

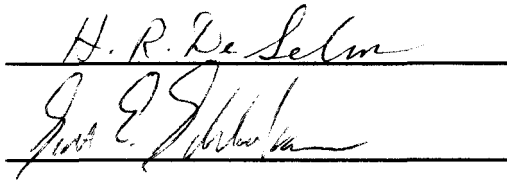
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DOES RUBUS CANADENSIS INTERFERE WITH
THE GROWTH OF FRASER FIR SEEDLINGS?

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

Eric Frank Pauley

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ABSTRACT

Vegetation change in the Great Smoky Mountains following balsam woolly adelgid-caused mortality of Fraser fir has included development of a dense Rubus canadensis shrub layer. Many fir seedlings have persisted in the forest understory, but the possible effects of Rubus on their annual growth have not been intensively studied.

This study had two objectives: (1) to determine if significant associations exist among density and shoot growth of Fraser fir seedlings, density/biomass of Rubus canadensis, canopy closure, and soil chemical parameters, and (2) to determine the effects of removal of aboveground Rubus stems on fir seedling shoot growth.

Eighty 1 x 1 m plots were used on Mount Collins, Great Smoky Mountains National Park, to characterize the understory habitat of Fraser fir seedlings. Terminal and lateral shoot lengths of the 1983-1987 growth were measured on fir seedlings. Seedlings were classified according to substrate type, surface type, substrate form, presence of adelgid damage, and age. Soil samples were taken for analyses of pH, potassium, phosphorus, and calcium. Overstory composition was characterized with prism plots. Fourteen 2 x 2 m plots were established to determine effects of Rubus removal on fir seedling growth, herbaceous cover, shrub/seedling counts, and soil parameters.

Rubus canadensis density was highest on the southwest-facing slope and lowest on the northeast-facing slope of Mount Collins. Fraser fir seedling density was highest on the northeast-facing slope and lowest on the southwest-facing slope. The Spearman rank correlation between Rubus density and fir seedling density was -0.376 ($P < 0.01$); a graph of these data showed variability in fir density to decrease with increasing Rubus density. Most years of fir terminal shoot growth showed positive associations with Rubus density ($0.309-0.396$, $P < 0.01$); a graph of these data showed no pronounced relationship. Rubus density and biomass were significantly correlated with soil phosphorus and potassium concentrations. All years of terminal shoot growth of fir seedlings measured showed positive associations with soil pH and potassium concentration.

Most fir seedlings were ≤ 25 cm tall. Only 38% were < 5 years old. More seedlings than expected occupied dead wood substrates, and more than expected were found on bryophyte-covered surfaces. More than 25% of seedlings showed adelgid damage; adelgid damage was more prevalent among seedlings ≥ 5 years old. Most seedlings showed a trend of increasing gains of terminal shoot growth over previous years of growth.

Removal of Rubus stems produced no significant effect on fir seedling shoot growth over one season. No Rubus-removal effects were found on any other understory variable

measured; Rubus itself responded to removal by rapid appearance and growth of new stems. Large seasonal changes in bryophyte cover and red spruce seedling density (from germination) occurred, but these changes were not affected by Rubus removal.

Germinal Fraser fir seedlings are scarce and are not likely to appear in large numbers unless existing understory firs reach reproductive age. Rubus appears to inhibit establishment of fir seedlings. Fir shoot growth does not appear to be associated with Rubus density or biomass. Fir shoot growth trends are probably consequences of normal growth patterns and recovery from adelgid infestation.

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CHAPTER 1

BACKGROUND

A. Introduction

Fraser fir (Abies fraseri) is a southern Appalachian conifer endemic to seven localities in North Carolina, Tennessee, and Virginia (Ramseur 1960). (Nomenclature for vascular plants follows that used by White (1982).) Fir is most abundant above 1500 m elevation, and its most frequent associates are red spruce (Picea rubens) and yellow birch (Betula lutea) (Oosting and Billings 1951; Whittaker 1956).

In the past three decades, Fraser fir has been devastated by a phloem-feeding insect, the balsam woolly adelgid (Adelges piceae Ratz.). The adelgid, native to Europe, was introduced into New England prior to 1908 (Kotinsky 1916). In the southern Appalachians, the adelgid was discovered on Mount Mitchell, North Carolina in 1957 (Speers 1958) and was found on Mount Sterling in the Great Smoky Mountains National Park (GSMNP) in 1962 (Ciesla et al. 1963, cited in Eagar 1984). The adelgid has since dispersed throughout the spruce-fir forest of the GSMNP and has killed most mature firs by disrupting water and nutrient transport to their crowns. With the loss of Fraser fir as a canopy dominant, the physical structure of

the forest has been greatly altered.

Vegetational changes following fir mortality include a large increase in the density of Rubus canadensis, thornless blackberry. Density of fir <2.5 cm diameter at breast height also increases as a result of seedling release (Boner 1979). DeSelm and Boner (1984) suggest, however, that the "considerable increase in the density of several shrubs raises the possibility of their interference with overstory regeneration" Also, Busing et al. (1988) state that Rubus "does appear to retard tree species recruitment" into taller height classes.

The most extensive population of Fraser fir exists in the GSMNP. Adelgid-caused mortality in the Park has been well documented (Johnson 1977; Eagar 1978) and post-adelgid vegetational changes have been described (Boner 1979). The growth responses of individual fir seedlings to understory development have not been intensively studied. This study was undertaken to determine if Rubus canadensis interferes with establishment/survival and growth of existing Fraser fir seedlings in the GSMNP.

B. The Great Smoky Mountains Spruce-Fir Forest

1. Topography

The GSMNP lies within the Blue Ridge physiographic province of the southern Appalachian Mountains (Fenneman 1938). In the Park, Clingmans Dome is the highest peak at 2025 m elevation. The main crest of the GSMNP rises over 1500 m elevation for about 40 km of its length (Ramseur 1960). Slopes are generally 40-60% within the spruce-fir forest but may reach 110% or more in some areas.

2. Geology and Soils

The largest portion of the GSMNP is underlain by rocks of the Great Smoky Group (Ocoee Series). Two formations are interbedded: the Thunderhead Sandstone (quartz, feldspar, granite, and quartzite) and the Anakeesta Formation (silty-clayey slate, phyllite, or schist with some free carbon and iron sulfides) (King et al. 1968).

These rocks weather into thin, stony Inceptisols or Spodosols that have high surficial organic matter (30-55%), low pH (3.4-4.4), low contents of basic cations (sum: 0.1-1.3 meq/100 g), and high exchangeable aluminum (2.3-7.1 meq/100 g) (McGinnis 1958; McCracken et al. 1962; Springer 1984). For the GSMNP spruce-fir forest, Oosting and

Billings (1951) provide general descriptions of soils, and Wolfe (1967) provides detailed soil descriptions and chemical analyses.

3. Climate

Annual precipitation in the GSMNP averaged 226 cm at 1524 m elevation for the years 1946-1951 (Shanks 1954; Stephens 1969). Recent data indicate somewhat lower precipitation. Annual totals at 1524 m elevation for 1983-1987 averaged 191 cm (Newfound Gap weather data provided by the Uplands Field Research Laboratory). Precipitation generally exceeds evapotranspiration (Shanks 1954), although some moisture stress probably occurs in summer and early fall (personal observation). At 1524 m, mean monthly temperatures may range from a low of 2° C. in February to a high of 18° C. in July (Shanks 1954).

4. Species Distribution

Three major overstory patterns are evident within the GSMNP spruce-fir forest: an increase in relative dominance of fir with elevation, a decrease in relative abundance of spruce toward lower, more mesic sites, and the interruption of the coniferous canopy by stands of beech (Fagus

grandifolia) (Russell 1953; Whittaker 1956; Fuller 1977; Pavlovic 1981). Understory patterns are more complex because of greater species richness compared to the overstory. Detailed descriptions of herbaceous and shrub patterns in the GSMNP are found in Crandall (1957, 1958) and Boner (1979).

5. Natural Disturbances

The most widespread natural disturbance in the GSMNP spruce-fir forest is the continual formation of canopy gaps <200 m² in area from single and multiple tree deaths. These small gaps occupy about 5-20% of the forest area (White et al. 1985). "Fir patches," arising from the cyclic death and regrowth of Fraser fir stands (Crandall 1958), occupy about 10% of the forest area (White et al. 1985). Large windthrow patches (>200 m²) and debris avalanches each occupy <2% of the forest area (White et al. 1985). Natural burned sites cover an insignificant portion of the GSMNP spruce-fir forest (White et al. 1985). Types, frequencies, and intensities of disturbance vary with topographic, elevational, and moisture gradients, species composition, species life history characteristics, and ecosystem-level characteristics such as litter accumulation and decomposition rates (Harmon et al. 1983).

6. Anthropogenic Disturbances

Only about 20% of the GSMNP area lacks historical anthropogenic disturbance (Pyle 1985, 1988). Corporate logging, fire, and concentrated settlement prior to Park establishment in 1934 continue to influence the species composition of the vegetation (Harmon 1980; Pyle 1985, 1988).

Historically, corporate logging was probably the most extensive human disturbance in the southern Appalachian spruce-fir forest. Logged spruce-fir forests are extremely susceptible to fire, and numerous logging-related fires have occurred (Korstian 1937; Pyle 1985, 1988).

Two other anthropogenic disturbances are currently known to be important in high-elevation forests of the GSMNP. First, an estimated 100 European wild boar (Sus scrofa L.) escaped into the mountains of North Carolina about 1920 (Stegeman 1938); boars have since spread into the GSMNP. Boar activity is concentrated in high-elevation deciduous forests dominated by beech, where rooting has caused intensive damage to understory vegetation (Bratton 1975; Huff 1977). Second, the balsam woolly adelgid has threatened the continued existence of Fraser fir (page 7).

Concern is increasing about the growth of Appalachian red spruce. In New England, major diebacks and radial

growth declines of red spruce have recently occurred (Siccama et al. 1982; Scott et al. 1984; Vogelmann et al. 1985). Spruce growth declines have been reported throughout the Appalachians (Adams et al. 1985; McLaughlin et al. 1987), including parts of the GSMNP. Busing et al. (1988), however, found no unusual mortality and no consistent trend in spruce radial growth in old-growth forests of Mount Collins, GSMNP. One complication in determining if spruce is showing a general decline is the history of logging in most Appalachian spruce and spruce-fir forests around the turn of the century. In some cases, growth rate declines are attributable to post-logging stand dynamics (Van Deusen 1987). Proposed contributing factors to observed declines include climatic stress, pathological agents, and air pollution (Hinrichsen 1987).

C. The Balsam Woolly Adelgid Problem

1. Adelgid-Fir Interactions

Adelgids are very small (<1 mm long) sucking insects which feed beneath the bark of Fraser fir boles. Adelgid saliva contains substances that cause abnormal xylem growth and impede water and nutrient transport to the tree crown (Eagar 1978, 1984, 1985). Larger trees support the highest adelgid populations (Johnson 1977), but seedlings and

saplings may also be infested and killed. Morphological changes in shoots and stems include swelling, twisting, and suppression of terminal shoot elongation. These changes are referred to as "gouting" (see Hay et al. 1978, p. 29). Lateral shoot growth is less affected by adelgid infestation than terminal shoot growth, and infested seedlings and saplings frequently acquire a characteristic flat-topped appearance. Young Fraser firs may recover from these effects and resume normal growth (Eagar 1984; personal observation). Fast-growing firs may support infestations for up to 20 years (Eagar 1985). Cone production may continue during infestation, but effects of the adelgid include reduced seed size, weight, and viability in Fraser fir (Fedde 1973).

2. Effects on Overstory Composition

Overstory fir mortality in the GSMNP has been extensive. Boner (1979) has constructed a chronosequence of forest changes following onset of overstory fir mortality. Density and basal area of overstory fir decreased sharply (to near zero) within 10 years, but subsequently increased because of recruitment. Density and basal area of spruce did not change substantially. For yellow birch, these parameters increased. Busing et al.

(1988), in a resample of two 0.4 ha plots on Mount Collins after more than 20 years, found similar results with fir and spruce basal areas.

3. Effects on Understory Composition

The understory of post-adelgid forests has undergone dramatic changes. Rubus canadensis density increased five-fold within 10 years and 10-fold within 20 years in Boner's (1979) chronosequence. Density of fir <2.5 cm diameter at breast height initially decreased but more than doubled within 20 years. Busing et al. (1988) estimated that Rubus canadensis patches now cover 25-50% of the Mount Collins plots. Fir sapling density increased in one of these plots but not in the other. Spruce sapling density increased significantly in both plots. Witter and Ragenovich (1986) examined fir regeneration on Mount Mitchell, North Carolina, where major overstory mortality occurred in the early 1960's. A large increase in density of fir >244 cm tall was found. However, density of smaller firs (<244 cm tall) decreased by half. Smaller spruces and hardwoods showed large increases in density. Rubus spp. "were by far the most common competing vegetation" (Witter and Ragenovich 1986). Height growth of taller fir seedlings showed signs of release, while that of shorter seedlings showed signs of suppression.

From these studies it appears that, generally, tree species recruitment is stimulated, but that response of Fraser fir specifically is variable. Data from Witter and Ragenovich (1986) suggest that few new fir seedlings are appearing and that existing small seedlings are being suppressed by competing understory vegetation.

D. Fraser Fir Growth

1. Seed Production, Viability, and Germination

Fraser fir produces large seed crops about every 3 years (Franklin 1974). Fraser fir in the GSMNP produced seed in 1987 (personal observation), although no cones were seen on any trees in the Park in 1988 (personal observation; observations by Uplands Field Research Laboratory and University of Tennessee personnel).

Seed viability in Fraser fir is typically low (S. E. Schlarbaum, personal communication). A period of stratification (cool, moist conditions) is required for substantial germination to occur (Franklin 1974). Germination in Fraser fir is highly sensitive to combinations of temperature regime, light exposure, and stratification period (Adkins et al. 1984; Blazich and Hinesley 1984). Seed longevity in forest soils is

apparently unknown, but viability may decrease after only one year under artificial storage (S. E. Schlarbaum, personal communication).

2. Early Seedling Survival

Many studies have described the ability of Fraser fir to colonize forest openings from logging, windthrow, fire, and canopy gaps (Korstian 1937; Crandall 1957; Crandall 1958; Boner 1979; Saunders et al. 1983; Busing 1985; White et al. 1985). Seedlings may also establish under a forest canopy and persist at low growth rates (personal observation). Early survival of seedlings is influenced by a large number of factors, including microclimate, soil, substrate type, and other ground layer vegetation (Harper 1977).

Brown (1953) transplanted 80 Fraser fir seedlings to an exposed grassy bald on Roan Mountain, Tennessee/North Carolina. Half were shielded from prevailing winds, while half were unprotected. After 10 years, 77% of the shielded seedlings survived, while only 35% of unprotected seedlings survived. Winter ice damage (broken twigs) was noted on most seedlings.

Gnegy (1970) assessed survival in Fraser fir Christmas tree plantations in West Virginia. Survival increased with increases in sand content of the soil. Mesic, well-drained

sites were regarded as most suitable for survival.

Busing (1985) examined distributions of Fraser fir seedlings among substrate types on Mount Collins, GSMNP. Of seedlings less than five years old, 39% occupied fallen logs and 49% occupied the forest floor. Of seedlings >25 cm tall and <12 cm diameter at breast height, 10% were on fallen logs and 75% were on the forest floor. Fallen logs appear to be well-suited to establishment but not to continued survival.

Warren et al. (1987b) studied survival of Fraser fir seedlings transplanted to a grassy bald at 1400 m elevation in North Carolina. After three years, survival was lower in bare soil than in other vegetation management programs. Most seedling mortality occurred in winter. Gnegy (1970) recommended "some type of weed control" to enhance survival of Fraser fir in plantations.

These studies suggest that Fraser fir seedling survival is best on sheltered, moist, well-drained forest floor sites. Some ground layer vegetation may be beneficial (by moderating temperature or water availability), but very dense vegetation may reduce survival.

3. Seedling Growth

Fraser fir is very shade tolerant. Height growth may not be reduced significantly unless shade reaches 76% (Hinesley 1986).

Shoot growth is sensitive to temperature regime and moisture availability. Hinesley (1981) found maximum height growth in 21-week old containerized Fraser fir seedlings at day/night temperatures of 30/18° C. Gnegy (1970) found a positive relation between height growth and sand content in Fraser fir plantation soils. Water stress reduced root and shoot dry weight of three year old Fraser fir (Tseng et al. 1988).

Warren et al. (1987a) assessed effects of nitrogen (N) fertilization and competition from orchard grass (Dactylis glomerata) and white clover (Trifolium repens) on growth of containerized Fraser fir seedlings. After 90 days, application of N enhanced dry weights of new shoots, stems, and roots. Competition reduced weights of these same plant parts, and also reduced phosphorus, potassium, and calcium concentrations in new shoots. Neither height nor diameter growth were affected by any treatment. Warren et al. (1987b) planted Fraser fir seedlings in a North Carolina grassy bald and applied several vegetation management programs. After three years, most types of vegetation control enhanced height growth over no vegetation control.

One major problem emerging from the last two studies is that there may be a time lag between an experimental treatment and its effects. Warren et al. (1987a) suggested that height growth may have required more than 90 days to respond to N fertilization. Likewise, Warren et al. (1987b) found significant differences in height growth among vegetation control programs only after a second season. Current growth of woody plants may be partially determined by conditions in the previous growing season (Kozlowski 1964). Shoot length of many species is associated with size of the bud producing the shoot, which is in turn affected by water deficiencies (Kramer and Kozlowski 1979).

E. Rubus Growth

Species of Rubus are perennial, but aboveground stems (canes) generally live for only two years. New canes are sterile the first year and are called primocanes; these canes flower the following year and are then called floricanes (Strausbaugh and Core 1970-1977). The primary mode of colony development in Rubus canadensis appears to be vegetative growth from rootstocks which occur 8-10 cm below the surface (personal observation; Flinn and Wein 1977). Rubus canadensis establishes quickly in forest

openings in the GSMNP if established conifer saplings are not too dense (Crandall 1957). Germination requires a stratification period (Core 1974). Seed longevity in Rubus canadensis is unknown, but seeds of R. idaeus may retain viability for up to 5 years in forest soil (Granström 1987).

F. Future Patch Dynamics in the Spruce-Fir Forest

The immediate future of Fraser fir depends strongly on the fate of existing seedlings in an environment with a persistent adelgid population. Seedlings that survive adelgid infestation may fail to produce viable seeds. Trees which mature and produce viable seeds may disperse those seeds into germination sites made unsuitable by herb and shrub species invasion.

Busing (1985) constructed a computer model of canopy dynamics in the old-growth spruce-fir forest on a northeast-facing slope of Mount Collins (Busing and Clebsch 1987). A variety of simulations was carried out, including fir survival with continuous adelgid infestation. In this simulation, fir remained a dominant species but made up a reduced fraction of the stand basal area. Fir relative density did not change substantially.

Busing's (1985) model applies to southern Appalachian spruce-fir forests whose disturbance regimes are dominated

by small gap formation. The topographic and compositional diversity of the GSMNP spruce-fir forest imposes great variability in type of and response to disturbance. One possible pattern is development of a mosaic landscape involving repeated stand growth, reproduction, infestation, and degeneration (White 1984). This scenario is partially dependent upon sufficient fir reproduction prior to adelgid-caused mortality. With increased frequency of canopy disturbance, seedling-understory interactions may influence tree species regeneration more strongly.

Balsam woolly adelgid infestation has greatly reduced the importance of Fraser fir in the forest canopy and caused death and growth abnormalities in understory firs. Canopy opening has caused rapid growth of shrub species, especially Rubus canadensis. Several authors suggest that Rubus does interfere with fir seedling establishment, survival, and growth (Boner 1979; Witter and Ragenovich 1986; Busing et al. 1988). This study examined Fraser fir seedling density and shoot growth specifically for associations with Rubus canadensis to determine if Rubus interferes with fir regeneration. The approach was to characterize the seedling-understory environment and to test for effects of Rubus removal on fir seedling growth.

G. Objectives and Hypotheses

This study had two primary objectives:

- (1) to determine if significant associations exist among density and shoot growth of Fraser fir seedlings, density/biomass of Rubus canadensis, canopy closure, and soil chemical parameters, and
- (2) to determine the effects of removal of aboveground Rubus stems on shoot growth of fir seedlings.

For objective (1), eleven principal hypotheses were tested:

- (a) Total density of fir seedlings is negatively associated with amount of canopy closure.
- (b) Density of fir seedlings established after overstory mortality is negatively associated with amount of canopy closure.
- (c) Rubus density and aboveground biomass are negatively associated with amount of canopy closure.
- (d) Total density of fir seedlings is negatively associated with Rubus density and aboveground biomass.
- (e) Density of fir seedlings established after overstory mortality is negatively associated with Rubus density and biomass.
- (f) Fir terminal and lateral shoot lengths of recent years' growth are negatively associated with amount of canopy closure.

- (g) Fir terminal shoot lengths of recent years' growth are positively associated with the density of fir seedlings themselves.
- (h) Fir lateral shoot lengths of recent years' growth are negatively associated with the density of fir seedlings themselves.
- (i) Fir terminal and lateral shoot lengths of recent years' growth are negatively associated with Rubus density and biomass.
- (j) Fir terminal and lateral shoot lengths of recent years' growth are positively associated with soil nutrient concentrations.
- (k) Rubus density and biomass are positively associated with soil nutrient concentrations.

For objective (2), the primary hypothesis tested was that 1988 fir shoot lengths would be greater in the Rubus-removal treatment than in an undisturbed control. Because Fraser fir height growth has responded positively to increased light levels (Hinesley 1986) and reduced vegetative competition (Warren et al. 1987b), removal of Rubus canadensis canes may cause increased seedling growth. Positive effects of Rubus-removal on herbaceous species cover, woody species densities, and soil nutrient concentrations were also hypothesized and tested.

CHAPTER 2

METHODS

A. Field Methods

1. Overstory Composition

Study site. Mount Collins in the Great Smoky Mountains National Park was the study area (Figure 1). That area was chosen because of accessibility, topographic uniformity, and prior history of vegetation study (Oosting and Billings 1951; Busing 1985; White et al. 1985; Busing et al. 1988). Adelgid-caused mortality of overstory fir occurred primarily during 1982 and 1983 (White et al. 1985; R. T. Busing, personal communication). Nearly all large firs were killed, foliage and smaller branches have fallen, and the forest canopy is discontinuous.

Most of the Mount Collins area is unlogged spruce-fir forest, but the northwest-facing slope (Figure 1) has been partially logged. Corporate logging prior to Park establishment was extensive in the Little River drainage, into which the northwest-facing slope drains (Pyle 1985, 1988). Maps prepared by Pyle (1985) show approximate boundaries of pre-Park disturbances. According to Map 36 of her set, all of the present study area should be in

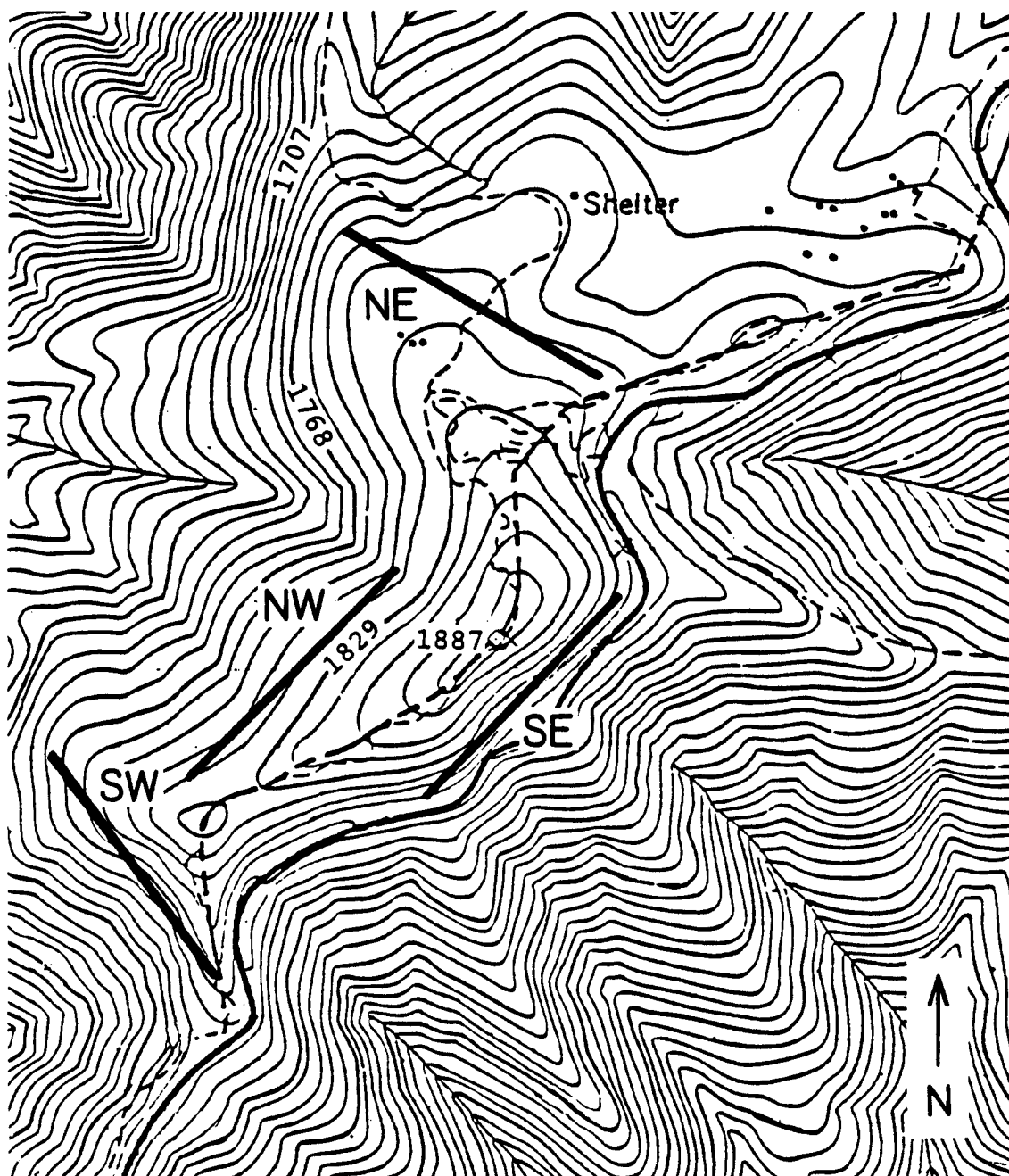


Figure 1. Map of Mount Collins, GSMNP, Clingmans Dome Quadrangle, USGS 7.5 minute topographic series. Straight lines are locations of transects used. Each transect is 500 m long. Dots are locations of control and Rubus-removal plots. Elevations are in meters.

unlogged spruce-fir forest. However, numerous cut stumps, few large spruce, and many large (now dead) fir were observed on the northwest-facing slope. Fir dominance is an expected consequence of logging (Weaver 1972; R. T. Busing, personal communication). Some cutting in the study area certainly occurred, although possibly not the "heavy cut" indicated for surrounding areas by Pyle's map.

Transect locations. On Mount Collins, four transects were oriented along arbitrary compass bearings across the slope. Locations were determined from a topographic map as areas of uniform topography and similar elevation, but of different aspect (Figure 1, Table 1; transects are labeled according to their aspect). Transects NE, SW, and SE were located in unlogged spruce-fir forest apparently undisturbed except for adelgid-caused mortality. Transect NW was located in forest which was logged to some extent.

Canopy measurements. Each transect was 500 m long, with sample points located at 50 m intervals. Each point served as the center of a 5-factor metric prism plot used to characterize the canopy stratum. Diameter at breast height (DBH; breast height = 137 cm) of each woody stem, alive or dead, reaching breast height in the prism plot was measured to the nearest 0.1 cm. Slope percent and aspect

Table 1. Site characteristics and sampling dates of transects used on Mount Collins.

	Transect			
	NE	NW	SW	SE
Aspect ($^{\circ}$)	30	310	230	135
Slope (%)	8-25	25-35	30-65	35-80
Elevation (m)	1780- 1810	1800- 1820	1760- 1790	1790- 1830
Sample date	6/24/88- 6/28/88	7/1/88- 7/5/88	7/7/88- 7/15/88	7/16/88- 7/20/88

were determined for each plot. Canopy closure was estimated using a convex mirror painted with regularly spaced dots. The mirror was viewed from the waist, and the proportion of dots (of 15) covered by canopy foliage was an estimate of canopy closure. The mirror was used twice at each sample point, once facing north and once facing south.

2. Seedling-Understory Characterization

Understory plot measurements. On the upslope and downslope sides of each sample point, a 1 x 1 m plot was placed 0.5 m away from the point to sample the understory. Plot sizes were not corrected for slope because most plots were located on gentle (<40%) slopes and corrections would have been minimal (<10%). Because slope correction involves enlarging plot sizes, some parameters (e.g., seedling densities) may have been slightly underestimated. In each plot, DBH of each living woody stem >137 cm tall was measured. Woody stems $\leq$ 137 cm tall (except Rubus canadensis) were counted and assigned to height classes. Height classes were: $\leq$ 25, 26-50, 51-75, 76-100, and 101-137 cm. Germinal seedlings (those emerging during the sampling season) were distinguished from others in the smallest height class only in transect SE. Rubus canes were counted and their basal diameters were measured with a

caliper to the nearest 0.1 cm. No distinction was made between primocanes and floricanes. Percent cover of plot area for each vascular herb species was estimated to the nearest 10 percent. Species with cover <10% were assigned a cover of 5% for data analysis because more precise visual estimates were not considered possible. Cover of lichens, bryophytes (collectively), litter (dead leaves, twigs, etc.), exposed rock, dead log (>5 cm diameter), dead root, live root, exposed mineral soil, and (in two transects) animal rooting were all estimated as above. A total of 40 sample points (80 1 x 1 m plots) was used.

Rubus biomass estimates. Size-biomass relationships in Rubus canes were determined from basal diameter measurements of 11 floricanes and 9 primocanes chosen to cover the range of the most frequent cane diameters (0.3-1.0 cm basal diameter). Canes were cut at ground level, dried in a forced-air oven for 24 hours at 70-80^o C., and weighed. Separate regression equations (REG procedure, SAS Institute 1987) of dry weight on basal diameter were calculated for floricanes and primocanes (Figure 2, Table 2). For all canes, explained variation using a log₁₀-log₁₀ regression ($r^2 = 0.80$) was greater than that using a normal-normal regression ($r^2 = 0.59$). A composite equation for all canes was used to estimate Rubus biomass in the

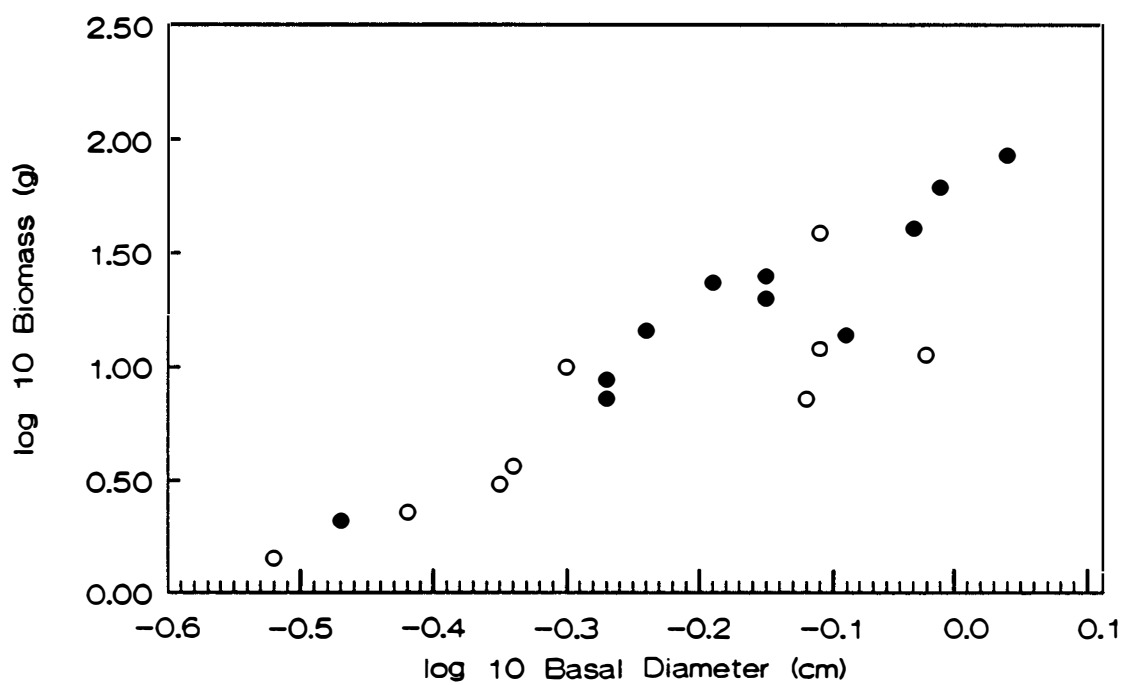


Figure 2. Graph of biomass in relation to basal diameter of *Rubus canadensis* canes. ● = floricanes, o = primocanes.

Table 2. Linear regression statistics for Rubus canadensis biomass as a function of basal diameter, derived from log(10) transformations of both biomass (g dry weight) and diameter (cm). Regression coefficients (b) are all significantly different from zero ($P < 0.01$). n = number of canes.

	n	b	y-intercept	r^2
Floricanes	11	2.94	1.74	0.91
Primocanes	9	2.05	1.26	0.88
All canes	20	2.58	1.55	0.80

transect plots, since the distinction between cane types was not made in the plots.

Fir seedling measurements. Seedling growth was measured using lengths of annually-produced shoots. "Shoot" is defined here as that stem tissue which emerges from an overwintering bud, elongates, and terminates in a new overwintering bud. Fraser fir normally produces only one increment of shoot growth per growing season (Wise et al. 1985). Each year's shoots are recognizable, in most cases, for at least five years. Shoot lengths are easily and non-destructively measurable and can usually be cross-compared among seedlings by each year's growth. These comparisons rest on the assumption that successive shoots represent successive years' growth. Although terminal bud abortion may occur, lateral shoots generally acquire apical dominance (Hinesley 1982; L. E. Hinesley, personal communication), thus preserving a continuous sequence of annual growth.

Fraser fir seedlings in the transect plots were recorded separately. Each seedling, alive or dead, was assigned to a height class. Its terminal shoot lengths of 1987 through 1983 growth were measured to the nearest 0.5 cm. The length of a shoot was recorded as the distance from the base of one set of bud scale scars to the base of the next set. Lateral shoot lengths of north-facing and

south-facing branches were determined in the same manner. To standardize the choice of lateral shoots to be measured, the following criterion was used: the longest shoot series on the lowest and northernmost/southernmost lateral branch not older than 1983 (see Figure 3). The seedling was also classified by substrate type (forest floor, dead log, dead root, live root, exposed rock), surface type (litter or bryophytes), substrate form (flat-level, flat-sloped, convex, concave), evidence of adelgid damage (gouting), other damage (browsing, mechanical damage, etc.), and whether the seedling was less than five years old (since overstory mortality occurred about 1983).

Soil sampling. From each pair of 1 x 1 m plots, a composite soil sample was taken with a soil tube. Samples were taken only from the top 25 cm of mineral soil. Stones, bryophytes, and large pieces of litter were discarded. Soil samples were placed in paper bags, air dried for several weeks, and analyzed by the University of Tennessee Soil Testing Laboratory in Nashville. Analyses included levels of water pH, phosphorus (P), potassium (K), and calcium (Ca). Mineral nutrient levels were expressed in concentrations of parts per million (ppm). To estimate the reliability of soil analyses, five samples were halved and each half submitted separately.

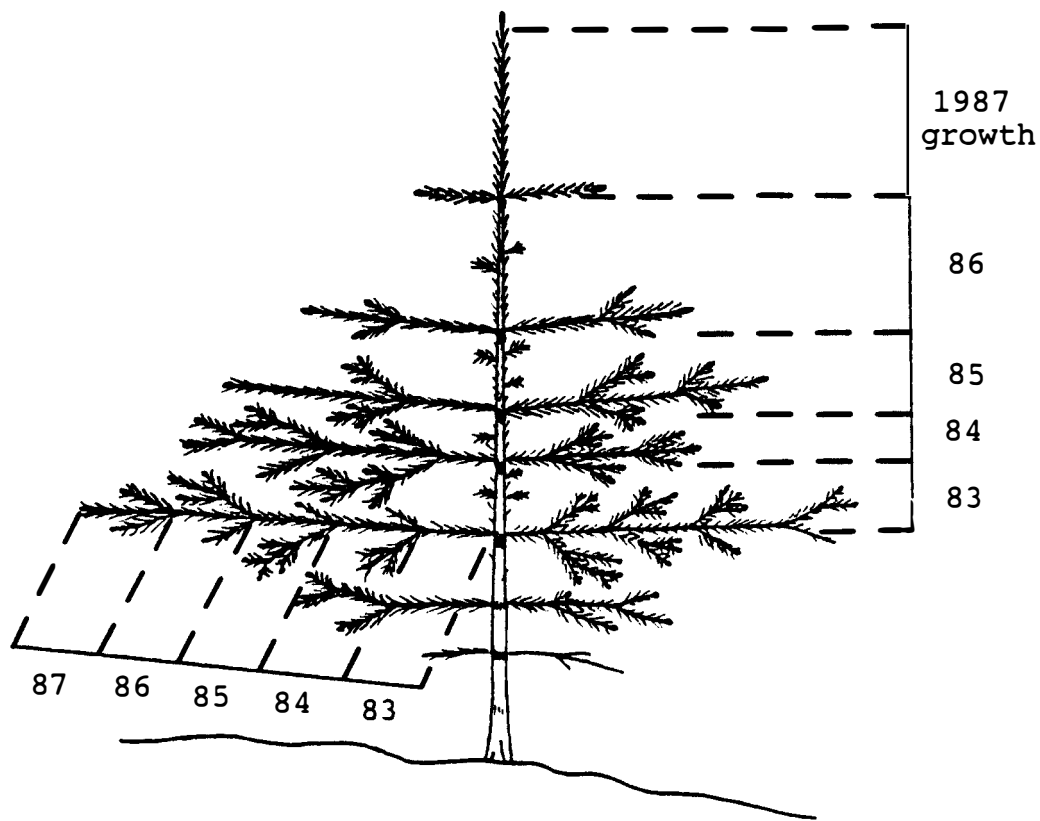


Figure 3. Fraser fir seedling, showing terminal and lateral shoot lengths measured.

3. Rubus-Removal Plots

Plot locations. A topographically uniform site was chosen on a gentle, north-facing slope of Mount Collins (Figure 1, page 20) for a test of effects of Rubus removal on growth of fir seedlings and other understory species. Fourteen 2 x 2 m plots were located attempting to apply these criteria: a substantial number of Rubus stems, at least five fir seedlings, and no woody stems >137 cm tall. Three of these plots were located on a separate site nearby (Figure 1, page 20). Because sites meeting these criteria were rare, two plots contained only four fir seedlings, and one plot contained a small spruce about 1.5 m tall. More fir seedlings per plot were desired, but fir seedlings and Rubus were seldom found together in abundance.

Initial plot measurements. Plots were initially evaluated during the period June 1-17, 1988. By this time, canopy, shrub, and Rubus foliage was well developed. Much foliage of herbaceous vegetation had emerged, and apparently spring growth was quite rapid in the study area. Most Fraser fir seedlings had broken dormancy but had not yet begun shoot elongation. This stage of development changed little over the first evaluation period.

Each plot was delimited by wooden stakes at the

corners. Shrubs, herbs, fir seedlings, etc. were measured identically to those in the transect plots. Germinal seedlings were not distinguished from others ≤ 25 cm tall. After plot measurement, the flip of a coin was used to determine if Rubus was to be removed. Rubus canes were cut with a knife at ground level and discarded at a distance from the plot. A composite soil sample was taken from each plot for analyses of the same chemical parameters as samples from the transect plots. Seven plots received the Rubus-removal treatment and seven plots were left undisturbed as controls.

Final plot measurements. During the period August 1-9, 1988, all plots were reevaluated in an identical fashion, and in the same sequence, as before. Germinal seedlings were distinguished in the reevaluation. At this time, the appearance of new vegetation of most species had stopped. Only Rubus and a fern, Athyrium asplenoides, showed recently emerged stems or foliage. Fir seedlings had completed most if not all shoot elongation and had begun to develop overwintering buds. Soil samples were again taken from each plot and submitted to the Soil Testing Laboratory for analyses of the same parameters as other soil samples. Five samples were halved and each half submitted separately to estimate reliability of analyses.

B. Data Analysis Methods

1. Overstory Composition

Canopy measurements, including canopy closure, basal area, and density, were summarized for each transect. Basal area and density for each species were calculated according to the methods of Husch et al. (1982) and Avery and Burkhart (1983).

2. Seedling-Understory Characterization

Choice of analytical methods. The distributions of most variables were highly non-normal and were not substantially affected by transformations suggested by Sokal and Rohlf (1981). Variances were extremely heterogenous, many data consisted of zero counts, and many differences among plots were slight (e.g., 2 seedlings versus 3 seedlings). Because of the irregular nature of the data, most data analyses used nonparametric statistics, which are calculated using the rank values of the data instead of the raw data (Sokal and Rohlf 1981). Analyses used Version 6.02 of the Statistical Analysis System (SAS Institute 1985, 1987). The 0.01 level of confidence was used in interpretation of all statistical tests.

Associations of variables. The eleven hypotheses regarding associations among seedling density/growth, canopy closure, Rubus density/biomass, and soil chemical parameters were all tested using Spearman rank correlations (FREQ procedure, SAS Institute 1985).

Substrate/surface type distributions. Distributions of seedlings among substrate and surface types were tested for departures from randomness using chi-square analyses (Sokal and Rohlf 1981). Expected distributions were generated using mean percent cover values of each substrate and surface type for all 80 plots (analogous to Collins and Pickett 1988). Direct estimates of cover of dead logs, dead roots, live roots, exposed rock, litter, and bryophytes were obtained; mean cover of forest floor substrate was obtained by subtracting cover of any other substrate type from 100% in each plot.

Substrate form/damage type distributions. Distributions of seedlings among substrate forms could not be tested in any fashion, since no estimates of percent cover were made for these attributes. No a priori estimates of seedling distribution among damage types (adelgid, mechanical, etc.) were possible, because other

data of these types do not exist for Fraser fir seedlings.

Shoot growth trends. Overall growth trends in Fraser fir seedlings were examined by calculating mean shoot lengths of each year's growth and by determining proportions of seedlings showing increases, decreases, and no changes of each year's growth over the previous year's growth.

3. Rubus-Removal Plots

Changes in understory and soil parameters. Analyses of results from experimental removal of Rubus candensis canes consisted of pairwise comparisons of changes in removal plots with changes in control plots. Changes tested included coverages of herbaceous species, densities of woody plants, and chemical parameters of soil samples. Analyses consisted of Wilcoxon rank sum tests (NPAR1WAY procedure, SAS Institute 1987), which are analogous to Student's t-tests (Sokal and Rohlf 1981). The rank sum test was chosen because of small sample sizes ($n = 7$).

Changes in fir seedling growth. Current growth response of fir seedlings in each treatment was tested two ways: (1) direct comparisons of 1988 terminal and lateral shoot lengths between treatments (using rank sum tests),

and (2) comparisons of product-moment correlation coefficients between 1987 and 1988 shoot lengths of individual seedlings.

CHAPTER 3

RESULTS

A. Overstory Composition

Mean canopy closure was highest on the SE slope (Table 3). That slope also had the highest spruce basal area and density (Tables 4 and 5). The NW slope, which had been logged, had the greatest total dead fir basal area and density (Tables 4 and 5). Canopy closure, spruce basal area, and spruce density were all lowest on that slope. Mean total basal area for transects NE, SW, and SE (all unlogged) was $54 \text{ m}^2/\text{ha}$, 40% of which was dead. Mean total density for the respective transects was 2223 stems/ha, 50% of which was dead.

B. Seedling-Understory Characterization

1. Herbaceous Species Composition

A total of 23 herbaceous taxa was described in the transect plots (Table 6). No attempt was made to differentiate species of bryophytes, although they were clearly important components of the ground layer of the study area, particularly on the NE slope. Ferns, including

Table 3. Mean percent canopy closure calculated for the Mount Collins transects. n = 10 sample points for all values.

Transect	Canopy closure (%)
NE	61.3
NW	58.3
SW	68.3
SE	93.7

Table 4. Basal areas (in m²/ha) of tree species (≥ 1.37 m tall) in 5-factor metric prism plots of the Mount Collins transects. n = number of prism plots.

		Transect				
		NE	NW	SW	SE	Mean
Species	n=	10	10	10	10	40
<u>Abies fraseri</u>						
	Live	0.5	0	0.5	3.0	1.0
	Dead	19.0	31.0	12.0	17.0	19.8
<u>Acer spicatum</u>						
	Live	0	1.0	0	0.5	0.4
	Dead	0	0	0	0	0
<u>Aesculus octandra</u>						
	Live	0	0	0.5	0	0.1
	Dead	0	0	0	0	0
<u>Betula lutea</u>						
	Live	4.5	10.0	8.0	7.5	7.5
	Dead	2.5	1.5	1.5	0	1.4
<u>Picea rubens</u>						
	Live	23.0	7.0	18.0	30.5	19.6
	Dead	5.5	0	5.5	1.0	3.0
<u>Prunus pensylvanica</u>						
	Live	0	1.5	0	0	0.4
	Dead	0	1.0	0.5	0	0.4
<u>Sorbus americana</u>						
	Live	0	0	1.0	0	0.3
	Dead	0	0	0	0	0
Total	Live	28.0	19.5	28.0	41.5	29.3
	Dead	27.0	33.5	19.5	18.0	24.5

Table 5. Densities (in stems/ha) of tree species (≥ 1.37 m tall) in 5-factor metric prism plots of the Mount Collins transects. n = number of prism plots.

		Transect				
		NE	NW	SW	SE	Mean
Species	n=	10	10	10	10	40
<u>Abies fraseri</u>						
	Live	398	0	663	160	305
	Dead	1622	1783	475	936	1204
<u>Acer spicatum</u>						
	Live	0	967	0	314	320
	Dead	0	0	0	0	0
<u>Aesculus octandra</u>						
	Live	0	0	1	0	<1
	Dead	0	0	0	0	0
<u>Betula lutea</u>						
	Live	23	367	830	408	407
	Dead	9	61	242	0	78
<u>Picea rubens</u>						
	Live	111	63	127	242	136
	Dead	18	0	25	3	12
<u>Prunus pensylvanica</u>						
	Live	0	29	0	0	7
	Dead	0	30	10	0	10
<u>Sorbus americana</u>						
	Live	0	0	53	0	13
	Dead	0	0	0	0	0
Total	Live	532	1426	1674	1124	1189
	Dead	1649	1874	752	939	1304

Table 6. Mean percent cover of herbaceous taxa sampled in the Mount Collins transects. n = number of 1 x 1 m plots.

Taxon	n=	Transect				Mean
		NE	NW	SW	SE	
		20	20	20	20	80
Bryophytes		42.5	18.3	19.5	21.3	25.4
<u>Athyrium</u> <u>asplenioides</u>		16.8	20.0	20.0	23.0	20.0
<u>Dryopteris</u> spp.		12.8	15.8	5.0	6.5	10.0
<u>Oxalis montana</u>		7.0	12.5	11.3	6.0	9.2
<u>Carex</u> spp.		1.3	4.5	3.3	14.5	5.9
<u>Cacalia rugelia</u>		6.8	3.3	5.3	4.5	5.0
Lichens		4.8	3.5	3.0	3.8	3.8
<u>Clintonia</u> <u>borealis</u>		0.3	7.8	0.3	0.5	2.2
<u>Aster acuminatus</u>		0.3	3.0	4.0	0.8	2.0
<u>Dennstaedtia</u> <u>punctilobula</u>		0	0	0.3	7.8	2.0
Other graminoids		0	2.5	1.8	1.5	1.5
<u>Solidago</u> <u>glomerata</u>		0	2.0	1.8	2.0	1.5
<u>Arisaema</u> <u>triphyllum</u>		0	2.3	0.5	1.3	1.0
<u>Lycopodium</u> <u>lucidulum</u>		0	0	0.8	2.3	0.8
<u>Aster chlorolepis?</u>		0	1.0	0.5	0	0.4
<u>Houstonia</u> <u>serpyllifolia</u>		0	0	0.8	0.5	0.3

Table 6. Continued.

Taxon	n=	Transect				Mean
		NE	NW	SW	SE	
		20	20	20	20	80
<u>Viola</u> sp.		0	0.5	0.5	0	0.3
<u>Laportea</u> <u>canadensis</u>		0	0.3	0	0.5	0.2
<u>Trillium</u> sp.		0.5	0	0	0.3	0.2
<u>Impatiens</u> sp.		0	0.5	0	0	0.1
<u>Eupatorium</u> <u>rugosum</u>		0	0	0	0.3	<0.1
<u>Medeola</u> <u>virginiana</u>		0.3	0	0	0	<0.1
<u>Stachys</u> <u>clingmanii</u>		0	0.3	0	0	<0.1
Total		93.4	98.1	78.7	97.4	91.9

Athyrium asplenoides and Dryopteris spp., covered relatively large areas of the forest floor. Oxalis montana cover was highest on west-facing slopes (NW and SW). Carex spp. formed substantial ground cover in some areas, particularly on the SE slope. Other graminoids were infrequent and did not contribute greatly to herbaceous cover in the study area. Total herbaceous cover was lowest on the SW slope.

2. Woody Species Composition

Ten woody species (≤ 137 cm tall) were found in the transect plots (Table 7). Both spruce and fir seedlings were most abundant on the NE slope. Spruce seedlings were also quite numerous on the SE slope. Separate counts of germinal spruces made on transect SE showed that these made up fully 76% of spruce seedlings on that transect. Density of Rubus canadensis was highest on the SW slope and lowest on the NE slope. Total density of woody stems ≤ 137 cm tall was highest on the NE slope.

3. Fir Seedling Population Characteristics

Data from White et al. (1985) indicate a fir seedling (stems ≤ 2 m tall) density of about 24,000/ha (2.4 stems/m^2) on the northeast-facing slope of Mount Collins. In the

Table 7. Mean densities (stems/m²) of woody species ≤ 137 cm tall sampled in the Mount Collins transects.
n = number of 1 x 1 m plots.

Species	n=	Transect				Mean
		NE	NW	SW	SE	
		20	20	20	20	80
<u>Picea rubens</u>		20.6	2.3	4.3	15.2	10.6
<u>Rubus canadensis</u>		2.1	5.9	8.5	3.3	5.0
<u>Vaccinium erythrocarpum</u>		3.9	1.6	2.7	5.9	3.5
<u>Abies fraseri</u>		8.2	1.6	1.5	2.2	3.4
<u>Betula lutea</u>		2.2	1.5	1.8	1.3	1.7
<u>Viburnum alnifolium</u>		0.5	1.2	0.8	0.4	0.7
<u>Sorbus americana</u>		0	0.3	0.8	0.2	0.3
<u>Acer spicatum</u>		0	0.4	0.1	0.1	0.2
<u>Prunus pensylvanica</u>		0	0.3	0.1	0.1	0.1
<u>Sambucus pubens</u>		0	0	0.2	0	<0.1
Total		56.4	15.1	20.8	28.7	30.3

present study, the NE slope (Table 7) showed a fir seedling density of 8.2 stems/m². If transect NE is representative of the area studied by White et al. (1985), then a recent increase in fir seedling density is evident at that site. In the present study, fir seedling density ranged from 0 to 72 stems/m². This peak density occurred on the NE slope.

The height class structure of fir seedlings showed a proponderance of seedlings ≤ 25 cm tall, except on transect SW (Table 8). Transect SW also showed the lowest total number of fir seedlings. Thirty-eight percent of fir seedlings were less than five years old (Table 9). Only two fir seedlings less than five years old were found on transect SW.

4. Substrate/Microhabitat Composition

Substrate and microhabitat patterns showed relatively low litter cover on the NE slope (Table 10). Dead logs made up a small fraction of the forest floor habitat. Animal rooting occurred primarily on the NW slope and was confined to four plots on the NW slope and one plot on the SW slope.

Table 8. Number of live Fraser fir seedlings in each height class in the Mount Collins transects. n = number of 1 x 1 m plots from which each distribution is derived.

		Transect				
		NE	NW	SW	SE	Total
Height class	n=	20	20	20	20	80
≤ 25 cm		155	25	12	41	233
26-50		6	3	12	0	21
51-75		0	4	4	2	10
76-100		0	1	1	0	2
101-137		1	0	0	0	1
Total		162	33	29	43	267

Table 9. Number of live Fraser fir seedlings less than five years old and five or more years old in the Mount Collins transects. n = number of 1 x 1 m plots from which each distribution is derived.

Transect	n	Number less than 5 years old	Number 5 or more years old
NE	20	60	102
NW	20	15	18
SW	20	2	28
SE	20	24	18
Total	80	101	166

Table 10. Mean percent cover of substrate and surface types in the Mount Collins transects. n = number of 1 x 1 m plots.

	Transect				Mean
	NE	NW	SW	SE	
n=	20	20	20	20	80
Litter	52.0	79.0	75.0	75.5	70.4
Dead log	14.3	4.5	6.3	9.0	8.5
Dead root	3.4	0.8	5.5	2.5	3.1
Exposed rock	0	1.0	4.8	1.0	1.7
Live root	0.8	1.5	0.5	2.5	1.3
Animal rooting	0	2.3	0.3	0	0.7
Mineral soil	0.5	0	0.3	0	0.2

5. Rubus Biomass Estimates

Estimated aboveground biomass of Rubus canadensis ranged from 0 to 837 g dry weight per 1 m² plot, with a mean of 106.6 g (Table 11). Mean biomass was highest on the SW slope and lowest on the SE slope.

6. Associations Among Vegetation Variables

A Spearman rank correlation matrix among selected vegetation variables appears in Table 12. Test results for the first nine hypotheses presented in Chapter 1 (Objectives and Hypotheses, pages 17 and 18) are described below.

(a) The rank correlation between total fir density and overstory canopy closure was not significant; a slight positive tendency was found.

(b) The rank correlation between density of seedlings less than five years old and canopy closure was not significant; as in (a), a slight positive tendency was found.

(c) Density and aboveground biomass of Rubus canadensis were not significantly correlated with canopy closure; negative tendencies were found.

Table 11. Mean estimated aboveground biomass of Rubus canadensis in the Mount Collins transects. Estimates are based on regression statistics for all canes, Table 2, page 26. n = number of 1 x 1 m plots.

Transect	n	Aboveground Biomass (g)	Range (g)
NE	20	81.3	0 - 837
NW	20	107.1	0 - 521
SW	20	187.2	0 - 751
SE	20	50.9	0 - 421
Mean	80	106.6	

Table 12. Spearman rank correlations (with sample sizes) among selected vegetation variables measured in the Mount Collins transects. Correlations with * are significant at the 0.01 level.

	Canopy closure	Total fir density	<u>Rubus</u> density	<u>Rubus</u> biomass
Total fir density (n)	0.183 (80)	-	-0.376* (80)	-0.426* (80)
Density of fir <5 yrs old	0.138 (80)	0.741* (80)	-0.365* (80)	-0.439* (80)
<u>Rubus</u> density	-0.172 (80)	-	-	0.889* (80)
<u>Rubus</u> biomass	-0.250 (80)	-	-	-
Terminal 87 growth	-0.224* (264)	-0.283* (264)	0.174 (264)	0.107 (264)
Terminal 86 growth	-0.027 (267)	-0.453* (267)	0.396* (267)	0.349* (267)
Terminal 85 growth	0.059 (260)	-0.405* (260)	0.352* (260)	0.370* (260)
Terminal 84 growth	0.141 (239)	-0.354* (239)	0.344* (239)	0.343* (239)
Terminal 83 growth	0.144 (150)	-0.287* (150)	0.309* (150)	0.367* (150)

Table 12. Continued.

	Canopy closure	Total fir density	<u>Rubus</u> density	<u>Rubus</u> biomass
N-lateral 87 growth	-0.150 (105)	-0.102 (105)	0.076 (105)	0.026 (105)
N-lateral 86 growth	0.449 [*] (63)	-0.018 (63)	0.051 (63)	0.141 (63)
N-lateral 85 growth	0.391 (36)	0.048 (36)	0.006 (36)	0.062 (36)
N-lateral 84 growth	0.673 [*] (26)	0.460 (26)	-0.017 (26)	0.039 (26)
N-lateral 83 growth	0.540 (14)	0.313 (14)	-0.042 (14)	0.036 (14)
S-lateral 87 growth	-0.230 (119)	0.051 (119)	-0.085 (119)	-0.027 (119)
S-lateral 86 growth	0.214 (74)	-0.021 (74)	0.214 (74)	0.304 [*] (74)
S-lateral 85 growth	0.430 [*] (40)	-0.066 (40)	0.117 (40)	0.233 (40)
S-lateral 84 growth	0.551 [*] (32)	0.249 (32)	0.181 (32)	0.235 (32)
S-lateral 83 growth	0.609 (15)	0.555 (15)	-0.074 (15)	0.001 (15)

(d) Significant negative rank correlations were found between Rubus density/aboveground biomass and total density of fir seedlings. A graph of fir density against Rubus density (Figure 4) illustrates the negative trend in variability with increasing Rubus density. Plots with more than 10 Rubus stems per m² rarely contained any fir seedlings.

(e) Significant negative rank correlations were found between density of fir seedlings less than five years old and Rubus density/aboveground biomass. The magnitudes of these correlations were similar to those in (d), and negative trends in variability of fir density were nearly identical to that in Figure 4.

(f) Five correlations between fir seedling shoot lengths and canopy closure were significant. These were either weak (in the case of terminal 1987 growth) or based on small sample sizes (in the cases of lateral growth).

(g) Every year of terminal shoot growth measured was significantly negatively correlated with density of fir seedlings themselves.

(h) No lateral shoot lengths measured were significantly correlated with density of fir seedlings themselves. Slight negative tendencies were evident in more recent growth (1985-1987), while positive tendencies

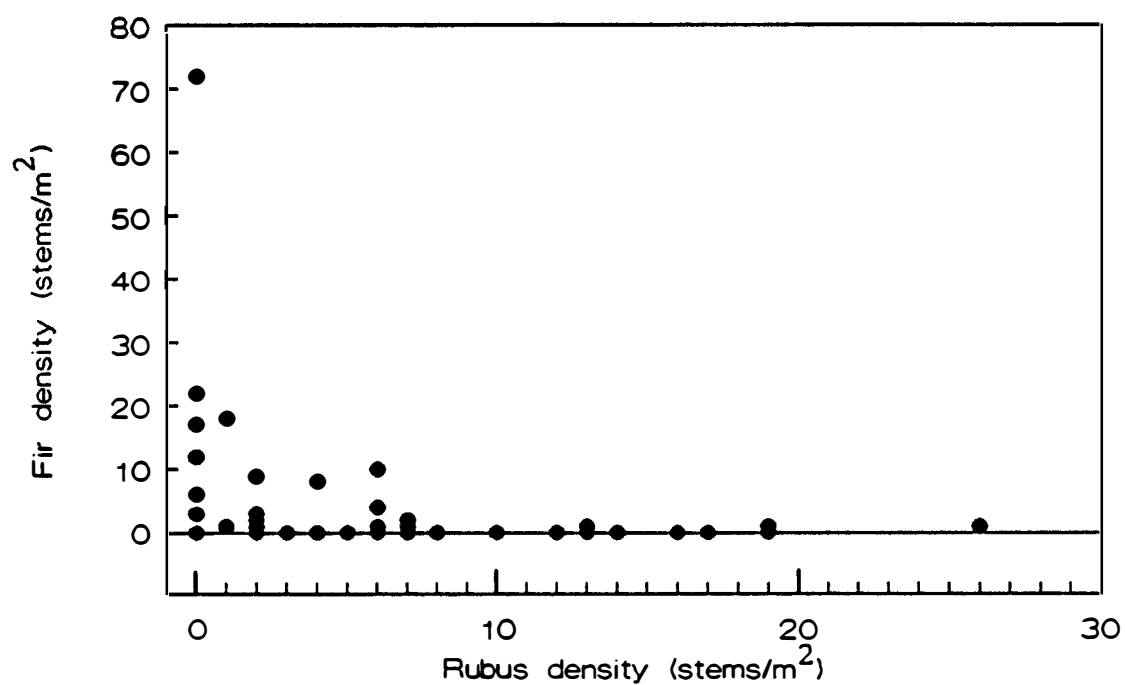


Figure 4. Graph of Fraser fir seedling (stems ≤ 137 cm tall) density in relation to Rubus canadensis density in the Mount Collins transects.

were evident in previous growth. Correlations in older growth were based on relatively smaller sample sizes.

(i) All but the most recent terminal shoot lengths measured were significantly positively correlated with Rubus density and aboveground biomass. A graph of the largest of these correlations (terminal 1986 growth with Rubus density) does not show a clear trend (Figure 5). Most seedlings have short shoots regardless of Rubus density.

Two other correlations in Table 12 were significant. Density of fir less than five years old was highly correlated with total fir density, since about one third of all seedlings were less than five years old (Table 9, page 46). Rubus density and biomass were also strongly correlated because biomass was calculated from density and basal diameter.

7. Soil Parameters

A summary of soil parameters by transect appears in Table 13. One sample in transect SW contained large amounts of litter and fine roots, and it showed concentrations of all nutrients that were considerably higher than in other samples. That outlier sample was not included in calculating means for that transect because the

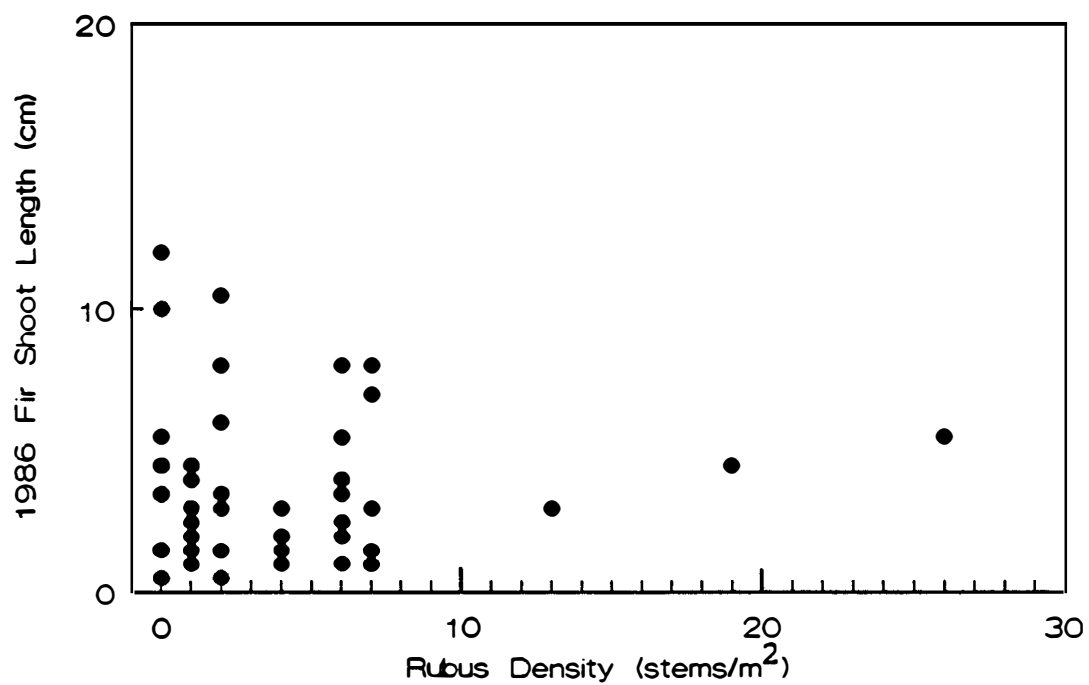


Figure 5. Graph of terminal 1986 shoot lengths of Fraser fir seedlings in relation to Rubus canadensis density in the Mount Collins transects.

Table 13. Soil chemical parameters in the transect plots. Values for P, K, and Ca are means ($\pm$ 1 standard error) in ppm; values in the same row with the same letter are not significantly different at the 0.01 level (T method, Sokal and Rohlf 1981). n = number of pairs of 1 x 1 m plots.

	Transect				Mean
	NE	NW	SW	SE	
n	10	10	9	10	39
water pH	3.92 a (0.06)	3.88 a (0.04)	3.78 a (0.05)	3.90 a (0.07)	3.87 (0.03)
P	2.6 a (0.5)	5.5 a (1.1)	6.2 a (1.7)	3.8 a (1.2)	4.5 (0.6)
K	36.8 c (3.6)	63.3 ab (5.4)	65.0 a (1.7)	46.5 bc (3.7)	52.6 (2.9)
Ca	11.5 a (1.1)	15.0 a (3.4)	21.1 a (8.7)	14.0 a (4.0)	15.3 (2.4)

sample was not representative of the mineral horizons. Concentrations of K varied significantly among transects; concentrations were highest on the west facing-slopes (NW and SW) and lowest on the NE slope. Water pH and concentrations of P and Ca did not vary significantly among transects. These low variabilities among samples may have reduced many of the correlations presented below. Student's t-tests between replicate samples (to determine reliability of analyses) showed no significant differences for any soil parameters.

8. Associations Between Vegetation and Soil Parameters

A Spearman rank correlation matrix among soil variables and selected vegetation variables appears in Table 14. Test results of the last two hypotheses presented in Chapter 1 (page 18) are described below.

(j) Significant positive correlations between terminal growth of 1984-1987 and water pH were found. Moderately strong positive correlations between all years of terminal growth and K concentration were also found. No correlations involving lateral shoot growth and soil parameters were significant.

(k) Significant positive correlations were found between Rubus density/biomass and P and K concentrations.

Table 14. Spearman rank correlations (with sample size) among selected vegetation variables and soil parameters measured in the Mount Collins transects. Analyses used only those Fraser fir seedlings growing on a "forest floor" substrate. Correlations with * are significant at the 0.01 level. "conc." = concentration (ppm).

	water pH	P conc.	K conc.	Ca conc.
Total fir density	0.019 (80)	-0.220 (80)	-0.239 (80)	-0.147 (80)
Density of fir <5 yrs old	0.086 (80)	-0.154 (80)	-0.325* (80)	-0.203 (80)
<u>Rubus</u> density	0.001 (80)	0.436* (80)	0.411* (80)	0.092 (80)
<u>Rubus</u> biomass	-0.084 (80)	0.449* (80)	0.445* (80)	0.150 (80)
Terminal 87 growth	0.492* (161)	0.097 (161)	0.475* (161)	0.060 (161)
Terminal 86 growth	0.428* (164)	0.144 (164)	0.625* (164)	0.086 (164)
Terminal 85 growth	0.319* (160)	0.094 (160)	0.566* (160)	0.035 (160)
Terminal 84 growth	0.407* (144)	0.071 (144)	0.591* (144)	0.015 (144)
Terminal 83 growth	0.228 (92)	0.051 (92)	0.513* (92)	-0.020 (92)

Table 14. Continued.

	water pH	P conc.	K conc.	Ca conc.
N-lateral 87 growth	0.289 (68)	0.153 (68)	0.079 (68)	0.259 (68)
N-lateral 86 growth	-0.005 (39)	-0.268 (39)	0.177 (39)	0.118 (39)
N-lateral 85 growth	-0.165 (26)	-0.452 (26)	-0.135 (26)	-0.166 (26)
N-lateral 84 growth	-0.273 (17)	-0.451 (17)	-0.415 (17)	-0.104 (17)
N-lateral 83 growth	0.339 (10)	-0.202 (10)	0.432 (10)	0.295 (10)
S-lateral 87 growth	0.237 (73)	-0.055 (73)	0.085 (73)	0.083 (73)
S-lateral 86 growth	-0.052 (51)	-0.290 (51)	0.349 (51)	-0.150 (51)
S-lateral 85 growth	0.043 (33)	-0.269 (33)	0.153 (33)	-0.376 (33)
S-lateral 84 growth	0.150 (27)	-0.488 (27)	0.256 (27)	-0.328 (27)
S-lateral 83 growth	-0.195 (14)	-0.546 (14)	0.128 (14)	-0.419 (14)

Neither Rubus density nor biomass were significantly associated with pH or Ca.

A significant negative correlation was found between density of fir seedlings less than five years old and K concentration.

9. Substrate Type Distribution

A distribution of fir seedlings among substrate types is shown in Table 15. A significant deviation from the expected distribution among substrate types was found. Seedlings are clearly not randomly distributed among substrate types. While dead wood (dead logs plus dead roots) occupied only 11.6% of the sample plots, more than 33% of all fir seedlings were found on that substrate. Student's t-tests (for single observations against a population, Sokal and Rohlf 1981) showed that K and/or Ca concentrations may be significantly higher in logs than in soil (Table 16).

10. Surface Type Distribution

A distribution of fir seedlings among surface types is shown in Table 17. A significant deviation from the expected distribution was found. Bryophytes covered only

Table 15. Distribution of Fraser fir seedlings among substrate types. n = 265 seedlings.

Substrate	Mean % cover	Predicted number	Actual number
Forest floor	85.4	226.3	164
Dead wood ^a	11.6	30.8	88
Other ^b	3.0	8.0	13
Chi-square = 126.395 [*]			
Chi-square _{0.01[2]} = 9.210			

^{*}significant at the 0.01 level.

^a"Dead wood" includes both dead logs and dead roots.

^b"Other" includes both live roots and exposed rock.

Table 16. Comparison of chemical parameters of forest floor soil samples (means of all transect data) and two rotting logs occupied by Fraser fir seedlings. Mineral nutrient concentrations ($\pm$ 1 standard error) are in ppm.

	Forest floor	Log A	Log B
n	39	1	1
water pH	3.87 (0.03)	4.0	3.9
P	4.5 (0.6)	6	6
K	52.6 (2.9)	115*	55
Ca	15.3 (2.4)	260*	120*

* significantly different from forest floor mean (t -test, $P < 0.01$)

Table 17. Distribution of Fraser fir seedlings among surface types. n = 265 seedlings.

Surface	Mean % cover	Predicted number	Actual number
Bryophytes	25.4	67.1	156
Litter	74.6 ^a	197.9	109
Chi-square = 157.871 [*]			
Chi-square _{0.01[1]} = 6.635			

^{*}significant at the 0.01 level

^aThis percentage differs from mean cover of litter in Table 10 (page 47) because seedlings growing on substrates such as dead logs were sometimes assigned a surface type of "litter."

25.4% of the sample plot area, yet 59% of seedlings occurred on this surface type.

11. Substrate Form Distribution

Most fir seedlings were found on convex (41%) or flat-sloped (32%) substrates (Table 18). The fewest were found on concave substrates. Many convex surfaces were bryophyte-covered (especially dead logs). A two-way distribution of fir seedlings among surface types and substrate forms is shown in Table 19. The largest number of seedlings (32%) were found on convex, bryophyte-covered surfaces. Flat-sloped, litter-covered surfaces were occupied by 21% of seedlings. Although no tests for departure from randomness are possible for these distributions, fir seedlings do not seem to be dispersed independently of substrate form.

12. Damage Type Distributions

More than one fourth of fir seedlings showed obvious gouting (Table 20). Gouting was seen in only 5% of seedlings less than five years old, as compared to 39% of those five or more years old.

Other, non-adelgid-related forms of damage were found in nearly 18% of fir seedlings (Table 21). Missing

Table 18. Distribution of Fraser fir seedlings among substrate forms.

Substrate form	Number of seedlings
Concave	26
Convex	108
Flat-level	46
Flat-sloped	86
Total	266

Table 19. Distribution of Fraser fir seedlings among surface types and substrate forms.

Substrate form	Surface type	
	Bryophytes	Litter
Concave	12	14
Convex	84	24
Flat-level	30	16
Flat-sloped	31	55

Table 20. Distribution of Fraser fir seedlings by presence or absence of adelgid damage (gouting).

	Number <5 years old	Number ≥5 years old
Gouting obvious	5	63
Gouting not obvious	95	100

Table 21. Distribution of Fraser fir seedlings among other damage categories. Total number of seedlings tallied is 266. Total of damage frequencies does not sum to this number because some seedlings showed more than one kind of damage.

Damage type	Number of seedlings
Undamaged (regardless of gouting)	219
Missing terminal bud	18
Terminal replacement	15
Mechanical damage	15
Aborted terminal shoot	5
Exposed roots	3
Multiple terminal shoots	3
Missing lateral bud	2
Aborted lateral shoot	1
Chlorosis	1
Frost damage?	1
Leaf base dieback	1

terminal buds (presumably from browsing), replacement of terminal shoots by lateral shoots, and types of mechanical damage (e.g., crushed, abraded) were most frequent.

13. Shoot Growth Trends

Mean lengths of terminal and lateral shoots on fir seedlings are shown in Table 22. A general increase in terminal shoot length since 1984 is apparent. North-facing and south-facing lateral shoot lengths do not show a common trend for all years, but a decrease since 1985 is evident in both sets of shoots.

Changes in shoot length over previous years' growth and the proportions of seedlings showing positive, negative, and no changes are shown in Table 23. In 1984, terminal shoots were, on average, no longer than the previous year's terminal shoots. Most seedlings (44%) actually grew less in 1984 than in 1983. By 1987, however, terminal shoots were, on average, 0.58 cm longer than the previous year's growth. Over half (57%) of the seedlings showed some increase of 1987 over 1986 growth. A trend toward increasing gains over previous terminal growth is evident, although the trend is not monotonic. Lateral shoots show more irregular patterns of increases and decreases.

Table 22. Mean shoot lengths of all Fraser fir seedlings in the Mount Collins transects for each year.
n = number of seedlings.

Year	Mean terminal shoot length (cm) (n)	Mean N-lateral shoot length (cm) (n)	Mean S-lateral shoot length (cm) (n)
1987	2.34 (265)	3.42 (105)	3.25 (119)
1986	1.80 (267)	3.66 (63)	3.25 (74)
1985	1.69 (260)	4.72 (36)	4.04 (40)
1984	1.36 (239)	3.83 (26)	4.56 (32)
1983	1.47 (150)	3.79 (14)	4.70 (15)

Table 23. Changes in Fraser fir seedling shoot growth over previous years' growth and proportions of seedlings showing increases, no changes, and decreases in the Mount Collins transects. n = number of seedlings.

Year	n	Mean change over previous year (cm)	% showing increase	% showing no change	% showing decrease
Terminal shoots					
1987	265	0.58	57	28	15
1986	260	0.10	38	30	32
1985	239	0.38	49	29	21
1984	150	0.00	23	33	44
N-lateral shoots					
1987	63	-0.21	38	19	43
1986	36	-0.49	17	22	61
1985	26	0.67	62	8	31
1984	14	-0.46	21	29	50
S-lateral shoots					
1987	73	-0.09	33	25	43
1986	40	-0.41	28	15	58
1985	32	-0.36	31	6	63
1984	15	0.10	40	13	47

C. Rubus-Removal Plots

1. Herbaceous Species Cover

Changes of herbaceous species cover in control and Rubus-removal plots are shown in Table 24. Substantial increases with time in bryophyte cover occurred in both treatments. Athyrium asplenioides cover also increased, and that species seemed to be continuing to produce new foliage at the time of reevaluation, as mentioned earlier. Dryopteris spp. cover decreased slightly. None of the changes in herbaceous cover differed significantly between treatments, so no evidence of a Rubus-removal effect was apparent.

2. Woody Species Densities

Changes in woody species densities in control and Rubus-removal plots are shown in Table 25. Large increases in density of spruce seedlings occurred in both treatments. Minor increases in density of Betula lutea and Vaccinium erythrocarpum occurred. No changes differed significantly between treatments.

Changes in spruce density by height class are shown in Table 26. The smallest height class showed the largest changes, indicating appearance of large numbers of germinal

Table 24. Changes in mean percent cover of herbaceous taxa in control (C) plots and Rubus-removal (R) plots between initial and final evaluation dates. n = 7 2 x 2 m plots for all values. No changes differed significantly between treatments (P > 0.01, Wilcoxon rank sum test).

Taxon	Treatment	Mean initial cover(%)	Mean final cover(%)	Change
<u>Arisaema triphyllum</u>	C	0	0.7	0.7
	R	0	0	0
<u>Aster acuminatus</u>	C	0.7	1.4	0.7
	R	0	0	0
<u>Athyrium asplenioides</u>	C	10.0	16.4	6.4
	R	3.6	5.7	2.1
Bryophytes	C	23.6	41.4	17.8
	R	31.4	51.4	20.0
<u>Cacalia rugelia</u>	C	6.4	7.1	0.7
	R	6.4	7.1	0.7
<u>Carex</u> spp.	C	2.1	2.1	0
	R	0	0	0
<u>Claytonia</u> sp.	C	0.7	0	-0.7
	R	0	0	0
<u>Clintonia borealis</u>	C	0.7	0.7	0
	R	0	0	0
<u>Dennstaedtia punctilobula</u>	C	0.7	0	-0.7
	R	0	0	0
<u>Dryopteris</u> spp.	C	14.3	10.0	-4.3
	R	15.7	13.6	-2.1
<u>Oxalis montana</u>	C	5.0	5.7	0.7
	R	5.0	5.0	0
Total	C	64.2	85.5	21.3
	R	62.1	82.8	20.7

Table 25. Changes in mean stem numbers of woody species ≤ 137 cm tall in control (C) plots and Rubus-removal (R) plots between initial and final evaluation dates. $n = 7$ 2 x 2 m plots for all values. No changes differed significantly between treatments ($P > 0.01$, Wilcoxon rank sum test).

Species	Treatment	Mean initial number	Mean final number	Change
<u>Abies fraseri</u>	C	16.1	15.9	-0.2
	R	17.9	17.9	0
<u>Acer spicatum</u>	C	0.3	0.6	0.3
	R	0	0.3	0.3
<u>Betula lutea</u>	C	2.4	4.9	2.5
	R	4.1	9.3	5.2
<u>Picea rubens</u>	C	25.3	79.7	54.4
	R	24.4	70.6	46.2
<u>Viburnum alnifolium</u>	C	6.3	7.9	1.6
	R	2.4	2.9	0.5
<u>Vaccinium erythrocarpum</u>	C	9.9	14.1	4.2
	R	6.6	8.3	1.7
Total	C	44.2	107.2	63.0
	R	37.5	91.4	53.9

Table 26. Changes in mean density of Picea rubens by height class in control (C) and Rubus-removal (R) plots between initial and final evaluation dates. n = 7 2 x 2 m plots for all values.

Treatment	Height class	Mean initial density	Mean final density	Change
C	≤25 cm	22.1	76.6	54.5
	26-50	1.3	1.6	0.3
	51-75	1.6	1.3	-0.3
	76-100	0.1	0.4	0.3
	101-137	0	0.1	0.1
R	≤25 cm	23.4	69.4	46.0
	26-50	1.0	1.1	0.1
	51-75	0	0	0
	76-100	0	0	0
	101-137	0	0	0

seedlings. (Changes in mean densities are not identical to those in Table 25 because of rounding errors.) At the final evaluation, germinal spruces made up 62% and 55% of all spruce seedlings in the control and Rubus-removal plots, respectively.

Changes in Rubus densities and estimated aboveground biomass in control and Rubus-removal plots appear in Tables 27 and 28, respectively. New primocanes appeared in somewhat higher numbers and new aboveground biomass was slightly higher in the Rubus-removal plots, but these differences were not significant. Basal diameter distributions of Rubus (Figures 6-9) show that appearance and growth of individual canes can be extremely rapid. The diameter distribution in the Rubus-removal plots at the final evaluation (Figure 9) is not greatly different from that at the initial evaluation (Figure 8), even though all canes at the final evaluation are 60-day old primocanes.

3. Soil Parameters

Changes in soil parameters in control and Rubus-removal plots are shown in Table 29. Water pH and nutrient concentrations in those plots are similar to those in plots from transect NE (Table 13, page 56), also on the northeast-facing slope of Mount Collins. Slight reductions are evident in all parameters between evaluation dates;

Table 27. Changes in Rubus canadensis densities in control (C) and Rubus-removal (R) plots. Values are mean numbers of canes in 2 x 2 m plots. n = 7 plots for all values.

Treatment	Mean initial density	Mean final density	Mean number of new canes
C	39.1	49.4	10.3
R	35.0	26.6	26.6
Wilcoxon mean rank scores for numbers of new canes:			
	C	5.143	
	R	9.857	
	Z = -2.049 ns		

ns = not significant at 0.01 level, Wilcoxon rank sums test.

Table 28. Changes in Rubus canadensis estimated aboveground biomass in control (C) and Rubus-removal (R) plots. Values are mean dry weights (g) in 2 x 2 m plots. n = 7 plots for all values.

Treatment	Mean initial biomass	Mean final biomass	Mean new biomass
C	493	630	137
R	717	187	187
Wilcoxon mean rank scores for new biomass:			
	C	5.429	
	R	9.571	
Z = -1.789 ns			

ns = not significant at the 0.01 level, Wilcoxon rank sums test.

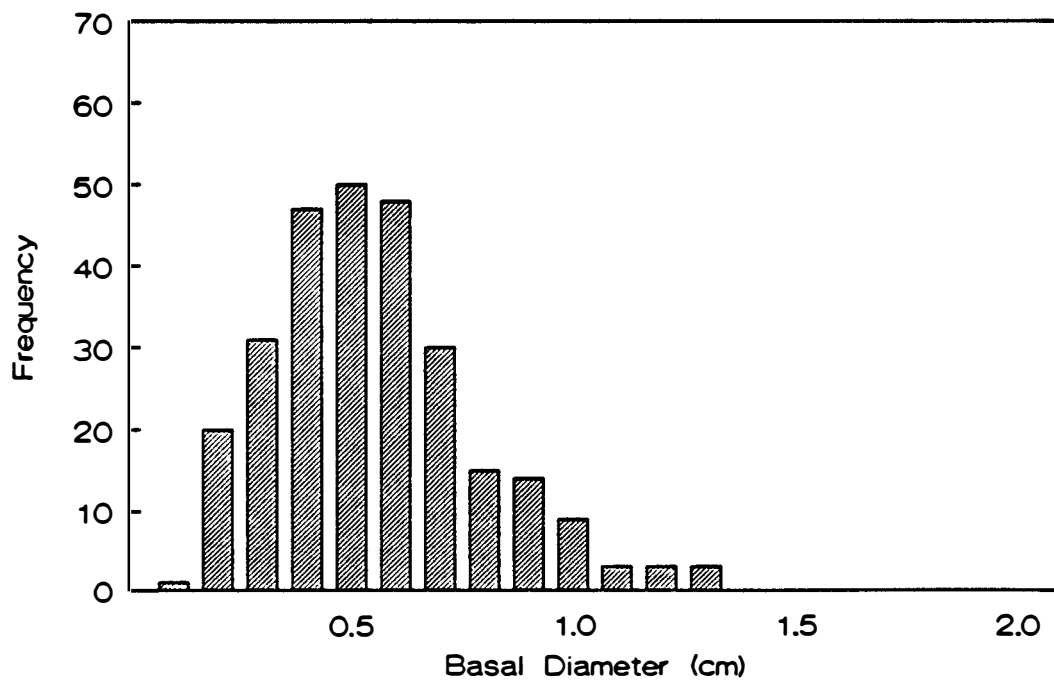


Figure 6. Diameter distribution of *Rubus canadensis* in control plots (all plots combined), initial evaluation date. Plot size is 2 x 2 m, n = 7 plots.

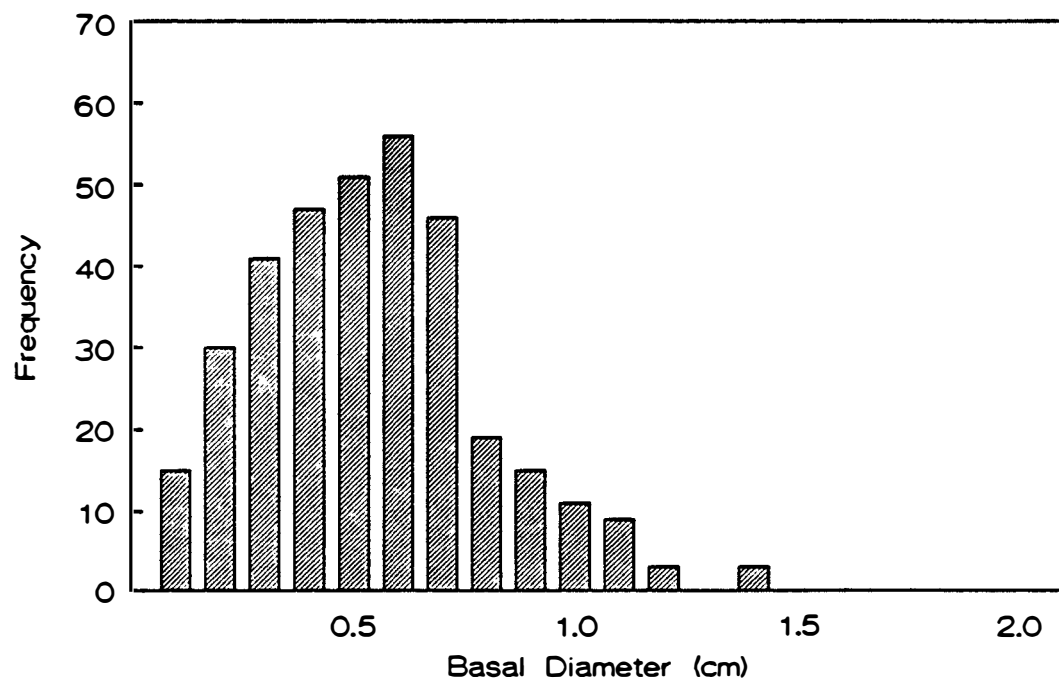


Figure 7. Diameter distribution of Rubus canadensis in control plots (all plots combined), final evaluation date. Plot size is 2 x 2 m, n = 7 plots.

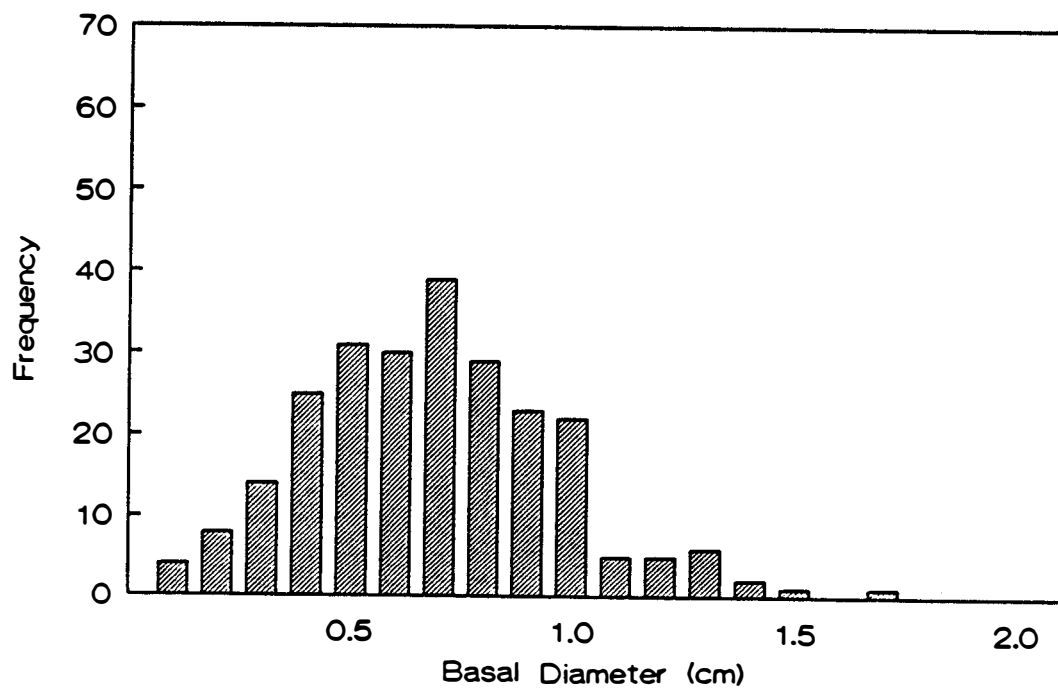


Figure 8. Diameter distribution of Rubus canadensis in Rubus-removal plots (all plots combined), initial evaluation date. Plot size is 2 x 2 m, n = 7 plots.

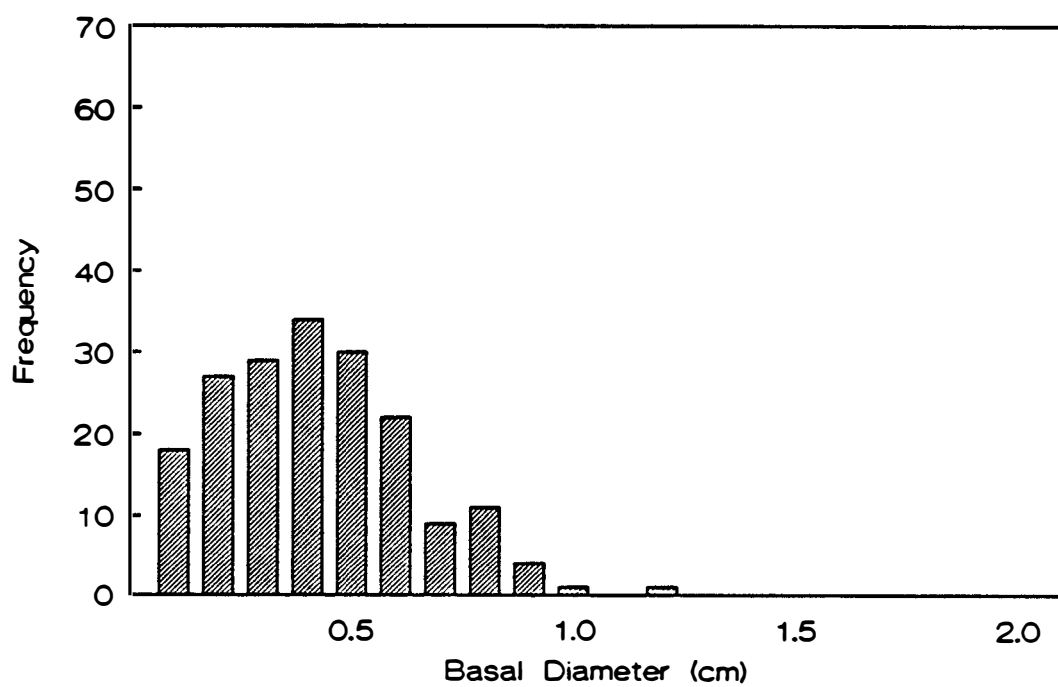


Figure 9. Diameter distribution of Rubus canadensis in Rubus-removal plots (all plots combined), final evaluation date. Plot size is 2 x 2 m, n = 7 plots.

Table 29. Changes in soil parameters in control (C) and Rubus-removal (R) plots. P, K, and Ca levels are means in ppm. n = 7 2 x 2 m plots for all values. No changes differed significantly between treatments (P > 0.01, Wilcoxon rank sum tests).

Parameter	Treatment	Mean initial value	Mean final value	Change
water pH	C	4.03	4.01	-0.02
	R	4.01	4.00	-0.01
P	C	2.9	2.0	-0.9
	R	2.0	2.0	0
K	C	30.0	24.3	-5.7
	R	27.9	25.7	-2.2
Ca	C	11.4	10.0	-1.4
	R	11.4	10.0	-1.4

those changes did not differ significantly between treatments. No effects of Rubus removal were found in these data. Student's t-tests between replicate soil samples (for reliability of analyses) showed no significant differences for any soil parameters.

4. Shoot Growth Comparisons

Wilcoxon rank sums comparisons of 1988 fir shoot growth between treatments appear in Table 30. Terminal, north-lateral, and south-lateral shoots all tended to be shorter in the Rubus-removal plots than in the control plots, but differences between treatments were not significant. Product-moment correlations between 1988 and 1987 shoot growth did not differ significantly between treatments (Table 31).

Table 30. Wilcoxon rank sums tests of 1988 Fraser fir shoot growth between control (C) and Rubus-removal (R) plots. n = number of seedlings. No mean ranks differed between treatments (P > 0.01).

Shoot	Absolute mean (cm) (n)		Mean rank		Z
	C	R	C	R	
terminal 1988	2.79 (116)	1.97 (127)	131.4	113.4	2.002
N-lateral 1988	2.28 (82)	1.47 (91)	96.8	78.2	2.484
S-lateral 1988	2.66 (52)	1.97 (61)	86.8	71.7	2.084

Table 31. Comparisons of product-moment correlation coefficients between 1988 and 1987 Fraser fir shoot growth between control (C) and Rubus-removal (R) treatments. n = number of seedlings. No coefficients differed significantly between treatments ($P > 0.01$).

Correlation	Treatment		Chi-square
	C	R	
terminal 1988/ terminal 1987 (n)	0.782 (116)	0.725 (127)	1.030
N-lateral 1988/ N-lateral 1987 (n)	0.792 (72)	0.653 (82)	3.218
S-lateral 1988/ S-lateral 1987 (n)	0.806 (52)	0.726 (61)	1.036

CHAPTER 4

DISCUSSION

A. Overstory Composition

The NE slope was dominated by conifers more than other slopes. Only three canopy species were encountered in the NE transect, and basal area and density of the single deciduous species (yellow birch) were the lowest of all slopes. Of the unlogged slopes (NE, SW, and SE), slope NE had the highest density of standing Fraser fir (nearly all of which are now dead).

The former dominance of live Fraser fir on the NW slope apparently resulted in greater changes in overstory composition following adelgid infestation than on other slopes. When that slope was logged, most large spruces were probably removed, allowing Fraser fir to gain dominance. Low spruce and high fir dominance were characteristic of other red spruce-Fraser fir stands several decades after logging (Weaver 1972). Following adelgid-caused mortality of fir, basal area and density of dead trees on the logged slope exceeded those on the unlogged slopes, and canopy closure became lower.

Conifers were less dominant on the SW slope than on the other unlogged slopes. Yellow birch basal area and

density were relatively high on that slope, suggesting a response to higher insolation. Yellow birch is classed as intermediate in shade tolerance (Fowells 1965) and the species regenerates primarily in canopy gaps in the GSMNP spruce-fir forest (Busing 1985).

The SE slope appeared to be the least affected by Fraser fir mortality. That slope had the highest basal area and density of live spruce, probably reflecting protection from prevailing winds (Busing and Clebsch 1988) and the drier aspect (Whittaker 1956). Canopy closure was nearly complete on that slope.

In general, fir mortality appears to have had the greatest effect on canopy composition of north-facing slopes. Canopy closure was lowest and dead fir basal area and density were highest on those slopes.

B. Seedling-Understory Characterization

1. Herbaceous Species Composition

Bryophytes are the most conspicuous feature of the herbaceous layer, particularly on the shaded, moist NE slope. Ferns are also important, with Athyrium asplenoides abundant on all slopes and Dryopteris spp. abundant on north-facing slopes. The Dryopteris

distribution may be related to the more mesic northern aspect (Boner 1979). The greater abundance of Oxalis montana on west-facing slopes may be associated with higher soil K concentrations on those slopes.

The relatively low total herbaceous cover on the SW slope results from the low cover of Dryopteris spp. on that slope. Dryopteris spp. cover is also low on the SE slope, but higher cover of Carex spp. there compensates for low Dryopteris cover.

2. Woody Species Composition

The NE slope of Mount Collins seems to favor conifer regeneration; both spruce and fir seedling densities were highest there. Spruce seedling densities were probably underestimated in transects sampled earlier in the season because appearance of germinal seedlings occurred during sampling. Comparisons of seedling densities among transects are confounded with time of sampling. Nevertheless, germinal seedlings seemed to form a large proportion of the spruce seedling population. Spruce produced a seed crop in 1987 (personal observation), so the large number of germinals appearing during 1988 may reflect a germination peak rather than typical yearly recruitment.

Fir seedling density is rather low in comparison to that of spruce. The low density of fir on the NW slope was

unexpected because the former canopy dominant was fir. Those canopy trees were almost certainly of reproductive age. One factor contributing to the paucity of seedlings on the NW slope may be that fir seedlings and saplings suffer especially severe adelgid infestation and mortality where overstory infestation is heavy (Eagar 1984).

Rubus canadensis density and biomass were highest on the SW slope of Mount Collins, suggesting that the species is more abundant on warmer, drier sites. Boner (1979) found a similar negative association of Rubus density with mesic aspect. The abundance of Rubus on the SW slope may partially explain the low total herbaceous cover there.

3. Fir Seedling Population Characteristics

Based on comparisons with data from White et al. (1985), density of fir seedlings has probably increased on the north-facing slope of Mount Collins following overstory mortality. Boner (1979) also found increases in fir seedling and sapling densities in a post-mortality chronosequence.

Most fir seedlings in this study were small (≤ 25 cm tall). In contrast to spruce, relatively few fir seedlings are very young. Apparently, germinal fir seedlings have become extremely scarce in recent years. No germinal fir

seedlings were observed in any transect plots. A few germinal seedlings were noted in other areas still having live overstory firs. Fraser fir seed crops are periodic (Franklin 1974), and some among-year variation in seedling appearance certainly occurs. Adelgid effects on mature firs are likely to decrease seed production. Sullivan and Pittillo (1988) noted reduced Fraser fir seedling appearance in a grassy bald after poor seed crops on nearby trees the previous two years; overstory firs had also suffered recent mortality from adelgid infestation. The sensitivity of seedling appearance rate to seed production supports the observation that Fraser fir seed viability may decrease after only one year (S. E. Schlarbaum, personal communication).

Germinal Fraser fir seedlings are not likely to appear in significant numbers until existing seedlings and saplings mature and begin to bear seed. First reproduction may occur in firs as young as 20 years; Fraser fir also becomes particularly susceptible to adelgid infestation at about this age (Eagar 1985). The GSMNP Fraser fir population has suffered mortality primarily within the past 25 years. Reproducing trees are much less numerous than before, and the pool of genetic variation among these trees has probably become smaller. The amount of variation among the progeny of surviving trees may become limited because of the increased likelihood of inbreeding. Li et al.

(1988) found significant variation in height growth among Fraser fir seedlings descended from different parent trees growing at the same site. A substantial amount of such "among family" (Li et al. 1988) variation may be lost in the next generation as a result of adelgid-caused mortality.

The effects of inbreeding in normally outcrossing species include accumulation of rare, deleterious recessive alleles, called inbreeding depression (Hartl 1980). If Fraser fir experiences significant inbreeding depression, the result may be local populations showing low growth rates. Li et al. (1988) found that Fraser fir seedlings grown from seeds collected on Roan Mountain, Tennessee/North Carolina showed lower height growth than seedlings from other southern Appalachian provenances.

4. Associations Among Vegetation Variables

Since rank correlations are not derived from the original data values, some information contained in those data are lost. Few of the correlations are especially large, and the chance of any one of them being spurious is accordingly high. Discussions of results for the specific hypotheses tested are presented below.

Hypotheses (a), (b), and (c). One contributing factor to the low correlations among canopy closure and other variables, such as fir seedling density and Rubus density/biomass, is the measurement of canopy closure directly above each sample point. Sunlight only rarely enters the forest vertically, so a more accurate estimate of the effect of sunlight on understory plant density would have had to account for sidelighting from neighboring gaps. Most seedlings predated canopy mortality; their distributions were determined by canopy and understory conditions which probably differed from current conditions. Rubus has been regarded as a gap colonizer species (Crandall 1957, 1958). The lack of correlation of Rubus density or biomass with canopy closure may also reflect effects of sidelighting from nearby canopy gaps.

Hypotheses (d) and (e). The negative associations between fir seedling density and Rubus density/biomass may be interpreted in several ways. Rubus may be inhibiting germination, establishment, and/or survivorship of fir seedlings. Fir may be inhibiting establishment and/or growth of Rubus. Alternatively, establishment of both species may be responsive to other variables which favor one species over the other. That fir would inhibit establishment or growth of Rubus seems least likely. The majority of fir seedlings (87%) are no more than 25 cm

tall, while Rubus canes are typically 1-2 m tall. Inhibition of Rubus by shading from fir seedlings cannot contribute much to the observed associations. Also, because fir seedlings show low overall densities, it seems unlikely that fir seedlings could significantly inhibit Rubus by competition for nutrients or root space, allelopathy, or other direct interactions. Rubus canadensis appears to inhibit establishment of Fraser fir seedlings.

Hypothesis (f). Correlations between fir shoot lengths and canopy closure were either small or likely to be spurious. Terminal 1987 shoot growth showed a slight negative tendency (which was expected) and lateral shoot growth showed a positive tendency. These correlations do not strongly suggest any real association between fir seedling shoot growth and canopy closure.

Hypotheses (g) and (h). Negative correlations between terminal shoot growth of fir seedlings and fir seedling density suggest a density-dependent effect on height growth. This result was contrary to expectation. Farmer et al. (1988) found greater height growth of jack pine with increasing seedling density. Mutual shading of fir seedlings is unlikely because seedlings are rarely dense

enough for their branches to overlap. Competition for some resource, allelopathy, or different responses by shoot growth and establishment to some external factor are possible explanations.

Hypothesis (i). Positive associations between fir terminal shoot growth and Rubus density and biomass were unexpected; height growth of Fraser fir seedlings has shown reductions under heavy shade (Hinesley 1986). Under low light conditions, many woody plants allocate more energy into height growth (Harper 1977; Ting 1982). If Rubus shade is producing such an effect on fir seedlings, this effect would be contrary to that found in nursery-grown seedlings (Hinesley 1986). Although the correlations were statistically significant, a graph of the actual data do not suggest a strong association between fir seedling shoot growth and Rubus density.

5. Associations Between Vegetation and Soil Parameters

Terminal growth of fir seedlings shows moderate positive associations with K concentration of the forest floor (Hypothesis (j)). McCracken et al. (1962) suggest that K availability in high elevation soils of the GSMNP may be regulated by weathering and atmospheric inputs. Mineral horizon concentrations of Ca and K are low because

these elements (among others) are readily lost to leaching. Positive responses of fir growth to K concentration indicate growth limitation by this element in some areas. Positive associations of Rubus density and biomass with P and K concentrations also suggest growth limitation (Hypothesis (k)). Alternatively, P and K concentrations may be affected by Rubus through foliar leaching, litter deposition, fine root decomposition, or some other mechanism.

Densities of all fir seedlings and those less than five years old showed tendencies toward negative correlations with soil nutrient parameters. Density of firs less than five years old and K concentration were significantly negatively correlated. These tendencies may reflect the negative associations of fir density and Rubus density/biomass, because Rubus density and biomass were positively associated with P and K concentrations.

The soil data indicate that K concentration is more variable from site to site on Mount Collins than other elements. K may thus be limiting in some areas and may detectably affect plant species distribution and growth. Information on N concentrations in the study area would have been a valuable addition to these data, but N determinations must be regarded with caution. Seasonal variations occur, and soil samples must be tested almost

immediately to prevent loss to volatilization (J. T. Ammons, personal communication).

6. Substrate and Surface Type Distributions

Existing fir seedlings are not randomly distributed in the study area. Dead wood (logs or roots) appears to be a particularly favorable substrate for establishment and/or early survival. Logs can be very important substrates for tree seedling establishment (Busing 1985; White et al. 1985; Harmon 1987). Establishment on logs may prevent competition with forest floor herbs (Harmon and Franklin 1989). On Mount Collins, Rubus canadensis was rooted almost exclusively in the forest floor. Fir seedlings established on logs thus should not be exposed to belowground interactions with Rubus. The present study indicates that concentrations of K and/or Ca are significantly higher in decaying logs than in the forest floor. Ca and N contents have been shown to increase with time in decaying boles of red spruce and balsam fir (Foster and Lang 1982), roots of lodgepole pine (Yavitt and Fahey 1982), and boles of western hemlock and Sitka spruce (Grier 1978). K content, however, decreased in these same species.

Bryophytes may constitute favorable surfaces for fir seedling establishment. Unlike substrate types, surface

types may not be independent of the plants occupying them. While fir seedlings may establish preferentially on bryophytes, bryophyte cover may also develop preferentially under seedlings.

7. Damage Type Distributions

The fraction of fir seedlings showing obvious gouting (26%) is probably an underestimate of the extent of balsam woolly adelgid effects among seedlings. Many understory firs have died from adelgid infestation (and subsequently decomposed), gouting is not the only effect of infestation, and gouting is not always serious enough to be distinguished from the normal growth forms of fir seedlings. Shoot origins are slightly larger in diameter than shoots themselves, and seedlings rarely grow perfectly straight. This fraction therefore represents only the extent of externally obvious adelgid effects among surviving seedlings.

8. Shoot Growth Trends

Shoot growth trends of fir seedlings indicate that terminal growth is increasing in successive years. This trend may reflect the early part of the typical sigmoidal

growth curve of plants (Ting 1982). Previous adelgid infestation may contribute to this trend. Following overstory mortality, the rain of adelgids from canopy trees has probably decreased, and a recovery from terminal suppression is occurring in many seedlings. An increasing trend in growth is not consistent with precipitation patterns at high elevations of the GSMNP. Recent annual precipitation totals have decreased since 1982. Shoot growth response to overstory mortality may also contribute to growth trends, but the small magnitudes of correlations between shoot growth and canopy closure indicate that that contribution is minor.

C. Rubus-Removal Plots

1. Herbaceous Species Cover and Woody Species Densities

Herbaceous species cover and woody species densities generally increased between evaluation dates. The slight decreases in Dryopteris spp. cover may be a result of changes in one of the common species, D. campyloptera. This species has been reported to be easily killed by low temperatures (Strausbaugh and Core 1970-1977). White-tailed deer also feed to some degree on ferns (personal observation). The appearance of large numbers of germinal spruces probably resulted from the previous year's seed

crop. Spruce produces large seed crops every 3-8 years, with most seed germinating the spring following dispersal (Fowells 1965). No Rubus-removal effect was detected for any herbaceous or woody species changes. Effects may become evident in subsequent seasons. Rubus itself is capable of rapid response to disturbance.

2. Soil Parameters

The slight reductions of soil nutrient concentrations indicate either uptake by growing vegetation (e.g., Rubus) and/or loss from leaching. Rubus-removal did not significantly affect these changes.

3. Shoot Growth Comparisons

The tendency for mean 1988 shoot lengths to be lower in the Rubus-removal plots may be an effect of increased light levels. High-light conditions suppress height growth in some plants (Ting 1982). Correlations between 1988 and 1987 shoot growth decreased slightly, indicating added variation to shoot lengths of seedlings in the Rubus-removal plots. No differences between treatments were significant, however.

CHAPTER 5

CONCLUSIONS

1. On Mount Collins, Fraser fir mortality from balsam woolly adelgid infestation appears to have had the greatest effect on canopy composition of north-facing slopes.
2. Bryophytes are the most conspicuous feature of the herbaceous layer of Mount Collins, particularly on the northeast-facing slope.
3. The northeast-facing slope of Mount Collins seems to favor conifer regeneration because of the high densities of Fraser fir and red spruce seedlings there.
4. The abundance of Rubus canadensis on the southwest-facing slope of Mount Collins may partially explain the low total herbaceous cover on that slope.
5. Density of Fraser fir seedlings has probably increased on the north-facing slope of Mount Collins following recent overstory mortality.

6. Germinal Fraser fir seedlings are very scarce and are not likely to appear in significant numbers unless existing seedlings and saplings reach reproductive age.
7. Reduced variability of Fraser fir seedling density with increasing Rubus canadensis density suggests that Rubus inhibits establishment of fir seedlings.
8. An association between Fraser fir seedling shoot growth and Rubus canadensis density is not apparent on Mount Collins.
9. Positive associations of Fraser fir shoot growth and Rubus canadensis density and biomass with soil potassium concentration indicate some growth limitation by this element.
10. Dead wood appears to be a favorable substrate for establishment of Fraser fir seedlings.
11. Bryophytes may constitute favorable surfaces for Fraser fir seedling establishment.
12. Balsam woolly adelgid effects are evident on about one fourth of Fraser fir seedlings, but this fraction is probably an underestimate of the extent of adelgid damage.

13. Terminal shoot growth is increasing in successive years as a consequence of normal growth habits and recovery from balsam woolly adelgid infestation.
14. No effect of Rubus canadensis removal was detected on herbaceous cover or woody species densities.
15. Rubus candensis itself is capable of rapid response to disturbance.
16. No effect of Rubus canadensis removal was detected on soil pH or phosphorus, potassium, or calcium concentrations.
17. No effect of Rubus canadensis removal was detected on 1988 Fraser fir shoot growth.

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