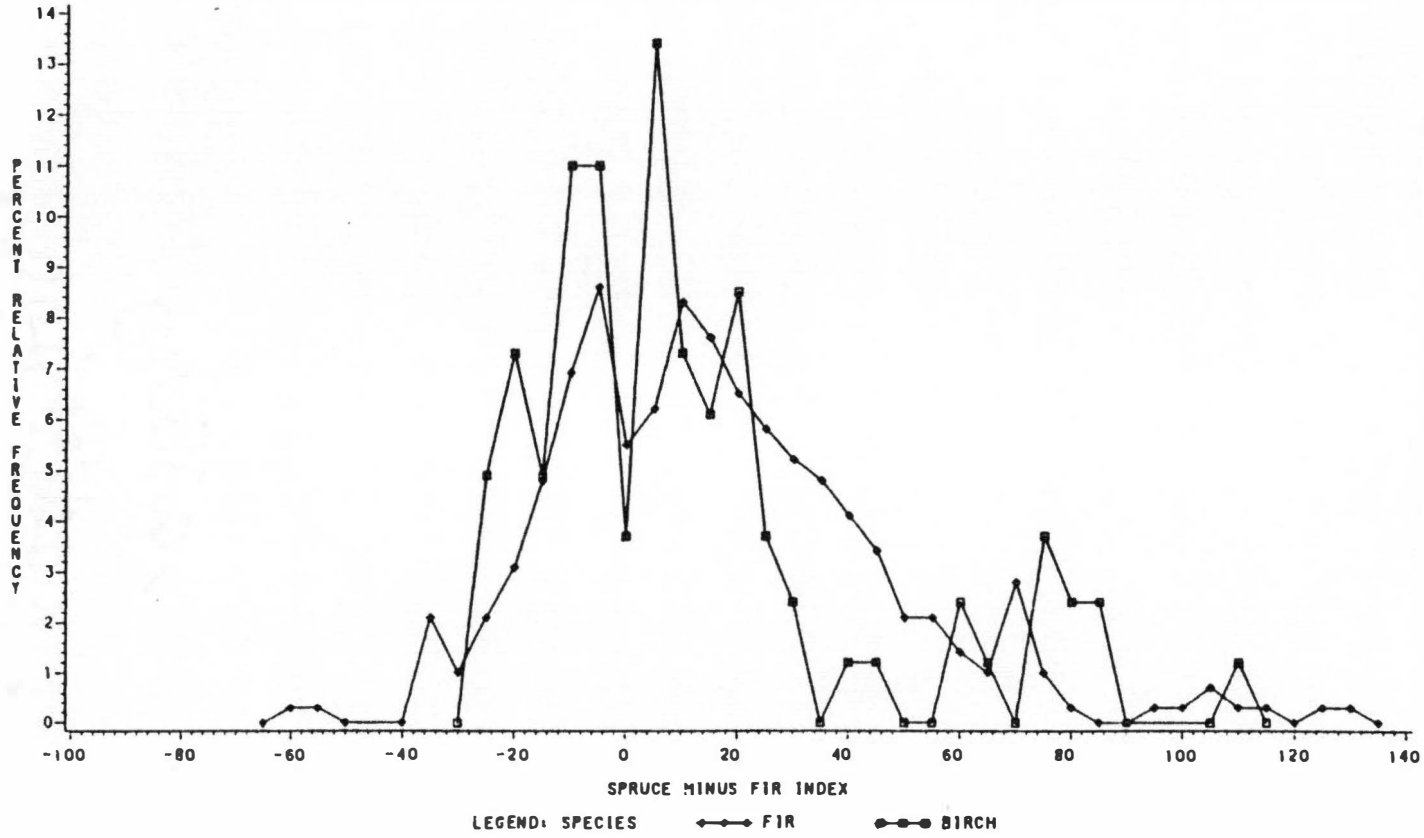


Fig. 11. Distribution of fir and birch saplings in relation to spruce and fir canopy trees as quantified by the spruce minus fir index. A significant difference between distributions was revealed by the rank-sum test ($p<0.05$).

The distributions of spruce minus birch index values for spruce, fir and birch seedlings are shown in Fig. 12. As noted above, values were most frequent near zero, indicating segregation of seedlings and canopy trees. No significant differences among these distributions were revealed by rank-sum tests (Table 13). The index distributions for saplings are shown in Fig. 13. Positive values are more frequent than negative values indicating spruce canopy influence. The distribution of fir sapling values is compared to those of spruce saplings and birch saplings in Figs. 14 and 15. In both comparisons, fir had higher frequencies for positive values. A significant difference between distributions of fir and birch saplings, and a highly significant difference between distributions of fir and spruce saplings were revealed by rank-sum tests (Table 13). In conclusion, fir saplings have a relatively strong tendency of proximity to large spruce trees as opposed to large birch trees.

The distributions of fir minus birch index values for spruce, fir and birch seedlings are shown in Fig. 16. High frequencies of slightly positive values indicate fir canopy influence. No significant differences among these distributions were revealed by rank-sum tests (Table 14). The index distributions for saplings are shown in Fig. 17. Again, slightly positive values were frequent and indicative of fir canopy influence. No significant differences among sapling distributions were revealed by rank-sum tests (Table 14).

Distributions of total canopy influence values for spruce, fir and birch saplings are shown in Fig. 18. The index is the total of all canopy species. Spruce and birch saplings are most frequent at

CANOPY INFLUENCE INDEX

SEEDLINGS

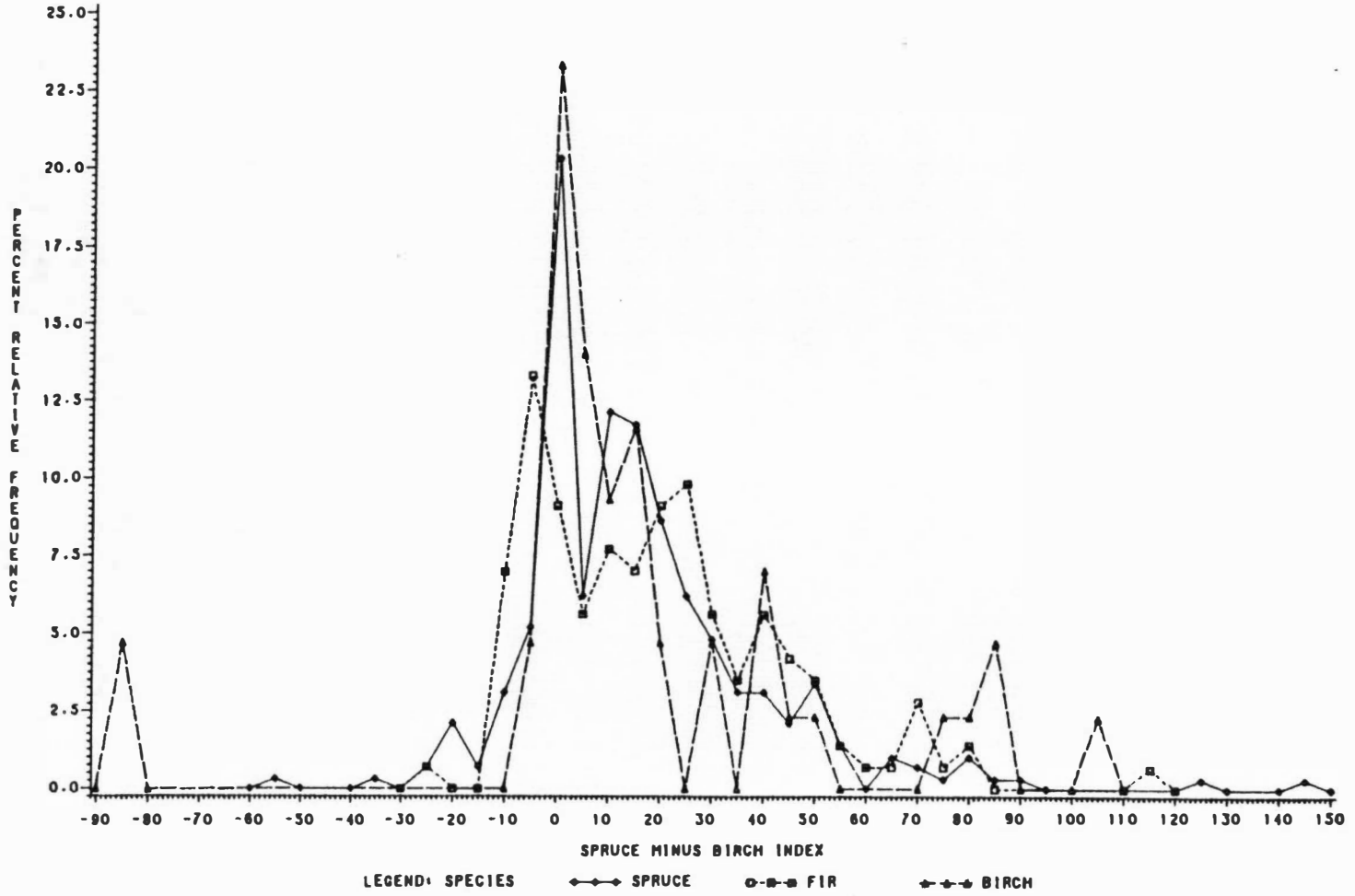


Fig. 12. Distribution of spruce, fir and birch seedlings in relation to spruce and birch canopy trees as quantified by the spruce minus birch index. No significant differences among distributions were revealed by rank-sum tests.

Table 13. Wilcoxon rank-sum results for the spruce minus birch index.

Understory Species Pair	n	Mean Score	z	Prob. >/z/	Significance
Picea-	108	160.7	-4.1445	<0.0001	**
Abies (saplings)	291	214.6			
Picea-	108	93.0	0.7178	0.4729	n.s.
Betula (saplings)	82	98.8			
Abies-	291	194.8	-2.4885	0.0128	*
Betula (saplings)	82	194.4			
Picea-	143	211.2	1.3665	0.1718	n.s.
Abies (seedlings)	290	228.7			
Picea-	290	167.0	-0.0102	0.9919	n.s.
Betula (seedlings)	43	166.9			
Abies-	143	94.1	-0.4781	0.6326	n.s.
Betula (seedlings)	43	94.5			

**Significant at .01.

*Significant at .05.

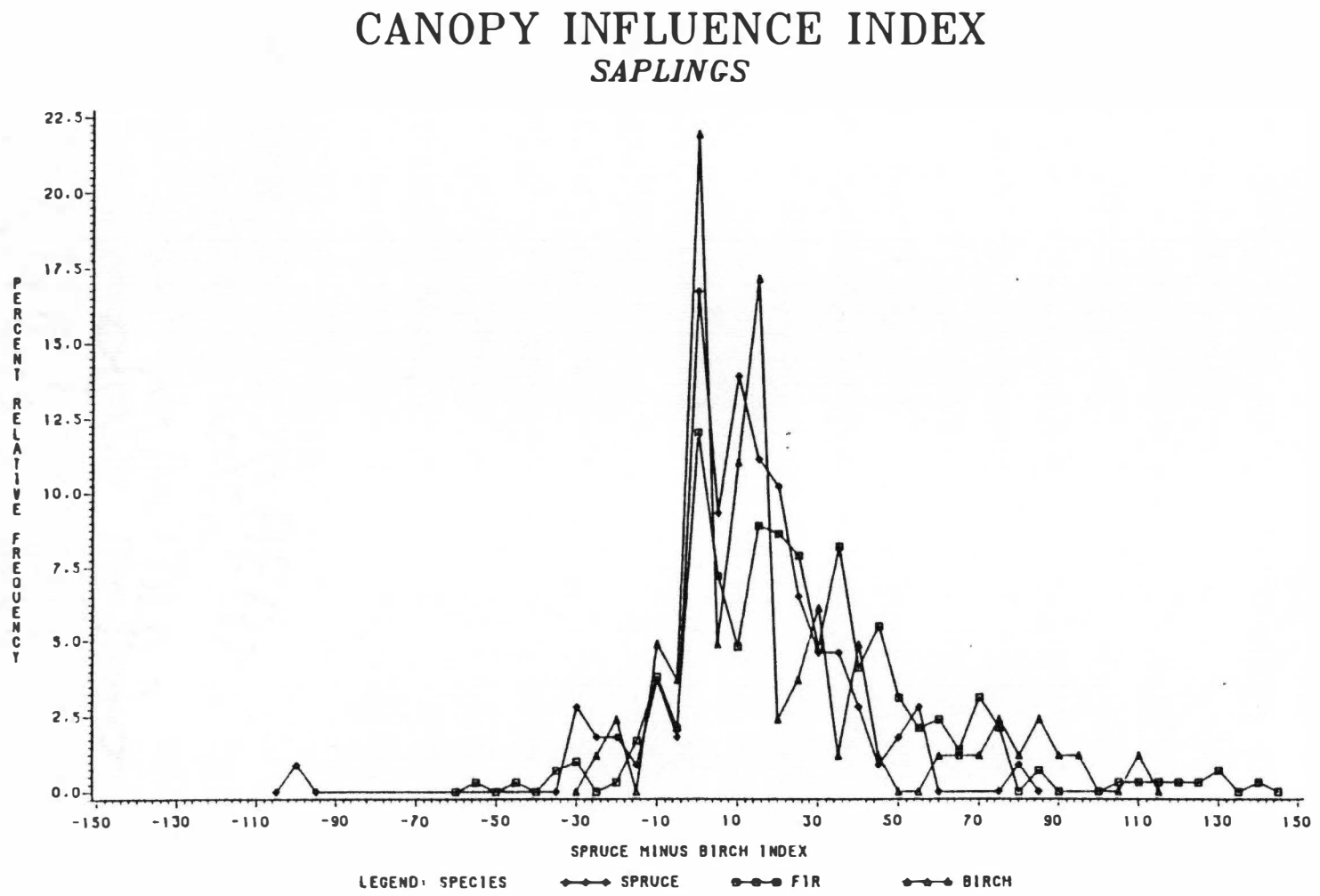


Fig. 13. Distribution of spruce, fir and birch saplings in relation to spruce and birch canopy trees as quantified by the spruce minus birch index.

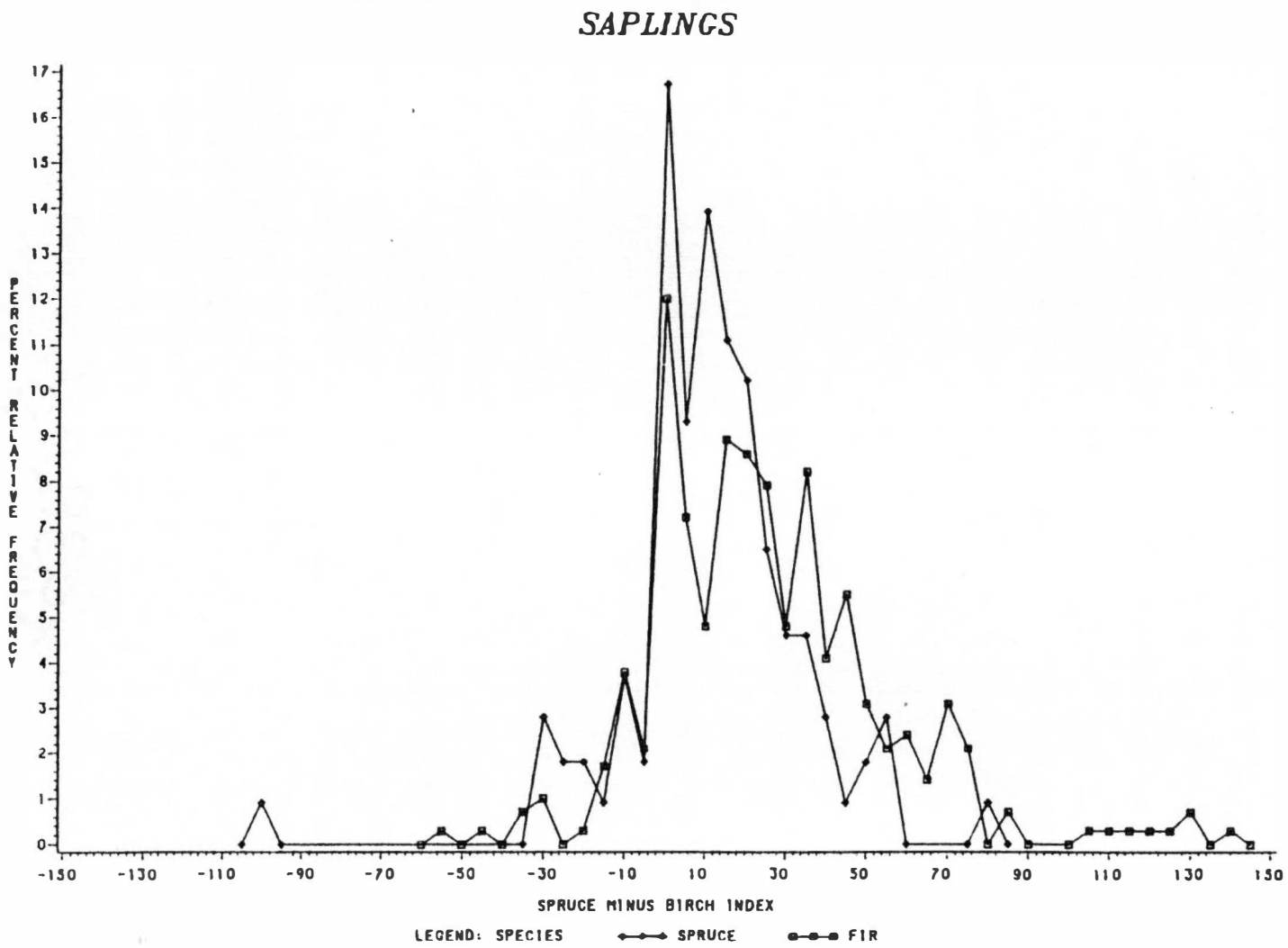


Fig. 14. Distribution of spruce and fir saplings in relation to spruce and birch canopy trees as quantified by the spruce minus birch index. A highly significant difference between distributions was revealed by the rank-sum test ($p<0.01$).

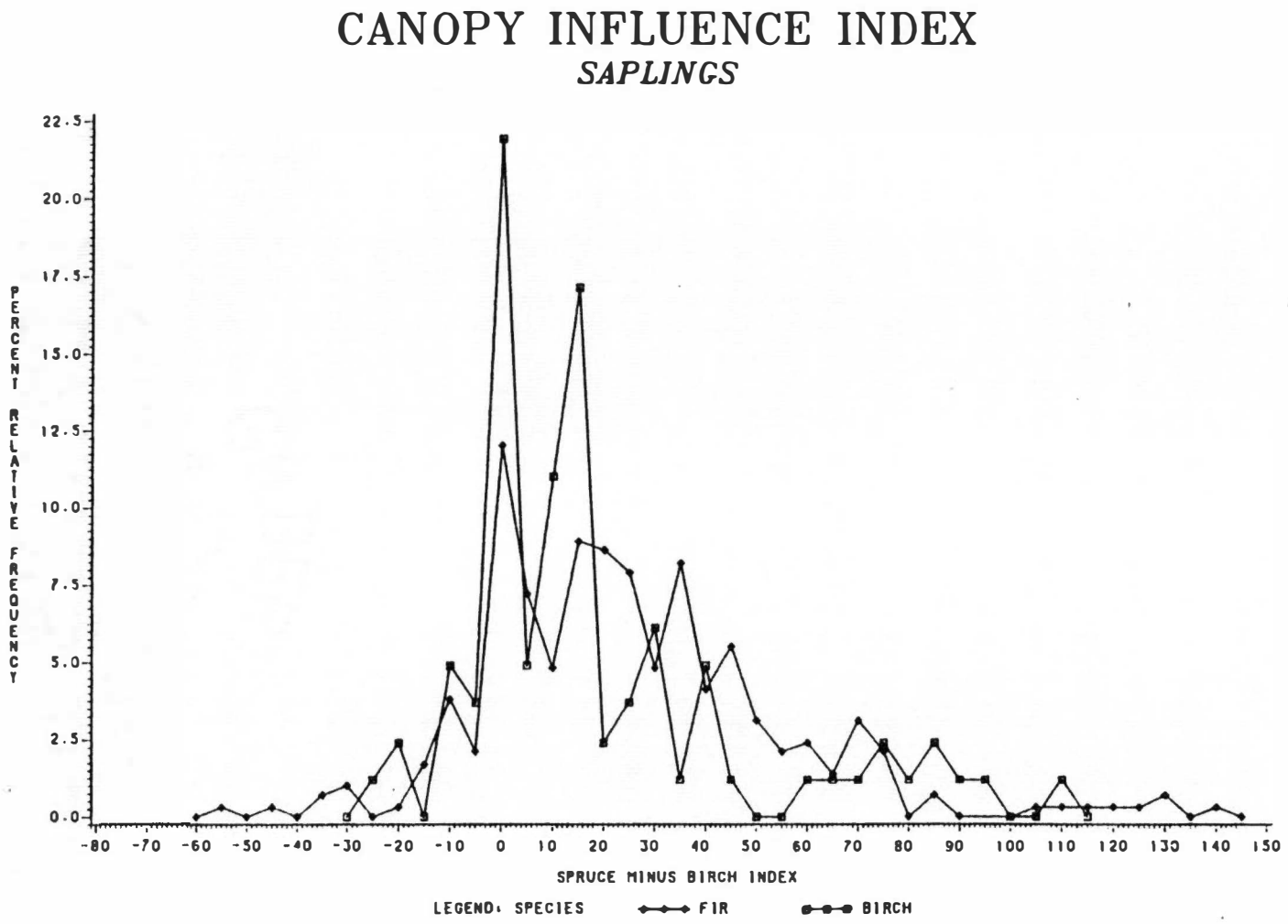


Fig. 15. Distribution of fir and birch saplings in relation to spruce and birch canopy trees as quantified by the spruce minus birch index. A significant difference between distributions was revealed by the rank sum test ($p<0.05$).

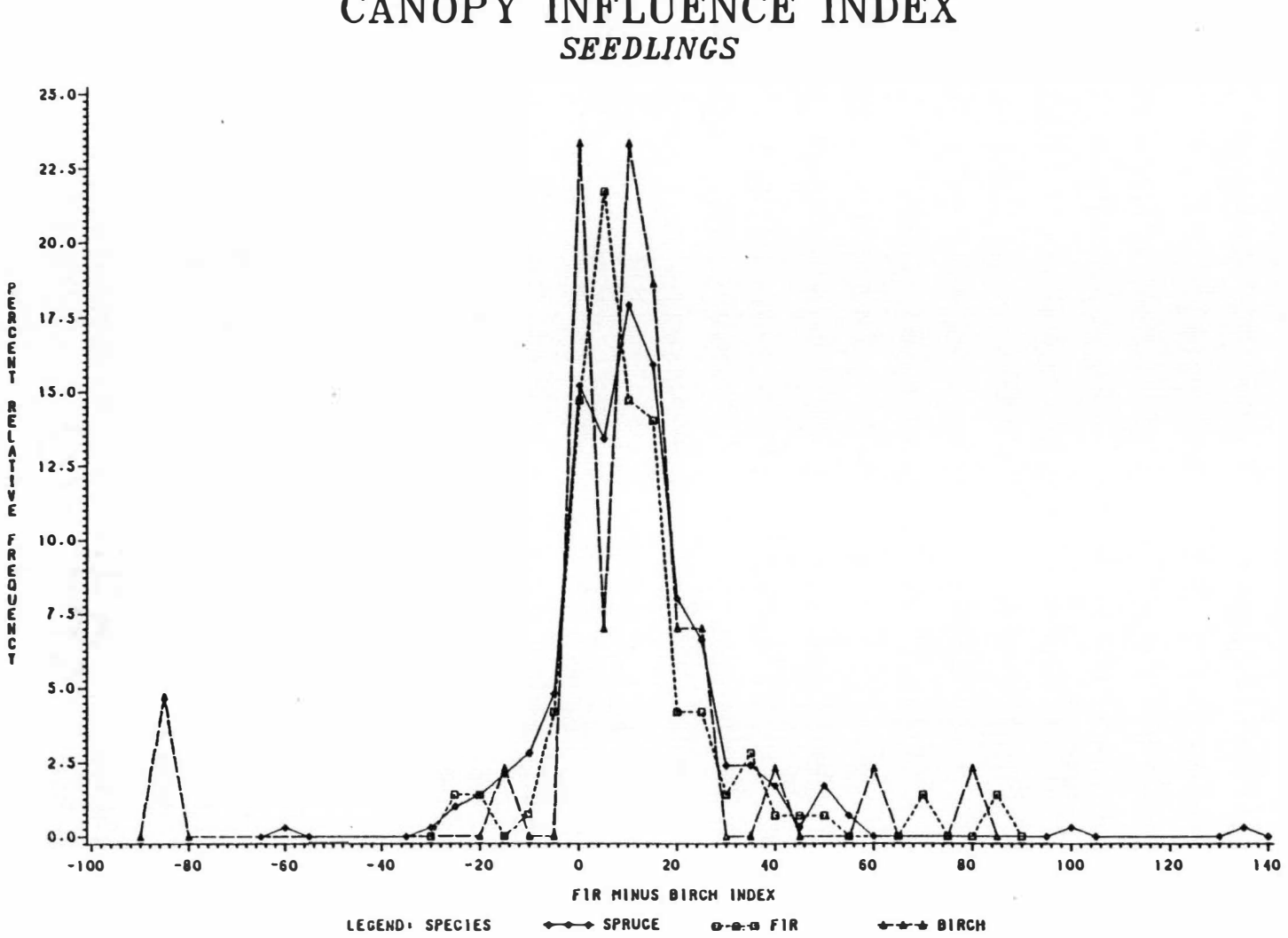


Fig. 16. Distribution of spruce, fir and birch seedlings in relation to fir and birch canopy trees as quantified by the fir minus birch index. No significant differences among distributions were revealed by rank-sum tests.

Table 14. Wilcoxon rank-sum results for the fir minus birch index.

Understory Species Pair	n	Mean Score	z	Prob. >/z/	Significance
Picea-	108	206.4	0.6727	0.5012	n.s.
Abies (saplings)	291	197.6			
Picea-	108	99.2	-1.0561	0.2909	n.s.
Betula (saplings)	82	90.7			
Abies-	291	188.0	-0.3293	0.7419	n.s.
Betula (saplings)	82	183.5			
Picea-	290	214.8	0.5181	0.6044	n.s.
Abies (seedlings)	143	221.4			
Picea-	290	167.1	-0.0450	0.9641	n.s.
Betula (seedlings)	43	166.4			
Abies-	143	94.4	-0.4167	0.6769	n.s.
Betula (seedlings)	43	90.5			

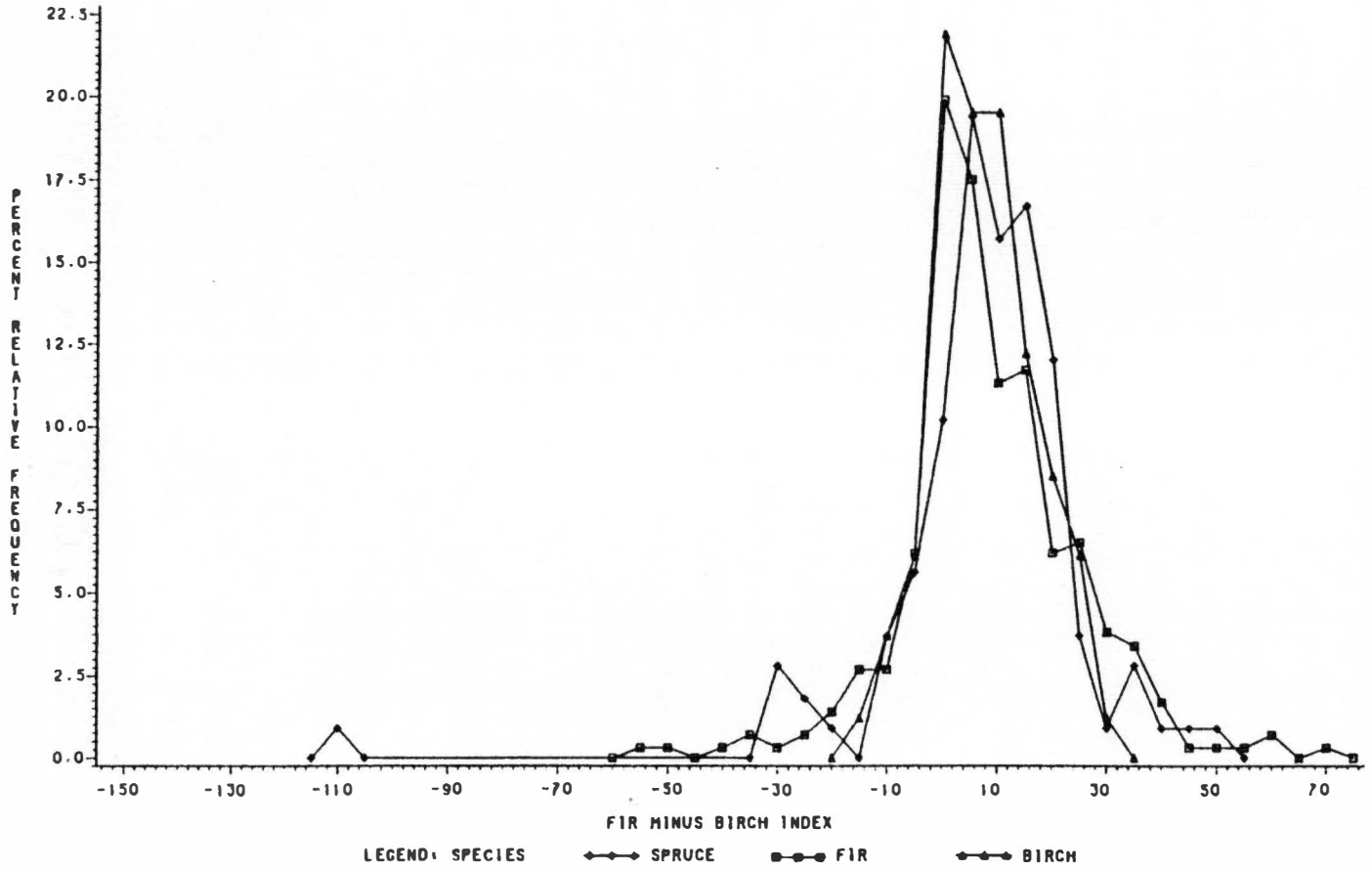


Fig. 17. Distribution of spruce, fir and birch saplings in relation to fir and birch canopy trees as quantified by the fir minus birch index. No significant differences among distributions were revealed by rank-sum tests.

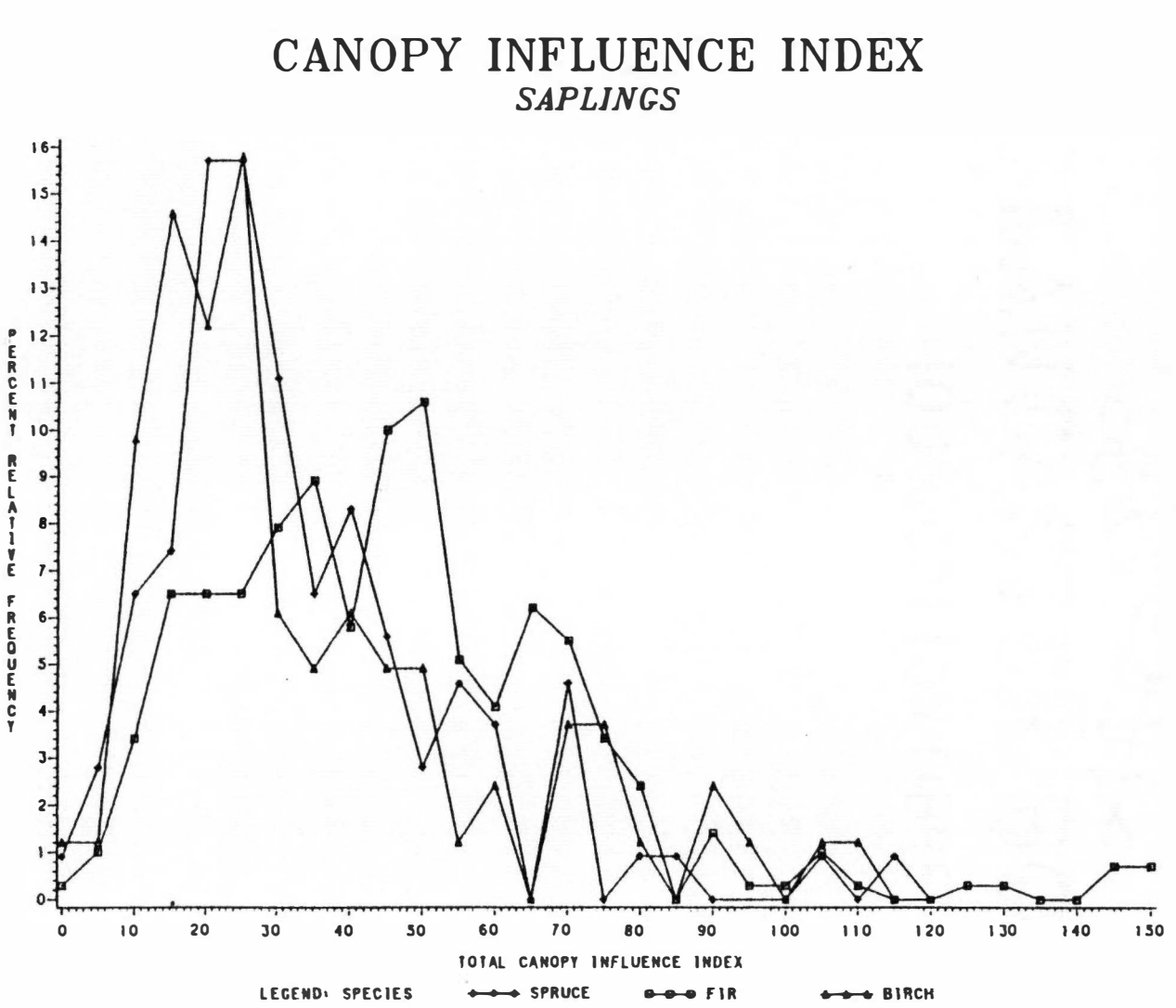


Fig. 18. Distribution of spruce, fir and birch saplings in relation to canopy trees as quantified by the total canopy influence index.

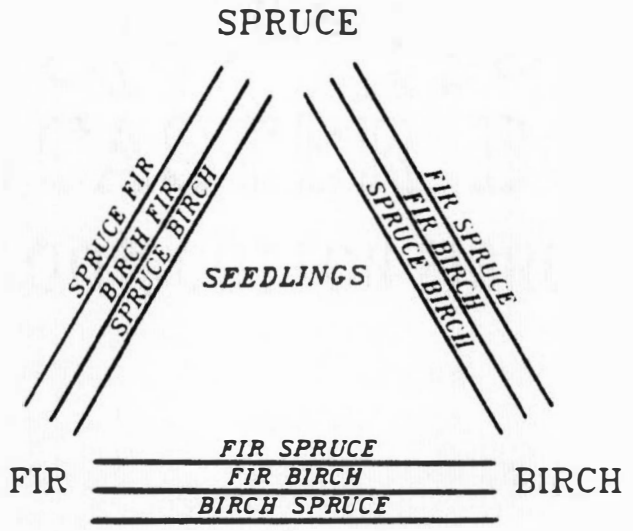
low values, ranging from 10 to 30, while fir saplings are most frequent at higher values, near 50. It can be concluded that fir saplings have a relatively strong tendency to grow near large trees.

The canopy influence index results are summarized in Fig. 19. There were no strong differences among the dispersion of seedling species in relation to spruce, fir and birch canopy trees. However, differences among sapling species were evident. Fir showed a strong affinity for spruce canopy trees in comparison with spruce and birch saplings.

Regeneration Substrates

Substrate suitability information for young seedlings of the forest dominants is presented in Table 15. Red spruce occurred predominantly on fallen logs and moss covered surfaces, while Fraser fir occurred predominantly on the forest floor litter and fallen logs. Yellow birch seedlings occurred almost exclusively on fallen logs. Further observations revealed that seedling density of these species is highest on moss covered logs. Such logs are excellent regeneration substrates because of their high resource availability (Harmon 1984).

Substrates of older individuals are tallied in Table 16. All species occurred predominantly on the forest floor. Yellow birch commonly grew on fallen logs and live roots as well. Sampling within canopy gaps revealed that even higher proportions of these populations occurred on the forest floor in canopy openings (Table 17). Relatively high resource availability in gaps may promote germination



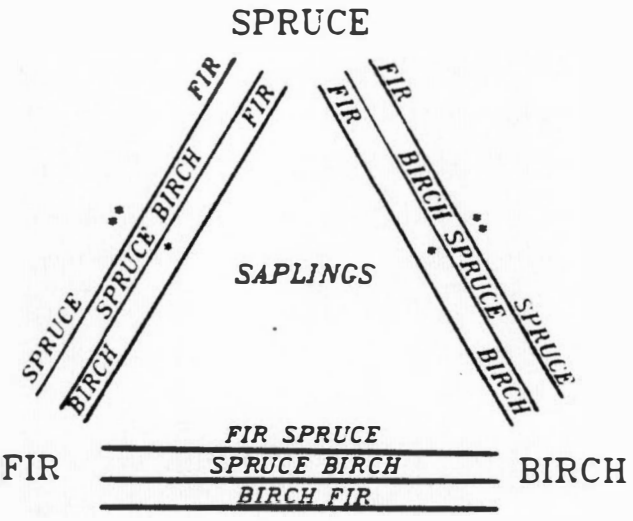


Fig. 19. Summary of canopy influence analyses. Canopy tree species are denoted at the angles of each triangle. Rank-sum test results of understory species comparisons are given between each canopy species pair: ** = significant at .01, and * = significant at .05. Each understory species is placed next to the canopy species it "prefers."

Table 15. Substrates of seedlings ($\leq$ 5 years old).

Species	n	Percent on Substrate			
		Forest Floor	Fallen Logs	Living Roots	Moss
Picea rubens	215	9	60	2	28
Abies fraseri	317	49	36	3	12
Betula lutea	31	22	77	0	0

Table 16. Substrates of individuals over 0.25 m tall and under 12 cm DBH.

Species	n	Percent on Substrate			
		Forest Floor	Fallen Logs	Living Roots	Moss
Picea rubens	395	69	20	10	1
Abies fraseri	495	75	10	15	0
Betula lutea	137	50	28	20	2
Acer spicatum	91	81	1	15	2

Table 17. Substrates of individuals invading gaps.

Species	n	Percent on Substrate		
		Forest Floor	Fallen Logs	Living Roots
Picea rubens	57	84	14	2
Abies fraseri	169	82	15	3
Betula lutea	37	65	32	3

and growth of individuals on the forest floor. The tendency of birch to grow on fallen logs is also evident in gaps.

Population Dispersion

All categories of populations sampled had a Morisita's index value greater than 1 indicating clumped dispersion of individuals (Table 18). The lowest index value (1.09) was obtained for Fraser fir stems which approached a random distribution. The highest index value (2.10) was obtained for yellow birch seedlings which had a strong tendency toward clumping. In all cases considered, seedling populations showed greater clumping than larger individuals of the same species. The patchiness of regeneration of each species suggests that microhabitat conditions regulate recruitment. Regeneration patch size tends to be small ($\leq$ 0.05 ha) and related to light gaps created by canopy tree mortality (Richards and Williamson 1975). Mortality of individuals within regeneration patches developing into mature stands is a likely cause for decreased clumping among larger individuals.

Interspecific nearest neighbor analyses of canopy trees revealed no interactions among spruce, fir and birch (Table 19). Pairwise segregation of canopy species was not evident from this analysis. Further study of intraspecific and interspecific canopy interactions involved the relationship of tree sizes and inter-tree distances between pairs of nearest neighbors. Figures 20-22 show this relationship for all pairwise combinations of spruce, fir and birch. Significant positive correlations were obtained for spruce-spruce, fir-fir and spruce-birch (Table 20). Large trees of these pairs tend

Table 18. Values of Morisita's population dispersion index.

Size Class	*Picea rubens*	*Abies fraseri*	*Betula lutea*	*Acer spicatum*
Stems (< 2.5 cm DBH)	1.66	1.51	2.10	--
Trees (> 2.5 cm DBH)	1.18	1.09	1.96	1.66

Table 19. Nearest neighbor Chi-square test results for canopy trees.[a]

Nearest Neighbor	Base Tree		Totals
	Picea	Abies	
Picea[b]	43 (46.54)	59 (55.46)	102
Abies	51 (47.46)	53 (56.54)	104
Totals	94	112	206
	Picea	Betula	
Picea[c]	43 (41.22)	13 (14.78)	56
Betula	10 (11.78)	6 (4.22)	16
Totals	53	19	72
	Abies	Betula	
Abies[d]	53 (51.59)	15 (16.41)	68
Betula	13 (14.41)	6 (4.59)	19
Totals	66	21	87

[a]Expected values are given in parentheses.

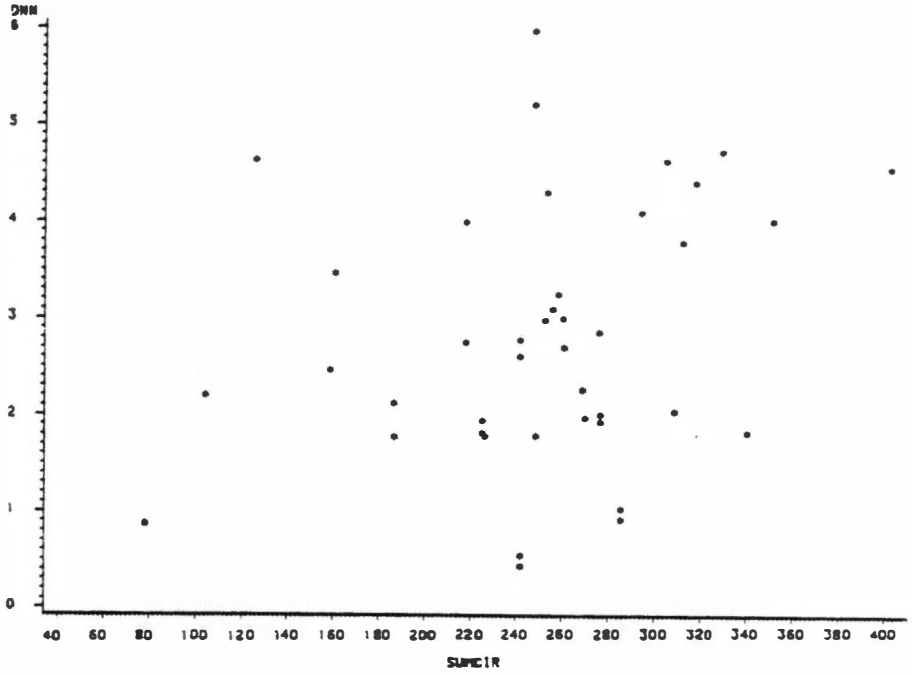
[b]$x^2 = 0.725$, n.s., p 0.05.

[c]$x^2 = 0.675$, n.s., p 0.05.

[d]$x^2 = 0.307$, n.s., p 0.05.

INTER-TREE DISTANCE VS SUM OF CIRCUMFERENCES

SPRUCE-SPRUCE



SPRUCE-FIR

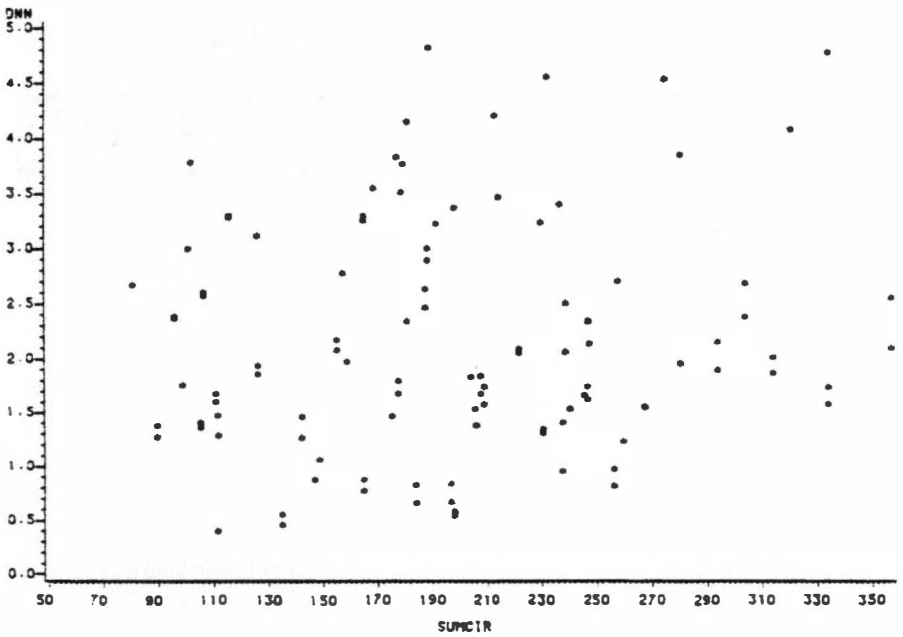


Fig. 20. Graphs of distance to nearest neighbor (m) vs. sum of trunk circumferences (cm) (spruce-spruce, spruce-fir). Correlation of spruce-spruce values was significant, while correlation of spruce-fir values was not significant.

INTER-TREE DISTANCE VS SUM OF CIRCUMFERENCES

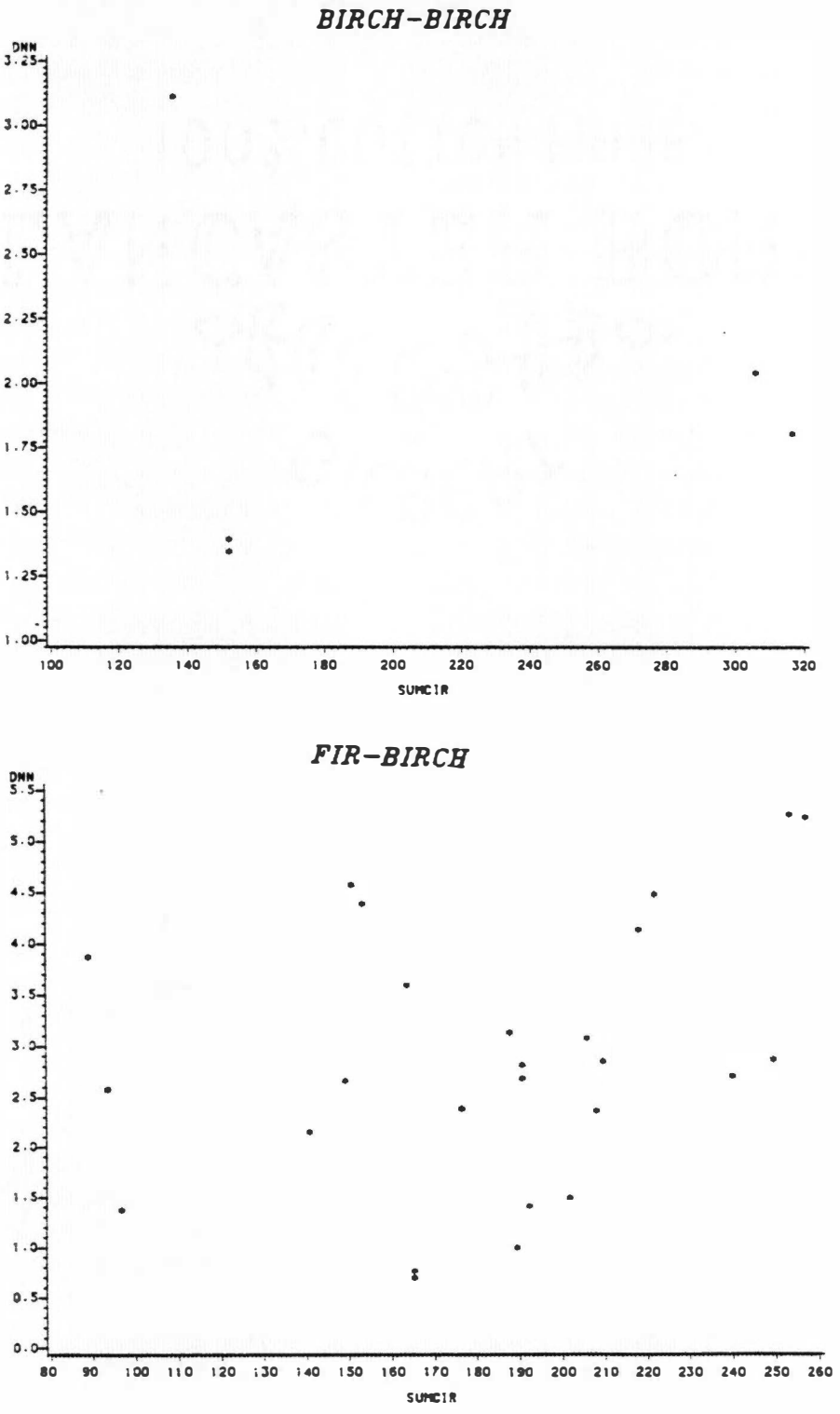


Fig. 21. Graphs of distance to nearest neighbor (m) vs. sum of trunk circumferences (cm) (birch-birch, fir-birch). Correlations of birch-birch values, and fir-birch values were both not significant.

INTER-TREE DISTANCE VS SUM OF CIRCUMFERENCES

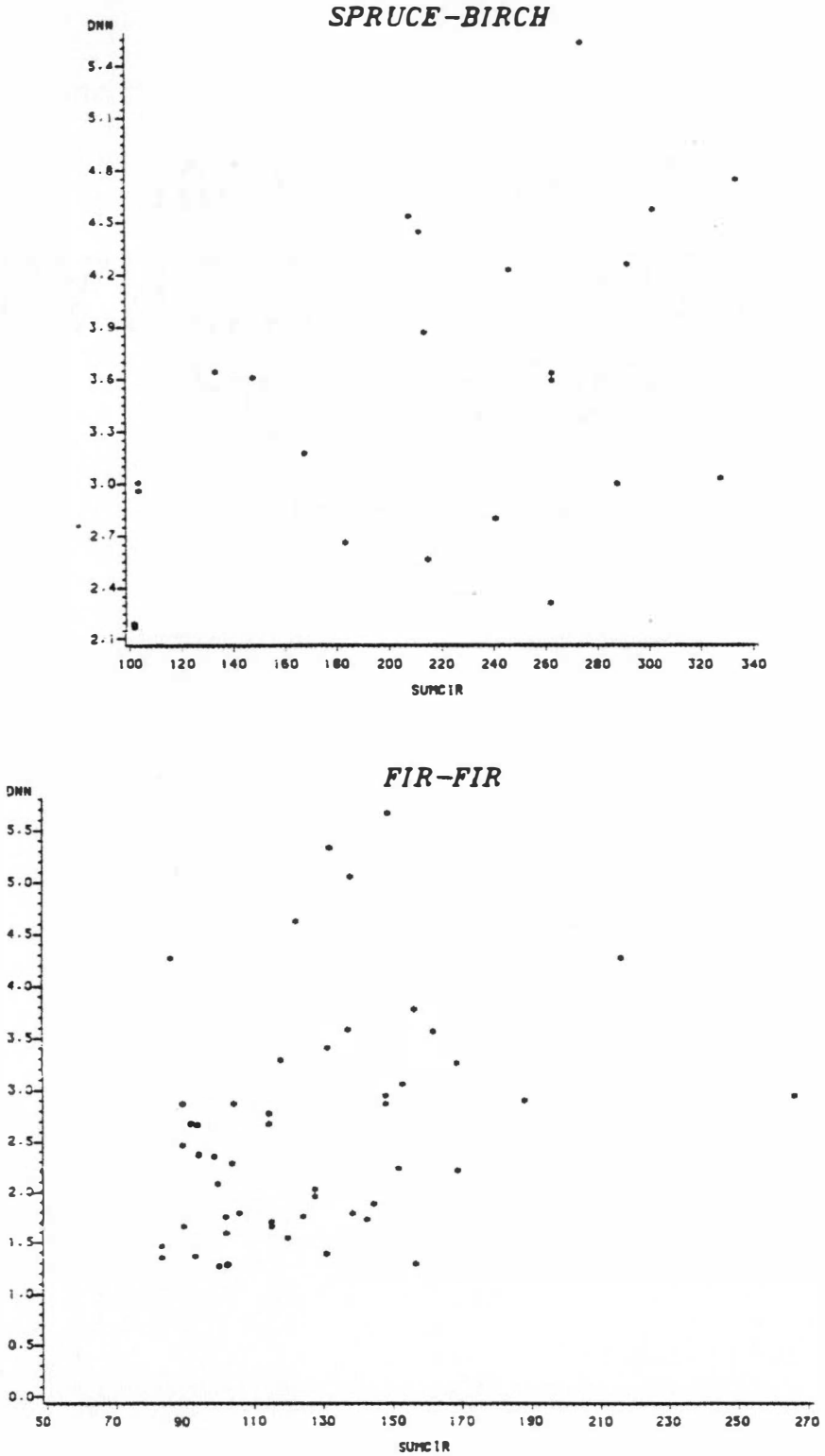


Fig. 22. Graphs of distance to nearest neighbor (m) vs. sum of trunk circumferences (cm) (spruce-birch, fir-fir). Correlations of spruce-birch values, and fir-fir values were both significant.

Table 20. Correlation analysis of distance to nearest neighbor vs. sum of trunk circumferences.

Canopy Species Pair	n	Correlation Coefficient	Prob. >/r/	Significance
Spruce-Spruce	43	0.314	0.040	*
Fir-Fir	53	0.334	0.015	*
Birch-Birch	6	-0.061	0.909	n.s.
Spruce-Fir	110	0.124	0.197	n.s.
Spruce-Birch	23	0.479	0.021	*
Fir-Birch	28	0.292	0.132	n.s.

*Significant at .05.

to be segregated from each other. Segregation may result from growth suppression and mortality caused by inter-tree competition (Pielou 1960, 1961).

Population Structure

Size-class distributions of red spruce and Fraser fir (Figs. 23 and 24) fit an inverse-J curve typical of undisturbed, self-perpetuating populations (Schmelz and Lindsey 1965, Whipple and Dix 1979). Individuals less than 5 cm DBH were abundant in both populations and frequencies declined rapidly in size classes greater than 5 cm. The maximum recorded size of spruce was 85 cm DBH, while the maximum recorded size of fir was 55 cm DBH.

Age-class distributions of red spruce and Fraser fir also fit an inverse-J curve (Fig. 25). Individuals under 5 years of age comprised over 70% of both populations. Few of the spruce trees sampled were more than 20 years of age, and few fir trees sampled were more than 60 years of age. The oldest spruce tree sampled was approximately 290 years of age, while the oldest fir tree was approximately 130 years of age. Both of these ages are considerably lower than the maxima of 359 and 168 years obtained by Oosting and Billings (1951) for southern spruce and fir, respectively. This suggests that very old trees comprise an extremely small portion of the spruce and fir populations.

The size-class distribution of yellow birch (Fig. 26) fits a decreasing curve (Whipple and Dix 1979). The frequency peak in 8-10 cm size-classes indicates a pulse of reproduction followed by a decreased rate of recruitment. Smaller peaks occurred in the 41 and

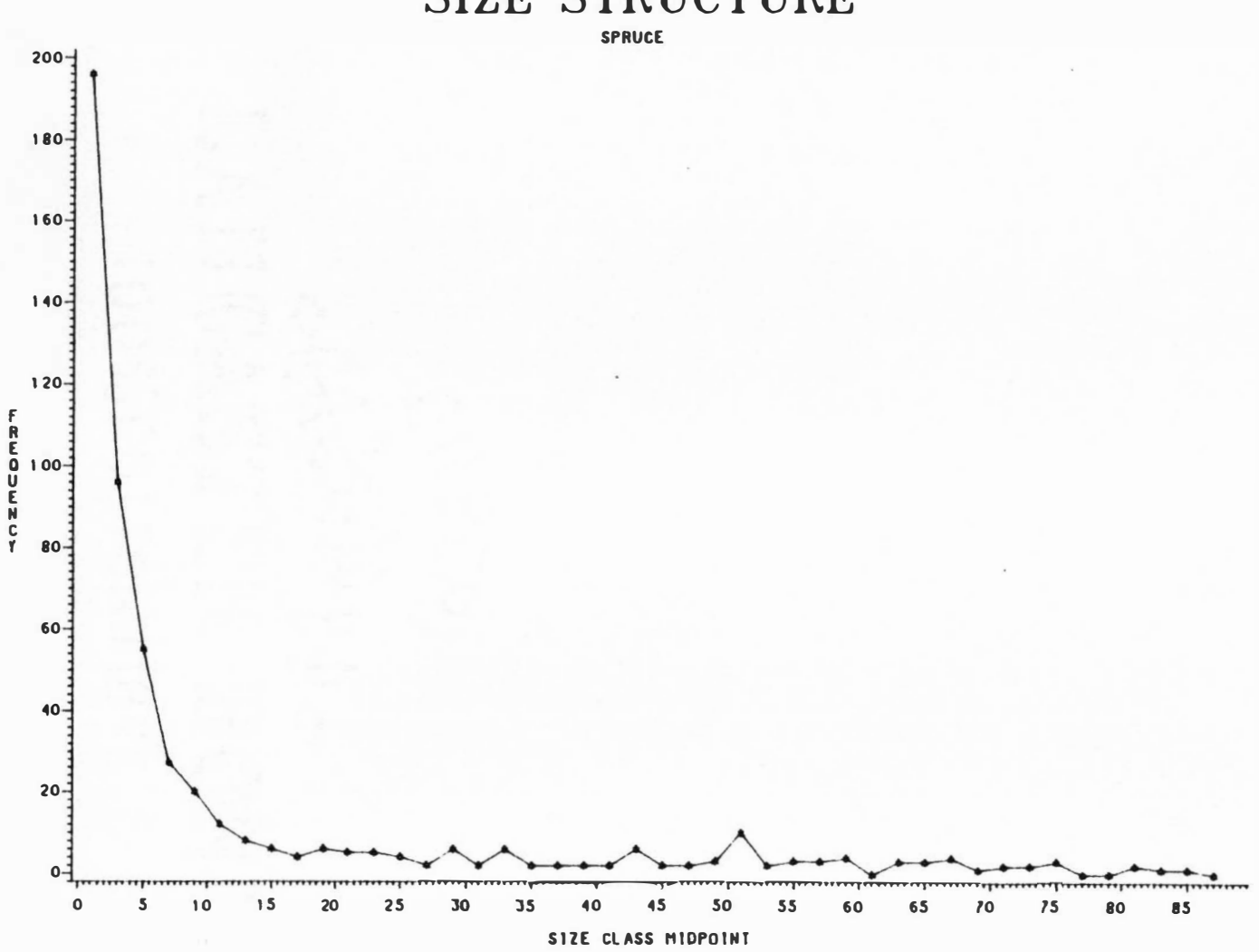


Fig. 23. Graph of red spruce size structure. Size is in cm DBH. Individuals less than 2.5 cm DBH are not included.

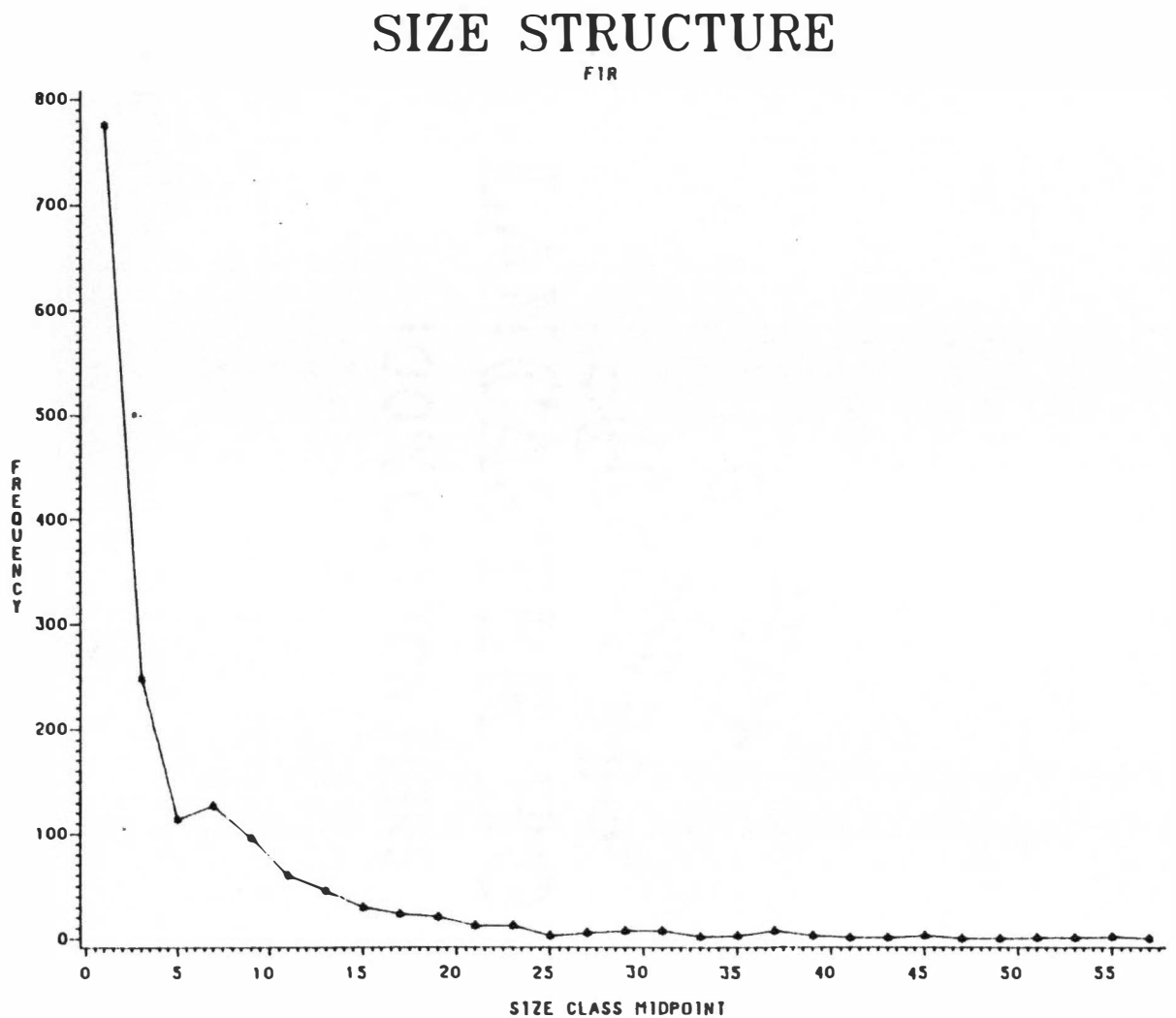


Fig. 24. Graph of Fraser fir size structure. Size is in cm DBH. Individuals less than 2.5 cm DBH are not included.

AGE STRUCTURE

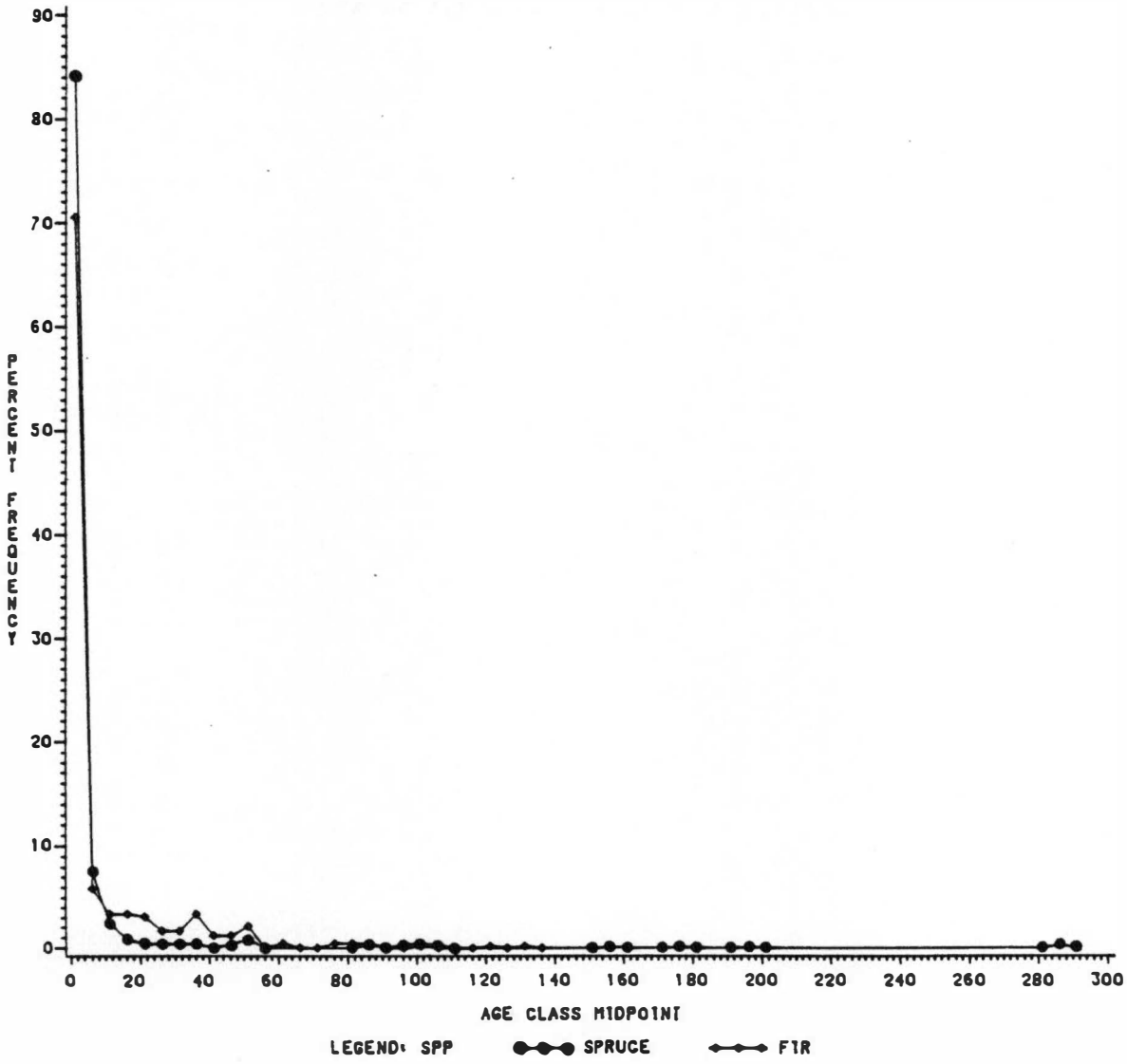


Fig. 25. Graph of red spruce and Fraser fir age structures. Sample sizes: spruce = 253 and fir = 431.

SIZE STRUCTURE

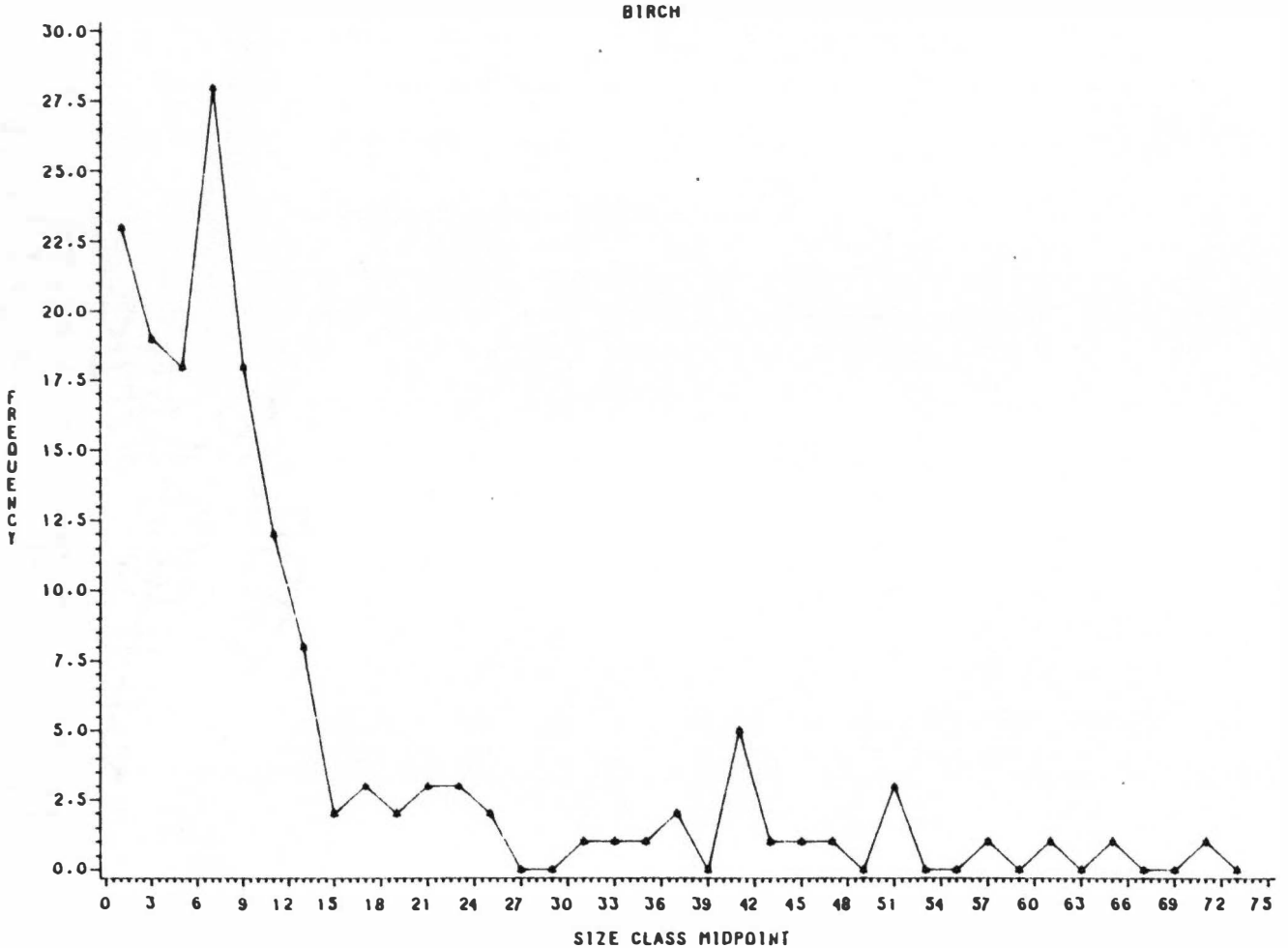


Fig. 26. Graph of yellow birch size structure. Size is in cm DBH. Individuals less than 2.5 cm DBH are not included.

51 cm size classes. These peaks were probably a result of reproduction pulses in response to synchronous small-scale natural disturbances which serve to perpetuate the birch population (Godman and Krefting 1960, White et al. 1985a).

The age-class distribution of yellow birch (Fig. 27) most closely resembles the inverse-J curve of Whipple and Dix (1979). Over 80% of the population was less than 5 years of age. Ages of other individuals sampled ranged from 40 to 250 years. The lack of pattern in the older age classes may have been caused by a small sample size (n=35) or by random regeneration pulses. The difference in shape of the age structure curve and the size structure curve resulted, in part, from the omission of individuals less than 2.5 cm DBH from the size structure distribution. Clearly, very small seedlings are highly abundant relative to saplings and canopy trees in the birch population. The mortality rate of birch seedlings less than five years of age appears to be very high (cf. Forcier 1975).

Size-class distributions of mountain maple and mountain ash are shown in Fig. 28. The distribution of ash resembles a bimodal curve which is characteristic of populations perpetuated by reproduction pulses (Whipple and Dix 1979). Maple was well represented in all size classes under 10 cm. Both populations were composed of relatively small trees (<20 cm DBH). Consequently, these two species are subdominants in the mature forest.

Approximate red spruce and Fraser fir survivorship curves generated from age-class distribution values are shown in Fig. 29. Linear regression results for the dependence of ln number of

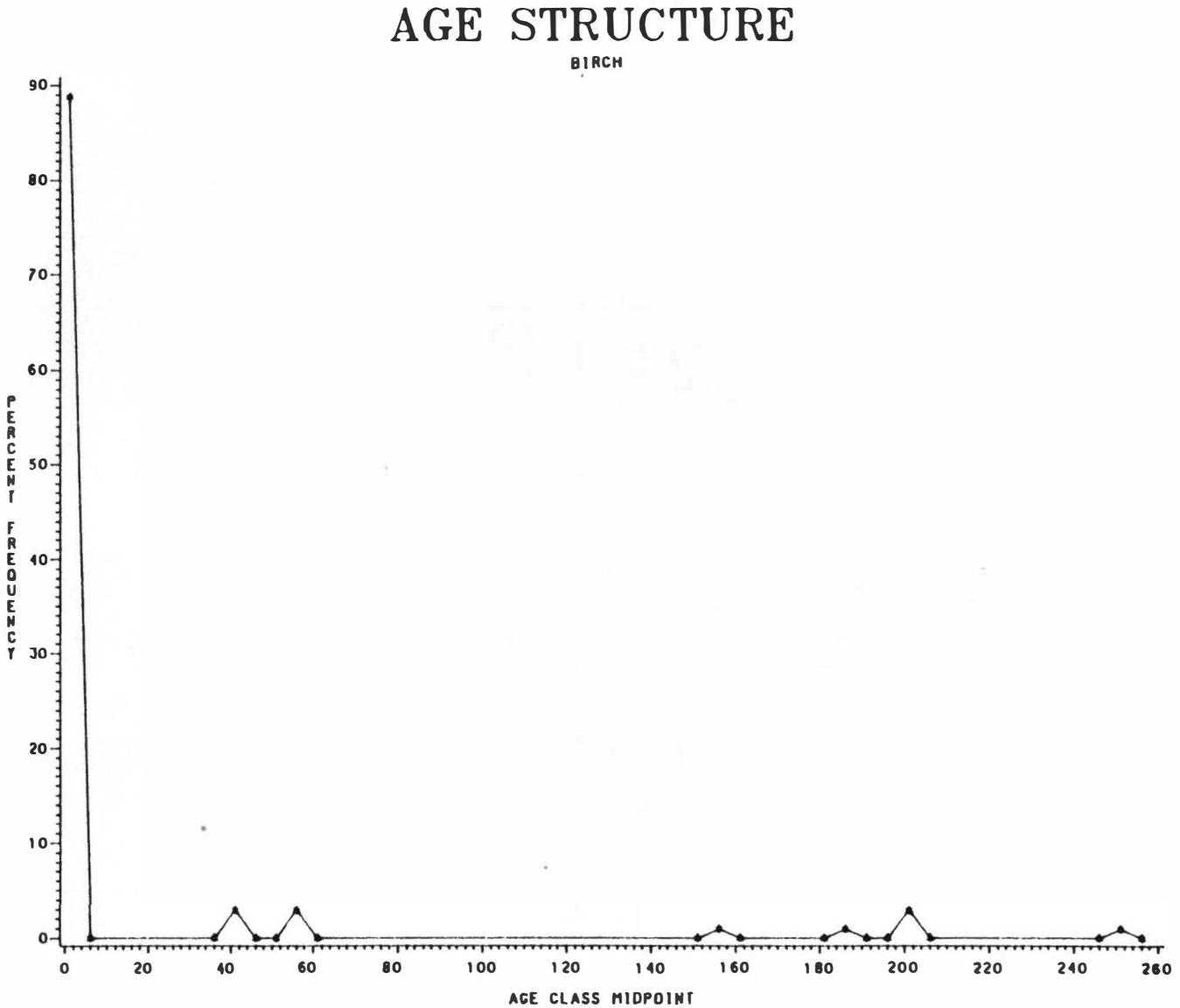


Fig. 27. Graph of yellow birch age structure.

SIZE STRUCTURE

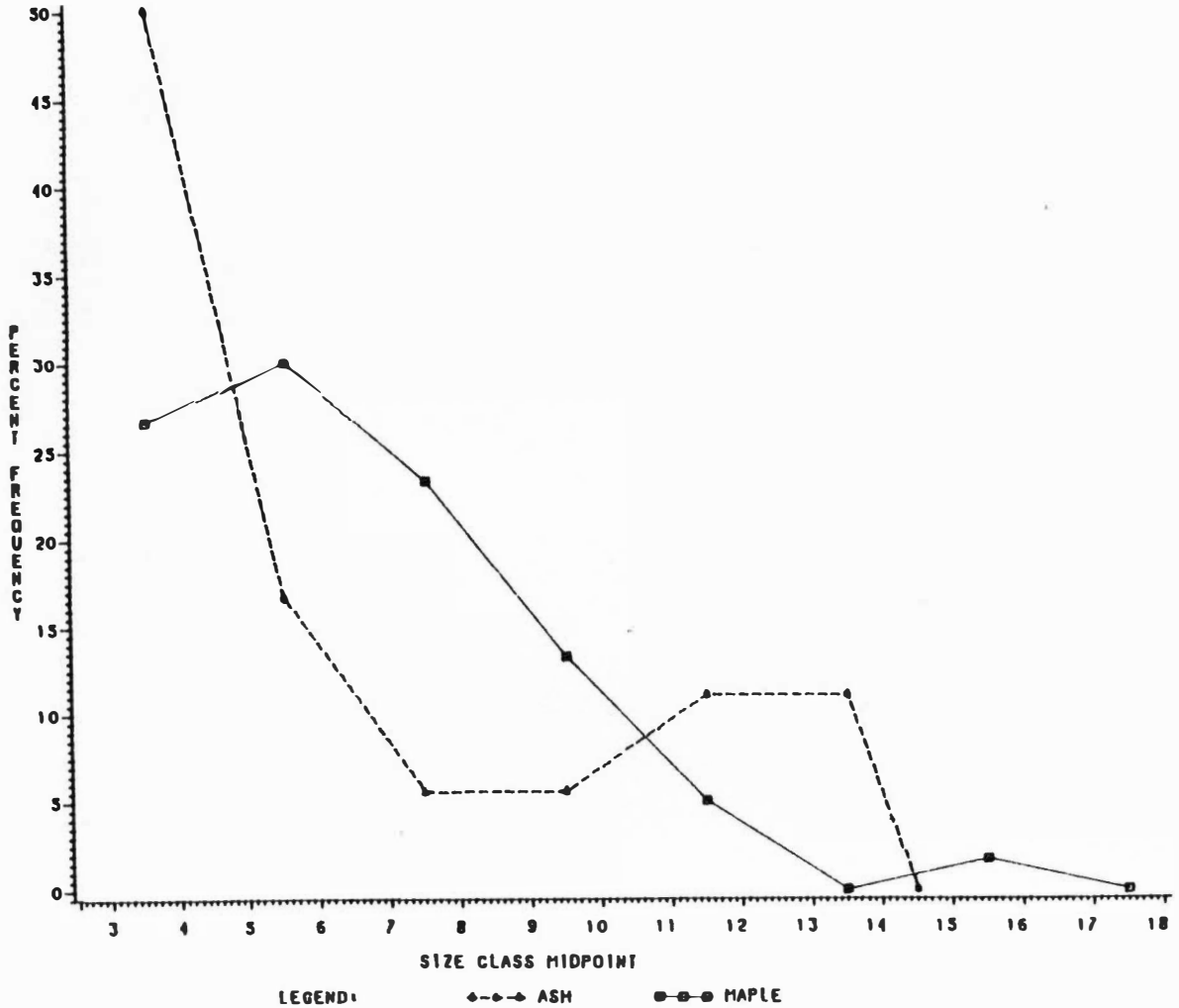


Fig. 28. Graph of mountain maple and mountain ash size structure. Size is in cm DBH. Individuals less than 2.5 cm DBH are not included.

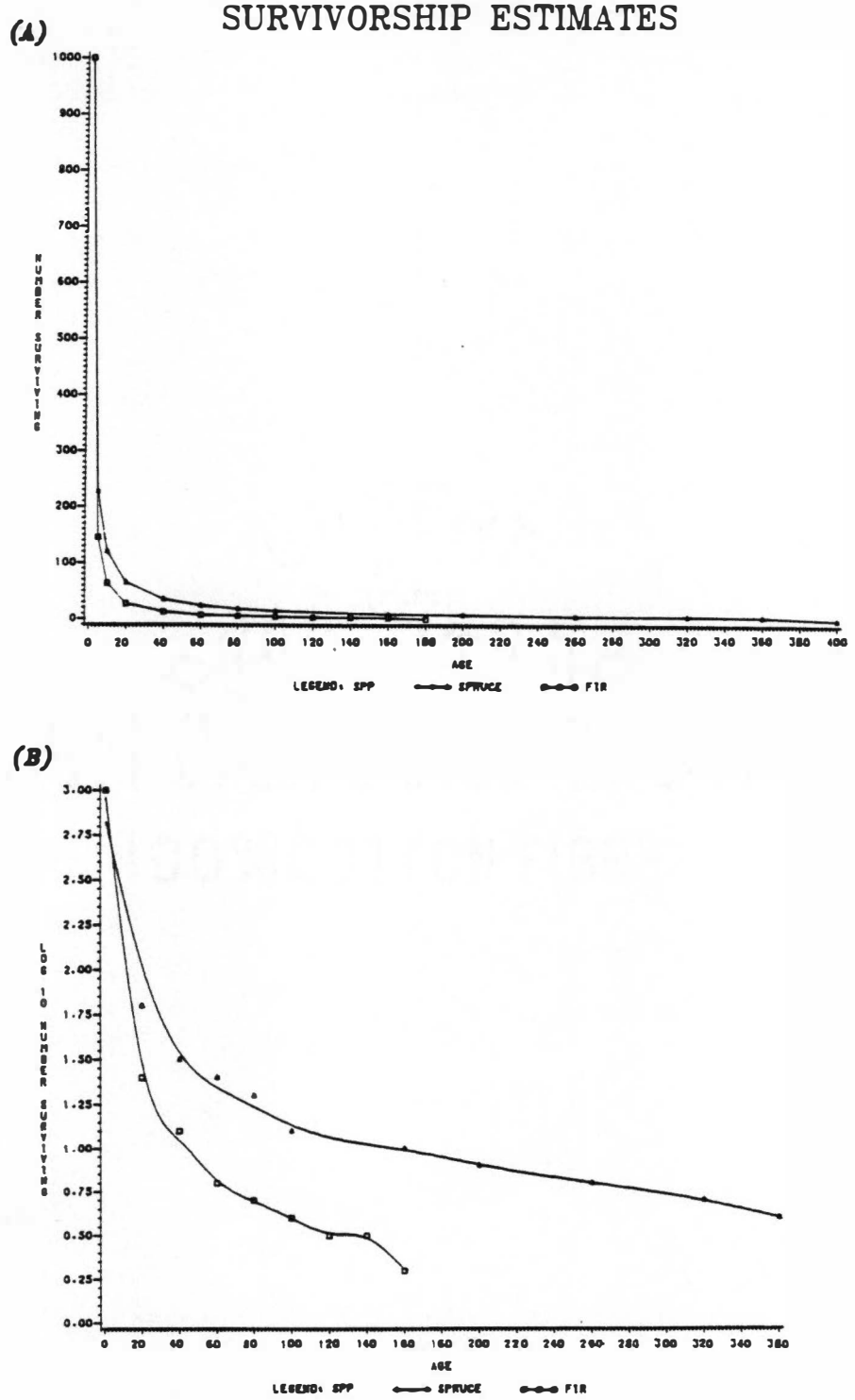


Fig. 29. Graphs of red spruce and Fraser fir survivorship estimates. These are: (A) actual survivorship vs. age and (B) $\log_{10}$ survivorship vs. age.

individuals on ln age are shown in Figs. 30 and 31. Regressions were highly significant for both species ($p<0.01$). The survivorship curves suggest a high mortality rate for individuals of both species less than 40 years of age. Mortality is low among 100-300 year old spruce trees and 70-130 year old fir trees. Life tables based on the approximated curves provide more detailed information (Tables 21 and 22). It should be noted that these tables are estimates based on the power function model of Hett (1971). The regression analysis performed to obtain these survivorship approximations may be an additional source of inaccuracy because of small sample sizes among the older age classes (>100 yr). Nonetheless, these estimates may serve in the comparison of model generated figures with actual survivorship figures. The model based life expectancy of spruce is highest in the age range from 100 to 180 years. For fir, the life expectancy is high among individuals 60 to 80 years of age. Life table values based directly on age-class data for spruce and fir are given in Table 23. When compared with the power function generated life tables, some notable differences emerge. Actual survivorship in the young age classes of fir (10-55 yr) is higher than that calculated with the power function. For spruce, actual survivorship in the young age classes (25-70 yr) is lower than that indicated by the calculated values. The age-class data suggest high survivorship for young fir relative to young spruce (<50 yr). Apparently, the power function of Hett (1971) is least accurate in predicting the survivorship of moderately young spruce and fir trees.

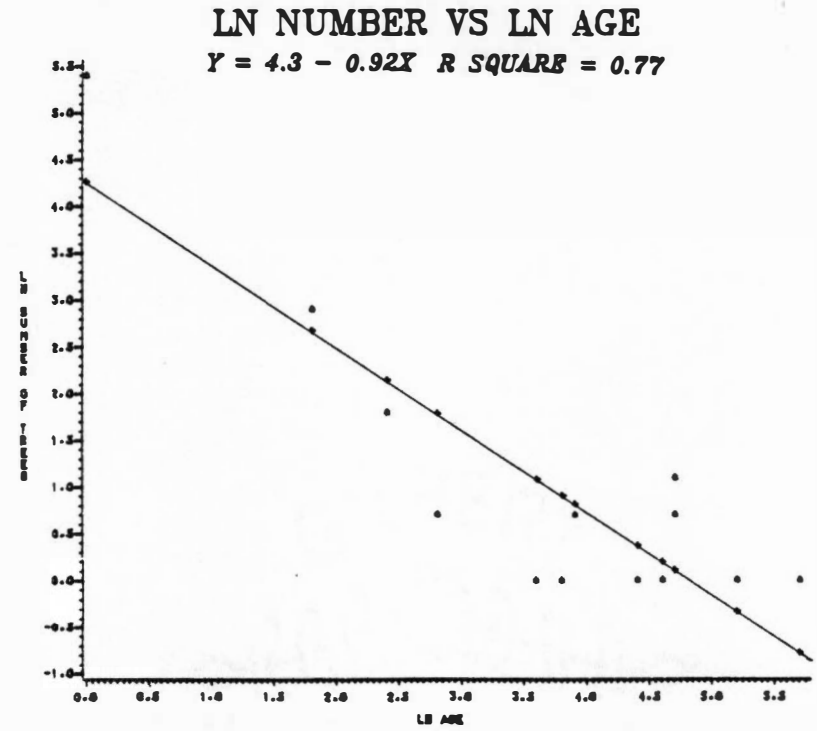


Fig. 30. Graph of red spruce survivorship with linear regression.

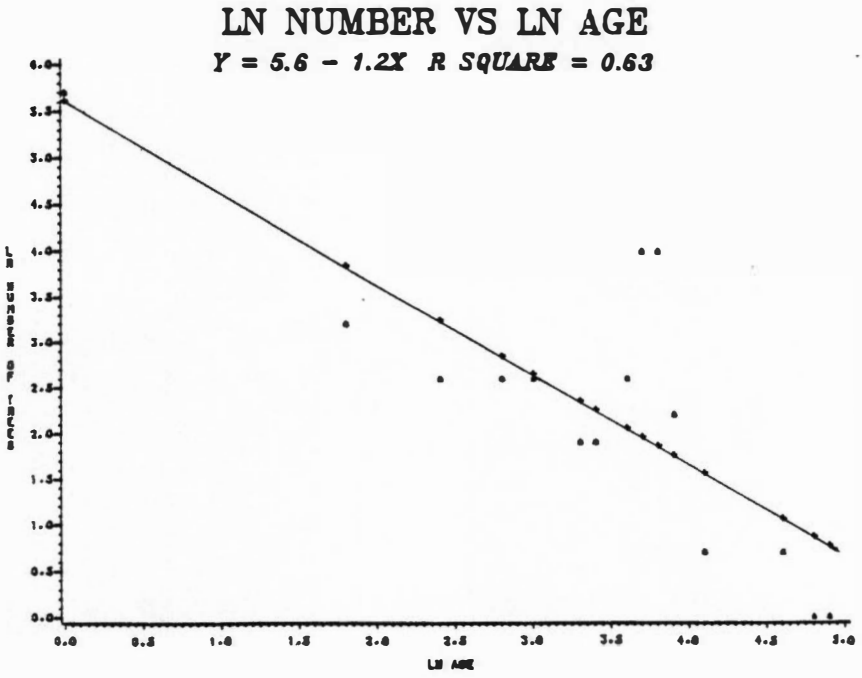


Fig. 31. Graph of Fraser fir survivorship with linear regression.

Table 21. Life table for Fraser fir based on the power function model of Hett (1971).

Age (x)	Survival (l_x)	Mortality (d_x)	Mortality Rate (q_x)	Average Years Lived (L_x)	Total Years Lived (T_x)	Life Expectancy (e_x)
1	1000	973	0.973	513.3	562.8	0.563
20	27	15	0.556	19.5	49.5	1.833
40	12	5	0.417	9.5	30.0	2.500
60	7	2	0.286	6.0	20.5	2.929
80	5	1	0.200	4.5	14.5	2.900
100	4	1	0.250	3.5	10.0	2.500
120	3	0	0.000	3.0	6.5	2.167
140	3	1	0.333	2.5	3.5	1.167
160	2	2	1.000	1.0	1.0	0.500
180	0					

Table 22. Life table for red spruce based on the power function model of Hett (1971).

Age (x)	Survival (l_x)	Mortality (d_x)	Mortality Rate (q_x)	Average Years Lived (L_x)	Total Years Lived (T_x)	Life Expectancy (e_x)
1	1000	936	0.936	532.0	749.0	0.749
20	64	30	0.469	49.0	217.0	3.391
40	34	11	0.323	28.5	168.0	4.941
60	23	5	0.217	20.5	139.5	6.065
80	18	4	0.222	16.0	119.0	6.611
100	14	2	0.143	13.0	103.0	7.357
120	12	1	0.083	11.5	90.0	7.500
140	11	2	0.182	10.0	78.5	7.136
160	9	1	0.111	8.5	68.5	7.611
180	8	0	0.000	8.0	60.0	7.500
200	8	1	0.125	7.5	52.0	6.500
220	7	1	0.143	6.5	44.5	6.357
240	6	0	0.000	6.0	38.0	6.333
260	6	0	0.000	6.0	32.0	5.333
280	6	1	0.167	5.5	26.0	4.333
300	5	0	0.000	5.0	20.5	4.100
320	5	0	0.000	5.0	15.5	3.100
340	5	1	0.200	4.5	10.5	2.100
360	4	0	0.000	4.0	6.0	1.500
380	4	4	1.000	2.0	2.0	0.500
400	0					

Table 23. Partial life tables for red spruce and Fraser fir based on age structure data.

	Age (x)	Survival (l_x)	Mortality (d_x)	Mortality Rate (q_x)
Picea rubens	1	1000	872	0.872
	10	128	114	0.891
	25	14	5	0.357
	40	9	0	0.000
	55	9	4	0.444
	70	5		
Abies fraseri	1	1000	822	0.822
	10	178	87	0.489
	25	91	4	0.044
	40	87	33	0.379
	55	54	47	0.870
	70	7		

Supplemental data on tree dimensions and age-to-size relationships are presented in the Appendix.

CHAPTER VI

GAP MODEL DEVELOPMENT AND DESCRIPTION

Introduction

A gap model (FORANAK) was developed for simulation of southern Appalachian spruce-fir forest dynamics in response to anthropogenic disturbances. The model was based on the FORET model of Shugart and West (1977) discussed earlier. Several major modifications of the original model were made in an attempt to improve its predictive capabilities. The most significant modification involved the simulation of regeneration. Alterations were made so that the position of each tree on a horizontal plane was monitored, producing a model with horizontal as well as vertical spatial considerations. The simulation was designed so that the input of seedlings on a simulated plot was low in areas near large trees. Seedlings of species tolerant to canopy trees were given higher probabilities of establishment near large trees. In effect, the model includes a fine-scale simulation of canopy influence on regeneration. Other modifications involved climatic effects, light competition effects, biomass estimation, regeneration by sprouting, plot size and the number of species considered. Specific alterations of program subroutines are discussed in the following section.

Model Description

The spruce-fir forest succession model is a FORTRAN computer program comprised of several subroutines designed to simulate forest

processes (Fig. 32). See the Appendix for a complete program listing. The main program regulates the order of operations by calling certain subroutines in sequence. Species and initial plot data are input first, then KILL, BIRTH, GROW and OUTPUT subroutines are called in an annual loop until the desired number of years of simulation is reached. This process is repeated if more than one plot is simulated. Alterations of the basic FORET program, discussed by subroutine, are as follows.

Subroutine KILL. The primary function of the KILL subroutine is to regulate individual tree mortality based on the maximum recorded age for the species and on the growth rate of the tree. Originally, the subroutine functioned solely as a regulator of tree mortality. In the FORANAK model stump sprouting of recently killed trees is also simulated here. The SPROUT subroutine of the FORET model was replaced by this addition to the KILL subroutine.

The simulation of regeneration by stump sprouting is relatively simple. When a tree dies it will be replaced by one individual with a DBH of approximately 1.27 cm if the species is capable of sprouting and the diameter of the dead tree is within a certain range. The trunk diameter range of each species was chosen so that medium sized trees, which tend to be vigorous, will give rise to stump sprouts.

Subroutine GROW. This subroutine determines the annual diameter growth increment of individual trees. In the FORET model the growth of each tree was a function of its potential growth rate, size, shade tolerance, response to climate and response to crowding. The FORANAK

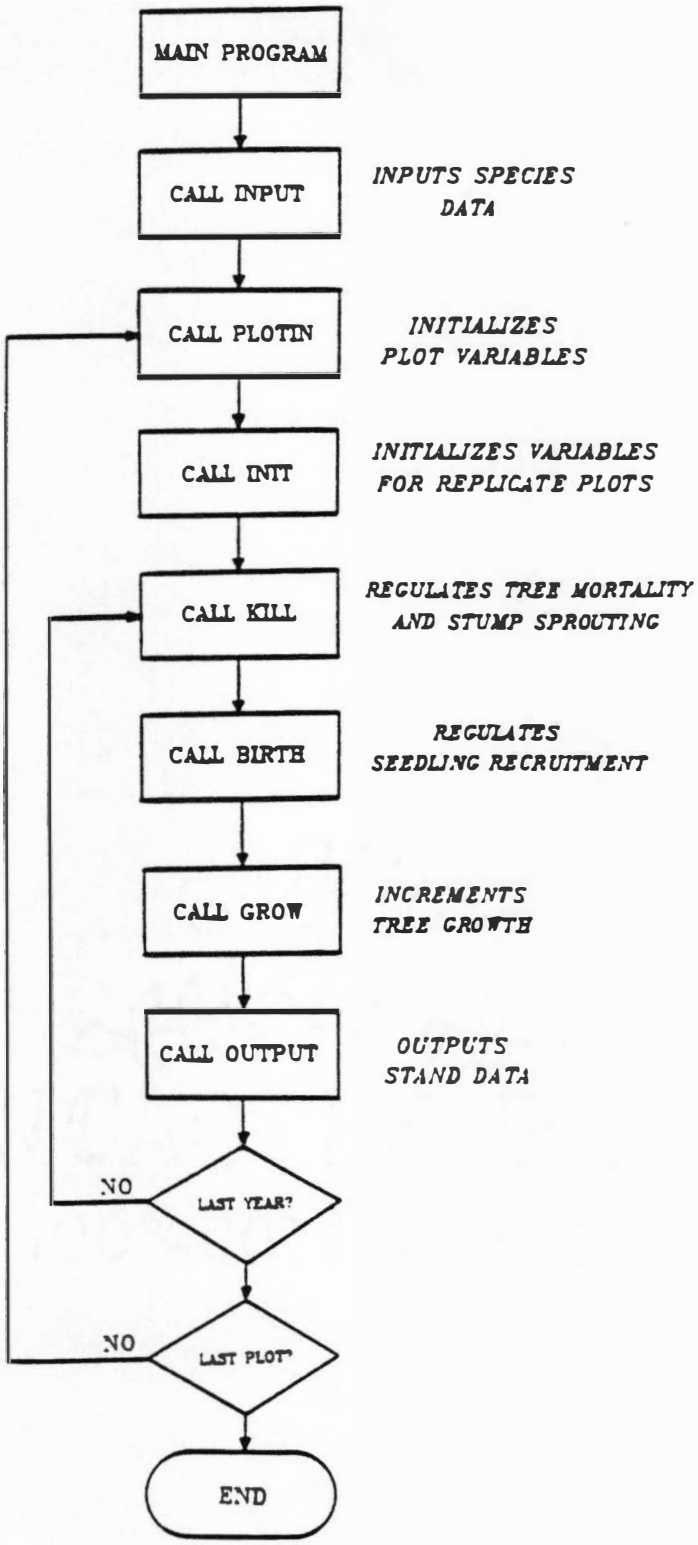


Fig. 32. Flow diagram and subroutine functions of the FORANAK model.

model includes all of these factors except for climatic effects. They were eliminated because of difficulties encountered in the early stages of model development. In the FORET model the growth of trees is drastically reduced near the limits to their climatic tolerance. For example, the simulated growth rate of red maple (Acer rubrum) is very low at 1820 degree-days, the climatic regime near the northern edge of its range. In the FORANAK model of the southern Appalachian spruce-fir zone, red spruce and yellow birch are near their climatic tolerance limits. The preliminary simulated growth rate of both species was so low that they were outcompeted by Fraser fir and other species. In reality, spruce and birch are forest dominants along with fir under this climatic regime. Apparently, the modeling of climatic effects on growth near the edge of a species' range is weak in FORET and inadequate for the FORANAK model. For this reason a variable climatic regime was not included.

The FORANAK model was adjusted to simulate gap dynamics in the 1770-1830 m elevation range of the Great Smoky Mountains spruce-fir zone. Seven tree species, commonly occurring at these elevations, were included in the model. They are red spruce, Fraser fir, yellow birch, mountain maple, mountain ash, fire cherry and serviceberry. Optimal growth of individual species was based on information from within this range (Oosting and Billings 1951; E.E.C. Clebsch, unpublished data). The model version presented herein is based on the assumption of a static climatic regime and is applicable only to spruce-fir forests within the 1770-1830 m elevation range of the southern Appalachians.

Another modification of the GROW subroutine involved the use of five shade tolerance classes instead of three. Growth increments for each of the five classes were calculated using the formulas of Waldrop (1983) which are simple modifications of the original shade tolerant and shade intolerant equations used in FORET.

A relatively small plot size of 0.03 ha was chosen for the model. Although White et al. (1985b) have shown that gap size in the southern Appalachian spruce-fir forest is typically less than 0.02 ha, Shugart (1984) has noted that dominant trees cannot attain their maximum size on simulated plots less than or equal to 0.02 ha in area. The maximum above-ground biomass estimate for a 0.03 ha area of spruce-fir is 10.9 t (362 t/ha). This estimate was obtained by calculating biomass based on individual tree diameters from the north slope of Mt. Collins (E.E.C. Clebsch, unpublished quadrat data). Species-specific equations provided by Tritton and Hornbeck (1982) were used in the biomass calculations. Other estimates of mature spruce-fir stand biomass are 300-340 t/ha (Whittaker 1966) and 351 t/ha (Shanks et al. 1961). An upper limit of 370 t/ha was used in the FORANAK model. Accordingly, the value of SOILQ was set at 11100 kg for the 0.03 ha plot size.

Calculation of plot biomass in the model involved the use of species-specific equations for the estimation of biomass from tree DBH's (Tritton and Hornbeck 1982). The form of the equations employed was:

$$\ln (wt) = C_1 + C_2 (\ln(DBH))$$

where wt is the tree biomass in lbs dry weight, DBH is the diameter in inches, and C_1 and C_2 are constants for the species. Biomass was converted from lbs to kg in the calculation of stand biomass.

A final modification of the GROW subroutine involved the growth of shaded red spruce trees. In the FORET model any tree with a calculated annual diameter increment less than 1.0 mm is not increased in size and is given a substantially greater probability of dying. Growth ring data collected for red spruce indicate that the annual growth increment of healthy trees is often much less than 1 mm. Additional studies have shown that suppressed red spruce trees may grow very slowly for several decades before release (Korstian 1937, White et al. 1985b). For this reason the 1 mm minimum growth increment did not allow accurate simulation of spruce mortality. The minimum required growth increment was reduced to 0.45 mm to decrease the mortality of suppressed spruce trees and thereby improve the accuracy of simulation.

Subroutine BIRTH. The BIRTH subroutine regulates seedling inputs. As in FORET, new trees enter a simulated plot at an average DBH of 1.27 cm. However, in FORANAK seedling regeneration is regulated in a very different manner; the number of seedlings entered is dependent upon the position and abundance of large trees on the plot, and the species of potential seedling. In most gap models to date only a few species are selected for input each year and the number of seedlings entered is randomly determined. This method is not adequate for spruce-fir forests because of the large discrepancy

in regeneration rates among species. For instance, Fraser fir seedlings are several times greater in abundance than other tree species in the forest. The relatively high regeneration rate of fir is a major reason for its codominance with spruce (White et al. 1985a). In FORANAK each species was given a maximum potential annual seedling input and the capability of regenerating each year.

The new seed regeneration procedure is a series of steps executed for each potential seedling to determine whether or not it should be recruited. In this simulation the 0.03 ha plot is a square grid of 0.5 m wide elements. Trees are located on gridpoints with no more than one tree per gridpoint. The following procedure is done a specified number of times for each species. First, a gridpoint is randomly selected to simulate the position of a seed. Second, the gridpoint is checked for occupancy. If the gridpoint is already occupied by a tree then the seedling cannot be recruited and input of the next potential seedling is attempted at another randomly selected gridpoint. Third, the total canopy influence at the selected gridpoint is calculated:

$$CIND = \sum^{n} \frac{DBH}{DIST}$$

where CIND is the total canopy influence index, n is the number of canopy trees (>12 cm DBH) within 5 m of the gridpoint, DBH is the canopy tree diameter in cm and DIST is the distance to the canopy tree in m. Repeating plot boundaries are used in the calculation of CIND for gridpoints within 5 m of the plot edge(s) (Fig. 33). A large CIND

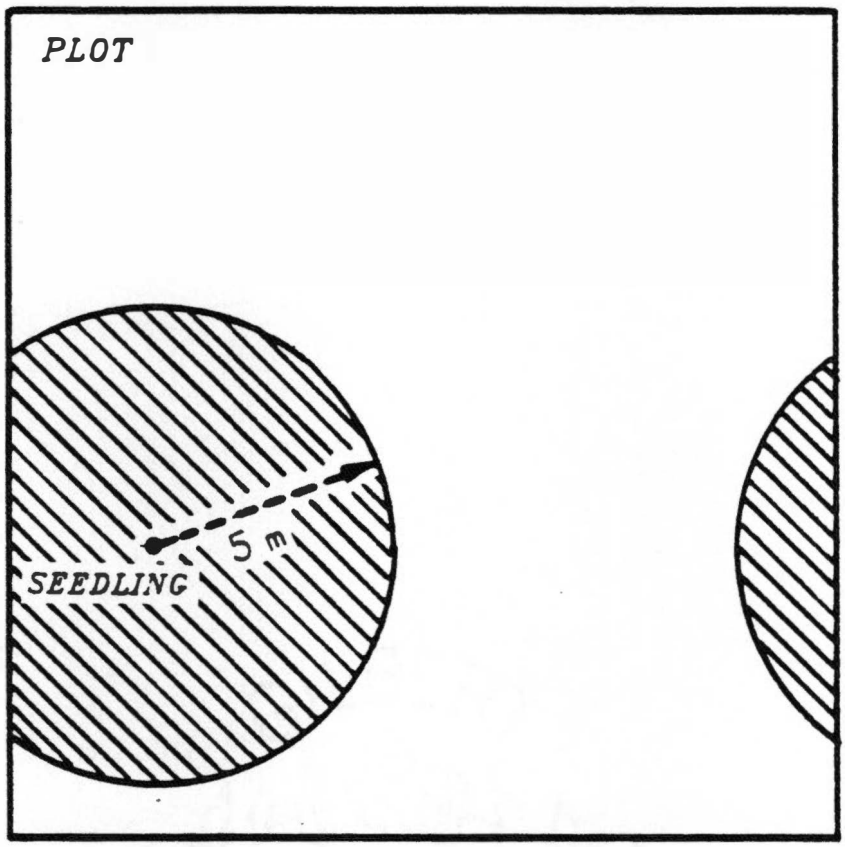


Fig. 33. Diagram of the repeating boundary condition on a simulated plot. Canopy trees in the shaded area are included in the calculation of canopy influence on the seedling.

value indicates the presence of large trees near the gridpoint. The fourth and final step of the regeneration procedure involves the generation of a random number and the comparison of that number to the CIND value. Each random number is the absolute value of a number picked from a normal distribution with a mean of zero and a species-specific standard deviation. Usually the random number will be less than CIND if large trees are nearby. In this case the seedling will not be input (Figs. 34 and 35). Each seedling species is given a certain standard deviation (CTOL) representing its tolerance to canopy trees: the larger the standard deviation, the greater the tolerance to canopy trees. These four steps are repeated a predetermined number of times (NSEDL) for each species. In essence, they regulate the positions of incoming seedlings based on the location and number of established trees.

The new BIRTH subroutine appears to be more realistic than earlier versions. It simulates actual events of seed regeneration in the spruce-fir forest annually. For example, the positioning of available seeds is random as would be expected for wind-dispersed seeds. Competition for space and associated resources is mimicked by competition for gridpoints. From a strategic viewpoint, each species' existence is dependent on its ability to win space and hold it (Harper 1977). When resources are plentiful, seedling species with fast growth rates are better able to win space. For this reason the simulation was designed so that species are given the opportunity to occupy gridpoints in order of their seedling growth rates: fire cherry > mountain ash > yellow birch > Fraser fir > mountain maple >

CANOPY INFLUENCE INDEX

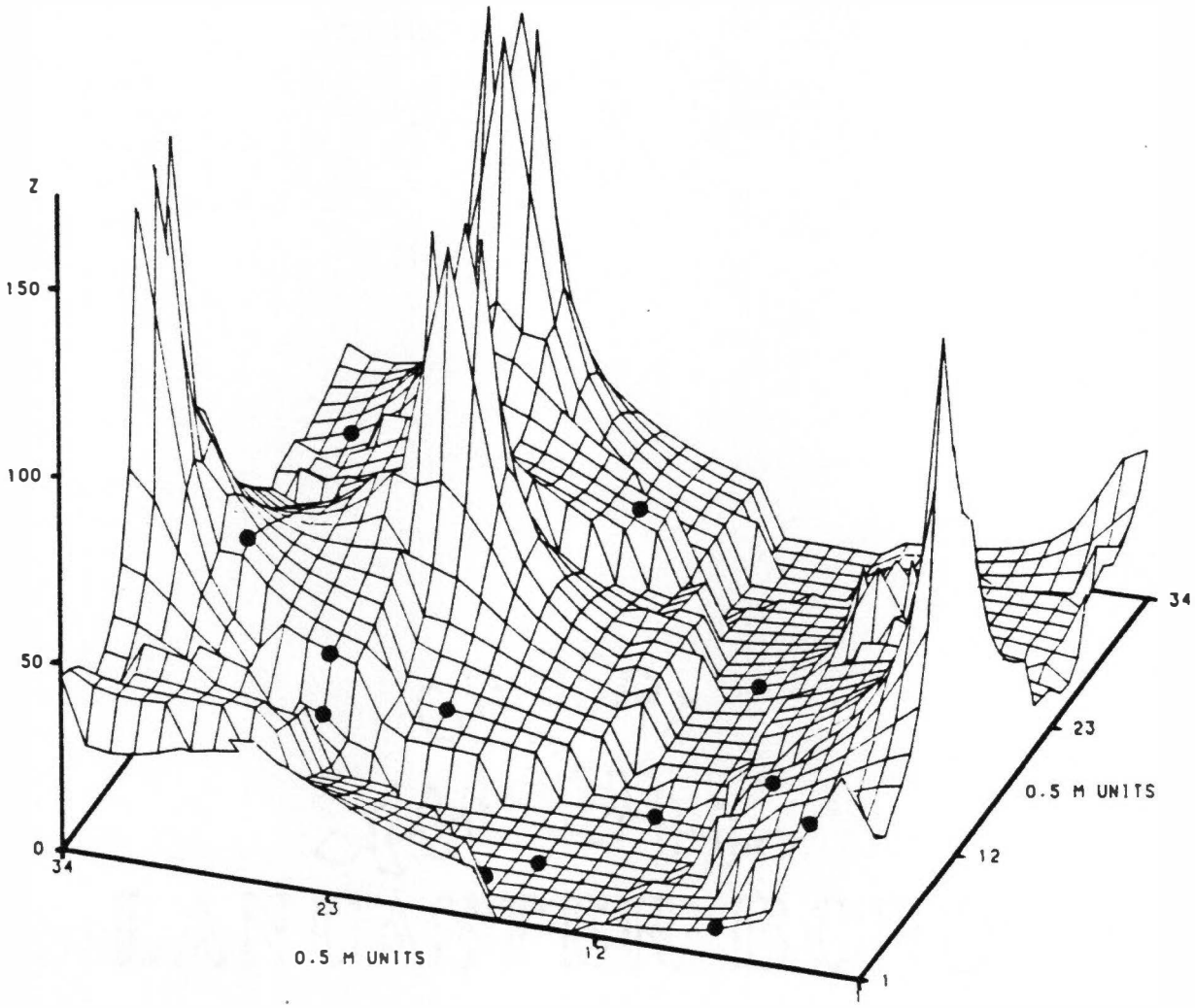


Fig. 34. Graph of total canopy influence on a simulated plot. Canopy influence index values (CIND) for each gridpoint are plotted along the z axis. Peaks occur at canopy tree locations. Dots represent incoming seedlings.

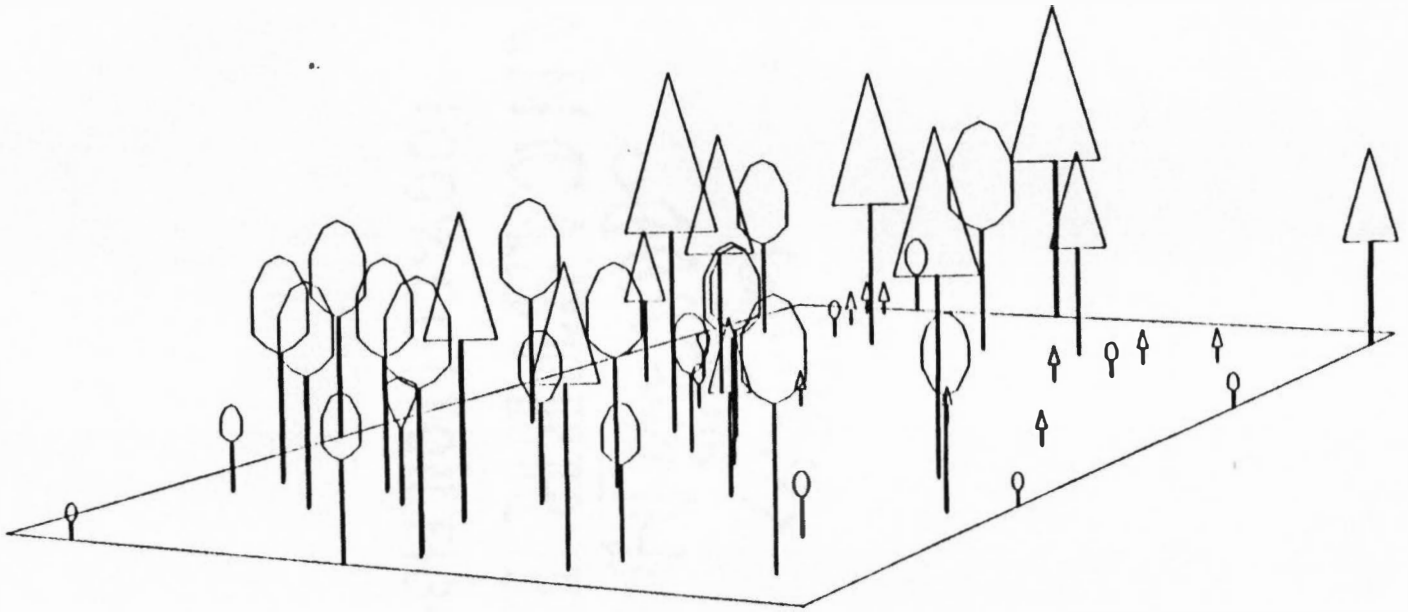


Fig. 35. Diagram of a simulated forest plot showing regeneration microsites. Note that regeneration is low in areas proximate to canopy trees.

serviceberry > red spruce. Finally, the survival of young seedlings in the forest is affected by canopy conditions which are monitored by the total canopy influence index. In brief, seedlings have a low probability of becoming established in locations where juvenile mortality is likely.

Model Parameters

The basic parameters used for species attributes in the FORANAK model are presented in Table 24. Parameters C_1 and C_2 are coefficients for the calculation of tree biomass (see page 100). These were obtained from Tritton and Hornbeck (1982). Parameters B_2 and B_3 are coefficients for the calculation of tree height (see page 32). They were calculated from the diameters and heights of large trees in the southern Appalachian spruce-fir zone (Saunders 1979; E.E.C. Clebsch, unpublished data). Equation (3) of Botkin et al. (1972) was used in the calculations. Shade tolerance classes (ITOL) were assigned in accordance with Daniel (1979) and field data on canopy influence. Maximum age values (AGEMX) for each species were determined based on information from Oosting and Billings (1951) and on field data. Determination of the growth scaling constant (G) for each species was a major task in model development. The calculation and adjustment of G values will be discussed below. Four of the seven species considered often regenerate by stump sprouting. They were assigned a SPRTND value of 1 indicating a stump sprouting capability in the event of a trees' death. SPRTMN and SPRTMX are the respective lower and upper limits of the trunk diameter range for sprouting.

Table 24. Basic parameters used in the FORANAK model.

Species	C_1	C_2	B_3	B_2	ITOL[a]	AGEMX	G	SPRTND	SPRTMN	SPRTMX
Abies fraseri	0.596	2.402	0.5251	73.51	1	160	80	0	0	0
Acer spicatum	0.939	2.380	0.9999	63.66	3	100	75	1	10	25
Amelanchier arborea	0.956	2.426	0.9999	83.15	4	150	70	1	10	25
Betula lutea	1.130	2.338	0.3686	62.66	4	280	75	1	20	50
Picea rubens	0.808	2.332	0.4275	76.96	2	380	50	0	0	0
Prunus pensylvanica	0.976	2.195	0.5469	53.59	5	40	150	0	0	0
Sorbus americana	0.956	2.426	0.6644	53.15	3	100	100	1	10	25

[a]ITOL is the shade tolerance class of each species (1 = very tolerant, 5 = very intolerant).

These values were chosen so that trees will sprout if killed before becoming large and senescent.

The growth scaling factor (G) is an important species parameter that determines optimal tree growth. Preliminary estimates of G values were obtained using two separate methods. The first method was based on the assumption that a tree will be 2/3 of its maximum diameter at 1/2 of its maximum age. Using equation (3.7) of Shugart (1984), one set of G values was calculated. The second method relied upon maximum diameter growth increments obtained for each species on the Mt. Collins study site. Using equation (3.8) of Shugart (1984), another set of preliminary G value estimates was calculated. Early simulations were done with these sets of estimates. Botkin et al. (1972) found it necessary to adjust some G values to produce realistic growth rates. In development of the FORANAK model the adjustment of G values was also required as most species were grown too fast, causing them to attain large size and die before expected. The final simulated age-to-size relationships are compared to those determined from field data in Figs. 36 and 37.

The species parameters CTOL and NSEDL are important in the control of seedling inputs in subroutine BIRTH. CTOL is a value representing the tolerance of seedlings to canopy trees. Values of CTOL for each seedling species were estimated from total canopy influence indices based on field data (Fig. 18). The effect of CTOL parameter alterations on regeneration is considerable (Table 25).

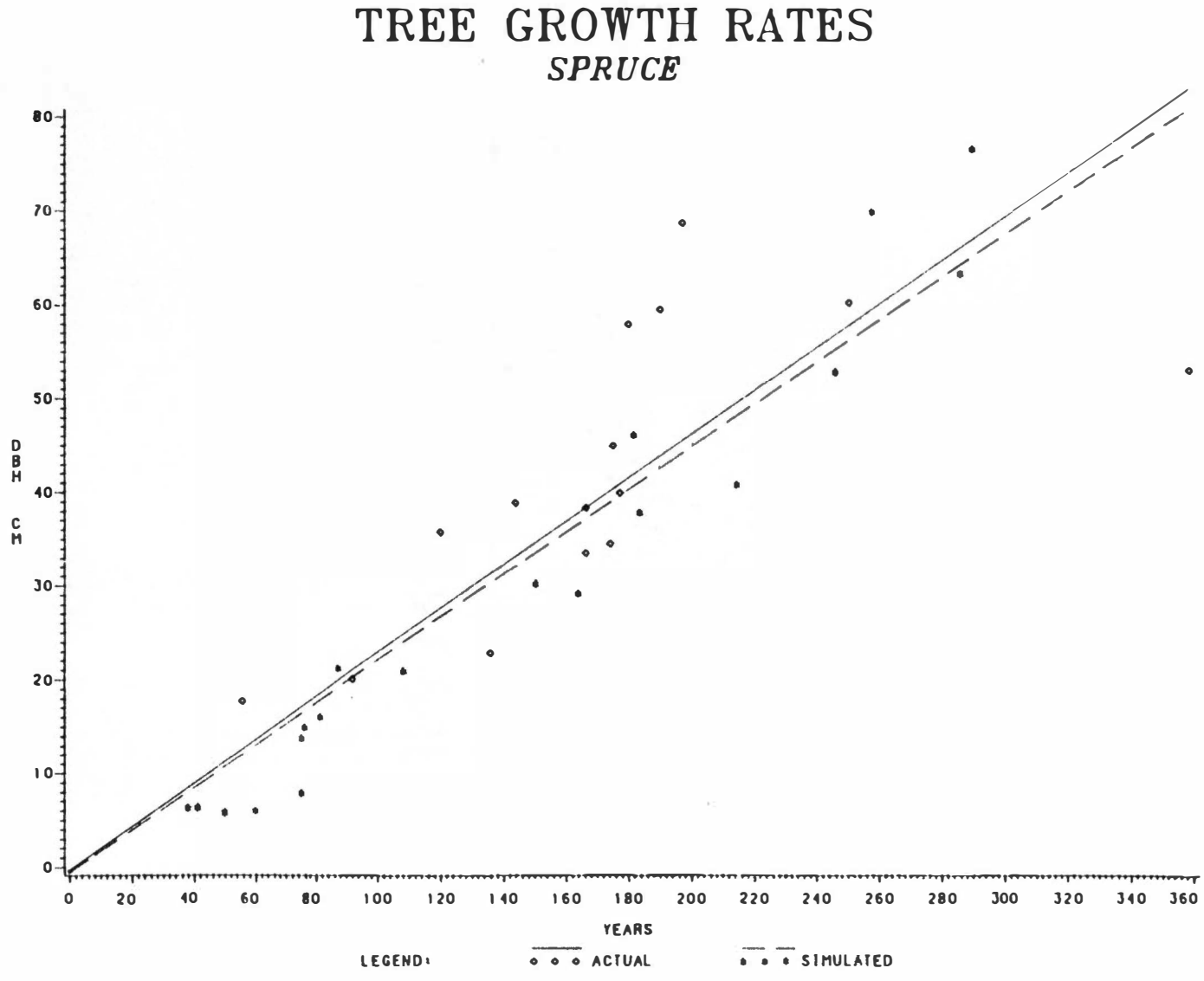


Fig. 36. Graph of simulated vs. actual red spruce growth rates with regression lines.

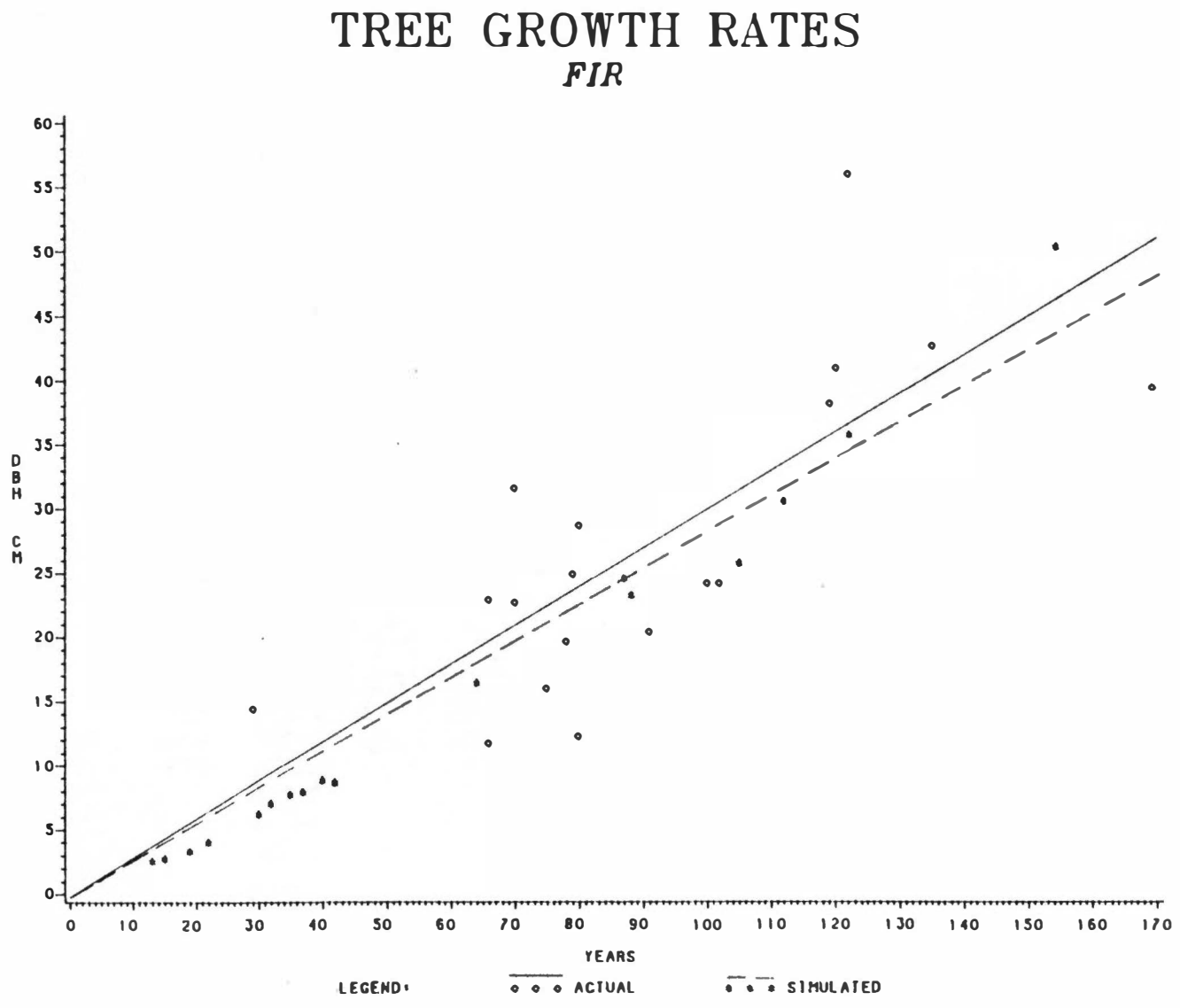


Fig. 37. Graph of simulated vs. actual Fraser fir growth rates with regression lines.

Table 25. Number of fir trees on simulated plots using two different CTOL values.

CTOL	Year						Mean
	50	100	150	200	250	300	
35	41	23	46	17	34	12	28.8
75	78	67	47	81	30	59	60.3

NSEDL is the maximum potential annual seedling input of a species. Estimation of NSEDL values was accomplished by comparing simulated species densities with densities from actual stands. Seedling input rates on bare plots were estimated using stand data from a 25 year-old burn in a spruce-fir forest of the Plott Balsam Mountains (Saunders et al. 1981). NSEDL values were adjusted until reasonable agreement between simulated and actual stand attributes were obtained. Seedling inputs on bare plots are much higher than in developing and mature spruce-fir stands. For this reason the value of NSEDL is reduced for each species, except spruce, when the leaf area of a simulated plot exceeds a critical value. NSEDL values for mature stands were adjusted to obtain simulated tree densities similar to those of old-growth stands on Mt. Collins.

Model Verification

Testing a model for agreement with data at hand is termed verification (Shugart and West 1980). An 800 year simulation of 40 plots was run to test for reasonable species composition changes during forest development. The simulated dynamics of biomass by species are dramatic (Fig. 38). During the first 10 years of forest

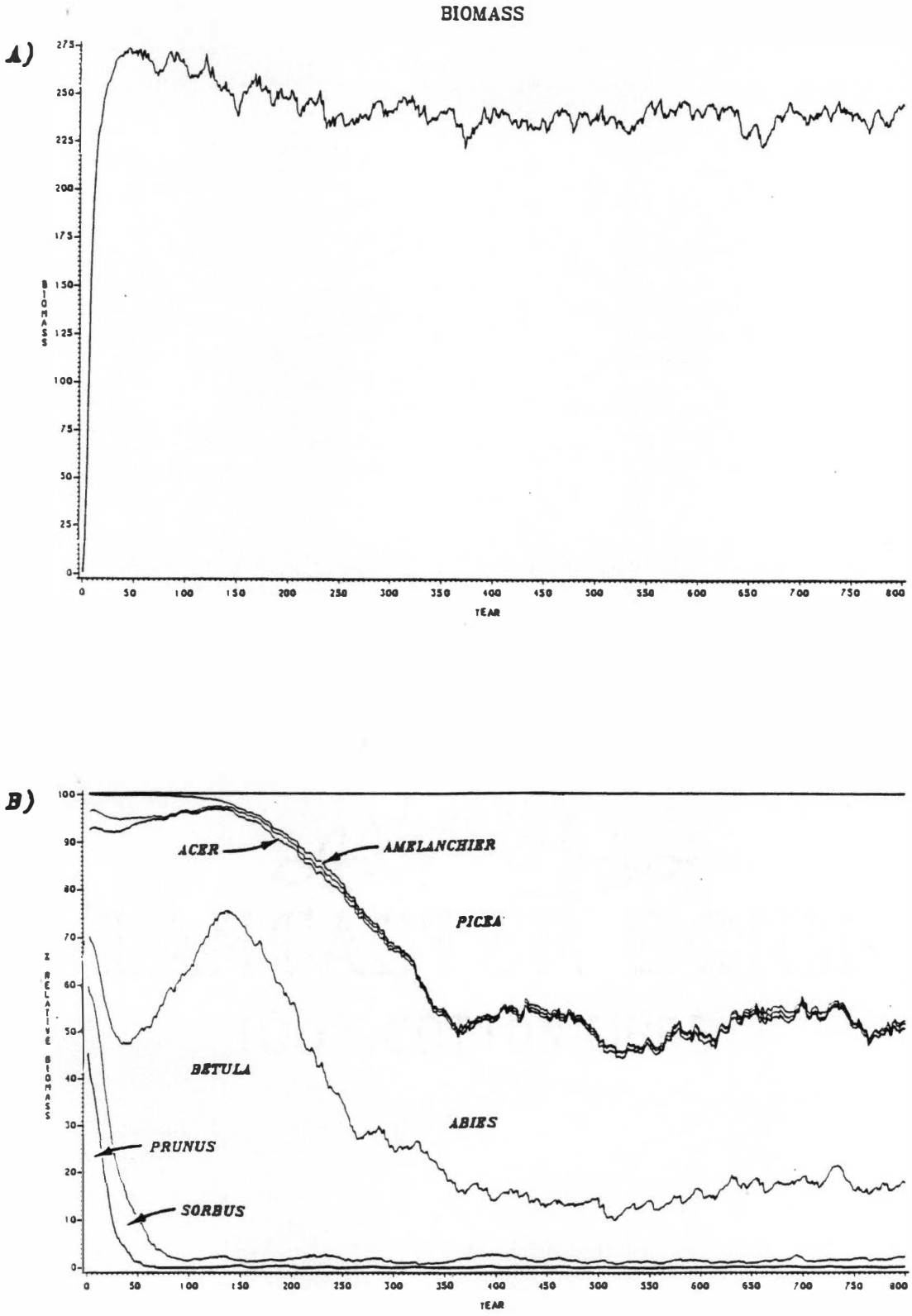


Fig. 38. Graphs of simulated biomass dynamics. These are: A) total biomass (t/ha), and B) relative biomass of individual species.

development fire cherry dominates the stand. By year 30 fir and birch have become the forest dominants. Between years 100 and 175 birch dominates as the colonizing stand of fir declines. By year 300 the importance of birch has diminished and spruce begins to codominate the forest with fir. A mature spruce-fir forest, dominated by spruce, has developed by year 400.

The long-term simulation initiated with bare plots produced successional trends compatible with those described for spruce-fir forests. The importance of fire cherry and yellow birch in successional stands is consistent with the observations of Davis (1930) and Ramseur (1960). Although Davis (1930) observed fir in young stands, he did not consider it to be an important component of colonizing stands. In contrast, Ramseur (1976) and Saunders et al. (1981) found fir to be an important component of stands invading areas subject to severe disturbance. Obviously, the species composition of colonizing stands is variable; it appears to depend on the type of disturbance and the availability of conifer seeds (Korstian 1937, Weaver 1972). In this simulation a population of fir seeds is available following disturbance and it gives rise to a large fir population (Fig. 39). The simulated recovery of spruce is slow (>150 yr). It becomes an important stand component after the first generation of hardwoods declines. These results are consistent with the observations of Korstian (1937) for severely disturbed spruce forests. In general, the long-term simulation produces results in agreement with information at hand. Additional simulation results are presented and further tested in the following chapter.

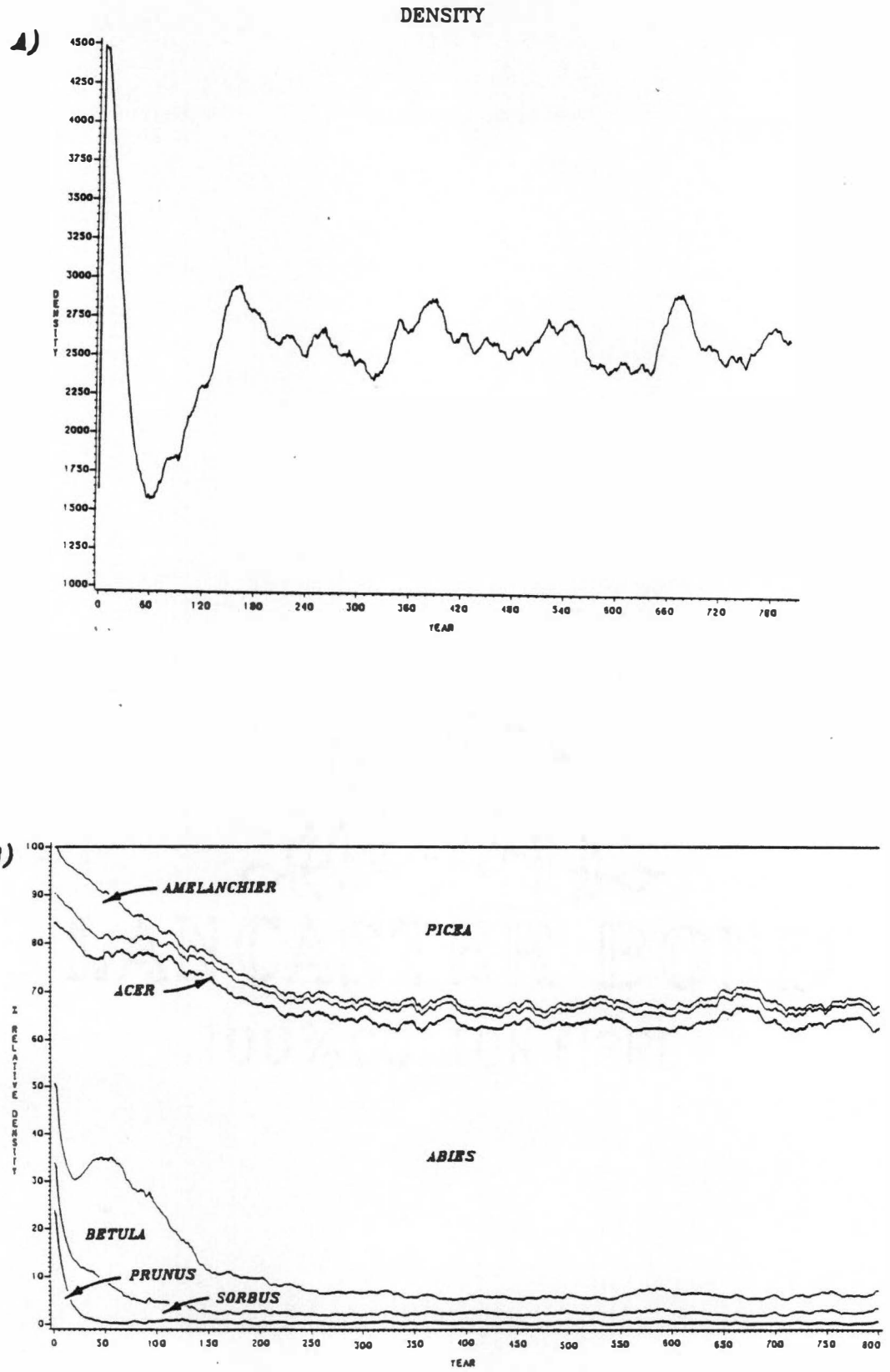


Fig. 39. Graphs of simulated density dynamics. These are: A) total density (stems > 1.27 cm DBH/ha), and B) relative density of individual species.

CHAPTER VII

GAP MODEL VALIDATION AND APPLICATION

Model Validation

Validation of a model involves testing for agreement with data independent of that used in model verification. The purpose of validation is to test the reliability of the model in order to insure that it will not produce unreasonable predictions (Shugart 1984). Several independent data sets quantifying forest responses to disturbance were used in model validation. Two of these sets were from second-growth forests generated by logging without subsequent burning. Density and basal area of tree species in stands approximately 35 and 50 years old were compared to those of simulated stands. Logging of an old-growth stand was simulated by the simultaneous death of all trees over 15 cm DBH in 40 plots representing a mature spruce-fir stand. The general predicted stand response was an increase in total density accompanied by increases in the relative densities of cherry, ash and birch (Fig. 40). Total stand basal area recovers rapidly (<30 yr). The relative basal area of fir increases sharply while that of spruce and that of birch decrease after logging (Fig. 41). Table 26 compares simulated and actual quantitative data for logged stands. The agreement between simulated and actual species relative densities is within 10 percentage points except for 35 year spruce and fir values. Spruce relative density was overestimated almost two times the actual value, while fir relative density was underestimated. Agreement between

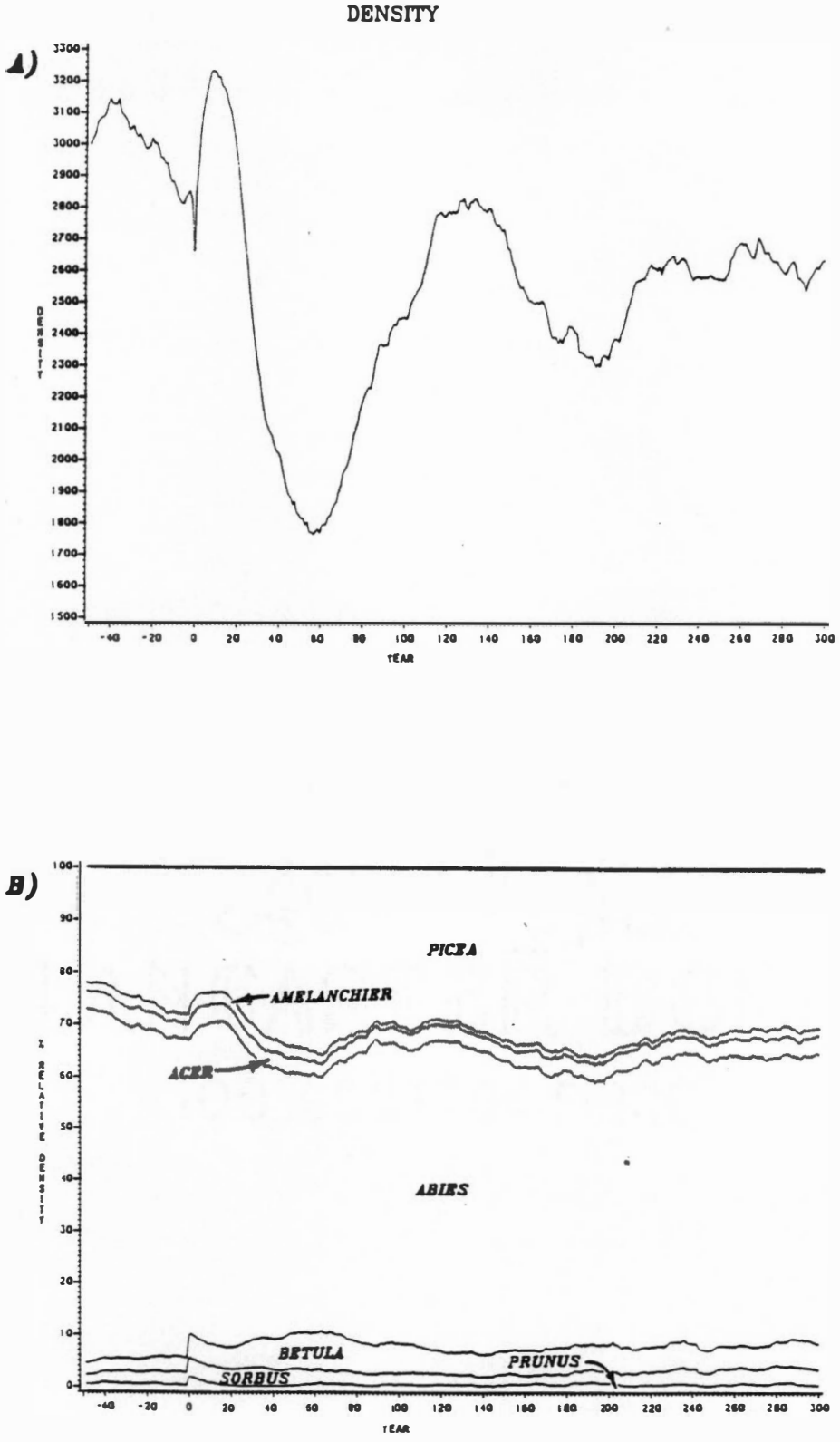


Fig. 40. Graphs of simulated density responses to logging. These are: A) total stand density (stems > 1.27 cm DBH/ha), and B) relative density. Logging occurs at year 0.

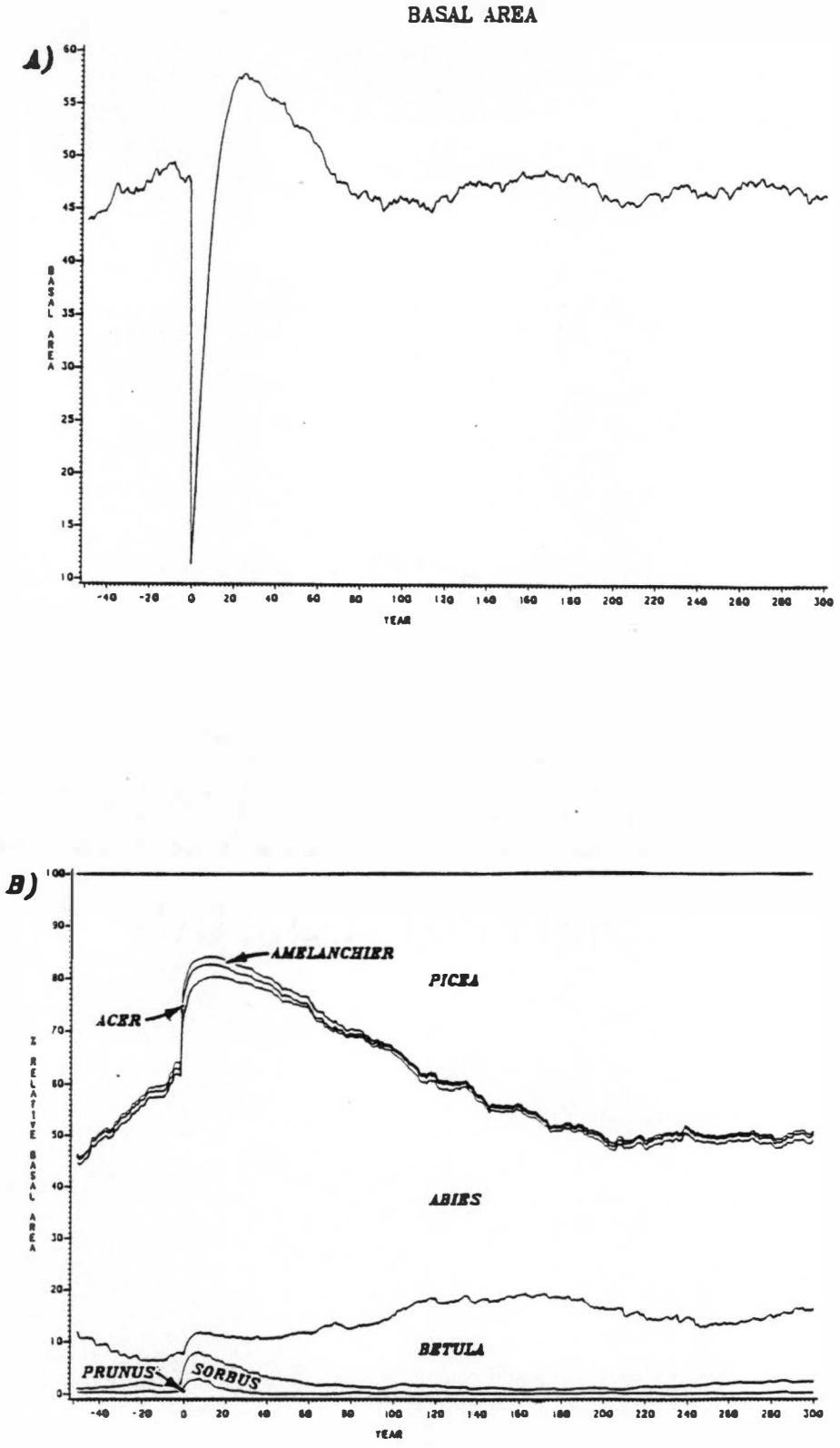


Fig. 41. Graphs of simulated basal area responses to logging. These are: A) total stand basal area (m^2/ha) and B) relative basal area. Logging occurs at year 0.

Table 26. Attributes of simulated and actual stands recovering from logging.[a]

Recovery Time	Species	Relative Density (%)	Basal Area (m^2/ha)	Relative Basal Area (%)
35 years[b]	*Picea rubens*	32(17)	11(8)	19(22)
	Abies fraseri	53(68)	37(36)	67(67)
	Betula lutea	6(5)	4(3)	7(5)
	Sorbus americana	4(10)	2(3)	4(5)
	Acer spicatum	3(<1)	1(<1)	2(<1)
50 years[c]	*Picea rubens*	34(33)	12(14)	22(26)
	Abies fraseri	50(59)	34(36)	64(62)
	Betula lutea	7(5)	5(1)	9(10)
	Sorbus americana	3(2)	2(<1)	3(<1)
	Acer spicatum	3(1)	1(<1)	1(<1)

[a]Actual values are given in parentheses.

[b]Actual values are from Shields (1962).

[c]Actual values are from Weaver (1972).

simulated and actual species basal areas was very good for both recovery times considered. All predicted and actual species basal areas differed by no more than 4 m^2/ha. The inconsistency between 35 year relative density values of simulated and actual stands is not unreasonable, and the fact that there is good agreement in relative density values for species of 50 year stands supports the reliability of the model. It appears that the quantitative predictions of the model in response to canopy tree removal are moderately accurate.

Another test of the model involved the simulation of mature forest response to aphid infestation. A stand-wide continuous infestation was simulated by increasing the mortality of large and/or suppressed fir trees which are the most susceptible to insect attack (Johnson 1977). Fir trees exceeding 15.5 cm DBH were given an additional 60% annual mortality probability while strongly suppressed trees were given an additional 95% annual mortality probability. The simulation results were compared to information on actual stands. Field observations on short-term responses (5-20 yr after loss of fir canopy) agree well with the simulation results. Although extensive quantitative studies on forest responses are incomplete at this time, general information is available. Pertinent findings include an increase in fir subsapling densities (Boner 1979), an increase in maple, ash and cherry sapling densities (DeSelm and Boner 1984), and an increase in the number of large spruce and large birch trees (Saunders 1977). Infested stands tend to be dominated by spruce and birch (Saunders 1977, DeSelm and Boner 1984). All of these short-term responses are predicted by the model. Total stand density increases

sharply after opening of the canopy (Fig. 42A). The relative density of fir increases while that of spruce decreases; other species maintain a constant relative density (Fig. 42B). Total stand basal area increases rapidly during stand recovery. The relative basal areas of spruce, birch, ash and maple increase in response to infestation. Similar biomass responses are predicted by the model (Fig. 43). Spruce and birch have the highest relative biomass values and are therefore the dominants of infested stands.

In conclusion, the model is reliable in simulations of moderately intense disturbances that open patches in the forest canopy. It has not predicted unreasonable species responses to disturbances of this kind. However, the model's adequacy may be limited to disturbances of low to moderate intensity. Severe disturbances involving the death of all trees, the disruption of seed sources and the alteration of soil conditions are probably beyond the predictive capabilities of this model.

Model Application

The model was used to predict future forest composition, structure and dynamics in the spruce-fir zone in response to several potential anthropogenic disturbances. The disturbances included: 1) continuous aphid infestation with fir regeneration, 2) infestation with complete elimination of fir, 3) retardation of spruce growth, and 4) increased spruce mortality. Long-term simulations of forest response were run for each of these disturbances and for the combined effects of declines in both spruce and fir populations.

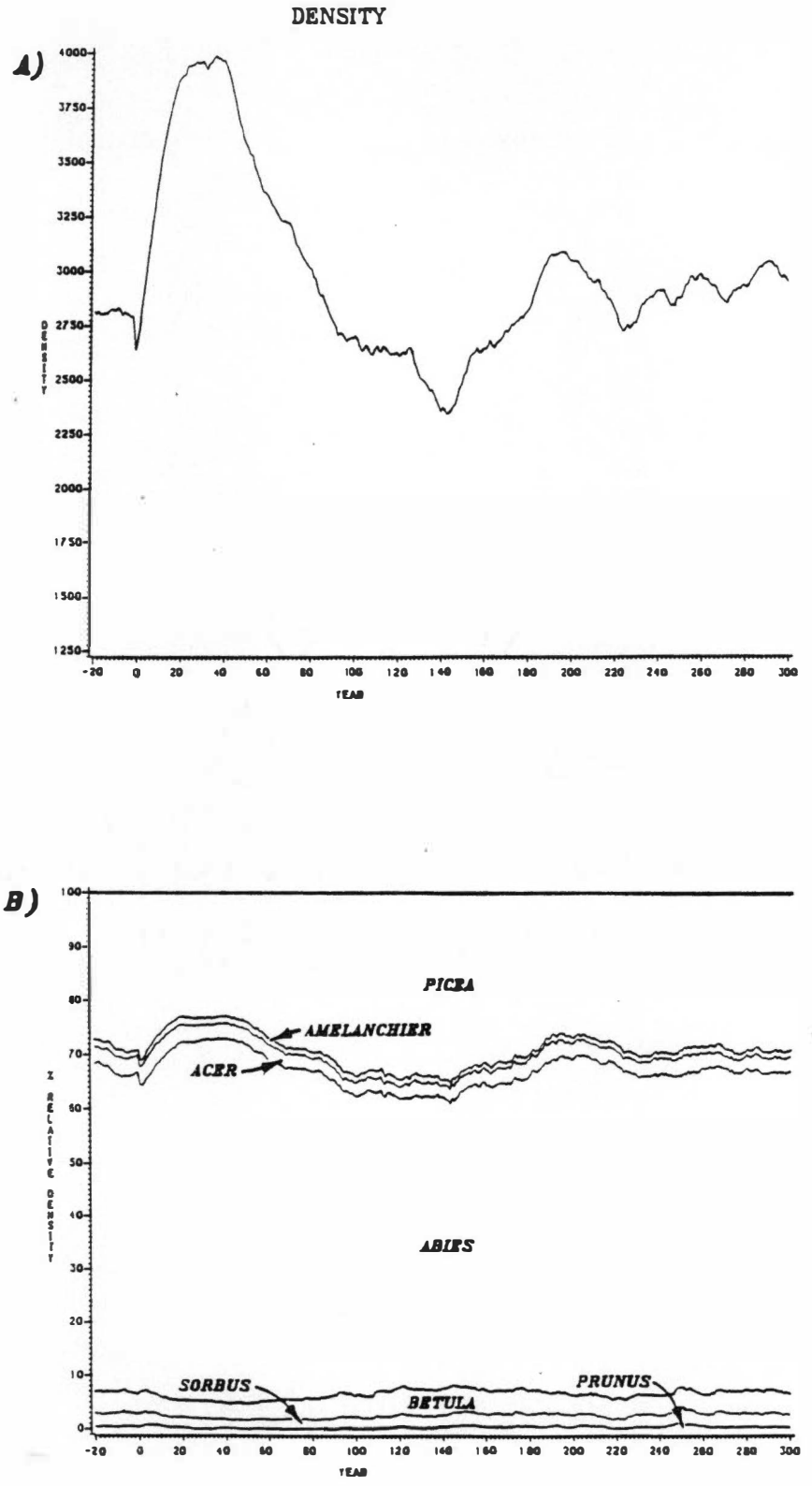


Fig. 42. Graphs of simulated density responses to continuous aphid infestation. These are: A) total stand density (stems > 1.27 cm DBH/ha), and B) relative density. Infestation begins at year 0.

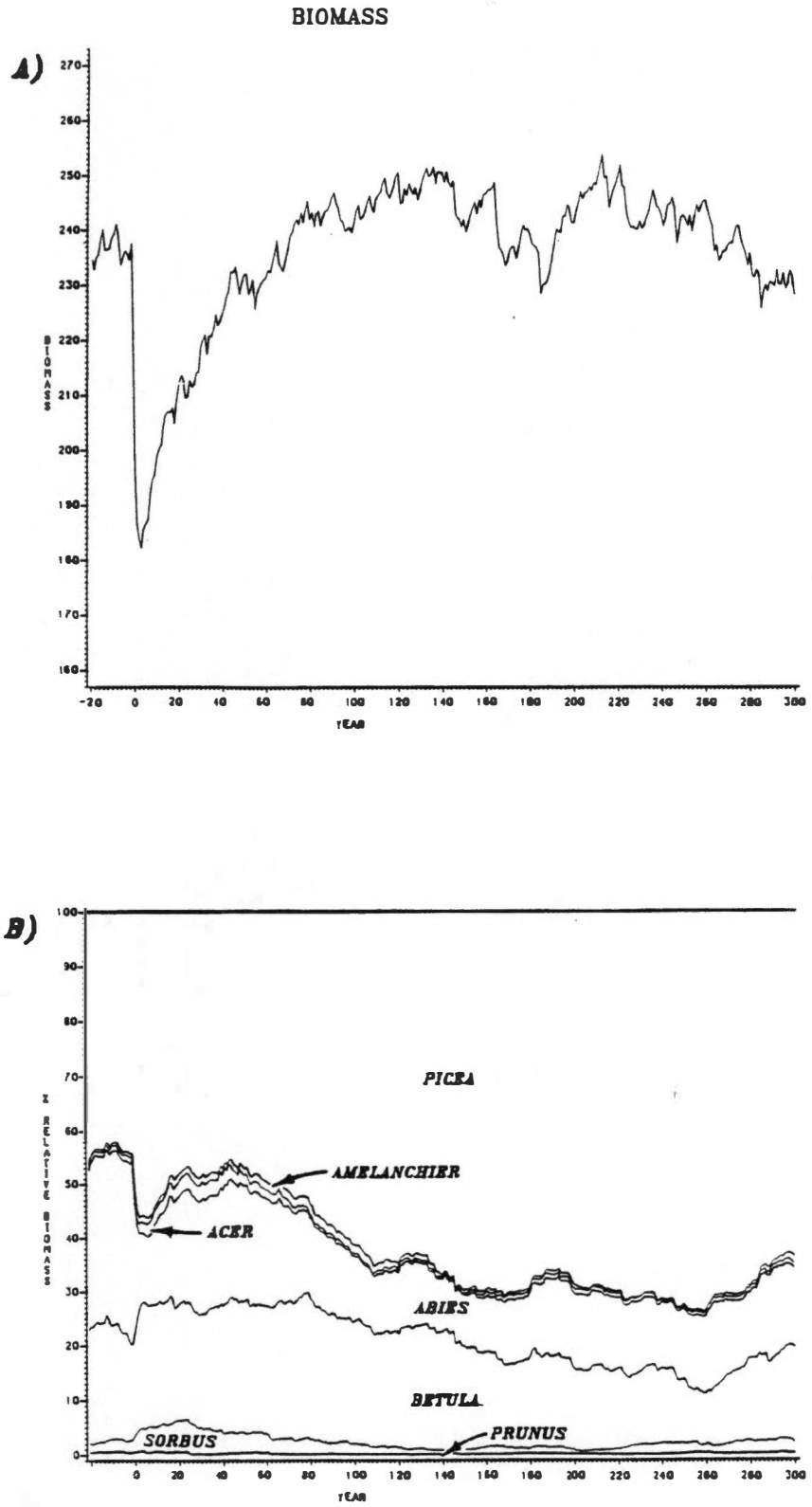


Fig. 43. Graphs of simulated biomass responses to continuous aphid infestation. These are: A) total stand biomass (t/ha), and B) relative biomass. Infestation begins at year 0.

A long-term simulation of mature spruce-fir forest dynamics without extrinsic disturbance produced a steady state condition lacking large fluctuations in stand density and biomass (Figs. 38 and 39). Over a 400 year period total stand density varied from 2400 to 2900 stems/ha. Spruce accounted for 29 to 33% of the total density, fir 55 to 61% and birch 2 to 5%. Total stand biomass varied from 220 to 250 t/ha. Spruce accounted for 43 to 51% of the total biomass, fir 31 to 41% and birch 9 to 20%. These figures will serve as a basis for comparison with simulations of disturbed stands.

The simulation of continuous aphid infestation with fir regeneration produced an increase in stand density (Fig. 42). Initially, stand density increased to 4000 stems/ha (30-40 yr) and exceeded 3000 stems/ha centuries after the onset of stand infestation. The relative density of fir also increased to a maximum of 68% (30-40 yr) and remained higher than in undisturbed stands. Spruce decreased in relative density, reaching a minimum of 22% (ca. 20 yr). Total stand biomass decreased sharply with the initial infestation and recovered to 240 t/ha within 80 years (Fig. 43). A slight increase in stand biomass is evident and biomass peaks exceeding 250 t/ha are not infrequent. Long-term changes in species relative biomass are apparent. The relative biomass of fir declined to less than 15%. Within the first 100 years of infestation, birch accounted for more than 18% of the total biomass, but gradually decreased in dominance thereafter. Spruce dominated the infested stands, often attaining more than 65% of the total biomass.

Examination of simulated fir population dynamics during a continuous infestation reveals cycles of fir stand growth and dieback. Accordingly, the biomass of fir on a simulated plot periodically decreases to minimal levels at an interval of 50 to 70 years (Fig. 44). At these times the fir population consists almost entirely of small individuals. Over a 50 to 70 year period these individuals grow and succumb to aphid attack upon reaching canopy tree size. This phenomenon of cyclic regeneration has been suggested as the probable outcome of aphid infestation (Hay and Eagar 1981). Continuous seed production is essential for such a cycle to occur. Because fir produces seed abundantly by 30 years of age, there should be no limitation on fir reproduction. In conclusion, fir stand growth and dieback cycles are a likely outcome of continuous stand infestation.

An alternative is the total elimination of fir propagules following infestation. The consequences of a cessation in seed production were simulated by gradually reducing seedling inputs to zero by the 25th year of infestation. As above, there is an initial increase in stand density during the first few decades of infestation (Fig. 45). However, by year 70 stand density has dropped to less than 1400 stems/ha with the lack of fir regeneration. The relative density of fir reaches zero by year 90 indicating the elimination of fir. Following the demise of fir, spruce accounts for more than 60% of the relative density, while birch and maple account for approximately 10% each. Total stand biomass recovers slowly (>100 yr) in the absence of fir (Fig. 46). The resulting forest is clearly dominated by spruce which comprises 68 to 79% of the total biomass. Birch is also an

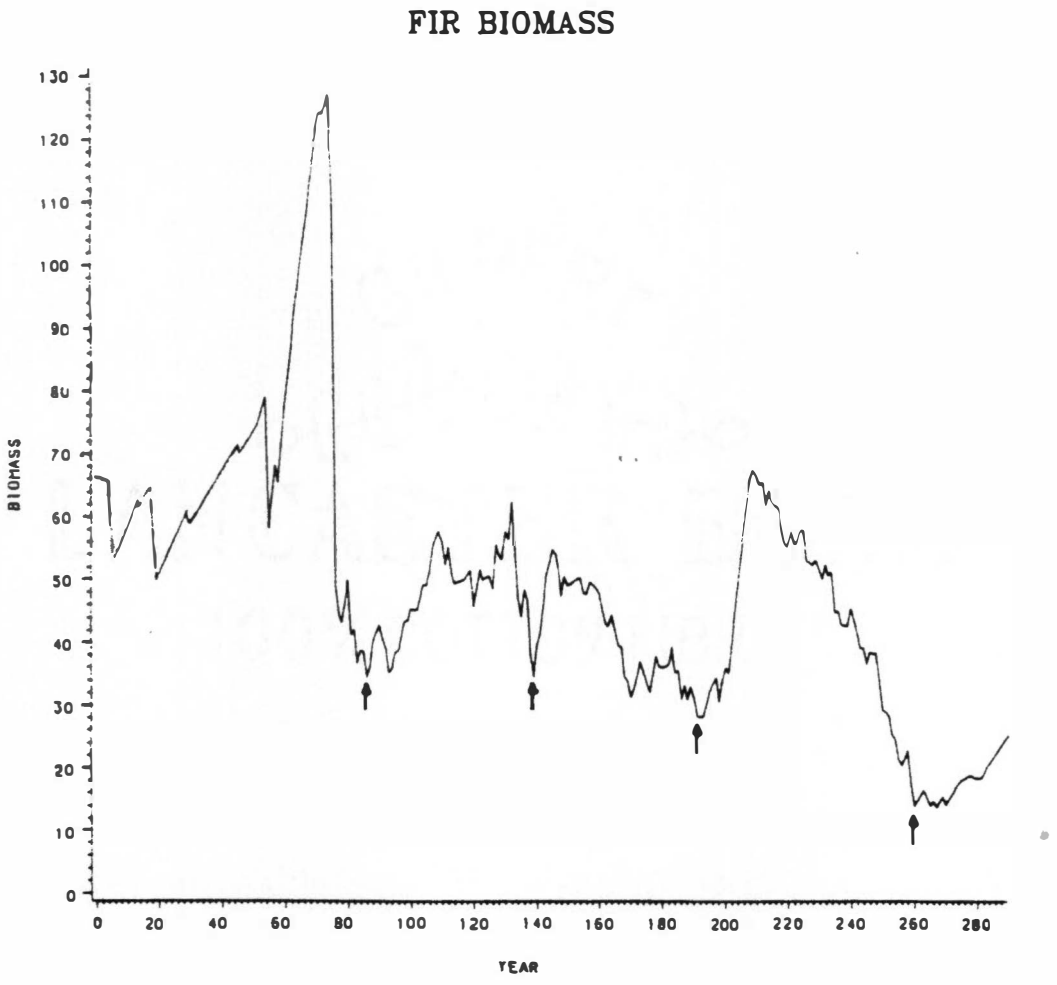


Fig. 44. Graph of fir biomass response to continuous aphid infestation on a simulated plot. Biomass is in t/ha. Infestation begins at year 75; arrows indicate periodic minima.

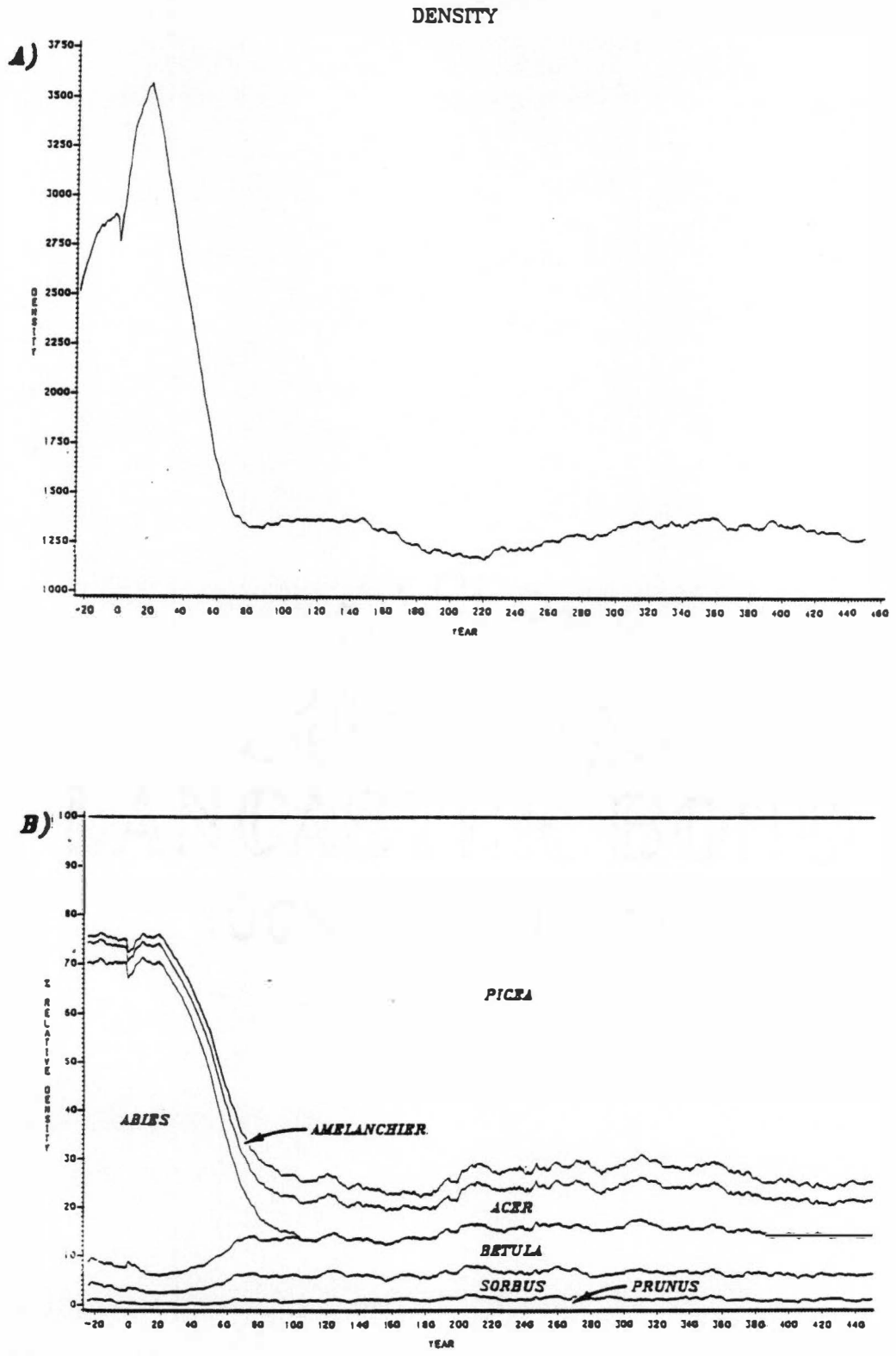


Fig. 45. Graphs of simulated density responses to the elimination of fir. These are: A) total stand density (stems > 1.27 cm DBH/ha), and B) relative density.

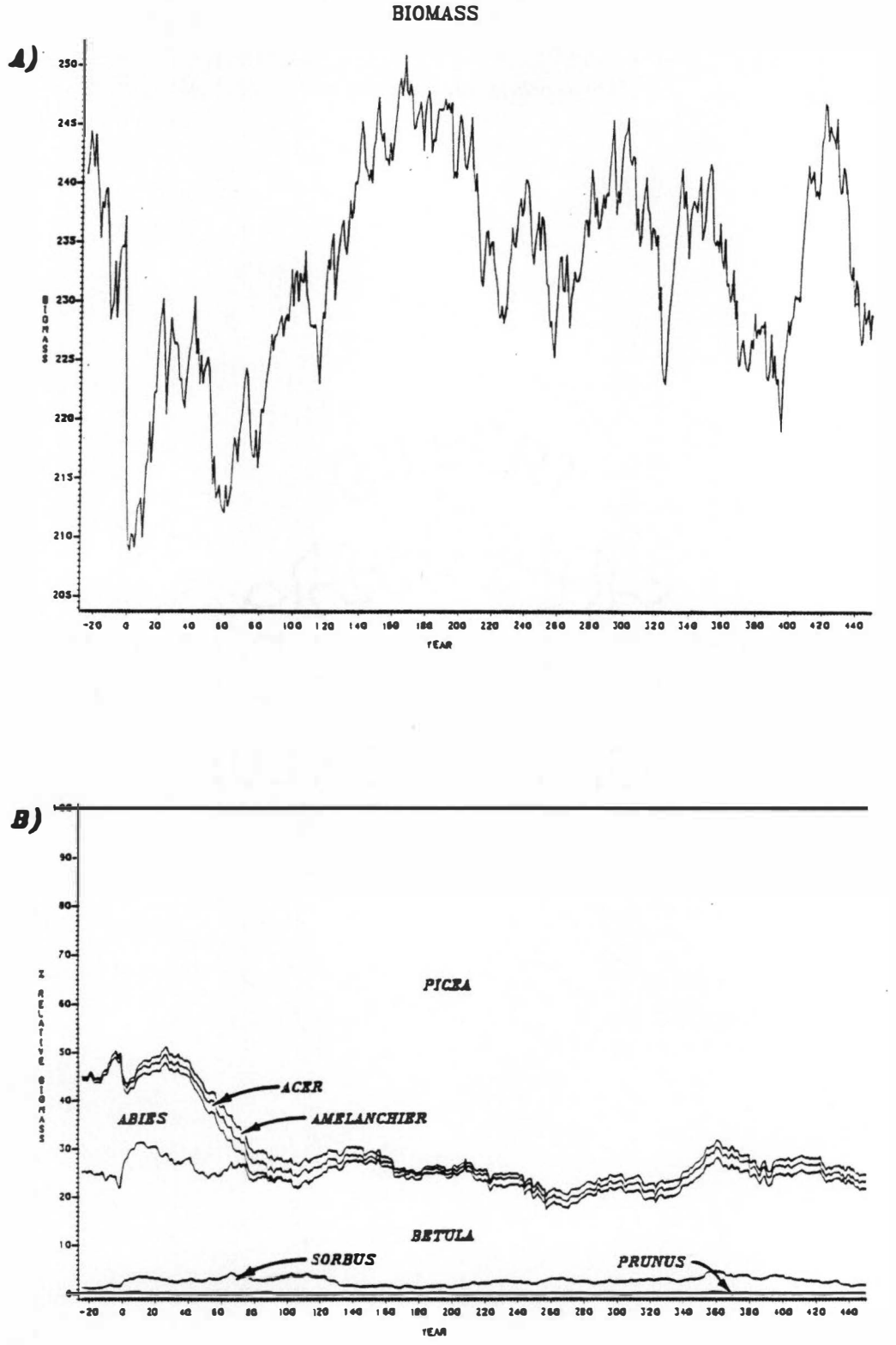


Fig. 46. Graphs of simulated biomass responses to the elimination of fir. These are: A) total stand biomass (t/ha), and B) relative biomass.

important stand component comprising 15 to 25% of the biomass. This forest has attributes similar to those of the spruce-birch vegetation type recognized by Golden (1974).

The ability of the forest to recover from an infestation was investigated by simulating a short-term (10 yr) infestation followed by undisturbed forest growth. Total stand density increases sharply to more than 3400 stems/ha upon infestation (Fig. 47). However, after 60 years of recovery (year 70) density has decreased to 2200 stems/ha as a result of canopy closure. By year 110 density moderates and remains within the limits simulated for an undisturbed stand. Changes in relative density are minor. The relative density of fir exceeds 60% in the interval from year 10 to 30, while that of spruce declines to less than 25%. Relative densities comparable to those of undisturbed stands are recovered by year 25. Total stand biomass also recovers rapidly (<30 yr; Fig. 48). An overshoot peak of 260 t/ha is attained at year 65 and biomass moderates shortly thereafter (year 75). The relative biomass of fir returns to undisturbed levels by year 50.

The effect of spruce growth decline on the forest was simulated by decreasing the growth scaling parameter (G) of spruce. Initially, the value of this parameter was decreased by 10%, the level of reduction applied by West et al. (1980) to moderately pollutant-sensitive trees. Spruce shows a slight simulated response to the growth reduction. It remains an important stand component although it decreases in relative biomass by approximately 10% (Fig. 49). An increase in the relative biomass of fir is associated with the slight

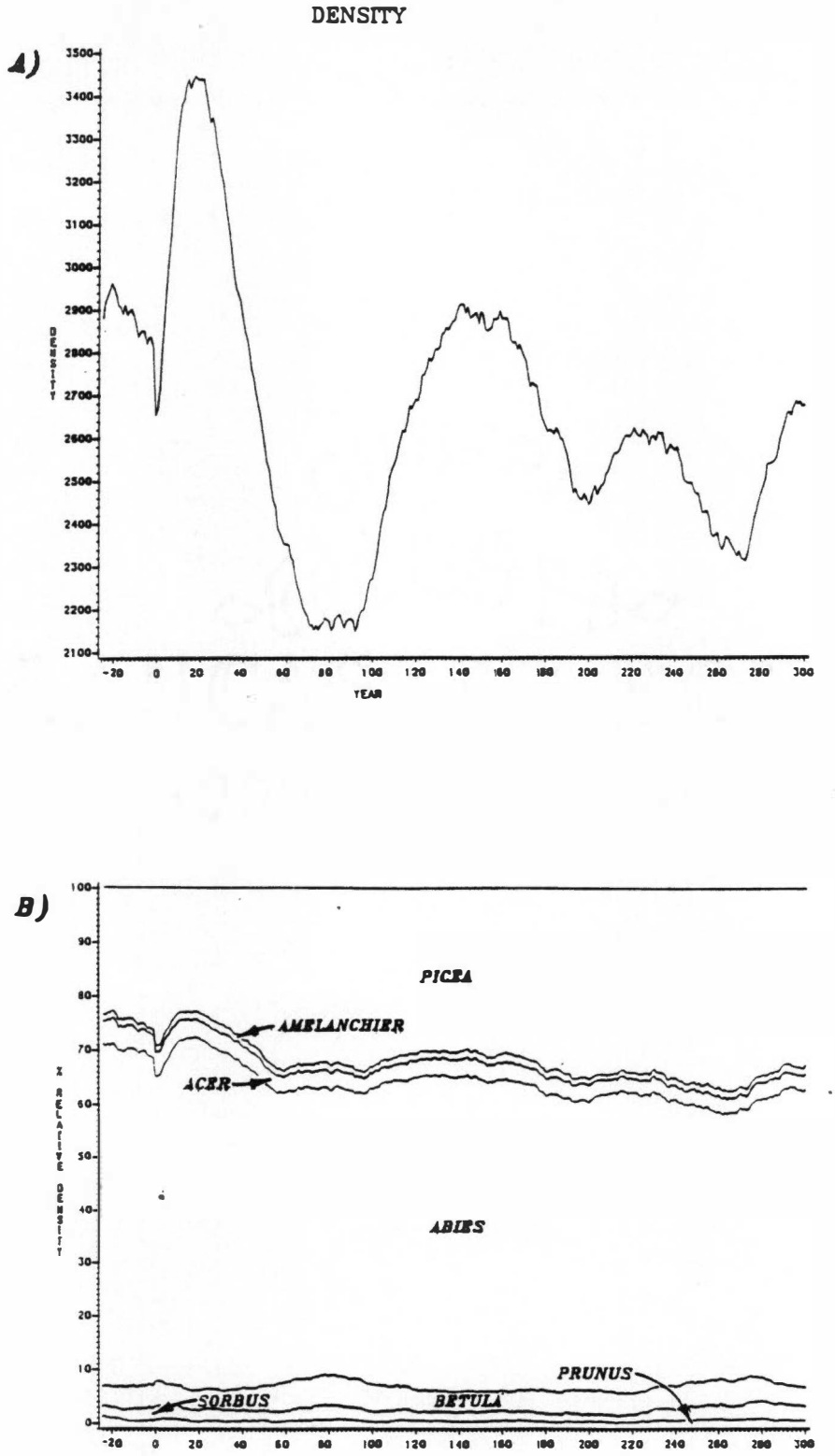


Fig. 47. Graphs of simulated density responses to a short-term fir infestation. These are: A) total stand density (stems > 1.27 cm DBH/ha), and B) relative density. The 10 yr infestation begins at year 0.

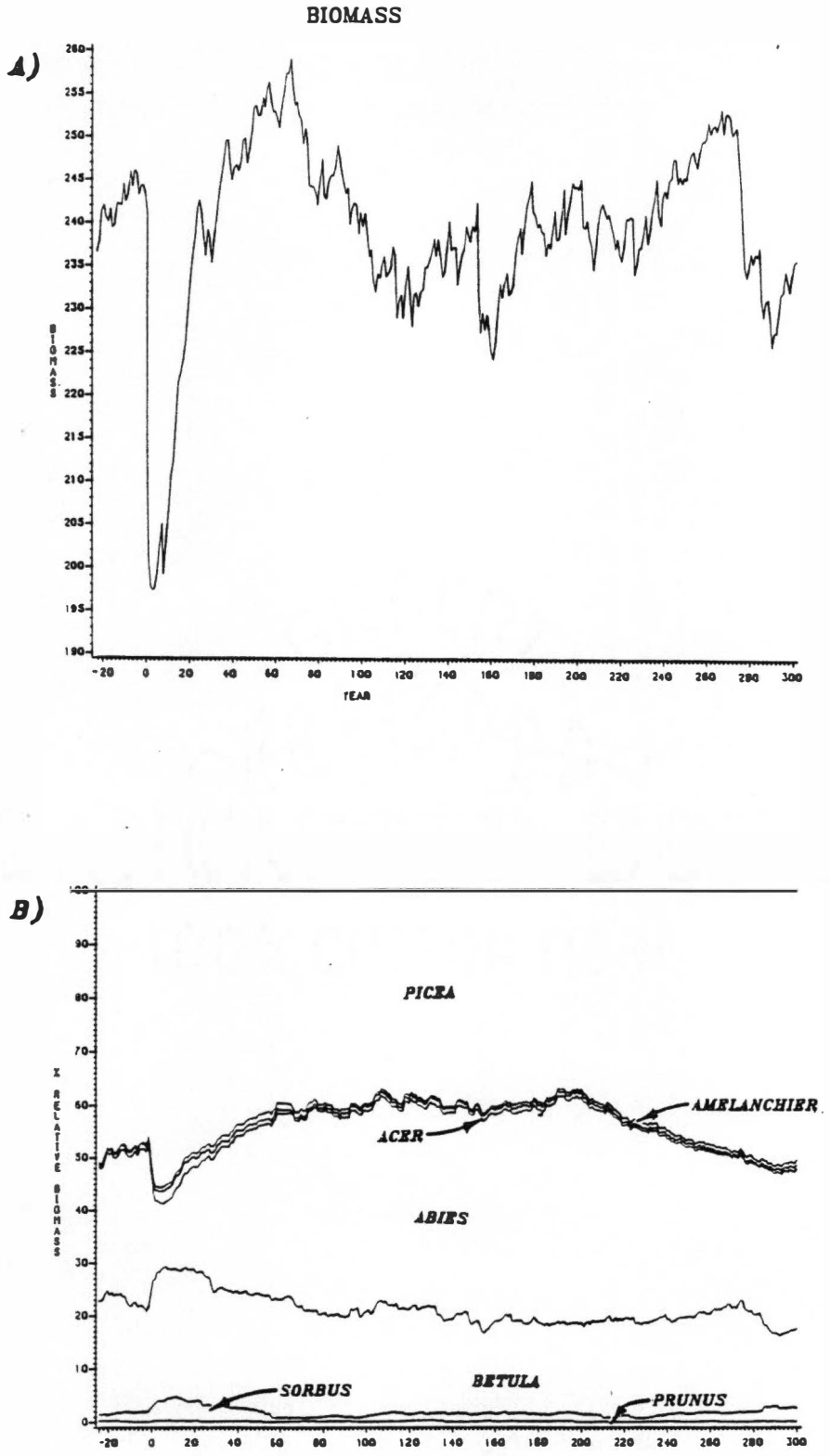


Fig. 48. Graphs of simulated biomass responses to a short-term fir infestation. These are: A) total stand biomass (t/ha), and B) relative biomass. The 10 yr infestation begins at year 0.

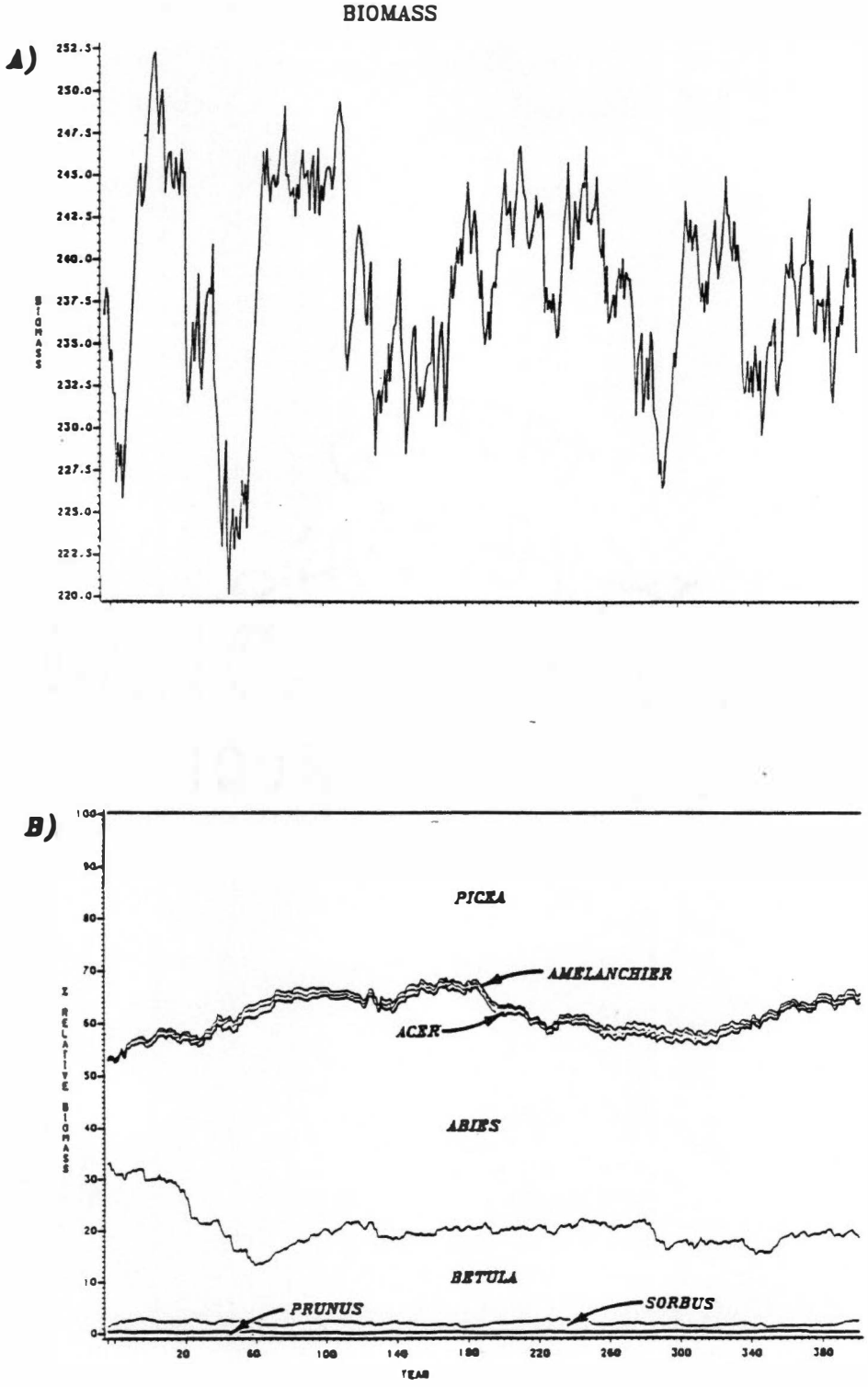


Fig. 49. Graphs of simulated biomass responses to a 10% spruce growth decline. These are: A) total stand biomass (t/ha), and B) relative biomass. Growth decline begins at year 0.

decline in spruce. In other aspects the stand resembles an undisturbed stand.

Further reduction of spruce growth was simulated by a 30% decrease in the growth scaling parameter (G). This reduction is on the order of actual growth decline measurements for red spruce in the southern Appalachians (McLaughlin and Braker 1985). It causes a dramatic decrease in the importance of spruce. The relative density of spruce diminishes to less than 15%, while that of fir increases to more than 70% (Fig. 50). Total stand biomass is generally unaltered by the spruce growth decline (Fig. 51). However, the proportions of biomass comprised by spruce and fir are greatly altered. By year 40 the relative biomass of spruce has declined to less than 30% and it continues to decline to approximately 15% by year 200, and to less than 10% by year 300. Fir clearly dominates the forest with a relative biomass of 50 to 75%. Birch also increases in importance, often comprising more than 25% of the biomass.

Forest recovery from a short-term decline in red spruce growth was simulated by reducing the growth scaling parameter of spruce by 30% for a 30 year period. The 30 year growth reduction only slightly affected forest composition. A gradual decrease in the relative biomass of spruce from 50% at year 0 to 35% at year 90 is evident (Fig. 52). The recovery of spruce, as indicated by relative biomass, is gradual. By year 170 spruce accounts for more than 40% of the total biomass, and by year 210 it accounts for more than 45%. It appears that the relative dominance of spruce is moderately resistant

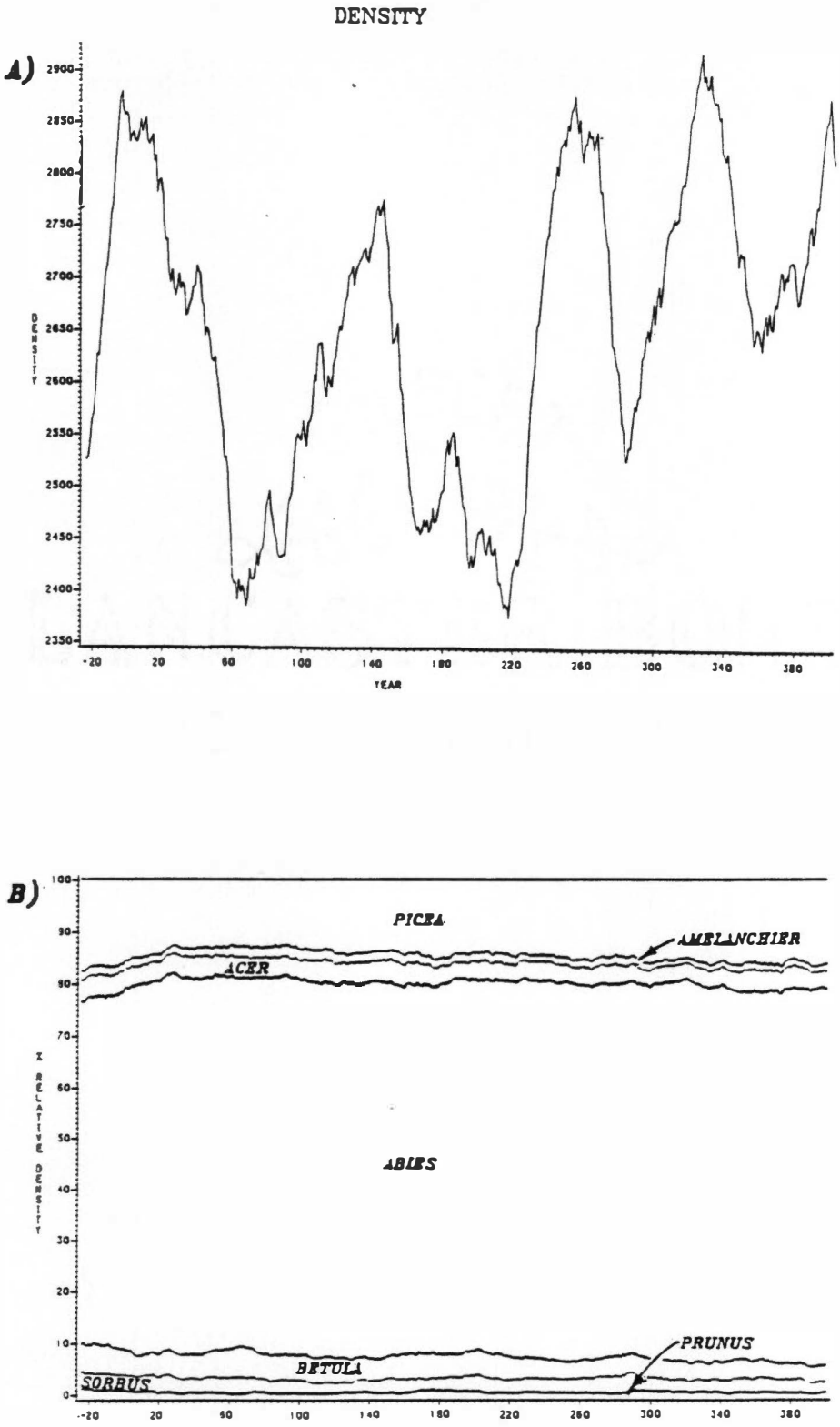


Fig. 50. Graphs of simulated density responses to a 30% spruce growth decline. These are: A) total stand density (stems > 1.27 cm DBH/ha), and B) relative density. Growth decline begins at year 0.

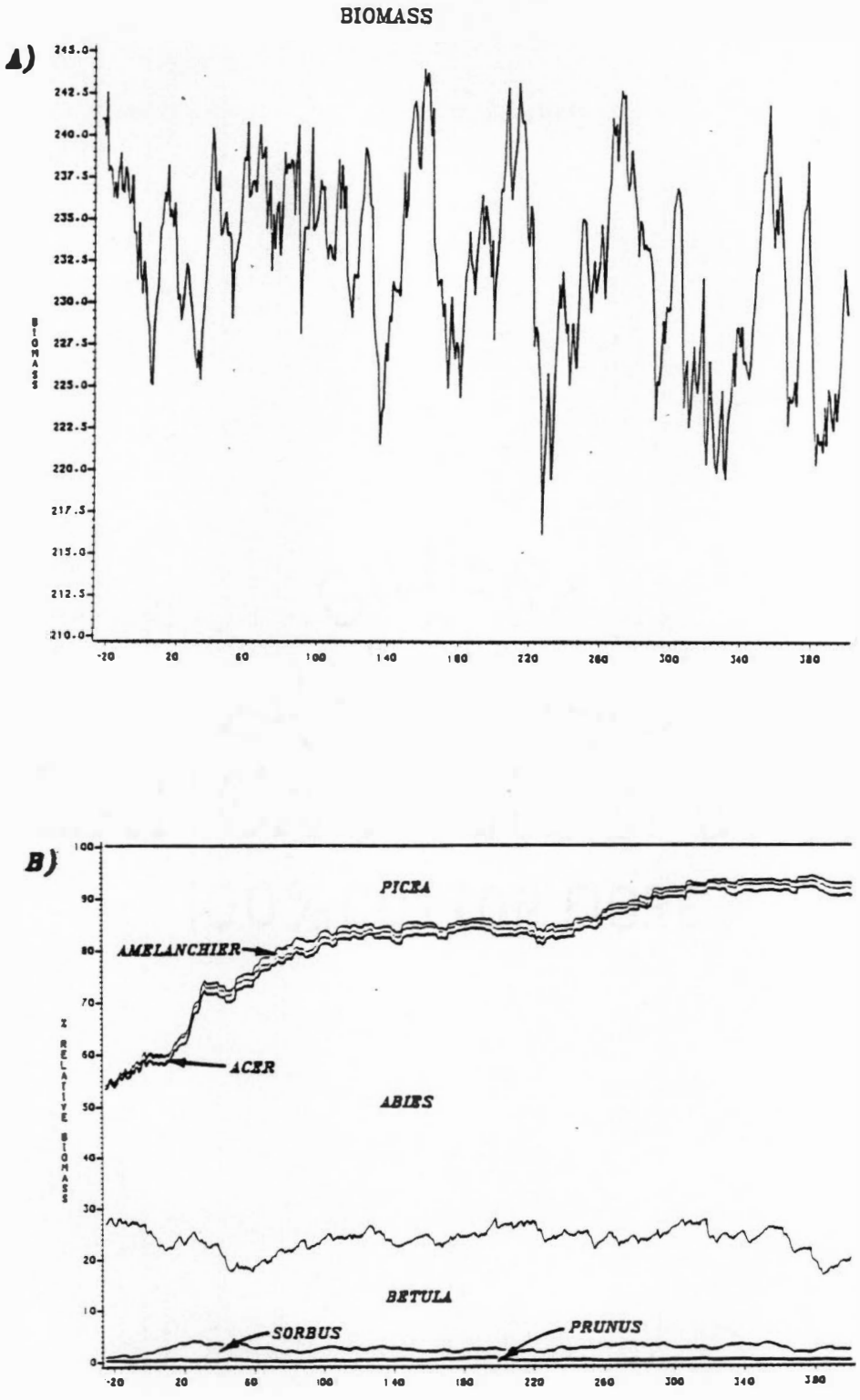


Fig. 51. Graphs of simulated biomass responses to a 30% spruce growth decline. These are: A) total stand biomass (t/ha), and B) relative biomass. Growth decline begins at year 0.

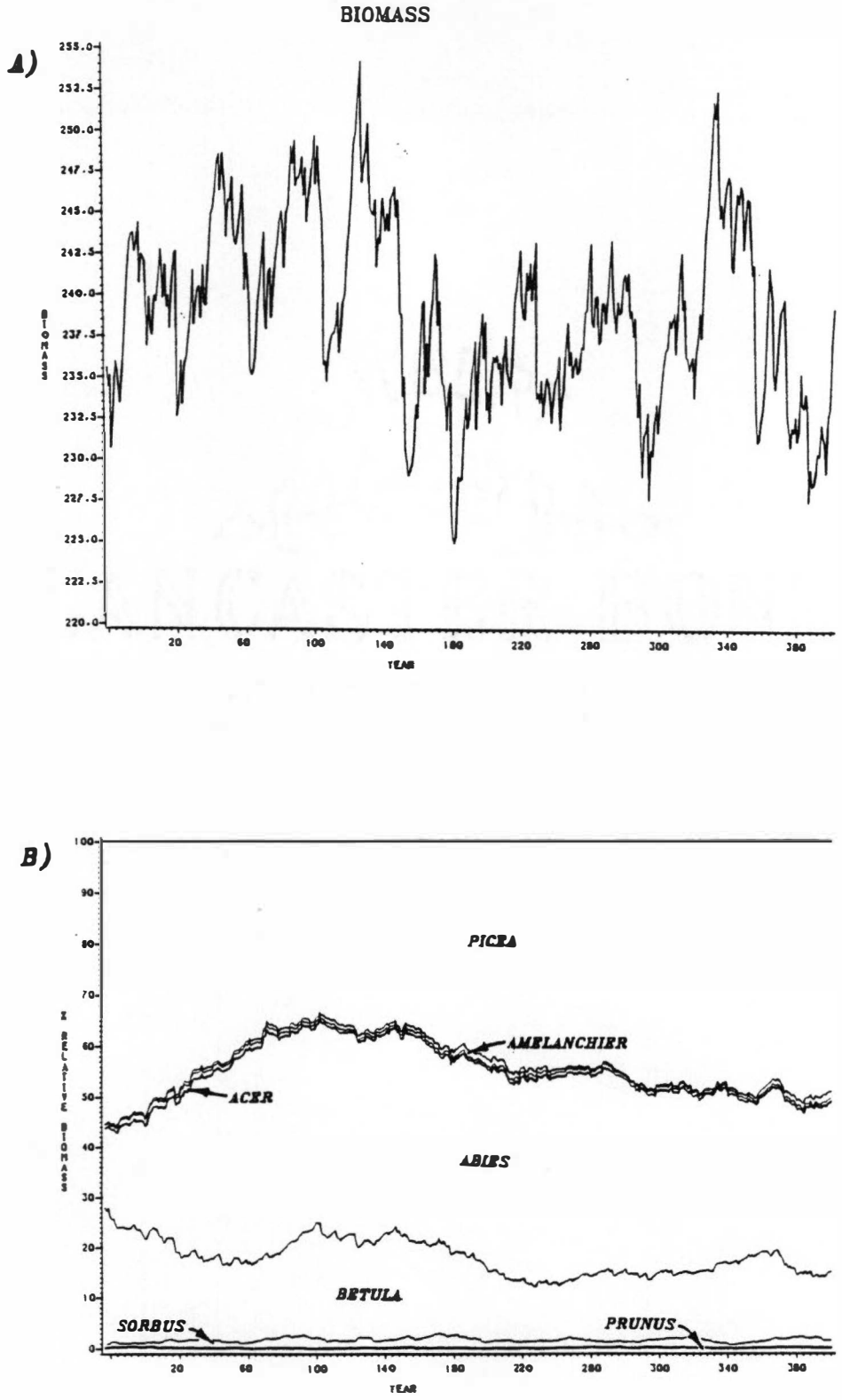


Fig. 52. Graphs of simulated biomass responses to a short-term, 30% spruce growth decline. These are: A) total stand biomass (t/ha), and B) relative biomass. The 30 yr growth decline begins at year 0.

to short-term growth reductions of 30 years or less, but the recovery time from even slight perturbations is great (>150 yr).

The combined effects of declines in spruce and fir populations on forest attributes were simulated in a similar manner. The initial simulation involved the simultaneous onset of a continuous aphid infestation of the fir population and a 30% growth decline in spruce trees. Shortly after disturbance total stand density increases rapidly to more than 4100 stems/ha (50 yr) and remains high (>3200 stems/ha) throughout the 400 year simulation (Fig. 53). An increase in the relative density of fir and a decrease in the relative density of spruce result from the combined disturbances. Total biomass declines immediately to less than 190 t/ha upon disturbance of the stand and remains low (<235 t/ha) thereafter (Fig. 54). Spruce and birch dominate the stand, accounting for 35 to 50% and 20 to 34% of the stand biomass, respectively. Fir is also an important stand component, comprising 18 to 27% of the biomass. In general, the disturbance regime produces a dense stand of small trees. Fir is by far the most abundant species in the stand, while birch is the only species that commonly attains large size (>60 cm DBH). Spruce dominates because it is more abundant than birch. The importance of spruce despite a 30% decline in its growth is notable. In the presence of mature, healthy fir trees spruce declined in importance when subjected to a 30% growth reduction (Fig. 51). The lack of competition from large fir trees allows spruce to dominate in this case.

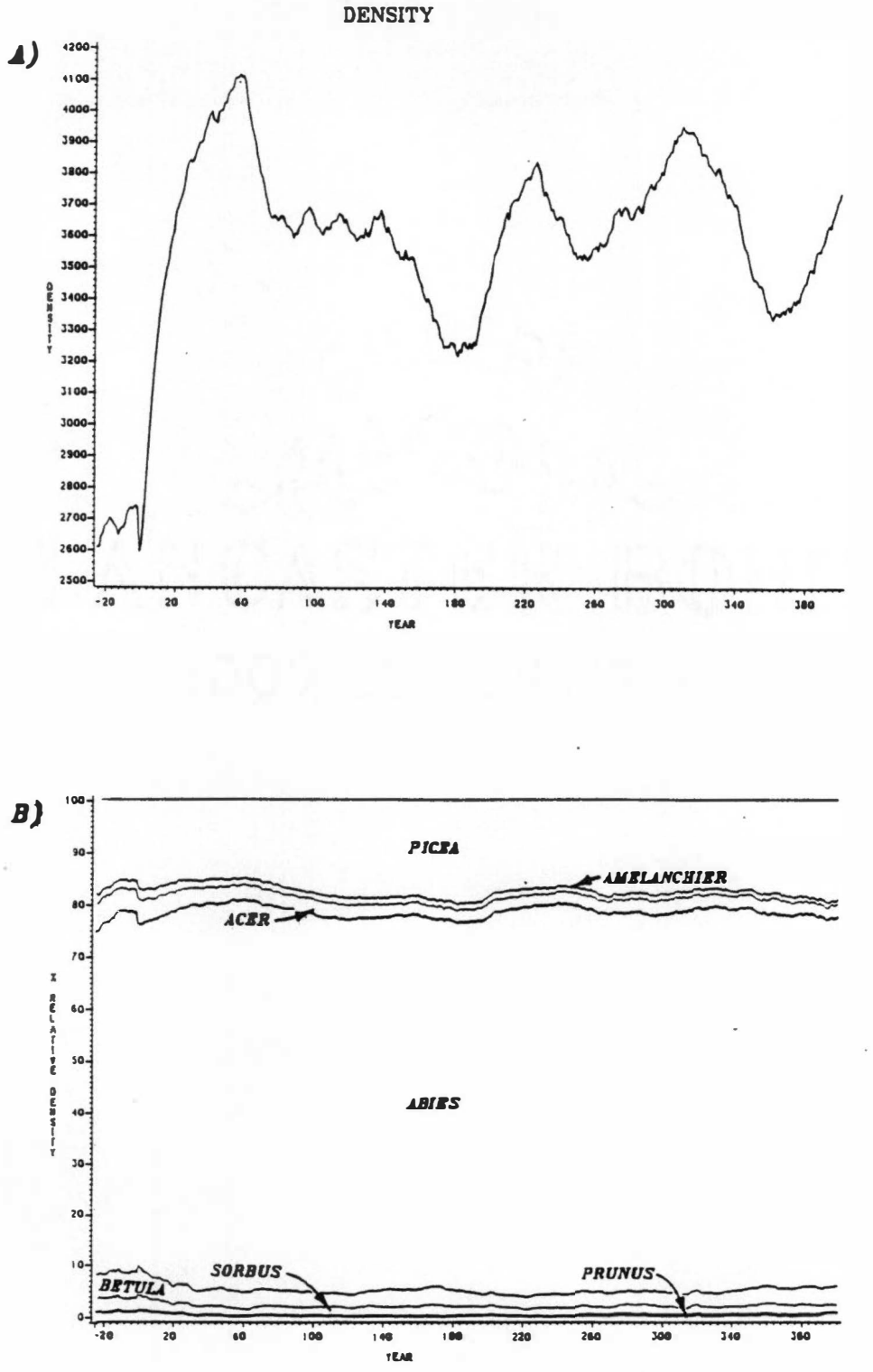


Fig. 53. Graphs of simulated density responses to continuous aphid infestation in combination with a 30% spruce growth decline. These are: A) total stand density (stems > 1.27 cm DBH/ha), and B) relative density. Disturbance begins at year 0.

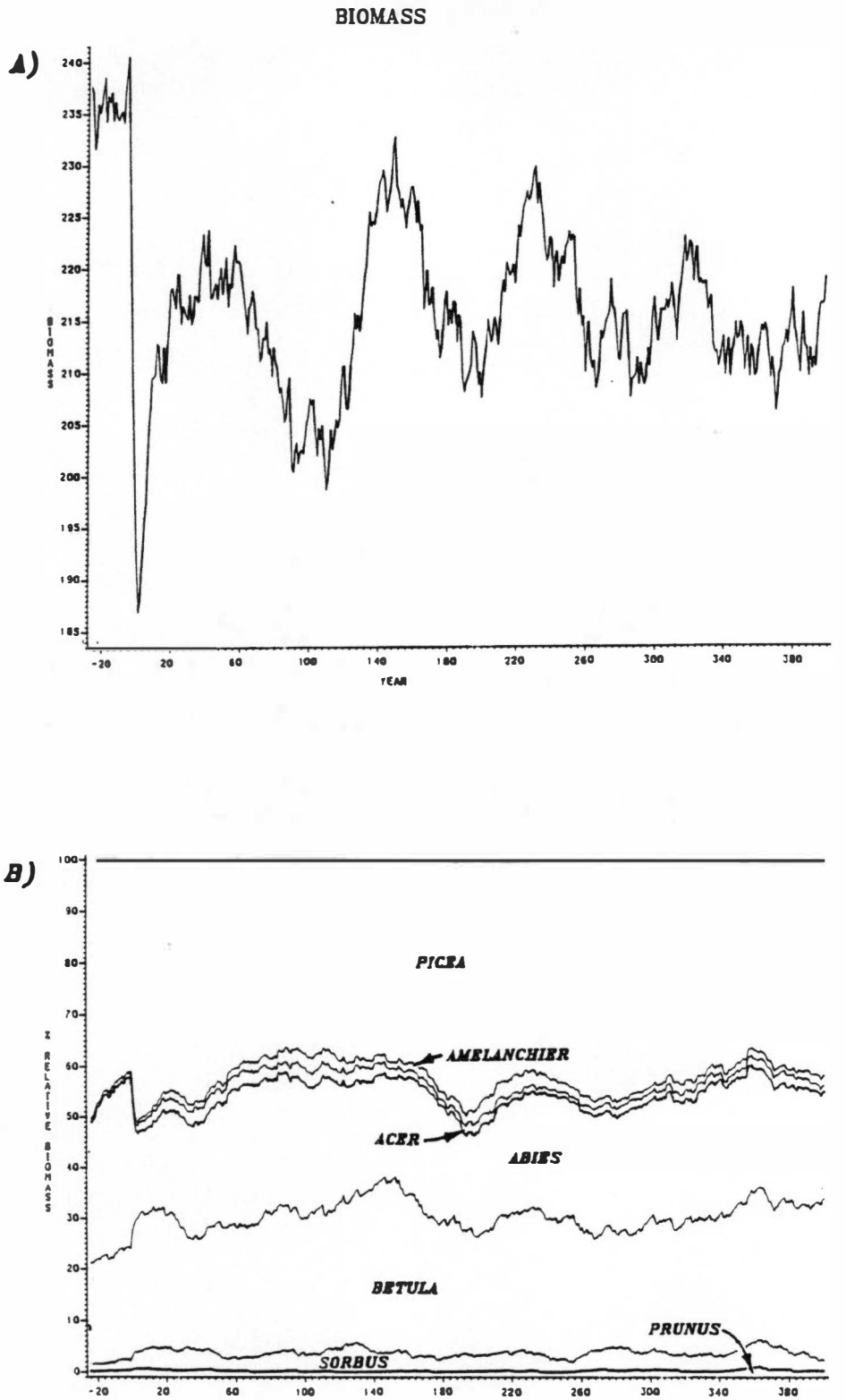


Fig. 54. Graphs of simulated biomass responses to continuous aphid infestation in combination with a 30% spruce growth decline. These are: A) total stand biomass (t/ha), and B) relative biomass. Disturbance begins at year 0.

The elimination of fir from such stands greatly reduces the total density (Fig. 55), and results in a spruce-birch forest. Spruce comprises 40 to 60% of the total biomass, while birch comprises 30 to 45% (Fig. 56). Total biomass of the disturbed stand is low and recovery to levels of 220 t/ha or more is slow (>90 yr). Although stand biomass increases over the 400 yr simulation, the increase is gradual and values characteristic of the undisturbed forest are infrequently attained.

Several important aspects of spruce-fir stand dynamics are revealed by these simulations. Of particular interest is the contrast in recovery times exhibited by spruce and fir following disturbance. Fir recovers rapidly (<50 yr) in response to short-term disturbances such as logging or an insect infestation. On the other hand, spruce recovers much more slowly. It does not regain dominance in a stand for at least 150 years after logging or an episode of declined growth. The slow recovery of spruce is attributable to its slow regeneration and growth rates in relation to fir. When fir is lost from a stand the total biomass returns to levels of undisturbed stands relatively slowly. In brief, fir plays a major role in stand recovery. Its high regeneration and growth rates facilitate rapid response to disturbance. The interaction between the forest dominants, spruce and fir, is another important aspect of stand dynamics. The dominance of spruce in the absence of fir canopy trees even while subjected to a 30% growth reduction suggests that competition among canopy trees is a factor in the growth and survival of spruce. In this case the reduction in competition allows spruce to endure moderately severe

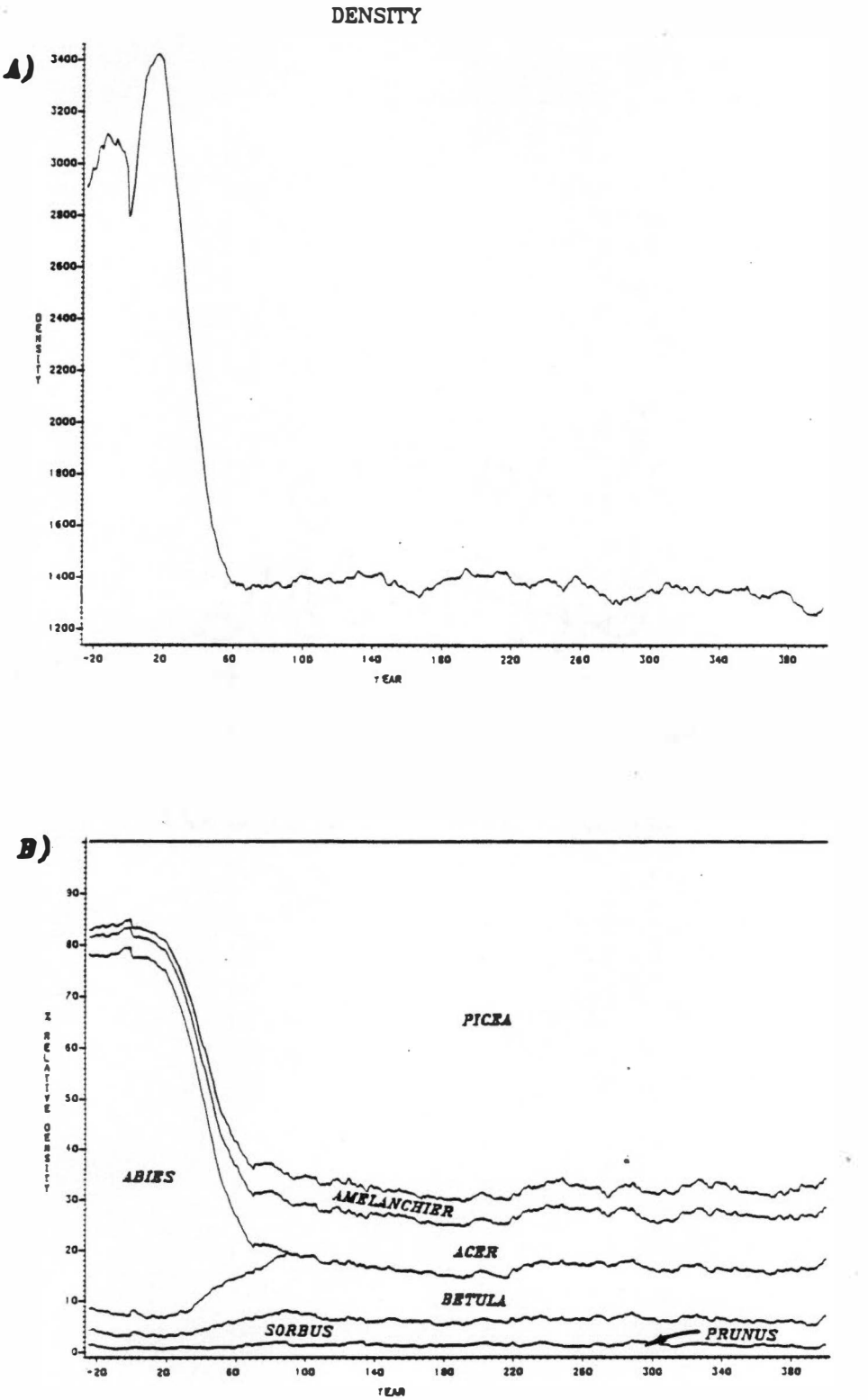


Fig. 55. Graphs of simulated density responses to the elimination of fir in combination with a 30% spruce growth decline. These are: A) total stand density (stems > 1.27 cm DBH/ha), and B) relative density. Disturbance begins at year 0.

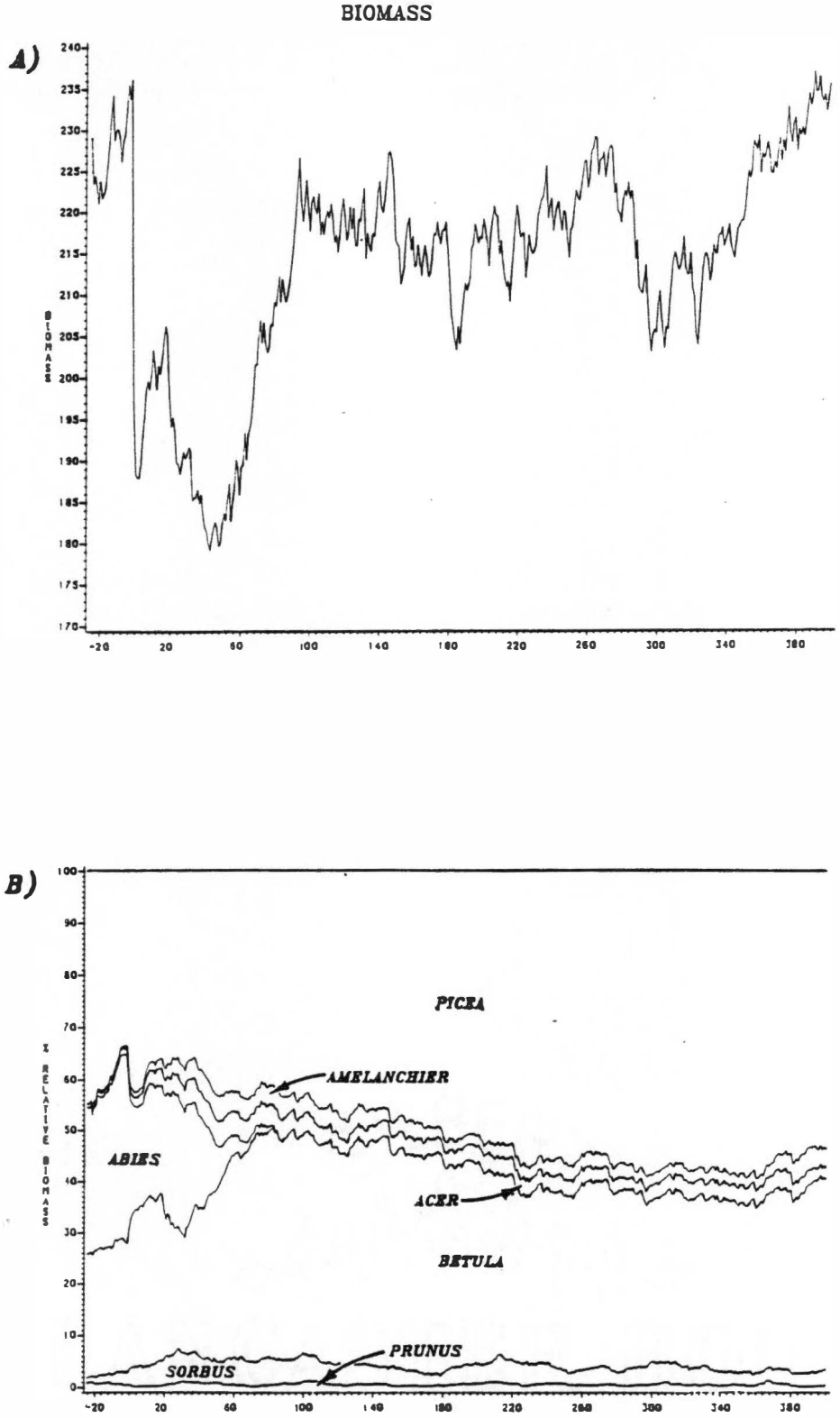


Fig. 56. Graphs of simulated biomass responses to the elimination of fir in combination with a 30% growth decline. These are: A) total stand biomass (t/ha), and B) relative biomass. Disturbance begins at year 0.

growth stress. Such phenomena serve to emphasize the importance of considering species interactions in the prediction of individual species' responses to disturbance.

CHAPTER VIII

SYNTHESIS

Introduction

The southern Appalachian spruce-fir forest is an assemblage of relatively few tree species. Only three species occupy a large majority of the mature forest canopy space. Of these species, red spruce and Fraser fir clearly dominate the mature forest. The relative simplicity of the spruce-fir forest system facilitates the study and understanding of the species interactions and mechanisms regulating forest dynamics. It allows the synthesis of autecological, environmental, and synergistic information in the formulation of a theory on dynamics of the system. The interrelations of the system are presented here. Beginning with autecological information on component species, and progressing to species interactions and gap dynamics, a theory of old-growth spruce-fir stand dynamics is constructed. Finally, a concept of landscape dynamics based on the overall outcome of many gap creation and capture events is presented.

Tree Species Life Histories

Some basic traits of southern Appalachian spruce-fir forest tree species were presented earlier (Table 4). The critical life history stages regulating population growth are further discussed and summarized here.

Red spruce, the mature forest dominant, reproduces exclusively from wind dispersed seeds. The annual seed population is generated in

late fall and winter by trees over 30 years of age. Seed survivorship is low beyond 2 years. Germination is most prevalent in the fall, late spring and early summer, and it occurs on any moist substrate. New seedlings are particularly abundant on moss, mineral soil and fallen tree boles. Seedling mortality commonly results from high temperatures and low soil moisture. Consequently, survivorship is low in large openings and on soils with thick organic layers. A ubiquitous population of suppressed saplings and subsaplings provides a source for canopy tree recruitment. Established individuals are very tolerant to shade and respond well to partial or full sunlight. Spruce grows slowly and approaches diameters of 95 cm in the spruce-fir zone. The tall canopy trees (30-35 m) are shallow rooted and subject to windthrow. Spruce is long-lived; some individuals may exceed 350 years of age.

Fraser fir also reproduces from wind dispersed seeds. Mature trees (>30 yr) produce annual seed crops from late summer to spring. Seed survivorship is low beyond 2 years. Germination occurs in the spring on any moist substrate. Seedlings are abundant on the forest floor and fallen tree boles. High temperatures and low soil moisture cause seedling mortality. Fir seedlings, however, are more drought resistant than spruce seedlings. Like spruce, fir canopy trees are typically recruited from a population of suppressed individuals. Established subsaplings are very shade tolerant and capable of rapid growth upon release. Canopy trees are subject to windthrow because of their shallow root system and susceptibility to heartrot. The maximum

life span of fir is approximately 170 years. Large trees rarely exceed 70 cm in diameter and 27 m in height.

Mature yellow birch trees (>40 yr) produce large wind-dispersed seed populations in the fall. Typically the seeds germinate in the following spring, but some seeds may remain dormant for at least one year. Cold stratification is a prerequisite for germination. Seedlings occur almost exclusively on logs and exposed mineral soil. Although first-year seedlings are often abundant on these substrates, their mortality rate is very high and few survive for more than 5 years. Establishment is best in small openings or on the edge of large openings. Birch is intermediate in shade tolerance and grows rapidly when provided adequate light and moisture. In the spruce-fir zone birch rarely exceeds 80 cm in DBH and 30 m in height. Large trees may be 250 or more years of age and heartrot is common among older trees. Vegetative reproduction occurs by way of stump sprouting. It is most frequent after the fall of a young birch.

Mountain maple is an understory tree in the spruce-fir zone that often reproduces vegetatively from trunk sprouts. Sexual reproduction occurs by way of wind-dispersed seeds. The development of seedlings appears to be restricted to mineral soil associated with windthrow mounds. Tree growth is moderately slow and mature trees are shade tolerant. It is possible that seed regeneration is enhanced by canopy openings, while trees persist in the shaded understory by vegetative regeneration. Individual trunks rarely exceed 18 cm DBH and the sometimes prostrate branches rarely exceed 8 m in height.

Mountain ash is a small boreal tree characteristic of the Appalachian spruce-fir forests. The animal dispersed seeds of this species are borne in fleshy fruits. Large fruit crops are typically produced at 3-year intervals (Stupka 1964). Apparently, there is no buried population of mountain ash seeds (Pavlovic 1981), and germination probably takes place soon after dispersal. Seedlings of mountain ash are most prevalent on windthrow mounds with exposed mineral soil. Rapid growth occurs in canopy openings where individuals may attain heights of 10 m or more. Diameters in excess of 30 cm are uncommon. The life span of mountain ash is short (<100 yr) and sprouting is a potential means of reproduction (Saunders 1979).

Fire cherry also exploits canopy openings in the mature spruce-fir forest. It reproduces from a population of dormant seeds in the soil (Marks 1974). Following the uprooting of a canopy tree it is often present on windthrow mounds where it grows very rapidly. In the mature forest this shade intolerant species occurs individually or in small clumps rather than in dense stands. It is not a major canopy tree because of its short life span (<60 yr) and low frequency in the old-growth forest.

Tree Population Dynamics

Population size and structure are typically regulated by a few critical life history stages. Among tree species, regeneration requirements and mortality sources are important considerations. An understanding of regeneration and mortality levels over time is vital.

In particular, the characterization of mortality levels at various life history stages is necessary.

The populations of spruce and fir appear to be stable in the old-growth forest. Both population structures fit an inverse-J curve indicative of undisturbed, self-perpetuating populations (Schmelz and Lindsey 1965). Undoubtedly, juvenile mortality is high for both species as individuals under 5 years of age account for more than 70% of each population. The likelihood of mortality is greatly reduced by the age of 10 to 15 years for individuals of both species. Most individuals in this age range are suppressed subsaplings which are capable of surviving for several decades in the shaded understory. The survivorship of established spruce in the understory is particularly high (ave. = 32 yr; White et al. 1985b). Even so, dead saplings of spruce and fir are not uncommon in dense stands. Opening of an overhead portion of the canopy allows vigorous sapling growth. Observations of fir suggest that adjacent openings, in addition to overhead openings, are sufficient for height growth into the canopy. In general, the mortality rate of vigorous overstory trees is believed to be low (Goff and West 1975). This applies best to spruce and fir entering the canopy. As trees become large they are more susceptible to wind and lightning damage. Their vulnerability to wind also increases with age. For example, fir is often weakened by heartrot and is therefore susceptible to trunk snapping in high winds (Crandall 1958). Although broken spruce trunks were observed, the shallow rooting habit of this species renders it susceptible to uprooting. Estimates of average canopy tree life spans are 225 and 137 years for

spruce and fir, respectively. Average spans of canopy residence are estimated at 153 years for spruce and 73 years for fir (White et al. 1985b).

Birch population structure of the old-growth forest also resembles an inverse-J curve when individuals under 5 years of age are included. Seeds germinate in abundance, but the majority of new seedlings die in the first 5 years. Establishment is episodic and disturbance related. Recruitment occurs in or near canopy openings. Vigorous overstory trees have low mortality rates; their average life span has been estimated at 154 years and their average canopy residence time has been estimated at 111 years (White et al. 1985b). Birch population dynamics are largely dependent on gap creation events in the mature spruce-fir forest. The role of natural disturbance in the perpetuation of birch and other hardwoods, including mountain ash and fire cherry, will be discussed in the following sections.

Gap Dynamics

Small, wind generated tree-fall gaps are the major form of natural disturbance in the southern Appalachian spruce-fir forest. Gap invasion and gap capture events following the death of a canopy tree are important elements of old-growth stand dynamics. Initial gap invasion involves the growth of individuals regenerated in advance near the gapmaking tree, and the regeneration of other species unable to survive beneath the closed canopy. Advanced regeneration is abundant in the mature forest. The advanced regeneration bank consists predominantly of suppressed spruce and fir individuals.

Within this bank fir is approximately four times more abundant than spruce. The relatively rapid growth rate of fir, in addition to its understory abundance, results in a high frequency of gap invasion. Spruce, on the other hand, is less frequent in gaps.

Gap invasion by advanced regeneration is presumably influenced by canopy-understory interactions prior to gap formation. Several studies have focused on species-specific interactions of this nature in southern Appalachian spruce-fir forests. A slight trend of reciprocal regeneration between spruce and fir was reported by White et al. (1985b). The analysis presented herein, based on canopy influence indices (Woods 1979), also suggests reciprocal regeneration (i.e., that spruce regenerates beneath fir and vice versa). Fox (1977) and White et al. (1985b) both reported high regeneration densities beneath spruce canopy trees relative to fir and birch canopy trees. An explanation for the high sapling and seedling densities beneath spruce can be based on canopy residence times and microsite conditions. Spruce is clearly the longest lived tree in the forest with an average canopy residence interval in excess of 150 years. During this interval suppressed individuals accumulate beneath the canopy of spruce. Furthermore, the moist, shaded understory typically develops a moss layer providing excellent seedling establishment conditions for spruce and fir. The saturated bank of advanced regeneration beneath spruce increases the chance that, in the event of gap formation, shade tolerant individuals will invade.

The role of gap invasion by newly regenerated individuals is of less significance in the old-growth forest. Birch is the only major

canopy species that commonly exhibits gap phase regeneration. Upon opening of the canopy, young birch seedlings receive enough light to become established. Without canopy disturbance the newly germinated seedlings perish in the light-limited understory. Other intolerant deciduous trees require the exposed mineral soil of windthrow mounds for germination and establishment. For example, healthy seedlings of mountain ash and fire cherry occur almost exclusively on windthrow mounds in the study site. Regeneration from seed in these species is clearly dependent upon wind created disturbances.

Regeneration is merely the first stage in a series of events during gap invasion that culminate in gap capture, the domination of a gap by one or more new trees. The interactions among species invading a gap are often complex and the outcome of a gap event is sometimes best viewed as stochastic. In this study, however, some relationships between gap characteristics and successor species were discernable. Characteristics such as gap size, gap age and species of gapmaker may influence canopy tree replacement (Barden 1981, Runkle 1984). In general, it is held that small gaps favor a shade tolerant successor, while large gaps favor a shade intolerant successor. The rapid growth rates of intolerant species under high light conditions are largely responsible for this replacement trend. Gapmaker species identity and type of death are related to gap size. For instance, spruce and birch have large crowns; consequently, they create large gaps upon treefall. If trees of these species die standing they create smaller gaps and theoretically, favor shade tolerant successors. Observations in the study site only correspond weakly with these hypothesized trends. One

example is the success of shade tolerant spruce in relatively small gaps. On a more general level, the shade tolerant species (spruce and fir) dominated over 70% of the gaps considered. Fir was highly successful in all gap types regardless of their size, age or species of gapmaker. Obviously the advanced regeneration strategy is very effective under the prevailing natural disturbance regime of small canopy gaps. Less tolerant species showed no clear replacement trends in relation to gap characteristics. Their ability to occasionally overtop the slower growing advanced regeneration enables them to persist in the mature forest.

As noted earlier, the species comprising the advanced regeneration are influenced by overlying canopy species. A pronounced trend of advanced fir regeneration beneath spruce was revealed in this study. Also a tendency of reciprocal regeneration between spruce and fir is suggested. Whether or not these regeneration patterns are reflected in gap phase tree replacement patterns is an important consideration. Judging from the gap capture observations, patterns of advanced regeneration and replacement are somewhat similar. However, there is no outstanding trend of reciprocal replacement in gaps. Spruce is most frequently replaced by fir, while self-replacement is infrequent. By contrast, fir is frequently self-replacing; replacement by spruce is clearly less frequent. The tendency of fir regeneration beneath spruce leads to a high frequency of fir domination in spruce created gaps. In general, the overwhelming abundance of fir in the advanced regeneration bank results in a high frequency of gap capture by fir regardless of gapmaker species.

Patterns of canopy tree replacement in gaps are summarized in Fig. 57. Again, the success of fir in gaps, particularly those created by spruce, is the overriding trend. Spruce is successful in fir and birch gaps. Its ability to regenerate in advance beneath these species leads to gap capture. Only rarely does spruce capture spruce created gaps; it is usually precluded by fir. Birch does not show any gapmaker species preference. By outcompeting the advanced regeneration it is able to capture gaps infrequently.

Stand Dynamics

Old-growth spruce-fir stand dynamics are influenced by canopy gap events. The response of individual species to gap events is an important aspect of stand dynamics. Also, the differing regeneration, growth and survivorship among tree species have a profound effect on stand structure and composition. For example, fir is not a particularly large tree, but it is able to codominate the forest because of its high regeneration and growth rates relative to spruce. It clearly dominates the understory and for this reason one might predict eventual stand dominance by fir. White et al. (1985a) have discredited the validity of such a prediction pointing out that it fails to account for the short canopy residence span of fir overstory trees. In terms of gap phase processes, the high gap capture frequency of fir is balanced by a high fir gap creation frequency. The end result is a stable fir population. Similar consideration of spruce's role in stand dynamics leads to the importance of its potentially long life span and large size. Spruce exhibits a low gap

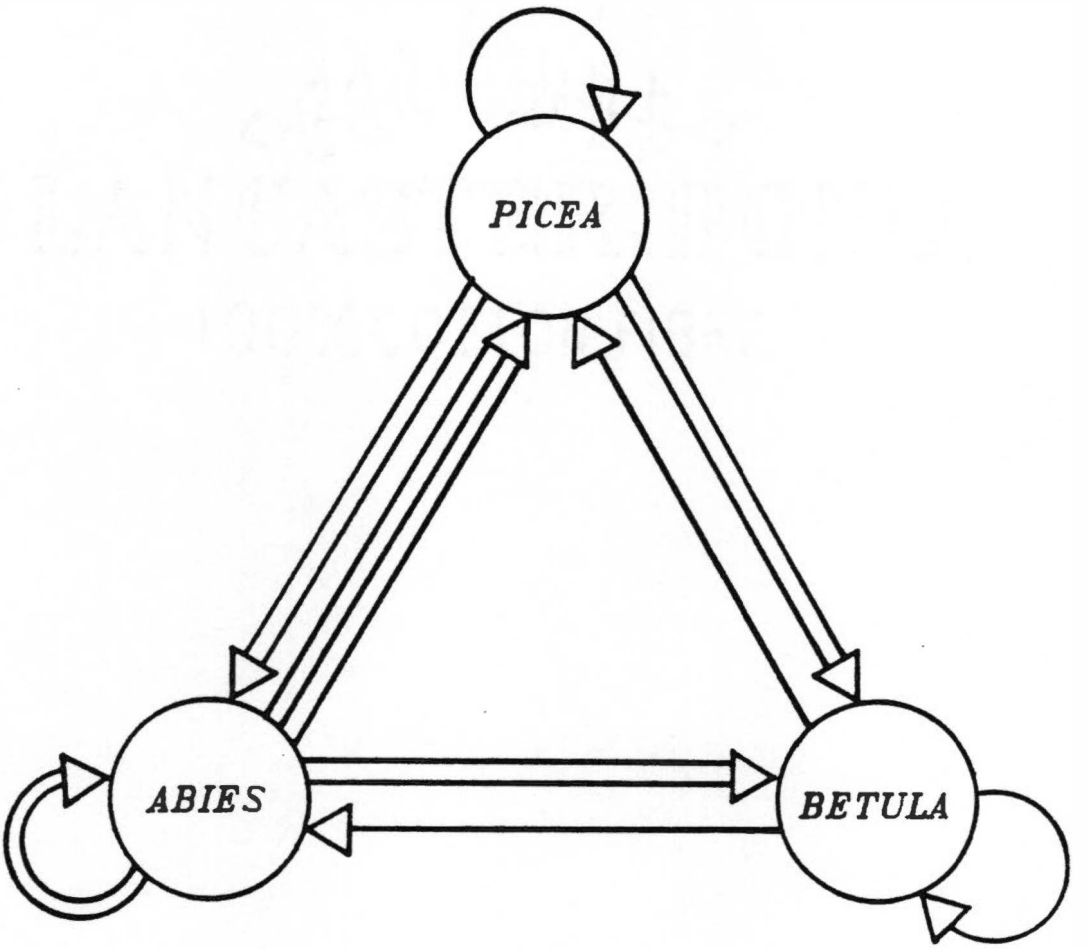


Fig. 57. Tree replacement trends in an old-growth spruce-fir forest. Arrows point toward the species being replaced. Several lined arrows indicate a strong replacement trend, whereas single lined arrows indicate a weak replacement trend.

capture frequency, but it remains in the overstory for an extended period of time. During this time interval it may attain large size and dominate local resources. In effect, the low gap capture frequency of spruce is compensated by its low gap creation frequency. Similarly, the low gap capture frequency of birch is compensated by its long canopy residence time relative to fir. A general concept of stand dynamics would hold that within the overstory fir individuals turn over in a rapid cycle of recruitment and mortality. Meanwhile the less profuse spruce and birch overstory populations are maintained by slower cycles of recruitment and mortality.

A more detailed examination of stand dynamics involves the recruitment of overstory individuals from understory populations. One means of assessing interactions among trees is to analyze their patterns of horizontal spacing. In this study spatial patterns of understory and overstory populations were considered separately in an effort to understand internal stand dynamics. Regeneration sites are potentially important factors in the spatial patterning of the understory population. Spruce, fir and birch stems (>0.25 m tall, <2.5 cm DBH) all show some degree of intraspecific clumping. Of these species, fir and spruce exhibit the least amount of clumping--presumably because of their shade tolerance which allows dispersion throughout the understory. Birch, on the other hand, is strongly clumped because of its restriction to microsites with favorable substrate and light conditions. Canopy influence analyses indicate that small spruce, fir and birch stems (<2.5 cm DBH) are not strongly affected by the species of overlying canopy trees. However, as stems

reach sapling size (>2.5 cm DBH) the degree of intraspecific clumping decreases and overlying canopy species appear to influence sapling survivorship. Fir has high survivorship beneath spruce in relation to other understory tree species. Interspecific nearest neighbor analyses indicate that fir saplings tend to be segregated from spruce and birch saplings which have their own microsite affinities. Spruce saplings are most abundant beneath fir canopies, while birch saplings are most abundant in canopy gaps (White et al. 1985b). The clumped pattern of birch is also evident in the overstory; large birch trees often occur together suggesting that more than one birch tree may capture a canopy gap. Conversely, large trees of spruce and fir exhibit intraspecific segregation. Thinning of these populations is evident in the gap capture process and it appears that only one or two trees of these species typically capture a small canopy gap. In conclusion, forest floor microsites influenced by the overstory affect understory composition and development. The clumped dispersion of understory birch leads to a similar pattern in the overstory. By contrast, spruce and fir overstory populations approach random or even hyperdispersed distributions because of thinning during overstory development.

A final aspect of stand dynamics is the response of mature stands to large-scale disturbance of moderate intensity. For example, the removal of canopy trees by logging causes an increase in stand density and dominance by fir. Along with the intolerant hardwood species, fir plays an important role in stand recovery. The high productivity of these species following disturbance results in a rapid return to

mature stand biomass levels. The importance of fir in stand recovery is demonstrated by simulations wherein fir is eliminated from a stand and the total biomass recovery interval is approximately 3 times that of a stand containing fir. Fire cherry and mountain ash are also a factor in the early stages of stand recovery. The nutrient retention capabilities of cherry (Marks 1974) are particularly important in this ecosystem where available nutrients can easily be lost by leaching. Although yellow birch may dominate forests recovering from severe disturbance, it does not appear to dominate forests recovering from logging or aphid infestation. In fact, it is of little importance during the first few decades of recovery. As a group, the birches are early to mid-successional forest trees, but within this group yellow birch is one of the slower growing and more shade tolerant species. In the spruce-fir zone yellow birch functions primarily as a mid-successional or a gap phase tree. It is of most importance in the later stages (>50 yr) of stand recovery. Finally, the recovery of spruce dominance is slow (>150 yr) because of its slow regeneration and growth rates.

Landscape Dynamics

Forest landscape-scale dynamics can be projected from smaller scale canopy gap dynamics. By treating the forested landscape as a mosaic of gap-sized patches, the dynamics of many individual gaps can be taken collectively to represent the dynamics of a forest landscape. Two assumptions are made in this abstraction to a larger scale: 1) that interactions among patches are minimal, and 2) that the potential

for tree regeneration and growth approaches uniformity across the landscape. Both assumptions are met in mature spruce-fir forests.

Using the spatial gap model, landscape level biomass responses can be investigated. Spruce-fir forest biomass recovery from disturbance is typified by a rapid increase in biomass to an overshoot peak followed by a slight decrease to relatively constant levels (Fig. 38). The overshoot peak is believed to be a common phenomenon especially in low-diversity forests (Bormann and Likens 1979a, Shugart 1984). An explanation for the peak has been based on the synchronization of patch biomass dynamics by a single large disturbance. In this situation individual patches recover to high biomass levels at approximately the same time producing a high average patch biomass (Bormann and Likens 1979a,b). However, in high-diversity forests the overshoot peak may be damped or absent because of asynchronous patch recovery resulting from the different biomass responses of species comprising each patch (Shugart 1984). This is certainly not the case in spruce-fir forests where recovering patches are typically dominated by one of two species: fir or birch.

The long-term compositional and structural dynamics of old-growth spruce-fir forests can also be investigated with gap model projections. One emphasis in vegetation ecology is to explore and predict community trajectory under certain regimes of disturbance and climate. The concept of an equilibrium community composition is useful as a theoretical trajectory endpoint. From a patch dynamics perspective this equilibrium state can be perceived as a "shifting-mosaic steady state" across the landscape (Bormann and Likens

1979a,b). Judging from the differential equation analysis of spruce-fir forest mosaic dynamics (Table 11), the old-growth forest studied here is close to equilibrium composition. The stable, all-aged structure of the dominant populations is further evidence for the quasi-equilibrium state (Shugart 1984). Clearly, anthropogenic disturbance will produce a nonequilibrium condition and in extreme cases such as the elimination of fir it may lead to a new quasi-equilibrium state. In the face of a moderately severe, short-term disturbance, however, the forest will return to the former quasi-equilibrium state within two centuries provided that natural disturbance and climatic regimes remain unaltered.

In comparison with other spruce-fir forests of eastern North America, the scale of natural disturbance in the southern Appalachian spruce-fir is small (White et al. 1985b). Boreal spruce-fir forests are repeatedly disturbed by intense fires covering large areas (fire rotation ca. 50-200 yr; Heinselman 1981, Cogbill 1985). Disturbances of this nature undoubtedly prevent the development of an equilibrium landscape. In northern Appalachian spruce-fir forests fire is less important (fire rotation >500 yr; Fahey and Reiners 1981) and wind is the primary agent of disturbance. The size of wind generated patches ranges from large windthrows created by major storms to small canopy gaps created by the death of one or a few trees (Reiners and Lang 1979, Foster and Reiners 1983). Patchwise disturbance at this scale is sufficient to prevent the development of an equilibrium over a small landscape area ($<10^6$ m^2; Shugart 1984). However, the development of a quasi-equilibrium over a larger landscape area is

conceivable in the northern Appalachian spruce-fir forest. By contrast, large disturbance patches are relatively rare in the southern Appalachian spruce-fir. Fire is insignificant and small tree-fall gaps are the predominant form of disturbance. Under this regime the development of a quasi-equilibrium is likely even over a small landscape area (ca. 10^4-10^5 m^2; Shugart 1984). In conclusion, natural disturbance in the southern Appalachian spruce-fir has allowed the forest to approach a level of equilibrium that has not been attained by its northern counterparts.

CHAPTER IX

CONCLUSIONS

The old-growth forest is comprised of stable, all-aged spruce and fir populations. Fir is more abundant than spruce, particularly in the understory. Spruce dominates the forest because of its potentially long life span and large size. Both spruce and fir exhibit advanced regeneration in the form of suppressed understory populations. The populations of birch and other hardwood species are maintained by gap phase regeneration in the mature forest.

Natural disturbance in the southern Appalachian spruce-fir forest is predominantly in the form of small, wind created tree-fall gaps. The different roles of tree species in gap phase processes are important aspects of forest dynamics. Shade tolerant spruce and fir saplings, regenerated in advance, are highly successful invaders of these small canopy gaps. Although a slight trend of reciprocal regeneration is evident between spruce and fir, there is no clear pattern of reciprocal replacement in canopy gaps. Fir captures a large proportion of gaps regardless of gapmaker species. Its success can be attributed to its high rates of regeneration and growth relative to spruce which is less frequent in gaps and does not appear to be self-replacing. The rapid growth rate of birch allows it to occasionally outcompete the advanced regeneration of spruce and fir to become established in the canopy.

Canopy turnover in old-growth stands is influenced by the potential life spans of canopy species. The life span of fir is

approximately half that of spruce, the longest lived species in the forest. Despite the understory abundance and high gap capture frequency of fir, its level of overstory dominance is stable rather than increasing. The high frequency of gap capture by fir is compensated by its short canopy residence interval. In contrast, spruce exhibits a long canopy residence interval and therefore has slower cycles of overstory mortality and recruitment. The turnover cycles of birch canopy trees also tend to be slower than those of fir.

Disturbances involving the decline of spruce and/or fir populations strongly affect stand composition, structure and dynamics. The simulated decline of fir results in a spruce-birch forest. In the absence of fir, stand biomass recovery is slow and total stand density is reduced. A long-term spruce growth decline (-30%) in the presence of an undisturbed fir population results in a fir-birch forest. However, in association with a fir population decline the effects of spruce growth stress are diminished. The reduction of competition with fir allows spruce to endure moderately severe growth stress.

The old-growth forest studied herein appears to be close to equilibrium composition. Disturbance patch size is small (<0.02 ha) and therefore forest composition, biomass and structure are relatively constant over a small landscape area (ca. 1-10 ha). This degree of equilibrium is unique among eastern North American spruce-fir forests.

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APPENDIX

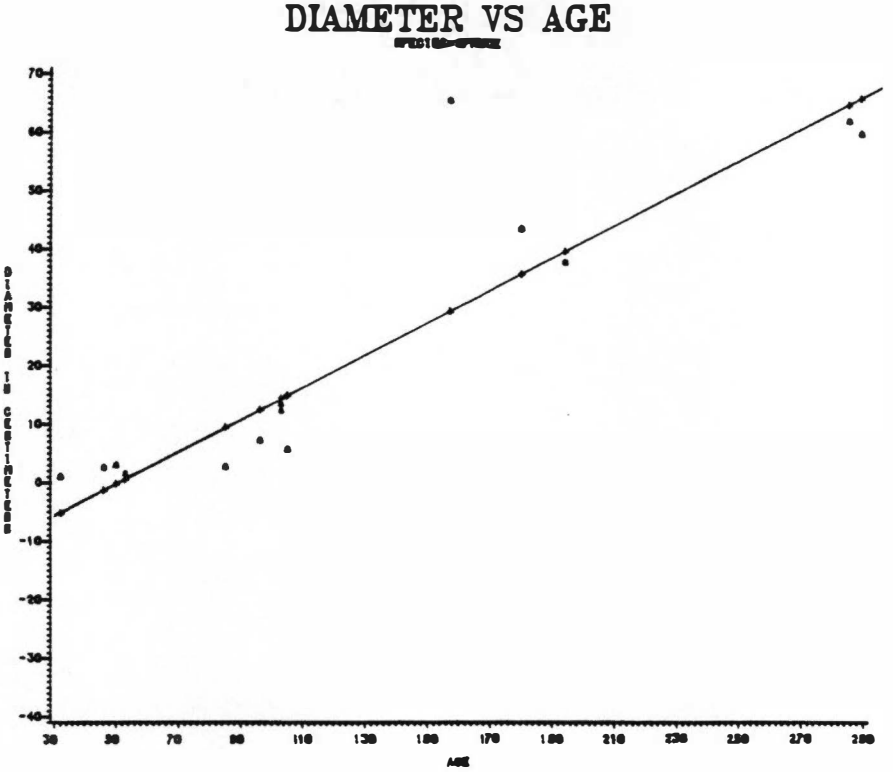


Fig. 58. Graph of red spruce diameter vs. age. Based on transect sampled individuals over 0 cm DBH. Linear regression r^2=0.79.

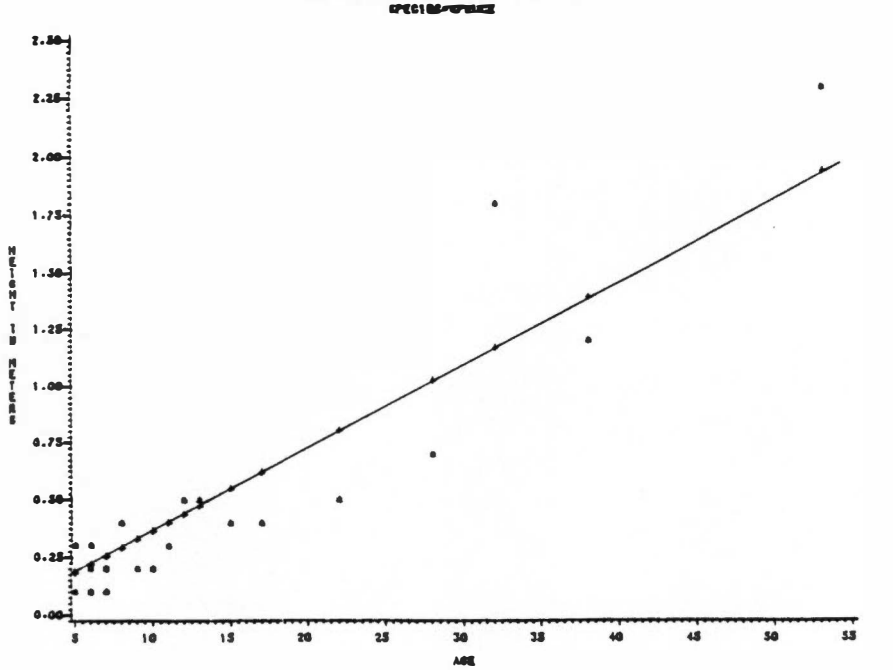


Fig. 59. Graph of red spruce height vs. age. Based on transect sampled individuals less than 2.3 m tall. Linear regression r^2=0.91.

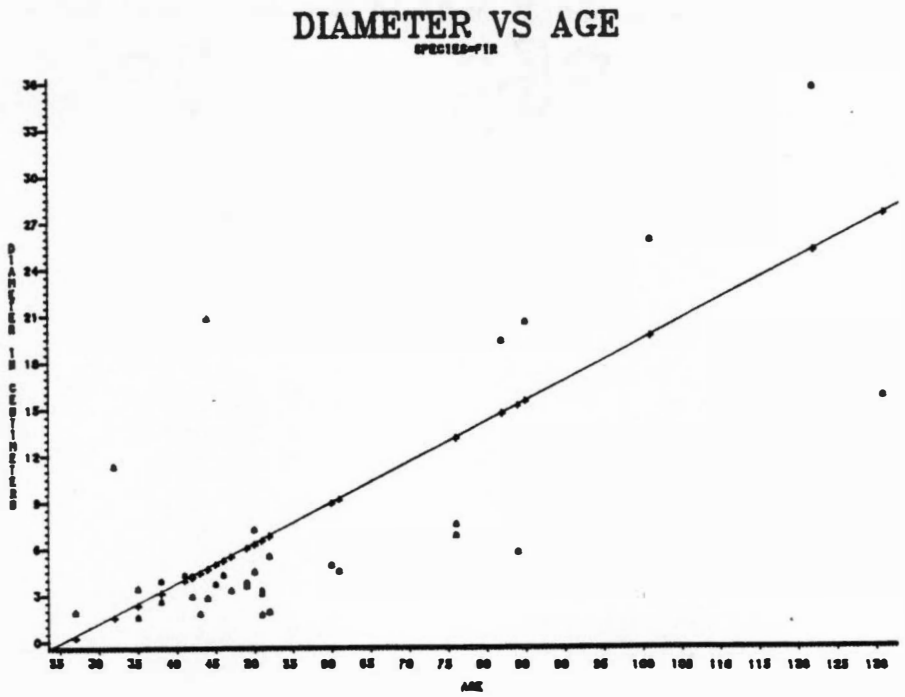


Fig. 60. Graph of Fraser fir diameter vs. age. Based on transect sampled individuals over 0 cm DBH. Linear regression r^2=0.71.



Fig. 61. Graph of Fraser fir height vs. age. Based on transect sampled individuals less than 2.0 m tall. Linear regression r^2=0.83.

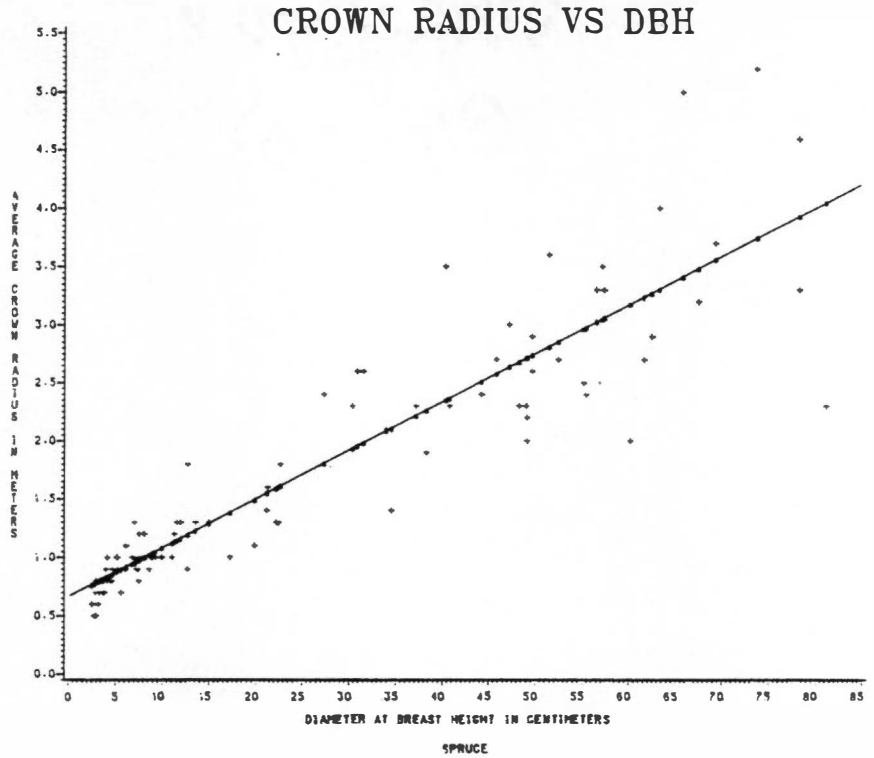


Fig. 62. Graph of red spruce crown radius vs. DBH. Linear regression r^2=0.83.

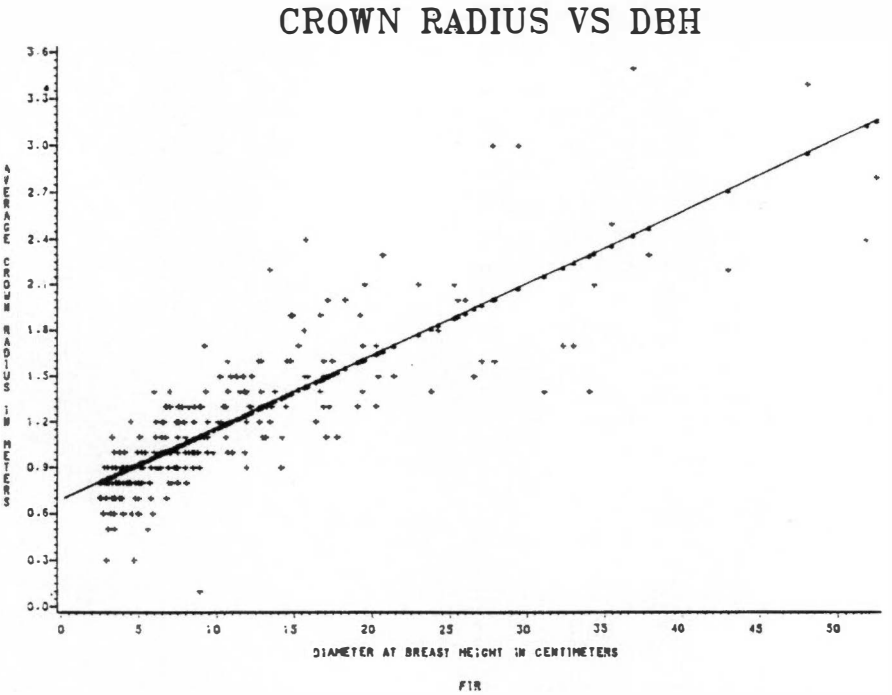


Fig. 63. Graph of Fraser fir crown radius vs. DBH. Linear regression r^2=0.69.

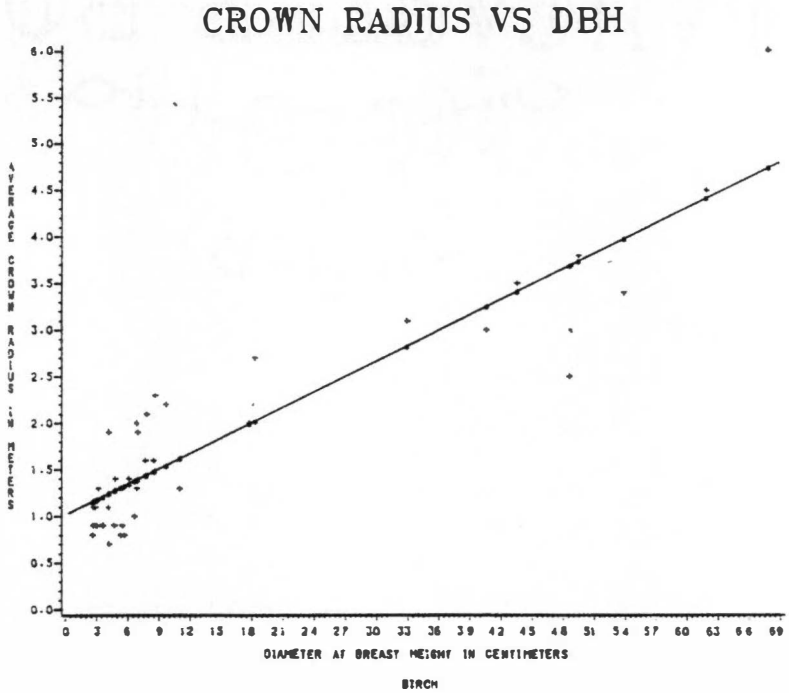


Fig. 64. Graph of yellow birch crown radius vs. DBH. Linear regression r^2=0.83.

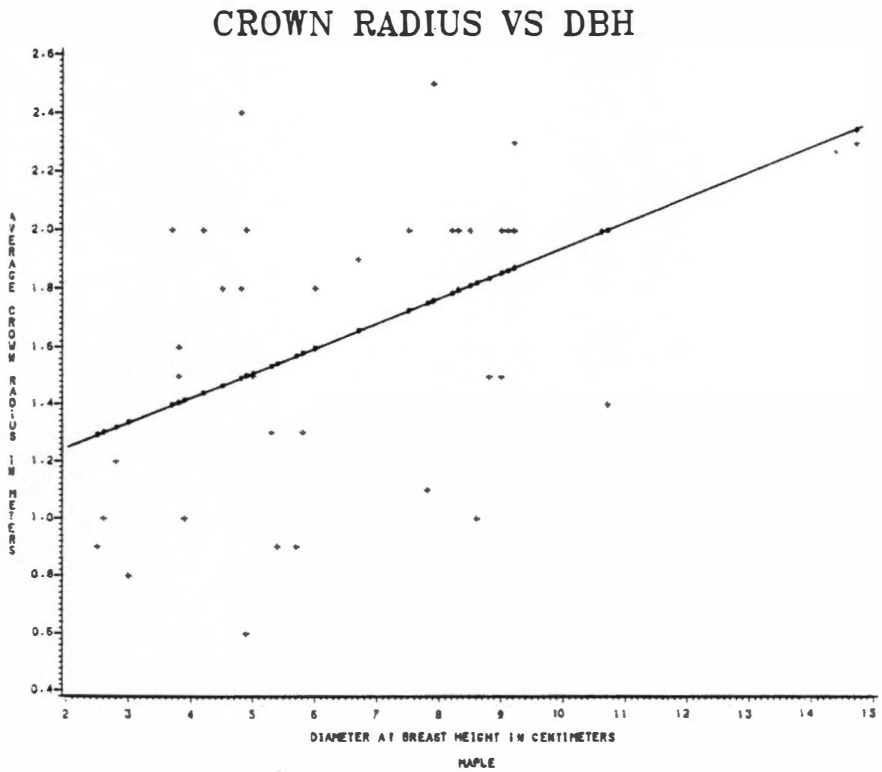


Fig. 65. Graph of mountain maple crown radius vs. DBH. Linear regression r^2=0.21.

QUADRAT MARKING

At least two corners of each 50 x 20 m quadrat were marked with colored pins. The color coding was as follows: N = north pin (blue), E = east pin (yellow-green), W = west pin (black), and S = south pin (red). A numbered aluminum tree tag was placed near each pin. See Fig. 3 for quadrat locations.

Quadrat 1

Long axis 100°; S pin 0.5 m from tree tag 75 at 190°; E pin 1.5 m from tag 69 at 280°; N pin 4.0 m from tag 73 at 305°.

Quadrat 2

Long axis 44°; S pin 0.5 m from tag 64 at 175°; N pin 6.8 m from tag 63 at 191°; W pin 8.0 m from tag 65 at 130°.

Quadrat 3

Long axis 350°; S pin 3.5 m from tag 72 at 270°; E pin 1.0 m from tag 66 at 250°.

Quadrat 4

Long axis 39°; S pin 2.0 m from tag 76 at 290°; N pin 4.0 m from tag 77 at 25°.

Quadrat 5

Long axis 135°; S pin 0.5 m from tag 78 at 335°; E pin 3.0 m from tag 80 at 88°; W pin 5.0 m from tag 81 at 165°.

Quadrat 6

Long axis 165°; S pin 4.0 m from tag 92 at 314°; N pin 4.5 m from tag 85 at 58°; W pin 4.5 m from tag 79 at 122°.

```
C.....FORANAK SOUTHERN APPALACHIAN SPRUCE-FIR FOREST SUCCESSION MODEL
C.....
C.....MODIFIED BY R.T. BUSING FROM THE FORET MODEL OF SHUGART AND
C.....WEST (1977).  THESE GAP MODELS ARE BASED ON THE JABOWA MODEL
C.....OF BOTKIN ET AL. (1972).
C.....
C.....ADDRESS: DEPARTMENT OF BOTANY, THE UNIVERSITY OF TENNESSEE,
C.....KNOXVILLE, TN 37916
C.....
C.....THIS PROGRAM WAS WRITTEN IN FORTRAN 77.  IT CAN BE RUN IN
C.....FORTRAN IV WITH A FEW MODIFICATIONS.
C.....
      COMMON/FOREST/NTREES(10),DBH(700),IAGE(700),KSPRT(100),
     >NEWTR(100),SUMLA(700),NEW(100),SWTCH(5),LOCUS(2,800)
      COMMON/PARAM/AAA(10,6),DMAX(10),DMIN(10),B3(10),B2(10),
     >ITOL(10),AGEMX(10),CURVE(10),G(10),SPRTND(10),SPRTMN(10),
     >SPRTMX(10),SWITCH(10,5),KTIME(10),C1(10),C2(10)
      COMMON/CONST/NSPEC,SOILQ,DEGD
      COMMON/RAN/YFL
      COMMON NSELCT(100)
      COMMON/OUTPT/IO1,IO2,PLOT,PRINT,LIST
      COMMON/PAREA/HTREE(700)
      COMMON/DEAD/NOGRO(700),NTEMP(700)
      COMMON/COUNT/NTOT,NYEAR
      COMMON/PASSX/ABM(1001,20),ABA(1001,20),AD(1001,20)
      COMMON/TEMP/DTEMP(700),ITEMP(700),LTEMP(2,800)
      COMMON/SEED/USEED(11),NSEED1,NSEED2,NSEED3,NSEED4
      DIMENSION Z(2)
      INTEGER USEED
      LOGICAL SWITCH,SWTCH,PLOT,PRINT,LIST
      DATA NCT/0/
C.....
C.....***********************************************
C.....ARRAYS USED IN THE MODEL
C.....NTREES - NUMBER OF TREES FOR EACH SPECIES
C.....DBH - DIAMETER AT BREAST HEIGHT FOR EACH TREE
C.....KSPRT - TREES THAT CAN SPROUT
C.....      (NOT CURRENTLY USED)
C.....NOGRO - TREES THAT DON'T GROW
C.....IAGE - THE AGE OF EACH TREE
C.....NEWTR - NEW TREES WHICH ARE ADDED TO PLOT
C.....SUMLA - LEAF AREA OF EACH TREE
C.....NEW - SPECIES ELIGIBLE TO SPROUT
C.....      (NOT CURRENTLY USED)
C.....LOCUS - X AND Y COORDINATES OF EACH TREE
C.....DTEMP - TEMPORARY STORAGE FOR DBH
C.....ITEMP - TEMPORARY STORAGE FOR TREE AGES
C.....LTEMP - TEMPORARY STORAGE FOR LOCUS
C.....***********************************************
        CONTINUE
C.....
C.....REFERENCE FOR RANDOM NUMBER GENERATOR - DESIGN AND USE OF COMPUTER
C.....SIMULATION MODELS - EMSHOFF AND SISSON - THE MACMILLAN COMPANY
C.....
C.....USEED(1) - KILL: TEST MAXIMUM AGE FOR EACH TREE
C.....USEED(2) - KILL: TEST GT .368 FOR TREE TO DIE
C.....USEED(5) - KILL: USED TO CALCULATE DBH FOR SPROUTS
C.....USEED(9) - BIRTH: USED TO DETERMINE SEEDLING INPUTS
C.....USEED(11) - BIRTH: USED TO CALCULATE DBH FOR SEEDLINGS
C.....
C.....INITIAL SEEDS FOR SUBROUTINE RANDOM
```

```
C.....
      USEED(1) = 13843
      USEED(2) = 25221
      USEED(3) = 29292
      USEED(4) = 41532
      USEED(5) = 75197
      USEED(6) = 18354
      USEED(7) = 79499
      USEED(8) = 35287
      USEED(9) = 78517
      USEED(10) = 12731
      USEED(11) = 97897
C.....
C.....INITIAL SEEDS FOR SUBROUTINE GGNORD
C.....
      NSEED1 = 31933
      NSEED2 = 36173
C.....
C.....INITIAL SEEDS FOR SEEDLING LOCUS
C.....
      NSEED3 = 45378
      NSEED4 = 78163
C.....
C.....SELECT OUTPUT MODE
C.....
      PLOT = .TRUE.
      PRINT = .TRUE.
      LIST = .TRUE.
C.....
C.....SET DEVICE SWITCHES
C.....
C.....SWITCH       IBM DEVICE #
C.....  IO1         5 (CARDS)
C.....  IO2         6 (PRINTER)
C.....  IO3         4 (TAPE)
C.....
      IO1 = 5
      IO2 = 6
      IO3 = 4
      CALL INPUT
C.....
C.....SET SIMULATION PARAMETERS
C.....
C.....KTIMES - NUMBER OF RUNS
C.....NYEAR - LENGTH OF RUN (YEARS)
C.....KPRNT - PRINT INTERVAL (YEARS)
C.....KPLOT - PLOT INTERVAL (YEARS)
C.....
      KTIMES = 1
      NYEAR = 200
      KPRNT = 50
      KPLOT = 900
      IF(.NOT.PLOT)     GO TO 10
      N3 = NSPEC+3
         DO 100 IVA=1,NYEAR
         DO 100 IVS=1,N3
        ABM(IVA,IVS)=0.
        ABA(IVA,IVS)=0.
        AD(IVA,IVS)=0.
  100   CONTINUE
C.....
```

```
C.....SITE VARIABLES
C.....SOILQ - THE MAXIMUM BIOMASS RECORDED FOR FORESTS IN THE AREA
C.....SOILQ IS IN KG/PLOT AREA IN HA
C.....PLOT AREA IS 0.03 HA
C.....AM - MEAN NUMBER OF DEGREE DAYS FOR AREA
C.....     (NOT CURRENTLY USED)
C.....S - STANDARD DEVIATION OF AM
C.....     (NOT CURRENTLY USED)
C.....
   10 SOILQ = 11100.0
      IPLOT = 0
      KYR = 0
      DO 200 JJ = 1,KTIMES
      CALL PLOTIN(IPLOT)
      WRITE(IO2,2000) IPLOT
 2000 FORMAT('1',58X,'PLOT NUMBER  ',I4)
      CALL INIT
      DO 250 I = 1,NYEAR
      KYR = I
      CALL KILL(KYR)
   50 CALL BIRTH(KYR)
      CALL GROW
      IF(((KYR/KPRNT)*KPRNT).EQ.KYR) CALL OUTPUT(KYR,IPLOT)
  250 CONTINUE
  200 CONTINUE
      IF(.NOT.PLOT)     STOP
      ZNYR = IPLOT
      NYR1 = NYEAR+1
      DO 300 IV1 = 1,NYR1
      TIMEX = IV1-1
         DO 350 IV2 = 1,N3
C.....
C.....AVERAGE BIOMASS, BASAL AREA AND DENSITY OVER PLOTS
C.....DETERMINE TOTALS AND WRITE THESE ARRAYS TO A FILE
C.....
        ABM(IV1,IV2) = ABM(IV1,IV2)/ZNYR
        ABA(IV1,IV2) = ABA(IV1,IV2)/ZNYR
        AD(IV1,IV2) = AD(IV1,IV2)/ZNYR
        ITIMEX=TIMEX
        WRITE(4,2020)ITIMEX,IV2,ABM(IV1,IV2),ABA(IV1,IV2),AD(IV1,IV2)
 2020   FORMAT(2I5,3F15.5)
  350 CONTINUE
  300 CONTINUE
      STOP
      END
C.....
C.....
C.....
      SUBROUTINE INPUT
      COMMON/PARAM/AAA(10,6),DMAX(10),DMIN(10),B3(10),B2(10),
     > ITOL(10),AGEMX(10),CURVE(10),G(10),SPRTND(10),SPRTMN(10),
     > SPRTMX(10),SWITCH(10,5),KTIME(10),C1(10),C2(10)
      COMMON/CONST/NSPEC,SOILQ,DEGD
      INTEGER SENSIT
      DIMENSION NSELCT(100)
C.....
C.....NSPEC - NUMBER OF SPECIES
C.....NSELCT - CONTAINS THE SPECIES NUMBER FOR THOSE SPECIES
C.....     THAT WILL BE USED IN THE SIMULATION
C.....
      READ(5,9000) NSPEC,(NSELCT(I),I=1,NSPEC)
```

```
C.....
C.....INPUT INDIVIDUAL SPECIES INFORMATION
C.....AAA - SPECIES NAME
C.....DMAX - MAXIMUM GROWING DEGREE DAYS
C.....     (NOT CURRENTLY USED)
C.....DMIN - MINIMUM GROWING DEGREE DAYS
C.....     (NOT CURRENTLY USED)
C.....B3 - INDIVIDUAL SPECIES CONSTANT USED IN GROW
C.....B2 - INDIVIDUAL SPECIES CONSTANT USED IN GROW
C.....C1 - INDIVIDUAL SPECIES CONSTANT USED TO CALCULATE BIOMASS
C.....C2 - INDIVIDUAL SPECIES CONSTANT USED TO CALCULATE BIOMASS
C.....ITOL - LIGHT TOLERANCE CLASS
C.....AGEMX - MAXIMUM AGE OF SPECIES
C.....CURVE - DENOTES TYPE OF CURVE FOR CALCULATING BIOMASS
C.....     (NOT CURRENTLY USED)
C.....G - SCALES THE GROWTH RATE OF EACH SPECIES
C.....SPRTND - TENDENCY TO STUMP SPROUT
C.....SPRTMN - MINIMUM SIZE TREE THAT WILL SPROUT
C.....SPRTMX - MAXIMUM SIZE TREE THAT WILL SPROUT
C.....SWITCH - REPRODUCTION SWITCHES USED IN BIRTH
C.....     (NOT CURRENTLY USED)
C.....KTIME - DESIGNATES SEED SOURCE LIMITATION FOR CERTAIN SPECIES
C.....      (NOT CURRENTLY USED)
C.....NUM - INDIVIDUAL SPECIES NUMBER
C.....SENSIT - DENOTES SENSITIVITY TO SULFUR DIOXIDE
C.....     (NOT CURRENTLY USED)
C.....
      J = 1
      REDUCE = 0.
      DO 10 K=1,100
         READ(5,9001) (AAA(J,I),I=1,6),C1(J),C2(J),B3(J),B2(J),
     >    ITOL(J),AGEMX(J),CURVE(J),G(J),SPRTND(J),SPRTMN(J),SPRTMX(J),
     >    (SWITCH(J,I),I=1,5),KTIME(J),NUM,SENSIT
         IF (NSELCT(J).NE.NUM) GO TO 10
         IF (REDUCE.NE.0.) G(J) = G(J)*(1.00-(SENSIT*REDUCE))
         WRITE(6,9002) (AAA(J,I),I=1,6),C1(J),C2(J),B3(J),B2(J),
     >    ITOL(J),AGEMX(J),CURVE(J),G(J),SPRTND(J),SPRTMN(J),SPRTMX(J),
     >    (SWITCH(J,I),I=1,5),KTIME(J),SENSIT,NUM
         IF (NUM.EQ.NSELCT(NSPEC)) GO TO 20
         J = J+1
   10    CONTINUE
   20 CONTINUE
      RETURN
 9000 FORMAT(40I2)
 9001 FORMAT(6A4,2F5.3,F5.4,F5.2,I1,F4.0,F2.0,F5.1,F2.0,F4.1,F4.0,
     > 5L1,I4,I5/I1)
 9002 FORMAT(' ',6A4,2F6.3,1X,F6.4,F6.2,I2,F5.0,F3.0,F6.1,F3.0,F5.1,
     > F5.0,5L1,I5,2I5)
      END
C.....
C.....
C.....
      SUBROUTINE INIT
      COMMON/FOREST/NTREES(10),DBH(700),IAGE(700),KSPRT(100),
     > NEWTR(100),SUMLA(700),NEW(100),SWTCH(5),LOCUS(2,800)
      COMMON/CONST/NSPEC,SOILQ,DEGD
      COMMON/DEAD/NOGRO(700),NTEMP(700)
C.....
C.....INITIALIZE VARIABLES TO ZERO FOR REPLICATE PLOTS
C.....
C.....KSPRT IS USED TO FLAG THE TREES THAT CAN SPROUT
```

```
C.....NOGRO IS USED TO FLAG THE TREES THAT DON'T GROW
C.....IAGE CONTAINS THE AGE FOR EACH TREE
C.....
C.....
      DO 10 I=1,NSPEC
         KSPRT(I) = 1
   10    CONTINUE
      NSPE1 = NSPEC+1
      DO 20 I=NSPE1,700
         NOGRO(I) = 0
         IAGE(I) = 0
   20    CONTINUE
      RETURN
      END
C.....
C.....
C.....
      SUBROUTINE PLOTIN(IPLOT)
      COMMON/FOREST/NTREES(10),DBH(700),IAGE(700),KSPRT(100),
     > NEWTR(100),SUMLA(700),NEW(100),SWTCH(5),LOCUS(2,800)
      COMMON/CONST/NSPEC,SOILQ,DEGD
C.....
C.....INITIALIZE VARIABLES TO START SIMULATION ON BARE PLOT
C.....NTREES CONTAINS NUMBER OF TREES FOR EACH SPECIES
C.....DBH CONTAINS DIAMETER AT BREAST HEIGHT FOR EACH TREE
C.....
      IPLOT = IPLOT+1
         DO 10 I=1,NSPEC
                  NTREES(I)=0
   10           CONTINUE
         NSPE1=NSPEC+1
         DO 20 I=NSPE1,700
                  DBH(I)=0.
   20           CONTINUE
      RETURN
      END
C.....
C.....
C.....
      SUBROUTINE RANDOM(NSEED)
      COMMON/RAN/YFL
C.....
C.....SUBROUTINE RANDOM CALLS THE UNIFORM RANDOM NUMBER GENERATOR AND
C.....    RETURNS THE RANDOM NUMBER IN YFL
C.....
      YFL = RANDU(NSEED)
      RETURN
      END
C.....
C.....
C.....
      SUBROUTINE KILL(KYR)
      COMMON/FOREST/NTREES(10),DBH(700),IAGE(700),KSPRT(100),
     > NEWTR(100),SUMLA(700),NEW(100),SWTCH(5),LOCUS(2,800)
      COMMON/PARAM/AAA(10,6),DMAX(10),DMIN(10),B3(10),B2(10),
     > ITOL(10),AGEMX(10),CURVE(10),G(10),SPRTND(10),SPRTMN(10),
     > SPRTMX(10),SWITCH(10,5),KTIME(10),C1(10),C2(10)
      COMMON/CONST/NSPEC,SOILQ,DEGD
      COMMON/RAN/YFL
      COMMON/DEAD/NOGRO(700),NTEMP(700)
      COMMON/COUNT/NTOT,NYEAR
```

```
      COMMON/TEMP/DTEMP(700),ITEMP(700),LTEMP(2,800)
      COMMON/SEED/USEED(11),NSEED1,NSEED2,NSEED3,NSEED4
      INTEGER USEED
      LOGICAL SWITCH,SWTCH
      KNT = 0
      DO 30 I=1,NSPEC
         IF (NTREES(I).EQ.0) GO TO 30
         NL = KNT+1
         NU = NTREES(I)+KNT
         DO 20 K=NL,NU
            CALL RANDOM(USEED(1))
C.....
C.....KILL TREES BASED ON PROBABILITY THAT ONLY 1% REACH MAXIMUM AGE
C.....
            IF (YFL.LE.(4.605/AGEMX(I))) GO TO 10
C.....
C.....CHECK TO SEE IF THERE WAS ANY GROWTH FOR TREE
C.....
            IF (NOGRO(K).EQ.0) GO TO 20
            CALL RANDOM(USEED(2))
            IF (YFL.GT.0.368) GO TO 20
   10       CONTINUE
            NTREES(I) = NTREES(I)-1
C.....
C.....CHECK TO SEE IF DEAD TREE CAN STUMP SPROUT. IF SO GIVE THE
C.....SPROUT NEW AGE, DBH AND NOGRO VALUES
C.....
        IF(SPRTND(I) .EQ. 0) GO TO 15
        IF(DBH(K).LE.SPRTMN(I).OR.DBH(K).GE.SPRTMX(I)) GO TO 15
         CALL RANDOM(USEED(5))
        DBH(K)=1.27+.3*(1.0-YFL)**3
        NTREES(I)=NTREES(I)+1
         IAGE(K)=0
         NOGRO(K)=0
         GO TO 20
C.....
C.....SET DBH OF DEAD TREES EQUAL TO -1.
C.....
   15       DBH(K) = -1.0
   20       CONTINUE
         KNT = NU
   30    CONTINUE
C.....
C.....REWRITE DIAMETERS AND AGES TO ELIMINATE DEAD TREES
C.....
      K = 0
      DO 40 I=1,700
         IF (DBH(I).EQ.0.) GO TO 50
         IF (DBH(I).LT.0.) GO TO 40
         K = K+1
         DBH(K) = DBH(I)
         IAGE(K) = IAGE(I)
         NOGRO(K) = NOGRO(I)
         LOCUS(1,K)=LOCUS(1,I)
         LOCUS(2,K)=LOCUS(2,I)
   40    CONTINUE
   50 NTOT = K
      IF (NTOT.EQ.0) RETURN
      NTOT1 = K+1
      DO 60 I=NTOT1,NU
         DBH(I) = 0.
```

```
         IAGE(I) = 0
         NOGRO(I) = 0
         LOCUS(1,I) = 0
         LOCUS(2,I) = 0
   60    CONTINUE
      RETURN
      END
C.....
C.....
C.....
      SUBROUTINE GROW
      COMMON/FOREST/NTREES(10),DBH(700),IAGE(700),KSPRT(100),
     > NEWTR(100),SUMLA(700),NEW(100),SWTCH(5),LOCUS(2,800)
      COMMON/PARAM/AAA(10,6),DMAX(10),DMIN(10),B3(10),B2(10),
     > ITOL(10),AGEMX(10),CURVE(10),G(10),SPRTND(10),SPRTMN(10),
     > SPRTMX(10),SWITCH(10,5),KTIME(10),C1(10),C2(10)
      COMMON/CONST/NSPEC,SOILQ,DEGD
      COMMON/RAN/YFL
      COMMON/DEAD/NOGRO(700),NTEMP(700)
      COMMON/COUNT/NTOT,NYEAR
      COMMON/TEMP/DTEMP(700),ITEMP(700),LTEMP(2,800)
      LOGICAL SWITCH,SWTCH
C.....
C.....DBH IS IN CENTIMETERS
C.....EACH TREE IS REQUIRED TO ADD A 1.0 MM GROWTH RING EACH YEAR
C.....(SPRUCE IS AN EXCEPTION - IT IS REQUIRED TO ADD 0.45 MM)
C.....
      TINC = .1
      PHI = 1.
C.....
C.....CALCULATE TOTAL NUMBER OF TREES
C.....
      NTOT = 0
      DO 10 I=1,NSPEC
   10    NTOT = NTOT+NTREES(I)
      IF (NTOT.EQ.0) RETURN
C.....
C.....SUM LEAF AREA OF ALL TREES THAT ARE OF APPROXIMATELY
C.....THE SAME HEIGHT
C.....
      DO 20 I=1,700
         NOGRO(I) = 0
   20    SUMLA(I) = 0.
      NL = 1
      SBIO = 0.
      DO 40 J=1,NSPEC
         IF (NTREES(J).EQ.0) GO TO 40
         NU = NL+NTREES(J) -1
         DO 30 K=NL,NU
C.....
C.....CALCULATE WT IN LBS, CONVERT TO KG (2.205)
C.....THEN CALCULATE STAND BIOMASS
C.....
         IF(DBH(K) .LE. 2.5) GO TO 25
           WT = C1(J) + C2(J) * (ALOG(DBH(K)/2.54))
           SBIO = SBIO + EXP(WT)/2.205
C.....
C.....HEIGHT PROFILE IS CALCULATED IN .1 METER UNITS
C.....
   25       IHT = (B2(J)*DBH(K)-B3(J)*DBH(K)**2)/10.+1.
            IF (IHT.GT.700) GO TO 90
```

```
            SUMLA(IHT) = SUMLA(IHT)+1.9283295E-4*DBH(K)**2.129
   30       CONTINUE
            NL = NL+NTREES(J)
   40    CONTINUE
         DO 50 J=1,699
            J1 = 700-J
            SUMLA(J1) = SUMLA(J1)+SUMLA(J1+1)
   50    CONTINUE
C.....
C.....CALCULATE AMOUNT OF GROWTH FOR EACH TREE
C.....
      NL = 1
      DO 80 I=1,NSPEC
         IF (NTREES(I).EQ.0) GO TO 80
         NU = NL+NTREES(I)-1
         DO 70 J=NL,NU
            HT = B2(I)*DBH(J)-B3(I)*DBH(J)**2
            IHT = HT/10.+2.
            SLAR = SUMLA(IHT)
            AL = PHI*EXP(-SLAR*.25)
            GR = (137.+.25*B2(I)**2/B3(I))*(0.5*B2(I)/B3(I))
            DNC = G(I)*DBH(J)*(1.0-(137.*DBH(J)+B2(I)*DBH(J)**2-B3(I) *
     >       DBH(J)**3)/GR)/(274.+3.0*B2(I)*DBH(J)-4.0*B3(I)*DBH(J)**2)
     >       *(1.0-SBIO/SOILQ)*4.0
            DINCT = 2.24*(1.-EXP(-1.136*(AL-.08)))*DNC
            DINCI = (1.0-EXP(-4.64*(AL-.05)))*DNC
C.....
C.....ADJUST DINC BASED ON SHADE TOLERANCE OF EACH SPECIES
C.....
      IF(ITOL(I).EQ.1) DINC=DINCT
      IF(ITOL(I).EQ.2) DINC=(3.0*DINCT+DINCI)/4.0
      IF(ITOL(I).EQ.3) DINC=(DINCI+DINCT)/2.0
      IF(ITOL(I).EQ.4) DINC=(3.0*DINCI+DINCT)/4.0
      IF(ITOL(I).EQ.5) DINC=DINCI
C.....
C.....CHECK INCREMENT LESS THAN 1.0 MM REQUIRED GROWTH
C.....
            TINC=.1
            IF(I .NE. 7) GO TO 55
            TINC=0.045
   55       IF (DINC.LT.TINC) DINC = 0.0
            IF (DINC.NE.0.) GO TO 60
            NOGRO(J) = -1
   60       IF(I .EQ. 7 .AND. DINC .LT. 0.1) DINC=0.0
            DBH(J) = DBH(J)+DINC
   70       CONTINUE
         NL = NL+NTREES(I)
   80    CONTINUE
      RETURN
   90 WRITE(6,9000)
      STOP
 9000 FORMAT('1 IHT EXCEEDED 700')
      END
C.....
C.....
C.....
      SUBROUTINE BIRTH(KYR)
      COMMON/FOREST/NTREES(10),DBH(700),IAGE(700),KSPRT(100),
     > NEWTR(100),SUMLA(700),NEW(100),SWTCH(5),LOCUS(2,800)
      COMMON/PARAM/AAA(10,6),DMAX(10),DMIN(10),B3(10),B2(10),
     > ITOL(10),AGEMX(10),CURVE(10),G(10),SPRTND(10),SPRTMN(10),
```

```
     > SPRTMX(10),SWITCH(10,5),KTIME(10),C1(10),C2(10)
       COMMON/CONST/NSPEC,SOILQ,DEGD
       COMMON/RAN/YFL
       COMMON/DEAD/NOGRO(700),NTEMP(700)
       COMMON/COUNT/NTOT,NYEAR
       COMMON/TEMP/DTEMP(700),ITEMP(700),LTEMP(2,800)
       COMMON/SEED/USEED(11),NSEED1,NSEED2,NSEED3,NSEED4
       DIMENSION NSEDL(10),CTOL(10),SMEAN(10),Z(1),LOCAT(2,100)
       DIMENSION NBARE(10),NCOVR(10)
       INTEGER USEED
C.....
C.....SAPLINGS ENTER THE PLOT AT AVERAGE SIZE OF 1.27 CM DBH
C.....
       SIZE = 1.27
         BIOM = 0.
         NL = 1
C.....
C.....INPUT SEEDLING PARAMETERS FOR EACH SPECIES
C.....
         DATA NBARE/10,6,13,20,4,5,0,0,0,0/
         DATA NCOVR/0,0,0,5,0,0,1,0,0,0/
         DATA SMEAN/0.,0.,0.,0.,0.,0.,0.,0.,0.,0./
         DATA CTOL/25.,45.,40.,75.,40.,35.,65.,0.,0.,0./
C.....
C.....CALCULATE BIOMASS (LEAF MASS) FOR EACH SPECIES
C.....
          DO 10 J=1,NSPEC
             IF (NTREES(J).EQ.0) GO TO 10
             NU = NL+NTREES(J)-1
             DO 5 K=NL,NU
                BIOM = BIOM+1.9283295E-4*DBH(K)**2.129
    5        CONTINUE
             NL = NL+NTREES(J)
    10       CONTINUE
C.....
C.....ASSIGN NSEDL VALUES DEPENDING ON PLOT CONDITIONS
C.....(BARE OR COLONIZED)
C.....
         IF(BIOM .GT. 0.5) GO TO 12
         DO 12 ICO=1,10
            NSEDL(ICO) = NBARE(ICO)
    12   CONTINUE
         IF(BIOM .LE. 0.5) GO TO 14
         DO 13 ICC=1,10
            NSEDL(ICC) = NCOVR(ICC)
    13   CONTINUE
          CALL RANDOM(USEED(9))
          IF(YFL .LT.      ) NSEDL(1)=NSEDL(1)+1
          IF(YFL .LT.      ) NSEDL(2)=NSEDL(2)+1
          IF(YFL .LT.      ) NSEDL(3)=NSEDL(3)+1
          IF(YFL .LT.      ) NSEDL(4)=NSEDL(4)+1
          IF(YFL .LT.      ) NSEDL(5)=NSEDL(5)+1
          IF(YFL .LT.      ) NSEDL(6)=NSEDL(6)+1
          IF(YFL .LT.      ) NSEDL(7)=NSEDL(7)-1
    14   CONTINUE
C.....
C.....TOTAL NUMBER OF TREES IN STAND
C.....
          NTOT = NL-1
C.....
C.....STORE VALUES FOR TREES IN TEMPORARY ARRAYS
```

```
C.....
         DO 15 I=1,NTOT
            ITEMP(I) = IAGE(I)
            DTEMP(I) = DBH(I)
            NTEMP(I) = NOGRO(I)
             LTEMP(1,I) = LOCUS(1,I)
             LTEMP(2,I) = LOCUS(2,I)
   15       CONTINUE
C.....
C.....DO THE FOLLOWING FOR EACH SPECIES OF SEEDLING
C.....
         DO 130 ISP=1,NSPEC
         MPLANT=0
        K=NSEDL(ISP)
C.....
C.....K IS THE MAXIMUM POTENTIAL SEEDLING INPUT/SPECIES/YEAR
C.....
      DO 75 IJS=1,K
C.....
C.....SET THE WIDTH OF THE SQUARE GRID IN 0.5 M UNITS
C.....
         IWIDTH=34
         CIND=0.0
         VAL=0.0
C.....
C.....RANDOMLY SELECT THE X AND Y COORDINATES OF A SEED
C.....
        IX=IWIDTH*RANDU(NSEED3)
        IY=IWIDTH*RANDU(NSEED4)
C.....
C.....CHECK TO SEE IF THAT GRIDPOINT IS OCCUPIED
C.....
         DO 17 M=1,MPLANT
         IF(IX .EQ. LOCAT(1,M) .AND.  IY .EQ. LOCAT(2,M)) GO TO 75
   17    CONTINUE
         DO 20 I=1,NTOT
         IF(IX .EQ. LOCUS(1,I) .AND. IY .EQ. LOCUS(2,I)) GO TO 75
   20    CONTINUE
C.....
C.....CHECK ALL TREES ON THE PLOT--IF THEY ARE OVER 12 CM DBH
C.....CALCULATE THEIR INFLUENCE ON THE SEED
C.....
   21  DO 40 I=1,NTOT
         IF(DBH(I) .LE. 12.0) GO TO 40
C.....
C.....USE REPEATING BOUNDARIES FOR SEEDLINGS WITHIN 5 M OF THE PLOT EDGE
C.....
          IDX=LOCUS(1,I)-IX
          INDI=0
   22    IF(IDX .GT. 10) GO TO 23
          IF(IDX .GE.-10) GO TO 25
          IF(INDI .EQ. 1) GQ TO 40
          IDX=IDX+IWIDTH
          INDI=1
          GO TO 22
   23    IF(INDI .EQ. 1) GO TO 40
          IDX=IDX-IWIDTH
          INDI=1
          GO TO 22
   25    IDY=LOCUS(2,I)-IY
          INDI=0
```

```
   26    IF(IDY .GT. 10) GO TO 29
         IF(IDY .LT.-10) GO TO 28
         IDISQ=IDX**2+IDY**2
C.....
C.....IF TREES ARE WITHIN 5 M OF THE SEED THEN A CANOPY
C.....INFLUENCE VALUE (VAL) IS CALCULATED FOR EACH TREE
C.....THE TOTAL FOR ALL TREES IS CIND
C.....
         IF(IDISQ .GT. 100) GO TO 40
         RDISQ=IDISQ
         DIST=SQRT(RDISQ)/2.0
         VAL=DBH(I)/DIST
         CIND=CIND+VAL
         GO TO 40
   28    IF(INDI .EQ. 1) GO TO 40
         IDY=IDY+IWIDTH
         INDI=1
         GO TO 26
   29    IF(INDI .EQ. 1) GO TO 40
         IDY=IDY-IWIDTH
         INDI=1
         GO TO 26
  40     CONTINUE
         IF (CIND .EQ. 0.0) GO TO 50
C.....
C.....IF CANOPY INFLUENCE IS GREATER THAN ZERO DRAW A NUMBER
C.....FROM ONE TAIL OF A NORMAL DISTRIBUTION--IF NUMBER IS
C.....GREATER THAN CIND THEN PLANT THE SEEDLING AT THE GRIDPOINT
C.....
         CALL GGNORD(NSEED1,NSEED2,Z)
         ZIND=SMEAN(ISP)+(CTOL(ISP)*Z(1))
         ZIND=ABS(ZIND)
         IF(ZIND .LE. CIND) GO TO 75
C.....
C.....TALLY NUMBER OF SEEDLINGS TO BE PLANTED (MPLANT)
C.....
   50    MPLANT=MPLANT+1
         LOCAT(1,MPLANT)=IX
         LOCAT(2,MPLANT)=IY
   75    CONTINUE
C.....
C.....CALCULATE AGE AND DIAMETER FOR NEW TREES
C.....
         NSUM = 0
         DO 80 IS=1,ISP
   80       NSUM = NSUM+NTREES(IS)
C.....
C.....PLANT RANDOM NUMBER OF SEEDLINGS
C.....
         NL = NSUM+1
         NUP = NTOT
          IF(MPLANT .EQ. 0) GO TO 130
         DO 90 J=1,MPLANT
            NTOT = NTOT+1
            IF (NTOT.GT.700) CALL ERR
            NSUM = NSUM+1
            NTREES(ISP) = NTREES(ISP)+1
            ITEMP(NSUM) = 0
            LTEMP(1,NSUM)=LOCAT(1,J)
            LTEMP(2,NSUM)=LOCAT(2,J)
C.....
```

```
C.....CALCULATE DBH FOR SEEDLINGS
C.....
            CALL RANDOM(USEED(11))
            DTEMP(NSUM) = SIZE+.3*(1.0-YFL)**3
            NTEMP(NSUM) = 0
   90       CONTINUE
         IF (NL.GT.NUP) GO TO 110
         N1 = NSUM+1
         DO 100 L=NL,NUP
            DTEMP(N1) = DBH(L)
            ITEMP(N1) = IAGE(L)
            NTEMP(N1) = NOGRO(L)
            LTEMP(1,N1) = LOCUS(1,L)
            LTEMP(2,N1) = LOCUS(2,L)
            N1 = N1+1
  100       CONTINUE
C.....
C.....REINITIALIZE ORIGINAL DBH AND AGE ARRAYS - INCLUDING NEW TREES
C.....
  110    DO 120 I=1,NTOT
            IAGE(I) = ITEMP(I)
            DBH(I) = DTEMP(I)
            NOGRO(I) = NTEMP(I)
            LOCUS(1,I) = LTEMP(1,I)
            LOCUS(2,I) = LTEMP(2,I)
  120       CONTINUE
  130    CONTINUE
  140    CONTINUE
C.....
C.....INCREMENT AGES
C.....
      DO 150 I=1,NTOT
         IAGE(I) = IAGE(I)+1
  150    CONTINUE
      RETURN
      END
C.....
C.....
C.....
         SUBROUTINE OUTPUT(KYR,IPLOT)
      COMMON/FOREST/NTREES(10),DBH(700),IAGE(700),KSPRT(100),
     > NEWTR(100),SUMLA(700),NEW(100),SWTCH(5),LOCUS(2,800)
      COMMON/PARAM/AAA(10,6),DMAX(10),DMIN(10),B3(10),B2(10),
     > ITOL(10),AGEMX(10),CURVE(10),G(10),SPRTND(10),SPRTMN(10),
     > SPRTMX(10),SWITCH(10,5),KTIME(10),C1(10),C2(10)
      COMMON/COUNT/NTOT,NYEAR
      COMMON/CONST/NSPEC,SOILQ,DEGD
      COMMON/PASSX/ABM(1001,20),ABA(1001,20),AD(1001,20)
      COMMON/OUTPT/IO1,IO2,PLOT,PRINT,LIST
      DIMENSION OUT(34,34),SNAME(10)
      DIMENSION PBIO(10),PBAS(10),PDEN(10)
      CHARACTER*3 OUT
      CHARACTER*1 SNAME
      CHARACTER*1 SIZE
      DIMENSION BAR(100),BAS(100)
      LOGICAL PRINT,PLOT
C.....
C.....ASSIGN EACH SPECIES A LETTER FOR GRID MAP OUTPUT
C.....
      DATA SNAME/'C','A','B','F','M','J','S',' ',' ',' '/
      KYR1 = KYR+1
```

```
      NL=1
      AREA=0.0
      TBAR=0.0
      TOBAS=0.0
      NTOT = 0
      DO 100 I=1,NSPEC
      BAR(I)=0.0
      BAS(I)=0.0
      PBIO(I)=0.0
      PBAS(I)=0.0
      PDEN(I)=0.0
      IF(NTREES(I).EQ.0) GO TO 100
      NU=NL+NTREES(I) - 1
      DO 150 J =NL,NU
C.....
C.....TOBAS - TOTAL BASAL AREA ON PLOT
C.....TBAR - TOTAL BIOMASS ON PLOT
C.....BAS(I) - BASAL AREA OF SPECIES I
C.....BAR(I) - BIOMASS OF SPECIES I
C.....AREA - LEAF AREA ON PLOT
C.....
      BAS(I)=BAS(I)+0.7854E-4*(DBH(J)*DBH(J))
      AREA=AREA+1.9283295E-4*DBH(J)**2.129
        IF(DBH(J) .LE. 2.5) GO TO 150
          WT=C1(I)+C2(I)*(ALOG(DBH(J)/2.54))
          BAR(I)=BAR(I)+EXP(WT)/2205
  150 CONTINUE
      TOBAS=TOBAS+BAS(I)
      TBAR=TBAR+BAR(I)
C.....
C.....CONVERSIONS TO PER HA
C.....
      PLTBAR=TBAR/0.03
      PLTBAS=TOBAS/0.03
      NTOT=NTOT+NTREES(I)
      NL=NL+NTREES(I)
  100 CONTINUE
      IF (PRINT) WRITE(IO2,2000) KYR
 2000 FORMAT('0YEAR',I5)
      IF (PRINT) WRITE(IO2,2010)
 2010 FORMAT('0SPECIES',15X,'STEMS',2X,'BASAL AREA',3X,'%',4X
     >,'BIOMASS',5X,'%',32X,'DBH AND AGE')
      NL=1
      DO 200 I =1,NSPEC
      IF(NTREES(I).EQ.0)        GO TO 200
      PER=(BAR(I)/TBAR)*100.
      PBA=(BAS(I)/TOBAS)*100.
      ATOT=NTOT
      ATREES=NTREES(I)
      PDEN(I)=(ATREES/ATOT)*100.
      PBIO(I)=PER
      PBAS(I)=PBA
      NU=NL+NTREES(I) - 1
      NLINES=((NTREES(I)-1)/8)+1
      NLINES=NLINES-1
      IF (NLINES.EQ.0)  GO TO 10
      L1=NL+7
      IF(PRINT) WRITE(IO2,2020)(AAA(I,J),J=1,6),NTREES(I),BAS(I),PBA
     >,BAR(I),PER,(DBH(II),II=NL,L1)
 2020 FORMAT('0',6A4,I3,2X,E9.3,F6.1,2X,E9.3,F6.1,5X,8(F6.1,2X))
      IF(PRINT) WRITE(IO2,2025)(IAGE(II),II=NL,L1)
```

```
 2025  FORMAT(67X,8(I6,2X))
       DO 250 J=1,NLINES
       L2=L1+1
       L1=L1+8
       IF (J.EQ.NLINES)  L1=NU
       IF (PRINT) WRITE(IO2,2030)(DBH(II),II=L2,L1)
       IF(PRINT) WRITE(IO2,2025)(IAGE(II),II=L2,L1)
 2030 FORMAT(67X,8(F6.1,2X))
  250 CONTINUE
       GO TO 20
   10 IF(PRINT) WRITE(IO2,2020)(AAA(I,J),J=1,6),NTREES(I),BAS(I),PBA
     >,BAR(I),PER,(DBH(II),II=NL,NU)
 2040 FORMAT('0',6A4,4X,I3,4X,E9.3,6X,F8.2,8X,8(F6.1,2X))
       IF (PRINT) WRITE(IO2,2025)(IAGE(II),II=NL,NU)
   20 NL=NL+NTREES(I)
  200 CONTINUE
       IF(PRINT) WRITE(IO2,2050) NTOT,PLTBAS,PLTBAR,AREA
 2050 FORMAT('0 TOTAL NUMBER=',I5,5X,'TOTAL BASAL AREA=',E12.3,
     >5X,'TOTAL BIOMASS=',E12.3,5X,'TOTAL LEAF AREA=',E12.3)
          NL=1
          MAP=1
C.....
C.....IF MAP IS SET UNEQUAL TO ZERO A MAP WILL BE DRAWN
C.....
          IF(MAP .EQ. 0) GO TO 3015
C.....
C.....ENTER ELEMENTS FOR GRID MAP OF TREE LOCATIONS
C.....
         DO 2055 IL=1,34
         DO 2055 JL=1,34
 2055    OUT(IL,JL)=' ..'
         DO 2060 I=1,NSPEC
         IF(NTREES(I) .EQ. 0) GO TO 2060
         NU=NTREES(I)+NL-1
         DO 2058 IT=NL,NU
         IF(DBH(IT) .LT. 5.0) SIZE='A'
         IF(DBH(IT) .GE. 5.0 .AND. DBH(IT) .LT. 10.0) SIZE='B'
         IF(DBH(IT) .GE. 10.0 .AND. DBH(IT) .LT. 15.0) SIZE='C'
         IF(DBH(IT) .GE. 15.0 .AND. DBH(IT) .LT. 20.0) SIZE='D'
         IF(DBH(IT) .GE. 20.0 .AND. DBH(IT) .LT. 25.0) SIZE='E'
         IF(DBH(IT) .GE. 25.0 .AND. DBH(IT) .LT. 30.0) SIZE='F'
         IF(DBH(IT) .GE. 30.0 .AND. DBH(IT) .LT. 35.0) SIZE='G'
         IF(DBH(IT) .GE. 35.0 .AND. DBH(IT) .LT. 40.0) SIZE='H'
         IF(DBH(IT) .GE. 40.0 .AND. DBH(IT) .LT. 45.0) SIZE='I'
         IF(DBH(IT) .GE. 45.0 .AND. DBH(IT) .LT. 50.0) SIZE='J'
         IF(DBH(IT) .GE. 50.0) SIZE='K'
C.....
C.....ASSIGN SPECIES NAME AND SIZE CLASS FOR TREES AT THEIR GRIDPOINTS
C.....
       IXC=LOCUS(1,IT)+1
       IYC=LOCUS(2,IT)+1
 2057 FORMAT('0',2I3,F7.1)
       OUT(IXC,IYC)=' '//SNAME(I)//SIZE
 2058 CONTINUE
          NL=NTREES(I)+NL
 2060  CONTINUE
       IF(PRINT) WRITE(IO2,3005)
 3005  FORMAT('0GRID MAP OF TREES - SPECIES AND SIZE CLASS')
       IF(PRINT) WRITE(IO2,3010)((OUT(I,J),I=1,34),J=1,34)
 3010  FORMAT('0',34A3)
 3015 CONTINUE
```

```
      IF(.NOT.PLOT)      RETURN
      DO 300 IV1 = 1,NSPEC
       ABM(KYR1,IV1)=ABM(KYR1,IV1)+PBIO(IV1)
       ABA(KYR1,IV1)=ABA(KYR1,IV1)+PBAS(IV1)
       AD(KYR1,IV1)=AD(KYR1,IV1)+PDEN(IV1)
  300 CONTINUE
      ATOT=NTOT
      N1 = NSPEC+1
      N2 = N1+1
      N3 = N2+1
       ABM(KYR1,N1)=ABM(KYR1,N1)+(TBAR/.03)
       ABA(KYR1,N2)=ABA(KYR1,N2) +(TOBAS/.03)
       AD(KYR1,N3)=AD(KYR1,N3)+(ATOT/.03)
      RETURN
      END
C.....
C.....
C.....
      SUBROUTINE ERR
      WRITE(6,9000)
      STOP
 9000 FORMAT('1 THE NUMBER OF TREES HAS EXCEEDED 700')
      END
C.....
C.....
C.....
      FUNCTION RANDU(SEED)
      REAL*4 RNEW
      INTEGER PLUS/Z1000000/,IBIT/Z40000000/,HEX/Z10003/
      INTEGER OLD,NEW,SEED
      LOGICAL*1 NORMAL/.FALSE./
      EQUIVALENCE(NEW,RNEW)
C.....
C..... THIS FUNCTION CALCULATES UNIFORM RANDOM NUMBERS
C.....
      OLD=HEX*SEED
      SEED = IABS(OLD)
      NEW=OLD/256
      IF (NEW.LE.0) NEW=NEW+PLUS
      NEW=NEW+IBIT
      RANDU = RNEW+0.0
      RETURN
      END
C.....
C.....
C.....
      SUBROUTINE GGNORD(NSEED1,NSEED2,Z)
      DIMENSION Z(1)
      DATA PI2/0.62831853E01/
C.....
C.....CALCULATES NORMALLY DISTRIBUTED RANDOM NUMBERS
C.....
      K = 0
      A1 = RANDU(NSEED1)
      A2 = RANDU(NSEED2)
      K = K+1
      Z(K) = SQRT(-.2E01*ALOG(A1))*SIN(PI2*A2)
      K = K+1
      Z(K) = SQRT(-0.2E01*ALOG(A1))*COS(PI2*A2)
      RETURN
      END
```

```
//GO.FT04F001 DD SYSOUT=A,DEST=DECFILE
//GO.SYSIN DD *
 7 1 2 3 4 5 6 7
PRUNUS PENSYLVANICA      0.9762.195.546953.595 40.1.150.00                    1

SORBUS AMERICANA         0.9562.426.664453.153100.1.100.01.10.  25.          2

BETULA LUTEA             1.1302.338.368662.664280.1. 75.01.20.  50.          3

ABIES FRASERI            0.5962.402.525173.511160.2.080.00.                   4

ACER SPICATUM            0.9392.380.999963.663100.1. 75.01.10.  25.          5

AMELANCHIER ARBOREA      0.9562.426.999983.154150.1. 70.01.10.  25.          6

PICEA RUBENS             0.8082.332.427576.962380.2. 50.00.                   7

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VITA

Richard T. Busing was born in Oak Ridge, Tennessee, on March 7, 1957. He attended public schools in Manchester, England (1962-1963), and Oak Ridge, Tennessee. In June 1975 he graduated from Oak Ridge High School.

He enrolled at Earlham College, Richmond, Indiana, in August 1975 where he received a Bachelor of Arts Degree in Biology, June 1979.

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