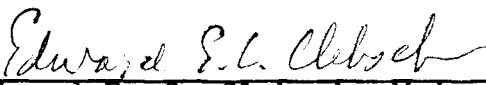
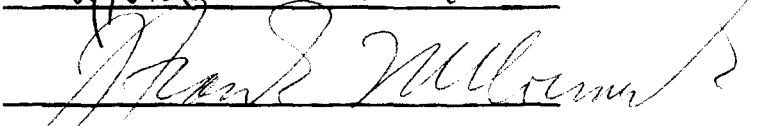
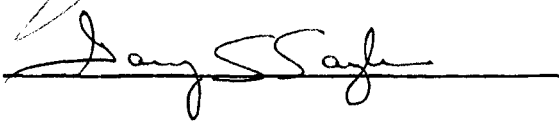


To the Graduate Council:

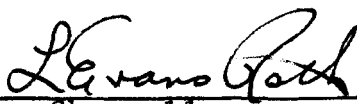
I am submitting herewith a thesis written by Robert Dale Fuller entitled "Why Does Spruce Not Invade the High Elevation Beech Forests of the Great Smoky Mountains?" I recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology.


Edward E. C. Clebsch, Major Professor

We have read this thesis
and recommend its acceptance:

Accepted for the Council:


Vice Chancellor
Graduate Studies and Research

Thesis
77
.F848
Copy 2

WHY DOES SPRUCE NOT INVADE THE HIGH ELEVATION BEECH
FORESTS OF THE GREAT SMOKY MOUNTAINS?

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

Robert Dale Fuller
December 1977

1345664

ACKNOWLEDGMENTS

The author wishes to express his most sincere appreciation to his major professor, Dr. Edward E. C. Clebsch, for suggesting the project and providing valuable advice and support throughout the study. Dr. Cornelius H. Muller is to be commended for developing the author's and many other students' interest in the discipline of plant ecology. The help of the author's committee in advice on experimental design and reading of the manuscripts was invaluable. Finally, the help and encouragement of friends, co-workers and the author's parents made the study possible.

The author wishes to express his thanks to the Graduate Program in Ecology and The University of Tennessee for providing financial support and research space and equipment throughout the course of the project.

ABSTRACT

Above 1,370 m, spruce-fir forests dominated by Picea rubens Sargent and Abies fraseri (Pursh) Poiret form a nearly continuous band across much of the landscape of the Southern Appalachian Mountains. Nearly pure stands of American beech (Fagus grandifolia Ehrhart) penetrate into the spruce-fir forest on south-facing concave slopes, near the tops of major ridges. Frequently the boundary between these two community types is very abrupt.

Important factors in the maintenance of these so-called "beech gaps" against red spruce invasion were investigated. Soil temperature, soil moisture, and the presence of biotic toxins were studied in the rooting environment of potentially invading spruce seedlings.

During the spring, while the beech canopy was still leafless, diurnal soil temperature (2 cm) variation was consistently greater in the beech gap than in the neighboring spruce-fir. Growth chamber experiments demonstrated that germination of red spruce was delayed and significantly reduced by beech gap soil temperature variation.

Soil moisture in the seedling rooting environment was found to be consistently higher in the beech gap than in the spruce-fir. It is therefore unlikely that deficiencies in soil moisture in the beech gap prevent the invasion of red spruce.

Spruce seed bioassays of beech litter, beech root, and beech gap soil extracts revealed the presence of potential inhibitors. Extracts of fall whole leaf litter, summer whole leaf litter, and summer fragmented leaf litter delayed spruce germination. These extracts and extracts of fall soil produced the greatest reductions in radicle elongation. The increased toxicity in summer litter extracts may be accounted for by toxic phenols generated by microbial degradation of lignin. Preliminary chemical analysis of whole leaf litter suggested the presence of p-hydroxybenzoic, vanillic, ferulic, and p-coumaric acids.

Artificial over-wintering experiments in intact beech gap and spruce-fir soil cores showed a small but significant inhibition of germination in beech gap cores. Natural over-wintering conditions of much longer duration may produce even greater inhibition of germination. Toxins leached from the beech litter may be responsible for this inhibition.

Field experiments suggested that animal destruction of seeds in beech litter contributes to seed mortality. Mortality of young seedlings also resulted from damping-off.

From these investigations, it appears that the high elevation beech gaps have been maintained against spruce invasion by a combination of interference mechanisms. These mechanisms progressively increase spruce seed and seedling mortality in the beech gaps.

TABLE OF CONTENTS

CHAPTER	PAGE
I. INTRODUCTION.	1
II. THE STUDY AREA.	7
Site Description and Location	7
Geology and Soils	9
Precipitation and Temperature	10
III. THE ENVIRONMENT OF THE SPRUCE SEED AND SEEDLING.	16
Soil Temperature.	17
Soil Moisture	20
Toxins in the Environment	23
Inhibition of germination	23
Toxicity under natural conditions	25
Effects on radicle elongation	29
Possible inhibitors	31
IV. GERMINATION AND ESTABLISHMENT	33
Germination in Programmed Environment Chambers.	33
Seedling Growth in Programmed Environment Chambers.	36
Establishment in Spring Field Cores	40
Mortality in Fall Field Plots	42
V. MAINTENANCE OF THE BEECH GAPS IN THE GREAT SMOKY MOUNTAINS	48
VI. VEGETATION DYNAMICS AT THE BEECH AND SPRUCE-FIR ECOTONE.	53
VII. CONCLUSIONS	56
LITERATURE CITED.	58
VITA.	65

LIST OF TABLES

TABLE		PAGE
I.	Bioassays of Red Spruce Germination, Expressed as Percent of Control	26
II.	Average Number of Germinating Seeds in Soil Cores after Artificial Over-Wintering Treatment	28
III.	Fate of Seeds in Growth Chamber Germination Experiment (No. of Seeds out of 100).	37
IV.	Growth Chamber Spruce Seedling Growth as Affected by Soil Source	39
V.	Seed Fate in Field Germination Cores.	41
VI.	Seed Fate in Over-Wintered Germination Plots. .	45

LIST OF FIGURES

FIGURE	PAGE
1. The Study Area.	2
2. Monthly Precipitation at Newfound Gap, Ten Year Average	12
3. Monthly Precipitation at Newfound Gap, 1976 . . .	13
4. Ten Day Averages of Maximum and Minimum Air Temperature (Below) and Diurnal Temperature Variation (Above) at Newfound Gap during 1976 .	15
5. Ten Day Averages of Maximum and Minimum Soil Temperatures at the 2 cm Depth under Spruce- Fir (---) and Beech Gap (—) Vegetation for 1976.	19
6. Soil Moisture as Percent Dry Weight under Beech Gap (—) and Spruce-Fir (---) Vegetation for 1976.	22
7. Reduction of Radicle Elongation in Various Extracts.	30
8. Cumulative Germination (Percent) in Growth Chambers.	35

CHAPTER I

INTRODUCTION

Above 1,370 m in the Southern Appalachian Mountains, coniferous forests dominated by red spruce (Picea rubens)¹ and Fraser fir (Abies fraseri) form a nearly continuous band of vegetation. Under certain conditions of topography and exposure, several other communities are found within the spruce-fir zone. On xeric ridge crests, "heath balds" dominated by ericaceous shrubs are common (Cain, 1930). At the border of the spruce-fir and deciduous forests zones, "grassy balds" dominated by Danthonia compressa occur (Mark, 1958; Gersmehl, 1973). On concave slopes above 1,370 m are frequently found stands dominated by deciduous trees, especially beech (Fagus grandifolia, the gray beech of Camp, 1951), and yellow birch (Betula lutea) (Crandall, 1958). On south-facing concave slopes, nearly pure stands of beech are bordered by spruce-fir forest on the adjacent convex slopes (Russell, 1953; Crandall, 1958) (Figure 1). These last distinctive communities have been termed "beech gaps," and are very limited in occurrence; probably no more than 4,000 hectares exist in the Southern Appalachian Mountains (Russell, 1953). The purpose of this study was

¹Nomenclature is after Radford et al. (1968).



Figure 1. The study area. The beech gap is on the left; the spruce-fir is on the right.

to investigate some of the factors which maintain the beech gaps against the invasion of spruce.

Russell (1953) was of the opinion that wind, funneling through the gaps, prevented the shallow rooted spruce from invading the gaps. While this may affect large trees, it seems unlikely that saplings and seedlings would be adversely affected. Beech gaps are typically found near 1,600 m in elevation, well above the lower altitudinal limit of red spruce on south-facing slopes (Whittaker, 1956). Germination studies with red spruce in the Southern Appalachian Mountains suggest that this species will germinate and survive at much lower elevations (Griffin, 1965). Planted stands of red spruce flourish at elevations as low as 600 m (Schofield, 1960). Studies of grassy balds at these elevations suggest that they are slowly but steadily being invaded by spruce and fir where seed sources are available (Ramseur, 1960, 1976; Bruhn, 1964; Radford, 1968). Schofield (1960) observed that established spruce trees in beech orchards will produce "a self-perpetuating and expanding clump that ultimately merges with the main body" of the spruce-fir forest nearby. These lines of evidence suggest that, in the absence of beech, spruce-fir forest could readily survive in the gaps.

The existence of these sharp boundaried (Ramseur, 1960) communities presented an ideal opportunity for the study of mechanisms of plant interaction. It was hypothesized

that some sort of interference mechanism(s) (Harper, 1961; Tinnin, 1972) caused by the dominance of beech was (were) preventing red spruce from invading the beech gaps.

Numerous hypothetical interference mechanisms can be advanced to account for the lack of spruce invasion. Shanks (1956) found that soil temperatures under the beech gap vegetation were higher, especially during the spring months, than under adjacent spruce-fir vegetation. This suggested the possibility that differences in soil moisture in the surface layers may also exist between the beech gap and spruce-fir forests. Winter and Bublitz (1953) and Mitin (1971) found evidence that the European copper beech (Fagus silvatica L.) may produce litter with an allelopathic potential.

Several potential interference mechanisms had to be deferred because of the limited scope of this study. Competitive interactions involving limiting nutrients were not investigated since few differences in concentrations of several extractable elements (Ca,Na,K,Mg) occur (Wolfe, 1967). Extractable manganese was much higher in soil profiles under beech vegetation than under spruce-fir vegetation. While the A horizon under the spruce-fir forest almost always had undetectable concentrations of extractable manganese, the beech gap All horizon had concentrations ranging up to 106 ppm (Wolfe, 1967). While this presents an intriguing problem in mineral cycling, it is questionable

that it is important in preventing the invasion of the beech gaps by red spruce. Lafond and Laflamme (1970) found that black spruce (Picea mariana) is, on the contrary, quite tolerant of manganese, growing normally at concentrations twice as high as those that produce toxicity symptoms in jack pine (Pinus banksiana Lamb.). Nevertheless, this aspect is worthy of investigation, since manganese can interact with iron to produce apparent deficiencies under low iron concentrations (Meyer et al., 1973; Lafond and Laflamme, 1970).

The purpose of this study was to measure and investigate the effects of soil temperature, soil moisture, and biotic toxins on spruce establishment in the beech gaps. Laboratory bioassays, growth chamber experiments, and field experiments were conducted to examine the importance of these factors. It was hoped that these experiments might also shed light on other potential interference mechanisms, including the effects of litter on seedling emergence, animal depredation, and attack by microorganisms.

The important influence of climatic change on vegetation dynamics is well established (Gleason, 1923; Oosting and Billings, 1951; Schofield, 1960; Davis, 1965; Bray, 1971). Plant species migrating in response to changing climates face potential interactions with already established populations. A knowledge of the interference mechanisms involved in the maintenance of a community permits

a greater understanding of both the origin of that community and its relationships to other plant communities through time.

CHAPTER II

THE STUDY AREA

I. SITE DESCRIPTION AND LOCATION

One beech gap was chosen for further study on the basis of its accessibility, resistance to spruce and fir invasion, and distinctness of boundaries with the neighboring spruce-fir forest. Located in Swain County, North Carolina, in the Great Smoky Mountains National Park, the gap is situated on a steep, south-facing slope 1.5 km west of Newfound Gap and Highway 441. It occupies the concave portion of the slope, while spruce-fir forest occupies the convex slopes on either side. A road runs through the bottom of the beech gap, while the ridge at the top forms the Tennessee, North Carolina border. The gap ranges from approximately 1,580 to 1,640 m in elevation. A portion of the spruce-fir forest immediately to the east of the beech gap was also studied (Figure 1, page 2).

The Unaka Mountain Range, which includes the Great Smoky Mountains, forms the southernmost extension of the Appalachian Mountain chain. Ranging in elevation from 500 to over 2,000 m, and having a variety of topographic features and exposures, these mountains have served as refugia during major plant migrations associated with periods of climatic change (Cain, 1943; Ramseur, 1960).

The high elevations of the Southern Appalachians contain many species characteristic of the northeastern United States and southeastern Canada. Oosting and Billings (1951), in a comparative study of southern high elevation and northern spruce-fir forests, found considerable similarity. Both contain red spruce (Picea rubens) as a major dominant. The southern forests contain Fraser fir (Abies fraseri) as a codominant, while in the north, Abies balsamea (L.) Mill. is its counterpart. They surmised that the northern and southern spruce-fir forests were continuous during the Pleistocene and have differentiated to some extent after being geographically isolated. Ramseur (1960) speculated that Southern Appalachian spruce-fir endemics may have failed to migrate north after the end of the Pleistocene.

The high elevation beech and birch forests form interruptions in a nearly continuous band of spruce-fir forest above 1,370 m in the Great Smoky Mountains (Whittaker, 1956). The beech forests are usually confined to flats and concave slopes (Crandall, 1958), reaching their greatest development on steep south-facing slopes (Oh, 1964). The vast majority of stems are of beech, with buckeye (Aesculus octandra), yellow birch (Betula lutea) and red spruce occurring in far fewer numbers. In the beech gap chosen for study, beech accounted for over 95% of all stems (Oh, 1964).

Whittaker (1956), in his study of the vegetation of the Great Smoky Mountains, subdivided these forest types on the basis of their understory vegetation. The lower half of the beech gap corresponds to Whittaker's "mesic type," while the upper part corresponds to his "sedge type" with Carex aestivalis being especially dominant. The portion of spruce-fir forest studied corresponds more closely to the subtype Whittaker described as occupying flats and north-facing slopes. Especially noticeable is the lack of Rhododendron catawbiense characteristic of the subtype occupying xeric south-facing ridges.

II. GEOLOGY AND SOILS

The study area is underlain by rocks of the Anakeesta formation, a complex series of interbedded slates, phyllites and sandstones, discussed fully by Hadley and Goldsmith (1963). Slate predominates in the lower soil horizons of the beech gap, while sandstone and slate dominate the lower layers of the spruce-fir soil. X-ray diffraction analysis of the clay fraction of the soils showed virtual identity (Wolfe, 1967). Wolfe (1967) concluded that "sharp boundaries between the two forest types were not caused by any considerable change in bedrock composition." Beech gaps are also found in areas underlain by sandstone (Wolfe, 1967). Depth to bedrock is very close under both vegetation types, on the basis of comparisons involving 17 gaps (Wolfe, 1967).

Wolfe (1967), in a study of high elevation soils of the Great Smoky Mountains, found that the majority of the soils were inceptisols, while spodosols were found on the tops of high peaks under spruce-fir vegetation. Adjacent spruce-fir and beech gap soils were very similar texturally and mineralogically. The contrasting vegetation did, however, have a pronounced effect upon the chemical characteristics of the soil. The less acid beech litter contains more bases than the spruce and fir needles and forms a looser and thinner litter layer. The A horizon in the beech gap is gray, contrasting with the black, highly organic A horizon under the spruce-fir canopy. The spruce-fir A horizon also has more organic carbon, lower pH, greater cation exchange capacity, and higher C/N ratios than the beech gap A horizon. Bases (Ca,Mg,K,Na) extractable with 1N ammonium acetate, however, showed few differences. Both soils showed accumulations of nitrogen in the litter and soil-litter interface. The A horizon of the beech gap contained less N than the spruce-fir, while the B horizons showed little difference.

III. PRECIPITATION AND TEMPERATURE

Ten years of daily precipitation and maximum and minimum temperature data were available from two weather

stations at Newfound Gap.² The weather stations are located near a parking lot in what was once a beech gap approximately 1 km northeast of the study site at an elevation of 1,550 m. Monthly averages of precipitation for the location are shown in Figure 2. Noteworthy aspects of monthly precipitation from this station include a winter maximum and early spring and fall minima (Whittaker, 1952; Smallshaw, 1953; Shanks, 1954; Stephens, 1969). Much of the winter precipitation maximum is associated with frontal activity from the West. Much of the summer precipitation occurs in the form of convectonal precipitation (Dickson, 1960; Stephens, 1969).

Annual precipitation for this station averaged 225.1 cm (88.6 in) for the eight complete years of data between 1967 and 1976, ranging from 187.2 cm (73.7 in) in 1976 to 258.9 cm (101.9 in) in 1972. Stephens (1969) and Smallshaw (1953) found yearly averages of 209.1 cm and approximately 226 cm, respectively, for the same location between 1946-1950 (Smallshaw) and 1947-1950 (Stephens). Figure 3 shows monthly precipitation for the period of study. It is noteworthy that April 1976 (4.7 cm) was the driest month in the 10-year period, while May 1976 (39.5 cm) was the wettest.

Ten day averages of maximum and minimum temperatures

²The author wishes to express his appreciation to the Tennessee Valley Authority for supplying these data.

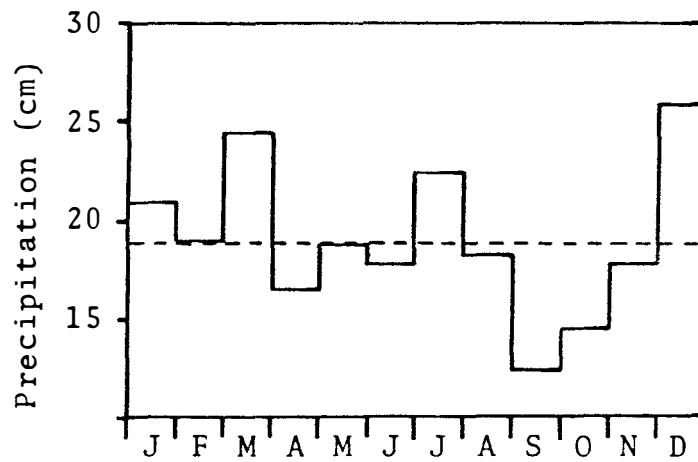


Figure 2. Monthly precipitation at Newfound Gap, ten year average. The dashed line represents the average monthly precipitation over this period.

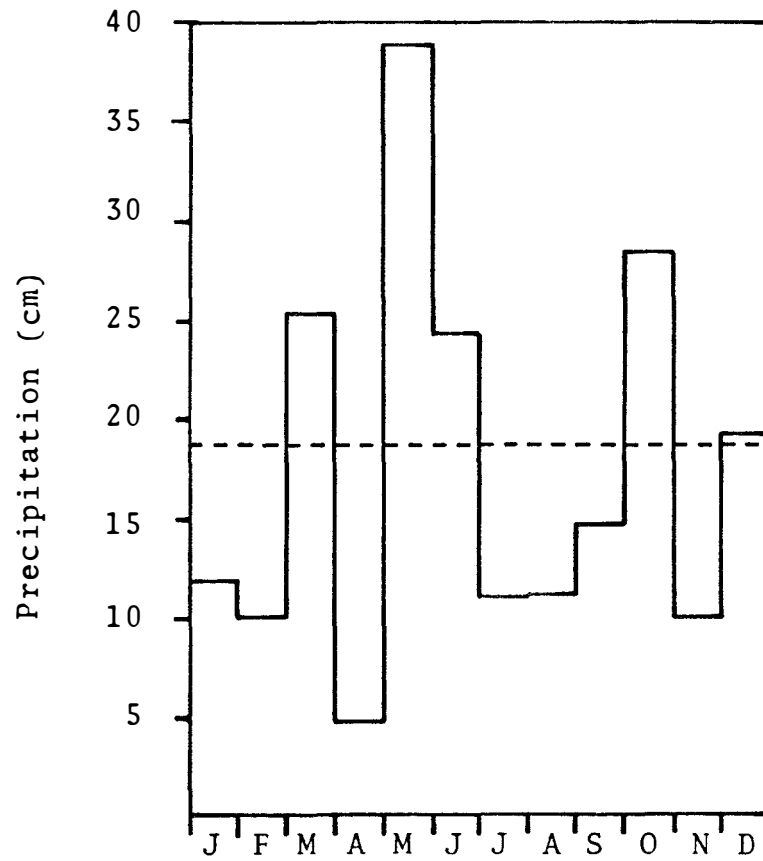


Figure 3. Monthly precipitation at Newfound Gap, 1976. The dashed line represents the average monthly precipitation for 1976.

from a standard weather station at Newfound Gap for 1976 are shown in Figure 4. An unseasonably warm period occurred in April, coinciding with the period of very low rainfall. A trend in diurnal temperature variation is also apparent. In the first five months of the year, 13 out of 16 dates had a diurnal temperature range greater than 10° C, while in the second five months only two out of 16 dates had a range greater than 10° C. Stephens (1969) noted a similar feature of diurnal temperature variation and found it to be inversely correlated with monthly precipitation.

The climate of the high elevations of the Smokies falls into the perhumid class according to the Thornthwaite system of climatic classification (Thornthwaite, 1948; Shanks, 1954; McCracken et al., 1962). Evaporation only rarely exceeds precipitation (McCracken et al., 1962). The high elevations of the Southern Appalachian Mountains have less winter snow and warmer winter temperatures than the spruce-fir forests of the northeastern United States (Oosting and Billings, 1951).

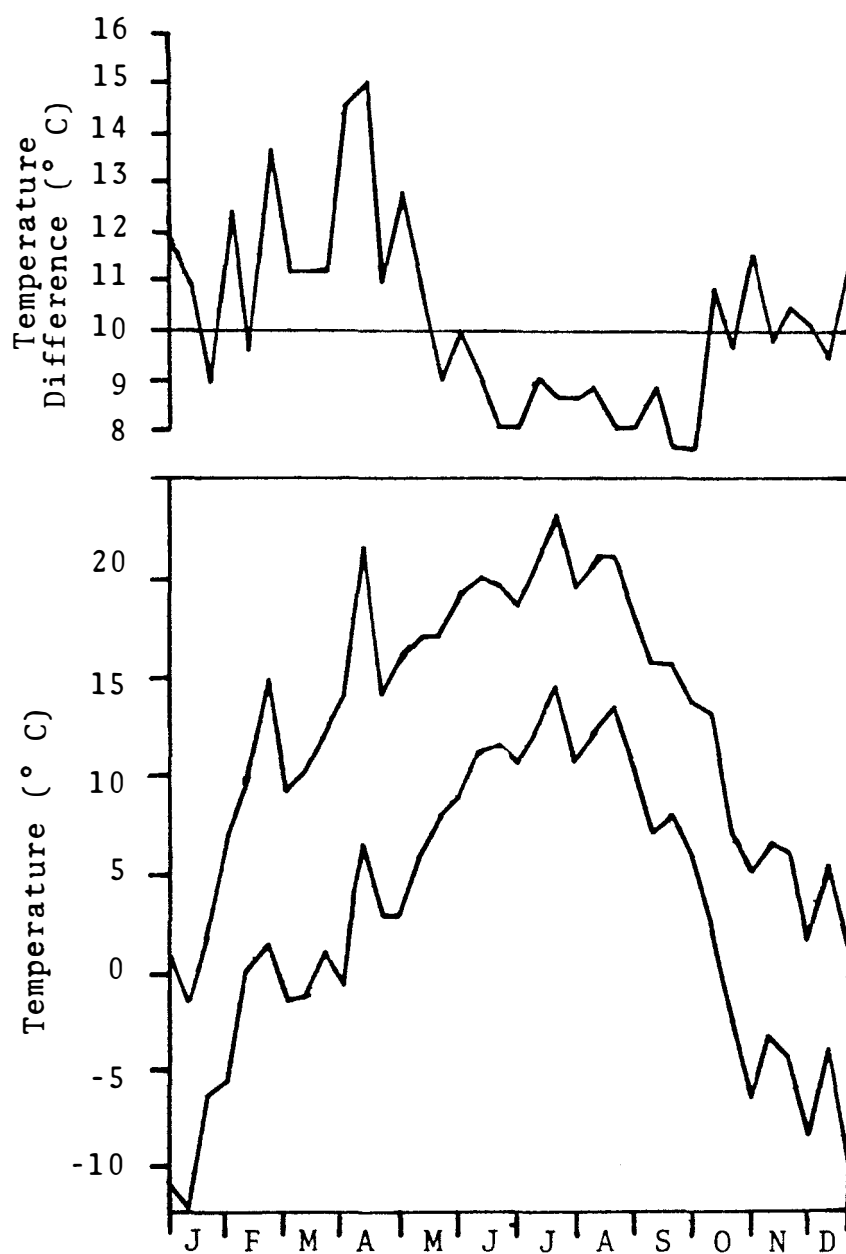


Figure 4. Ten day averages of maximum and minimum air temperature (below) and diurnal temperature variation (above) at Newfound Gap during 1976. The solid line in the upper graph represents 10°C of diurnal temperature variation.

CHAPTER III

THE ENVIRONMENT OF THE SPRUCE SEED AND SEEDLING

Several aspects of the immediate environment of spruce seeds and seedlings in the beech gap were investigated. Soil temperature and soil moisture in the seedling rooting zone were monitored through one growing season. In addition, the presence of potentially inhibitory toxins in beech gap soil, litter, and roots was examined seasonally.

The absence of spruce in the beech gap could conceivably result from a failure of spruce seeds to reach it. The presence of large cone bearing trees of red spruce immediately adjacent to and above the beech gap (Figure 1, page 2) should insure that a large number of spruce seeds will fall or be blown into the gap. Five 725 cm² seed collectors, coated with vaseline, were set out in late summer. The use of premarked seeds revealed that seeds were being washed off the collectors by rainfall, negating the use of any quantitative data. In early November spruce seeds were found in four of the five collectors, indicating that spruce seeds do indeed reach the gap, and apparently begin falling in late fall (Murphy, 1917). The lack of spruce invasion into the beech gap should thus be the result of the failure of these seeds to germinate and become established.

For purposes of comparative sampling, two 20 by 50 m plots were established, one near the middle of the beech gap, the other in the neighboring spruce-fir vegetation on the convex slope to the east. The long axes of both plots were on the same contour at 1,620 m. The closest ends of the two plots were within 30 m of each other, approaching the ecotone between the two forest types. The opposite end of the beech gap plot extended to the middle of the concave portion of the slope, while the opposite end of the spruce-fir plot extended to the ridge of the convex slope. It was assumed that samples taken randomly within these plots would give a representative approximation of conditions within the two vegetation types.

I. SOIL TEMPERATURE

Soil temperatures were monitored in the beech gap and spruce-fir between April and December of 1976 using a Dixon thermocouple with recorder in each plot. In the beech gap, the probe was placed 2 cm beneath the consolidated soil material, while in the spruce-fir the probe was placed 2 cm below the surface layer of fresh spruce and fir needles. Shanks (1956) monitored soil temperatures at 15 cm and found that even single soil temperature measurements were sufficient to compare microclimates under different types of cover in the Great Smoky Mountains. In the present study, the probes were placed at a shallow

level in order to sample the seedling rooting environment.

Figure 5 shows 10 day averages of maximum and minimum soil temperatures under both vegetation types. Particularly noticeable is the strong influence the canopy plays in damping diurnal temperature variation (Shanks, 1956; Geiger, 1965). In the spring, the leafless beech canopy allows full incident radiation to the litter surface during the day, while permitting almost unhindered re-radiation during the night. In the spruce-fir, the canopy serves to insulate the litter surface from both effects. During the summer, soil temperatures under both vegetation types increased and converged with respect to diurnal variation. At this time the beech canopy had leafed out and the lush herbaceous growth was at its peak.

In late summer, spruce-fir soil temperatures fell more rapidly than beech gap soil temperatures and diurnal variation increased under both vegetation types. Defoliation of many of the larger fir trees in the spruce-fir plot occurred at the same time as a result of attack by the balsam woolly aphid. Examination of the canopy revealed a large hole directly above the probe. A number of large spruce trees downslope (southwest) from the probe shaded it from low angle incident sunlight. The hole in the canopy may have permitted greater re-radiation while the downslope trees intercepted incoming radiation. This would account for both the more rapid decline in soil temperature and

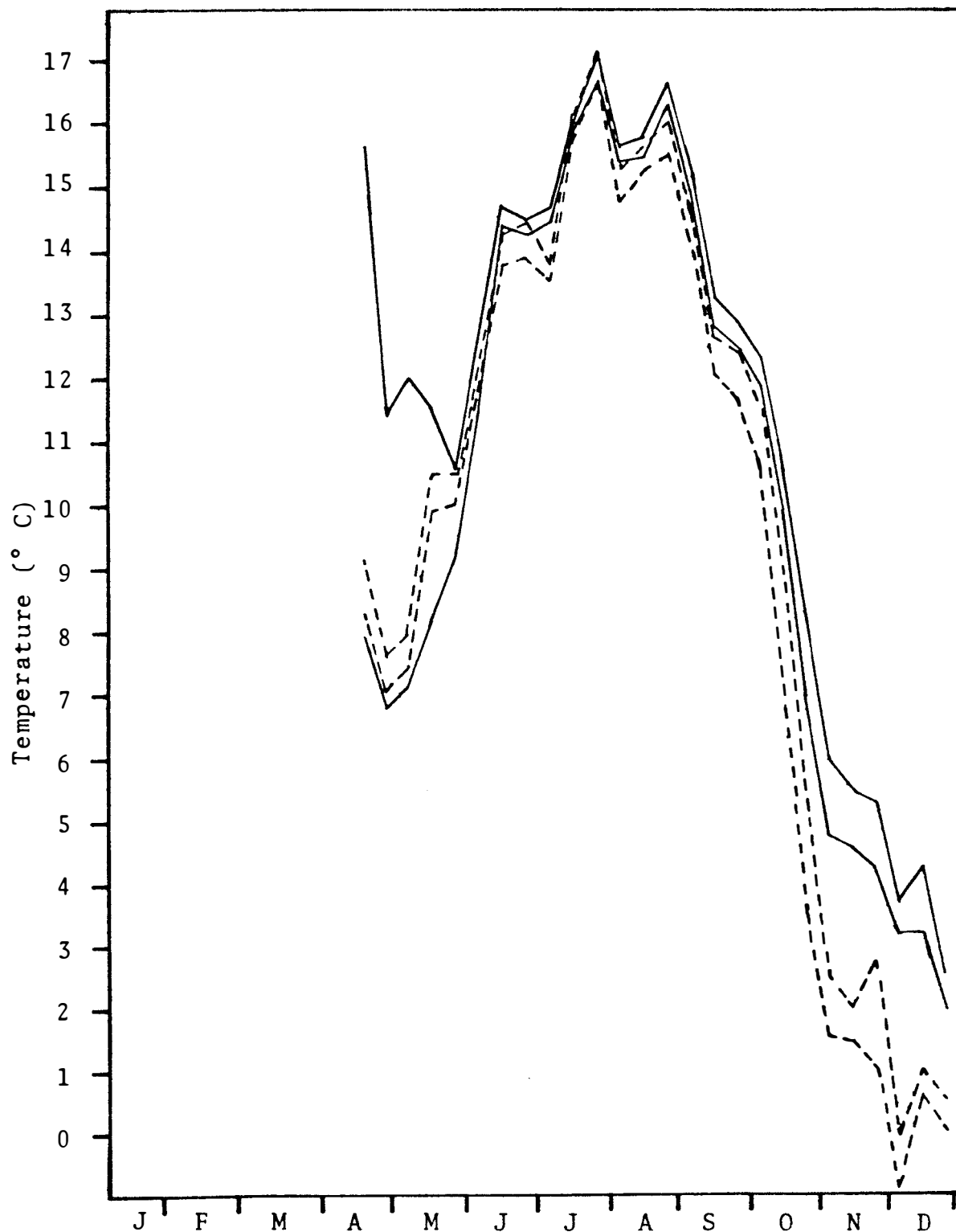


Figure 5. Ten day averages of maximum and minimum soil temperatures at the 2 cm depth under spruce-fir (---) and beech gap (—) vegetation for 1976.

the increased diurnal temperature variation in fall under the spruce-fir canopy.

Shanks (1956), in a study comparing soil temperatures in these same locations, noted higher soil temperatures in the beech gaps, especially during the early spring months. This study supports those observations, but soil temperature differences were not as pronounced during the summer and the necessity of examining diurnal soil temperature variation is indicated.

II. SOIL MOISTURE

From March to November of 1976, soil moisture was measured in the rooting zone of young spruce seedlings. In the beech gap plot, surface litter was removed and the top 4 cm of consolidated soil was collected. In the spruce-fir plot, the top 4 cm of material immediately under the layer of fresh needles was collected. This matrix was composed of varying proportions of decomposing needles, decomposing wood, and mucky mineral soil (Wolfe, 1967). Ten samples were collected in each plot in seamless cans at approximately two-week intervals and were subsequently weighed, dried at 105° C for 48 hours, and re-weighed. Soil moisture was expressed as percent of dry weight.

To compare available water in soils of differing densities, it was necessary to relate moisture as percent of dry weight to specific moisture tensions in each soil

type. In January of 1977, five randomly selected 50 by 50 cm soil blocks from each plot were stripped of the rooting zone soil as described previously for both vegetation types. A composite soil from each vegetation type was prepared by combining the five blocks. The composite soils were screened through 6 mm mesh to remove pebbles and intact root systems. Moisture levels of each composite soil were determined at one-third bar (field capacity) and one bar using a ceramic pressure plate (Soil Moisture, Inc.).

Figure 6 shows soil moisture at the two sites in relation to soil moisture constants. The spruce-fir site was below field capacity for 10 of the 18 sampling dates, while the beech gap site was below this level only four times. The spruce-fir site was below the one bar tension level eight times, while the beech gap was below this level only once. From these data it is apparent that the spruce-fir site is physiologically drier than the beech gap site. Moore (1917) found drier conditions under a spruce tree than in adjacent open habitats and attributed the difference to crown interception of rainfall. While this may be true in the present case, greater evapotranspiration on the more exposed ridge site may be of importance also. Benecke and Mayer (1971) compared soil moisture conditions under a native copper beech (Fagus silvatica L.) stand and a nearby spruce plantation [Picea abies (L.) Karst.] using tensiometers. They also found slightly drier conditions under the coniferous species.

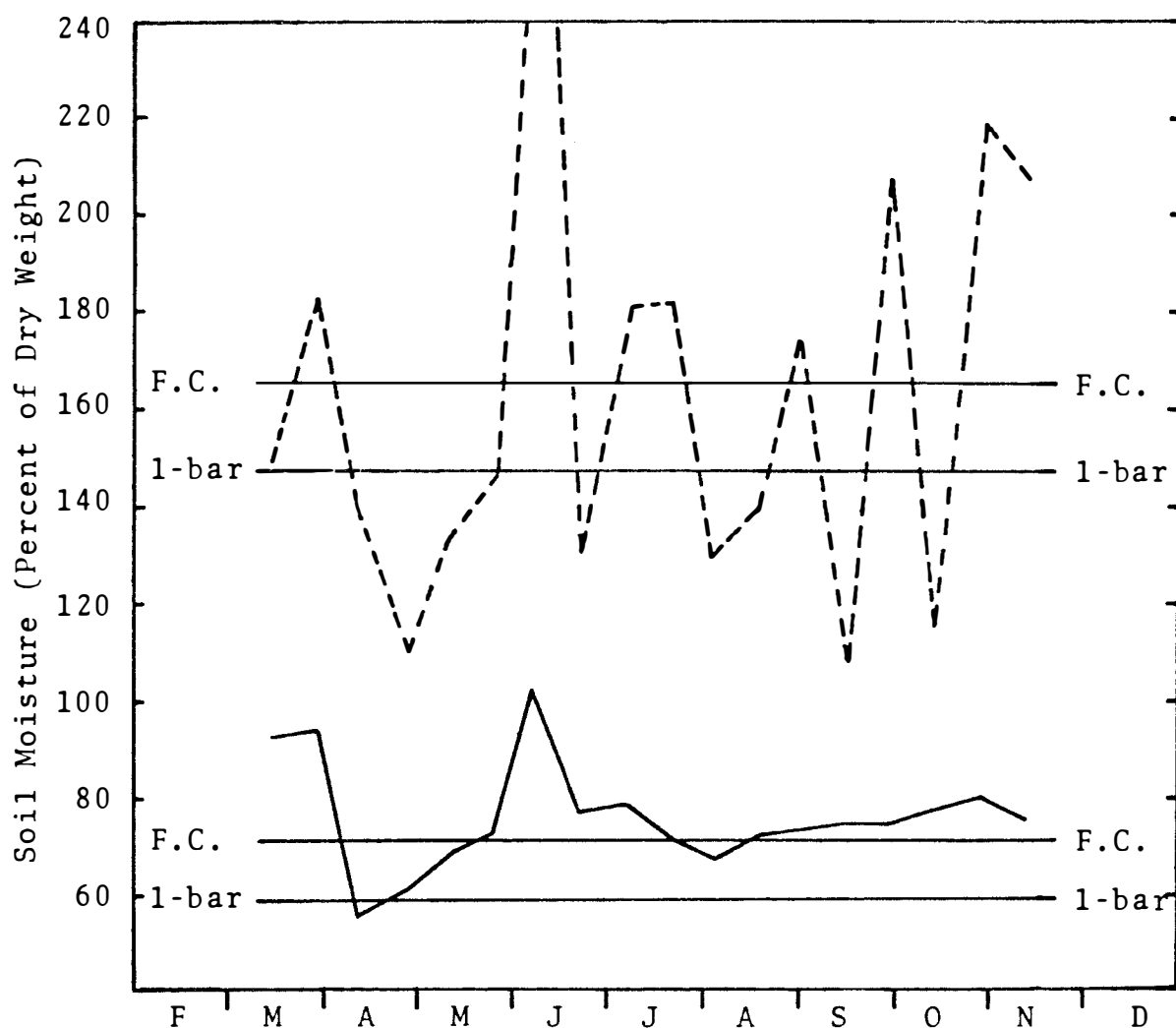


Figure 6. Soil moisture as percent dry weight under beech gap (—) and spruce-fir (---) vegetation for 1976. The solid lines represent moisture tension at 1-bar and at field capacity (F.C.).

Soil moisture tended to follow precipitation trends (Figure 6). The spring and fall minima and summer maximum in precipitation were also pronounced in soil moisture measurements. The high amount of annual precipitation is reflected in the uniformly high soil moisture values. Even during the driest month recorded in the last nine years (April, 1976), soil moisture was well above the wilting point.

III. TOXINS IN THE ENVIRONMENT

Inhibition of Germination

From early spring to late fall of 1976, litter, soil, and roots were sampled at two-week intervals from five random locations in the beech gap plot. Soil and root (0-3 mm) samples were taken from the 0-4 cm zone. All samples were stored in sealed plastic bags and frozen until further use.

The five random samples of each fraction (roots, litter, soil) at each sampling date were combined. Samples from four sampling dates in the middle of each of spring, summer, and fall were combined to form a composite sample for each fraction from the middle of each season. Soil particles were washed off roots, and all samples were oven dried at 50° C for 48 hours. The litter fraction was screened through 2 cm mesh to separate the whole leaf fraction from the partially decomposed or fragmented litter

fraction. Roots and the two litter fractions were ground through a 2 mm mesh Wiley mill to a small flake consistency. Each fraction was extracted with ten parts (volume/weight) distilled water by blending in a Waring blender for two minutes, then filtering through two thicknesses of Whatman #3MM filter paper. All soil extracts were lyophilized to a powder and taken up in one-fifth the initial volume. This produced 12 solutions representing four fractions (roots, soil, fragmented litter, and whole leaf litter) from the middle of three seasons (spring, summer, and fall).

To test for the presence of possible germination inhibitors in these aqueous extracts, bioassays were performed on spruce seed germination. High viability red spruce seeds from New York State (collected at 600 m) were used in all assays. A variation of Christensen and Muller's (1975) "glass wool bioassay" was found superior to other techniques. Three 6 by 6 cm glass wool squares each approximately 1.5 mm thick were laid in a glass petri plate. Sixteen plump, dark spruce seeds were laid on top and covered with one additional layer of glass wool. Ten ml of the extract to be tested were pipetted onto the glass wool (sufficient to saturate it). Distilled water was used as a control in all cases. All plates were incubated for 15 days at 25° C, the temperature optimum for red spruce germination (Baldwin, 1934). Each plate was checked for progress of germination at 24-hour intervals.

Table I shows the results of the germination bioassays after 9 and 15 days. Bioassays against root extracts were not performed since it was reasoned that these components would probably not come into contact with spruce seeds. After 9 days, significant inhibition was discovered in the summer and fall whole leaf litter extracts and in the summer fragmented litter extracts. No inhibition was apparent after 15 days, indicating that germination is only delayed and not suppressed entirely by any of these extracts. Peterson (1965) found similar germination delay using extracts of Kalmia angustifolia with black spruce (Picea mariana) seed.

Toxicity under Natural Conditions

The results of the spruce seed germination bioassays suggested that seeds over-wintering in the partially decomposed litter layer (O2 horizon) might be exposed to toxins leaching out of freshly fallen leaves. In order to test this hypothesis, an experiment was designed which would account for as many factors as possible while maintaining conditions approaching those in the field.

In early spring of 1977, 20 soil cores 5 cm in diameter and 10 cm deep were taken at regular spatial intervals from both the beech gap and spruce-fir plots. Litter was removed from the beech gap cores and replaced with litter collected from the previous fall. The whole leaf litter was cut into 2-3 cm squares so that water

TABLE I
BIOASSAYS OF RED SPRUCE GERMINATION, EXPRESSED
AS PERCENT OF CONTROL

Season of Collection	No. of Days	Whole Leaf Litter	Fragmented Litter	Soil
Spring	9	76.0	76.0	86.0
	15	96.4	95.2	97.6
Summer	9	42.0 ^a	62.0 ^b	84.0
	15	88.0	85.7	90.5
Fall	9	60.0 ^b	86.0	68.0
	15	92.9	91.7	94.0

^aDifference at .01 level, using Duncan's new multiple range test.

^bDifference at .05 level.

would not be diverted to the side of the cores. All cores were encased in heat-shrinkable PVC (Galbreath, Inc.) with a screen under the bottom, after the method of Van Hook et al. (1974) and Ausmus and O'Neill (1977). Ten red spruce seeds from New York were placed in each core: in the beech gap cores they were placed in the fragmented litter layer (02), while in the spruce-fir cores they were pressed down into the freshly fallen needles, flush with the top of the core. The cores were covered and placed in the cold room at a temperature of 5° C for 45 days. The cores were watered lightly every three days to keep them uniformly wet. They were subsequently removed to room temperature for seven days, after which germination was tabulated.

A significant reduction in germination of 15.4% was found in the beech gap cores (Table II). Since temperature and moisture conditions were uniform, it seems likely that toxins leaching from the whole leaf litter layer are responsible for this reduction. Under natural conditions, spruce seed may lie dormant in this litter layer for up to 7 months before germinating (Murphy, 1917; Baldwin, 1934; personal observation). Extended exposure to conditions of low toxicity, perhaps interacting with other stresses during the winter months, may cause much higher mortality rates than were observed in this relatively short-term experiment.

TABLE II
AVERAGE NUMBER OF GERMINATING SEEDS IN SOIL CORES
AFTER ARTIFICIAL OVER-WINTERING TREATMENT

Source of Soil Cores	Average Germination in Each Soil Core $\pm$ 1 Standard Deviation
Spruce-fir	8.10 $\pm$ 1.46
Beech gap	6.85 $\pm$ 1.45 ^a

^aDifference at .05 level, using Student's t-test.

Effects on Radicle Elongation

To determine if growth inhibiting toxins were present in beech gap components, a series of growth bioassays was initiated using the 12 extracts described previously. Four 6 by 25 cm strips of approximately 1.5 mm thick glass wool were rolled into a cylinder and placed in a plastic vial 7 cm deep and 4 cm in diameter. Eight pre-germinated New York red spruce seeds were imbedded in the top of the glass wool cylinders. Thirty-five ml of solution were pipetted onto the glass wool which saturated it down to the bottom of the vial. Five vials (40 seeds) of each extract were incubated at 25° C for 7 days. Preliminary tests indicated that this procedure was superior to others using sand, filter paper, or perlite for spruce radicle growth rate and uniformity.

Ten of the 12 extracts significantly inhibited radicle elongation (Figure 7). All fractions except soil were most inhibitory during the summer. The greatest inhibition was seen in summer fragmented litter, while fall fragmented litter was completely nontoxic. Fall soil extracts and fall whole leaf litter extracts also were very inhibitory. Winter and Bublitz (1953) found that dead January leaves of copper beech (Fagus silvatica L.) which over-wintered on the tree inhibited growth while those which over-wintered on the ground did not. This is similar to the present situation in which fall whole leaf litter is very inhibitory while spring whole leaf litter is non-toxic.

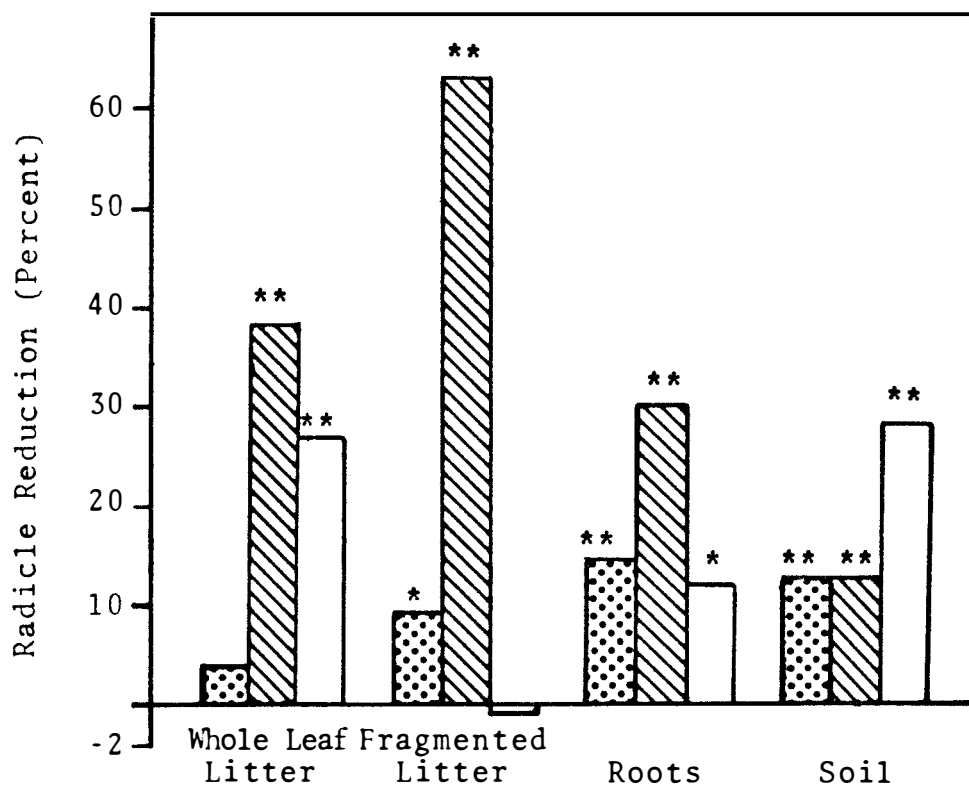


Figure 7. Reduction of radicle elongation in various extracts. Distilled water was used as the control solution. Spring (•••), Summer (///), and Fall (). Asterisks represent significance at the .05 (*) and .01 (**) level (Duncan's new multiple range test).

In the early summer of 1977, litter was collected from under the beech gap and processed as described previously. Bioassays against radicle elongation again showed inhibition at a significant level, although to a lesser degree.

Possible Inhibitors

Several authors have examined the chemistry of both litter and living leaves of the European copper beech (Fagus silvatica L.). Tissut (1967, 1968) found that living leaves of copper beech contained caffeic and chlorogenic acid and the flavanoid aglycones quercitin and kaempferol in addition to several glycosides of these compounds. Robinson and Smith (1955) reported the presence of cyanidin-3-galactoside in living leaves. Boquel et al. (1970) found p-hydroxybenzoic acid, vanillic acid, and p-coumaric acid in copper beech litter in addition to several other carboxylic acids. Winter (1961) indicated that copper beech litter contains ferulic acid in addition to the three phenolic acids reported by Boquel et al. (1970). Unfortunately, little work has been reported on the secondary plant chemistry of the American beech (Fagus grandifolia).

In an attempt to identify potential inhibitors, an aqueous extract of fall whole leaf litter was lyophilized to a powder and taken up in methanol. Two-dimensional paper chromatography of the methanol soluble portion of the extract revealed seven compounds. Due to poor separation of

these compounds in several solvent systems, elution and spectrophotometric determinations were not attempted. Instead, the extract and known standards of ferulic, vanillic, p-hydroxybenzoic, and p-coumaric acids were chromatographed in two dimensions. Solvent systems were isopropanol-ammonia-water (200:10:20) and 6% acetic acid. Spraying with diazotized p-nitroaniline and sodium carbonate (Ribereau-Gayon, 1972) indicated the presence of all four of these simple phenolic acids. The author stresses that these results are not conclusive without further spectrophotometric and chromatographic work.

These compounds and other simple phenols have been shown to be inhibitors of germination and growth in too many cases to enumerate. For a more complete discussion, the reader is urged to consult Rice (1974). All are common in the plant world, being produced during the synthesis and decomposition of lignin (Christensen and Muller, 1975; Robinson, 1967; Pearl, 1967). Increased lignin decomposition during the warm summer months may render large quantities of these and other simple phenols. This may account for the increased toxicity observed in summer extracts.

CHAPTER IV

GERMINATION AND ESTABLISHMENT

To test the effects of soil, litter, and microclimate under the two canopy types on spruce germination and establishment, growth chamber experiments were conducted using soil temperature data gathered the season before. Field experiments were performed to assess the success of establishment in the beech gap with known seed additions under natural conditions.

Germination in Programmed Environment Chambers

One hundred 5 cm diameter by 10 cm deep soil cores were taken from under each canopy at regular spatial intervals in early spring and were subsequently randomized. All cores were encased in heat-shrunk PVC after the method of Van Hook et al. (1974). Due to disturbance, the litter layer was removed and replaced with litter collected nearby. Whole leaves were cut into 2-3 cm squares to prevent the diversion of water to the side of the cores. Five stratified red spruce seeds (New York source) were placed near the center of each core. In the beech gap cores, the seeds were placed in the 02 litter layer, while in the spruce-fir cores, they were pushed down into the freshly fallen needles.

Twenty cores each from spruce-fir and beech gap horizons were placed in a 20 cm deep wooden box and

surrounded with coarse sand. Two such boxes, each containing 40 cores, were placed in programmed environment chambers. One chamber was programmed to simulate soil temperature at 2 cm in the beech gap, while the other mimicked those in the spruce-fir (Figure 5, page 19). Relative humidity was maintained in both growth chambers at 60%, the maximum attainable under those temperature conditions in available growth chambers. Comparison of light intensities in the photosynthetic wavelengths in the field and growth chambers revealed that the maximum attainable lighting in the programmed environment chambers was between full and partial shading in the spruce-fir

For the first 20 days, each core was sprayed with the equivalent of 1 cm of rainfall every fifth day using distilled water. Subsequently this was increased to 2 cm, corresponding to the summer maximum in rainfall. Analysis of rainfall data over the past 10 years for April and July revealed average periods between rainfalls of 6 mm or more to be 3.87 and 3.84 days, respectively. Because of this, watering every fifth day was deemed appropriate throughout the course of the experiment.

The experiment lasted for a period of 70 days, mimicking temperature conditions from mid-April to the end of August, a period of 140 days. Establishment was regarded as complete when the seed coat was shed from the cotyledons and the seedling was above the litter layer. Figure 8

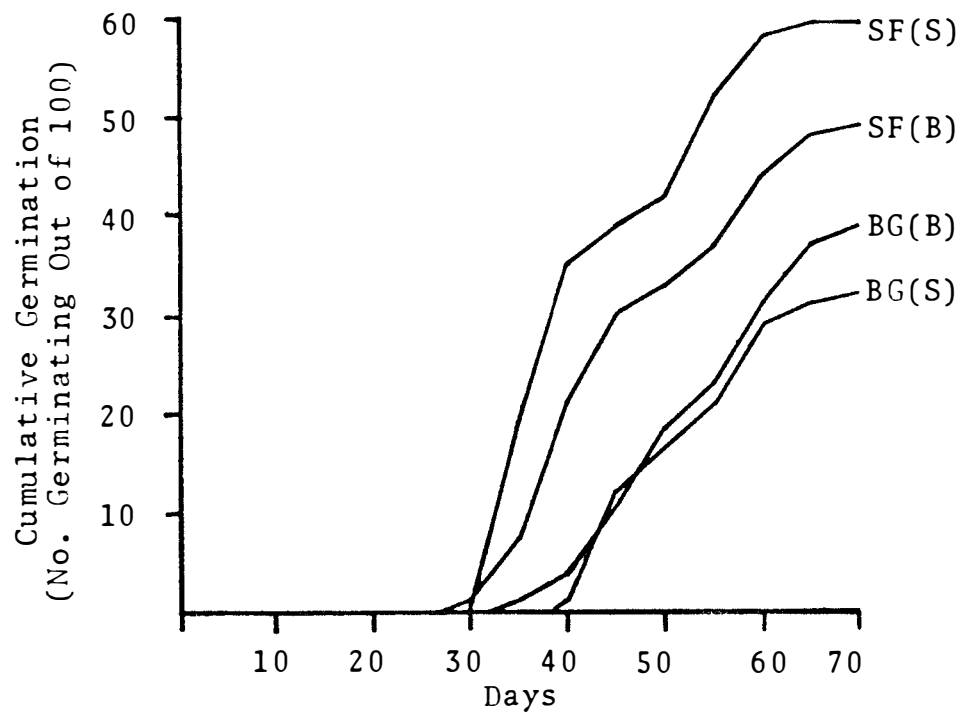


Figure 8. Cumulative germination (percent) in growth chambers.

SF = Spruce-fir microclimate.
 BG = Beech gap microclimate.
 (S) = Spruce-fir soil cores.
 (B) = Beech gap soil cores.

illustrates the course of cumulative germination over the length of the experiment. The shape and location of the curves suggests a 10-20 day delay and less overall establishment in the beech gap soil temperature regime. Analysis of variance revealed significant microclimatic effects by the end of the experiment. These effects may be due to much greater diurnal variation in the beech gap regime during the first 25 days of the experiment.

Table III shows the fate of most of the seeds in the experiment. Many of the recovered seeds germinated readily on moist glass wool at room temperature, indicating that they were still viable.

Murphy (1917) and Moore (1933) hypothesized that red spruce seeds may have difficulty reaching the moist mineral soil when germinating in hardwood litter. Provided that the seeds reach the O2 litter layer, the results of this experiment suggest that their hypothesis may be unfounded for the present conditions of litter thickness and type.

Seedling Growth in Programmed Environment Chambers

A third box containing 20 soil cores from each vegetation type was placed in the "spruce-fir" chamber after the 20th day of the germination experiment, just as seeds were beginning to germinate. At this time, temperature conditions in the two environment chambers were beginning to

TABLE III
FATE OF SEEDS IN GROWTH CHAMBER GERMINATION
EXPERIMENT (NO. OF SEEDS OUT OF 100)

Microclimate Soil Origin	Spruce-Fir		Beech Gap	
	Spruce-Fir	Beech Gap	Spruce-Fir	Beech Gap
Total seeds germinated and established	59 ^a	49 ^a	39	32
Germinated, immature	0	0	0	0
Germinated, dead radicle	8	2	5	3
Seeds recovered/ germinated on glass wool ^b	22/13	36/27	53/41	49/40

^aSignificant microclimatic effects at the .05 level, using analysis of variance.

^bNumber of nongerminated seeds recovered at the end of the experiment/total germinated on glass wool squares at room temperature.

converge (Figure 5, page 19). One pre-germinated spruce seed with a radicle between 1 and 3 mm in length was placed in the middle of each core. Seedlings were grown for 75 days, with temperature conditions for the last 25 days conforming to those of late summer. Emerging herbs were clipped at the soil surface to reduce competitive effects.

Seedlings were removed intact and desiccated for 48 hours at room temperature before weighing. No significant differences were found due to soil source between either root or shoot weights using the Student's t-test (Table IV). Toward the end of the experiment, it appeared that shoot growth in the spruce-fir soil cores was greater than in the beech gap cores. This experiment bears repeating under both growth chamber and field conditions through at least the fall months. This would test the possibility that fall soil toxins may affect growth as demonstrated in the bio-assay series (Figure 7, page 30).

Seedlings in the field usually pause in their elongation after forming cotyledons and several additional needles (Edward E. C. Clebsch and the author, personal observations). Moore (1917) found in southern Maine that growth had slowed by July 10 and winter buds had formed by August 10. However, if a warm period ensued, a second growth period started. Growth chamber seedlings were decidedly more robust than field seedlings, often forming 40 or more needles in 75 days of growth.

TABLE IV
GROWTH CHAMBER SPRUCE SEEDLING GROWTH AS
AFFECTED BY SOIL SOURCE

Seedling Growth	Spruce-Fir Cores	Beech Gap Cores
Mean root weight (g) ± 1 S.D.	0.012 ± .004	0.014 ± .006
Mean shoot weight (g) ± 1 S.D.	0.089 ± .035	0.074 ± .040

Establishment in Spring Field Cores

Two soil core boxes, each containing 20 spruce-fir and beech gap cores, were placed in the field on May 2, 1977. One box was placed near the center of the beech gap plot, while the other was placed near the middle of the spruce-fir plot. Both boxes were covered with 6 mm mesh screen to prevent disturbance. Herbaceous growth was not removed during the course of the experiment. The cores were removed on July 15 and germination and initial growth were assessed. Germination was considered complete when the seed coat was shed from the cotyledons.

Analysis of variance revealed significant effects due to soil origin on germination. However, close examination of Table V will reveal that these results may be spurious. Spruce-fir cores in the spruce-fir microclimate contained 12 seeds which germinated but failed to make the maturation cutoff. Spruce-fir cores under the beech gap had approximately 20 more seeds which could not be accounted for than did the other treatments.

Seedlings grown in the spruce-fir microclimate had significantly longer radicles than those grown under the beech canopy. Defoliation of Fraser fir, allowing more mid-day radiation to the spruce-fir forest floor, may have caused this difference. It is also possible that spring differences in diurnal temperature variation may have delayed beech gap germination, resulting in shorter radicles.

TABLE V
SEED FATE IN FIELD GERMINATION CORES

Microclimate Soil Origin	Spruce-Fir		Beech Gap	
	Spruce-Fir	Beech Gap	Spruce-Fir	Beech Gap
No. of seeds planted	100	100	100	100
Total germinated	57	71 ^a	51	69 ^a
No. surviving	40	54	41	52
No. killed by damping-off	17	17	10	17
No. germinated but immature	8	2	4	3
Germinated, dead radicle	4	0	0	0
Seeds recovered/ no. germinated ^b	8/2	2/0	2/0	5/0
No. accounted for	77	75	57	77
Mean radicle length of surviving seedlings	<u>28.23</u>	<u>28.15^c</u>	<u>21.63</u>	<u>20.35^c</u>

^aSignificant microclimatic effects at .05 level (analysis of variance).

^bPlaced on moist glass wool squares at room temperature.

^cNumbers not connected by underline are significantly different at .05 level (Duncan's new multiple range test).

The first explanation is the more likely. The opening of the canopy in the spruce-fir forest increased diurnal variation there also, and the late starting date (May 2) only allowed two weeks before canopy closure in the beech gap.

Of particular interest is the number of seedlings killed by damping. Presumably of fungal origin, this source of seedling mortality is promoted by high air humidity around the aerial portion of the seedling (Daubenmire, 1959). High humidity around the hardwood litter may increase mortality due to damping-off, although this was not discernible in the experiment. Moore (1917), however, noticed that red spruce seed germinating in well watered plots suffered much less from damping-off than those in drier humus.

Mortality in Fall Field Plots

Red spruce seeds might germinate soon after seed dispersal in late fall (Murphy, 1917). To determine if beech gap microclimate allows fall germination with subsequent high winter mortality, a series of seed plots was established. On November 1, 1976, four 1/2 m square plots were established near the middle of the beech gap. Treatments were as follows:

1. Recognizable litter removed, 6 mm mesh screen enclosure, 500 spruce seed added.

2. Litter left intact, 6 mm mesh screen enclosure, 500 spruce seed added.
3. Five cm deep square of intact spruce-fir substrate laid into excavated hole, 6 mm mesh screen enclosure, 500 spruce seed added.
4. Recognizable litter removed from half the plot, no enclosure, no seeds added.

One plot was also established in the spruce-fir with the litter left intact, no enclosure, and 500 seeds added.

The date these plots were established preceded by 10 days the first seed fall found in fall seed collectors. Seeds were extracted from fallen immature cones collected 1 kilometer from the research site. Cones were opened by heating for 24 hours at 38° C (Safford, 1974). Seeds were removed from the cones in a shaker, and de-winged while moist by stirring with a plastic scraper (Safford, 1974). Viability in these seeds was low, ranging from 10-20% depending on seed lot. It is not known whether this was a result of the immature cone seed source or the method of extraction.

All four plots were observed closely through the fall of 1976. No spruce germination was apparent in any of them. Any hypotheses regarding premature fall germination in the beech gap appear to be untenable.

During the winter of 1977, a fir tree fell onto and disrupted the plot maintained under the spruce-fir canopy.

The other plots, however, remained available for analysis the following summer. These plots were observed once in June and were scraped clean and carefully sorted through in mid-July.

Germination was greater on the beech gap mineral soil cleared of litter (Table VI). A number of investigators have noticed this same effect with red spruce seed on various types of mineral soil (Moore, 1926; Westveld, 1926, 1930; Baldwin, 1934; Griffin, 1965). The poor ability of red spruce to become established in hardwood litter is also well known (Pinchot, 1898; Murphy, 1917; Moore, 1917; Baldwin, 1934). A mat of hardwood leaves under the seed may prevent emerging radicles from reaching moist mineral soil (Murphy, 1917; Moore, 1926). Once germinated, a seedling may not be able to reach the surface of the litter (Moore, 1917), or it may become susceptible to microbial attack (Murphy, 1917). Three of the five emergent seedlings visible in the intact litter in June were not seen in July. Although these seedlings had already made it up through the litter, they may have suffered from damping-off, or else downslope litter movement may have smothered them. Four of the five seedlings seen in June were in the upper third of the 1/2 m square plot where litter movement had thinned the whole leaf litter considerably.

It is doubtful that an inability to grow up through the litter layer is the prime cause of seedling mortality.

TABLE VI
SEED FATE IN OVER-WINTERED GERMINATION PLOTS

Seed Fate	Spruce Soil Litter Intact	Beech Soil Litter Removed	Beech Soil Litter Intact
No. seeds planted	500	500	500
No. germinated, 6/1/77 estimate	3	20-25	5 ^a
No. germinated, 7/15/77	4	17	2
Whole seeds recovered	168	100	43
Empty or damaged seeds recovered	72	39	81
Empty or damaged seeds as percent of total recovered	30%	28%	65%
No. of whole seeds germinated on glass wool squares at room temperature	0	0	0

^aFour of the five were in the upper third of the plot where downslope movement had considerably thinned the litter.

Spruce seedlings are capable of epigeal growth (Safford, 1974), allowing them to grow up through 3-5 cm of litter by elongation of the hypocotyl (personal observation). Spruce seedlings are unable to grow up through the litter layer only if it is exceedingly thick or matted down into many impenetrable layers. Cayford and Waldron (1962) found that white spruce (Picea glauca Moench) would readily grow up through six layers of aspen leaves.

Analysis of recovered seeds revealed that a larger fraction of those over-wintered under intact beech litter were empty than in the other two treatments. Most of these seeds had suffered animal depredation, with a large ragged hole in one side of the seed. It is unknown whether this represents emerging insect larvae or foraging. Whole seeds were recovered from all three plots. Attempts to germinate these seeds on moist glass wool at room temperature for 14 days failed.

Failure of germination in the spruce-fir plot and intact beech litter plot may have been affected by allelopathic mechanisms. Bublitz (1953) found that spruce litter contained substances inhibitory to spruce [Picea abies (L.) Karst.] seed germination. Spruce seeds which over-winter in litter of low toxicity may be inhibited a great deal. Chronic exposure to toxins over a period of 6 months, in conjunction with other environmental stresses, may affect mortality severely.

Growth chamber and field experiments revealed that many factors may increase seed and seedling mortality in the beech gaps. These include high diurnal temperature variation in the beech gap in spring, damping-off, down-slope litter movement, and, at least potentially, allelopathic mechanisms. It is difficult to partition these effects without much more extensive field testing.

CHAPTER V

MAINTENANCE OF THE BEECH GAPS IN THE GREAT SMOKY MOUNTAINS

Germination of red spruce seeds and establishment of seedlings is a rare event under most conditions of canopy coverage. The long lived, shade tolerant spruce (Murphy, 1917) need only rarely successfully complete reproduction in order to insure the replacement of canopy individuals. Although red spruce seeds do reach the beech gap, it seems likely that fewer arrive there than in the spruce-fir forest directly below the seed source. Seedfall in red spruce occurs from October to March (Murphy, 1917), but many of the seeds which fall in the later months are empty (personal observation).

Red spruce seeds which fall into the beech gap in fall will reside somewhere in the litter layer for a period of at least 6 months until germination in late May to July (Fowells, 1965). There they are exposed to conditions which may bring about increased mortality. Toxins which leach out of the fresh fall litter may seriously affect viability, and animal depredation of the seeds in the intact litter may also be of great consequence. The effect of low temperatures and occasional freezing of soil during the winter months is unknown though potentially stressful.

itself may contain toxins in high enough concentrations to affect the spruce seedling.

The effects of competition on red spruce seedling success are unknown, though often speculated upon (Murphy, 1917; Moore, 1917; Baldwin, 1934). Competition has been defined as the deleterious effect of one plant upon another through the removal of some limiting resource (Muller, 1974; Oosting, 1956). A deleterious effect caused by the proximity of neighbors has been termed "interference" (Harper, 1961; Tinnin, 1972) and would properly include both competitive and the other deleterious interactions discussed so far. Wolfe (1967) found no major differences in concentrations of several important elements (Ca, Mg, K, Na) between the stands, and this study indicated that soil moisture is indeed higher in the beech gap. Thus, for at least these resources, there appears to be no basis for assuming competitive interactions. Differences are seen in extractable nitrogen, however; concentrations in the upper 5 cm of the A horizon are up to 65% higher in the spruce-fir (Wolfe, 1967). The potentially complex states of this nitrogen, and its relationship to quantities of organic carbon, make comparisons very difficult.

Beech gaps contain an especially lush herbaceous cover compared to the neighboring coniferous forests (Russell, 1953), usually ranging between 80-110% during the summer months (Bratton, 1975). Although the beech

canopy itself is small and stunted (Bratton, 1975; Russell, 1953), the additional cover of the herbaceous layer may be effective in reducing incident radiation to a critically low level.

Because of the differences in topography and vegetation type, any number of hypotheses could be advanced to explain the lack of spruce invasion in the beech gap. It is apparent from this study that no one factor is of overriding significance in the prevention of invasion. The maintenance of the beech gaps may depend in large part upon a series of factors which progressively increase spruce seed and seedling mortality. Many of these factors, however, are dependent upon the integrity of the litter layer. Isolated coniferous species within the beech gap will occasionally block hardwood litter fall in places, and successful germination will occur in the needle litter (personal observation). Self-perpetuating clumps of red spruce which may expand into the spruce-fir forest are formed (Schofield, 1960).

Bratton (1975) found that the recently introduced European wild boar (Sus scrofa) does considerable damage to the herbaceous layer in high elevation forests often reducing herbaceous cover to less than 10% of the original in areas intermediate on a moisture gradient. While rooting, the hogs frequently mix the O, A, and B horizons, resulting in the exposure of mineral soil. Although the

effect of exposing mineral soil on increasing spruce germination is well established (Moore, 1926; Westveld, 1926, 1930; Baldwin, 1934; Griffin, 1965), it is not known how this will affect the integrity of the beech gaps.

Several beech gaps that were once nearly pure beech are yielding to spruce and fir invasion (Schofield, 1960, personal observation). In many places, the spruce-fir forest seems to be encroaching upon high elevation beech forests by the establishment of clumps which gradually expand and merge with the main coniferous forest (Schofield, 1960). The interference mechanisms which maintain the beech gaps may only be operative when very high densities of beech are present, enough to dominate the litter layer. The sharp borders between the two forests may indeed be transitory phenomena which move across the landscape in response to climatic change.

CHAPTER VI

VEGETATION DYNAMICS AT THE BEECH AND SPRUCE-FIR ECOTONE

Whittaker (1956) noted that red spruce occurs at elevations above 1,370 m except in the southwest section of the park. Although there are over 15 continuous km southwest of the spruce border above 1,370 m, none of this area has peaks above 1,730 m. Whittaker theorized that during the xerothermic (hypsithermal period), a temperature rise displaced the lower limit of the spruce forest upward over 300 m in elevation. This effectively limited spruce to the northern half of the park where the only peaks above 1,730 m are found. Beech, northern red and white oaks, and chestnut, species adapted to high elevations, moved in and replaced the spruce. In the cooler period since the hypsithermal, spruce has readily migrated downward to 1,370 m, but has been stopped in its lateral advance, perhaps by the beech forests at Double Springs Gap. Whittaker was apparently unaware of a small stand of native spruce on Miry Ridge, 7 km west of Double Springs Gap.

The hypsithermal period occurred approximately 3,000 to 9,000 years before present (Deevey and Flint, 1957), and is recorded in the pollen records from a number of sites (Davis, 1965). The lack of pollen records from the Southern

Appalachians necessitates the assumption of such a warm period for this area. Temperatures have cooled since the hypsithermal with minima approximately 2,800 and 225 years before present (Bray, 1971), the latter known as the "little ice age." Since 1900 average temperatures in temperate latitudes have been increasing to the middle of this century (Dorf, 1959).

The origin of the beech gaps and the extensive beech forests southwest of the present spruce boundary, most probably lies in these climatic fluctuations of the post-Pleistocene. As the lower elevational limits of spruce were pushed upward during the hypsithermal, beech and other mesic hardwoods replaced it in the mesic coves, while the more xeric hardwoods or perhaps pines or ericaceous shrubs replaced it on the ridges. Since the hypsithermal, the spruce forests have migrated downward, occupying the convex slopes and ridges within their range, but being excluded from the beech gaps by interference mechanisms already discussed. In the western part of the Great Smokies, northern red and white oaks (and until recently, chestnut) have persisted at these elevations in the absence of spruce (Whittaker, 1956). Schofield (1960) advanced this same hypothesis to account for the origin of the beech gaps, assuming that the effects of beech stands on the microclimate would be adequate to prevent subsequent spruce invasion.

Numerous palynological studies have been performed in the northeastern United States, where bogs and ancient glacier formed ponds are found. Davis (1965), in a study from northern Vermont near the present boundaries of northern hardwood and spruce-fir forests, found a virtual absence of spruce pollen during the hypsithermal period. Corresponding increases in sugar maple (Acer saccharum), beech, hemlock (Tsuga canadensis), birch (Betula spp.), and ash (Fraxinus spp.) were found. Since the end of the hypsithermal, spruce and fir pollen have both increased considerably. Assuming that these climatic changes also occurred in the Southern Appalachians, as the present-day distribution of spruce indeed suggests, this sequence lends evidence for the origin of the beech gaps in the hypsithermal.

CHAPTER VII

CONCLUSIONS

Monitoring of the spruce-fir and beech gap soil temperature regimes at 2 cm revealed greater diurnal temperature variation in the beech gaps during the early spring months when the deciduous beech canopy is leafless. Analysis of soil moisture revealed that adjacent spruce-fir soils are physiologically drier than beech gap soils in the spruce seedling rooting zone, even during the spring months when beech gap soil temperatures were up to 5° C higher than in the spruce-fir.

Growth chamber experiments indicated that high temperatures, or just high diurnal temperature variation in spring, may delay or inhibit germination. Toxins leaching out of the freshly fallen beech litter over the winter months inhibit seed germination. Animal depredation of spruce seeds is higher in the intact beech litter than on mineral soil or in spruce-fir litter. The hardwood litter may increase damping-off of young spruce seedlings by increasing the relative humidity around the stem. The litter itself may prevent the radicle from reaching moisture, or may prevent the shoot from extending above it under certain conditions. A number of other hypotheses can be advanced based on the differences in canopy type and topography.

A theory is advanced for the origin and subsequent persistence of the beech gaps in these mountains, based on an extension of ideas advanced by Whittaker (1956) and Schofield (1960). During the warm hypsithermal period (Deevey and Flint, 1957), beech and other mid-elevation species advanced in elevation behind the retreating spruce. As the climate again cooled, beech stands were able to maintain themselves from the advancing spruce by specific interference mechanisms. This theory is consistent with Whittaker's observation of the failure of spruce to extend laterally over many square miles of area above the present lower elevational limit of red spruce in the Great Smoky Mountains.

High elevation beech gaps have been maintained against spruce invasion by a combination of interference mechanisms which include allelopathy. These mechanisms progressively increase spruce seed and seedling mortality in the beech gaps.

LITERATURE CITED

LITERATURE CITED

- Ausmus, B. S. and E. G. O'Neill. 1977. Comparison of carbon dynamics of three microcosm substrates. In press. Soil Biology and Biochemistry.
- Baldwin, H. I. 1934. Germination of red spruce. Plant Physiology 9:491-532.
- Benecke, P. and R. Mayer. 1971. Aspects of soil water behavior as related to beech and spruce stands. Some results of the water balance investigations. In H. Ellenberg, ed., Integrated Experimental Ecology. Methods and Results of Ecosystem Research in the German Solling Project. Springer-Verlag, New York.
- Boquel, G., S. Bruckert, and L. Suavin. 1970. Inhibition de la nitrification par les extraits aqueux de litiere de hêtre (*Fagus silvatica*). Revue D'Ecologie et de Biologie du Sol 7(3):357-366.
- Bratton, S. P. 1975. The effect of the European wild boar, *Sus scrofa*, on gray beech forest in the Great Smoky Mountains. Ecology 56:1356-1366.
- Bray, J. R. 1971. Vegetational distribution, tree growth and crop success in relation to recent climatic change. In J. B. Cragg, ed., Advances in Ecological Research. Academic Press, New York.
- Brown, R. T. and P. Mikola. 1974. The influence of fruticose lichens upon the mycorrhizae and seedling growth of forest trees. Acta Forestalia Fennica 141:5-23.
- Bruhn, M. E. 1964. Vegetational succession on three grassy balds of the Great Smoky Mountains. Master's thesis. The University of Tennessee, Knoxville.
- Bublitz, W. 1953. Über die Keimhemmende Wirkung der Fichtenstreu. Naturwissenschaften 40(9):275-276.
- Cain, S. A. 1930. An ecological study of the heath balds of the Great Smoky Mountains. Butler University Botanical Studies 1:177-208.
- . 1943. The tertiary character of the cove hardwood forests of the Great Smoky Mountains National Park. Bulletin of the Torrey Botanical Club 7(3):213-235.

- Camp, W. H. 1951. A biogeographic and paragenetic analysis of the American beech (Fagus). American Philosophical Society Yearbook 1950:166-169.
- Cayford, J. H. and R. M. Waldron. 1962. Some effects of leaf and needle litter on greenhouse germination of white spruce and jack pine seed. Forestry Chronicle 38:229-231.
- Christensen, N. L. and C. H. Muller. 1975. Effects of fire on factors controlling plant growth in Adenostoma chaparral. Ecological Monographs 45(1): 29-55.
- Crandall, D. L. 1958. Ground vegetation patterns of the spruce-fir area of the Great Smoky Mountains National Park. Ecological Monographs 28:337-360.
- Daubenmire, R. F. 1959. Plants and Environment. Second edition. John Wiley and Sons, New York. 422 pp.
- Davis, M. B. 1965. Phytogeography and palynology of the northeastern United States. In H. E. Wright and D. G. Frey, eds., The Quaternary of the United States. Princeton Univ. Press, Princeton, N. J.
- Deevey, E. S. and R. F. Flint. 1957. Postglacial hypsithermal interval. Science 125:182-184.
- Dickson, R. R. 1960. Climates of the states: Tennessee. United States Department of Commerce, Weather Bureau, Climatology of the United States, No. 60-40, 16 pp.
- Dorf, E. 1959. Climatic changes of the past and present. Contributions to the Museum of Paleontology, University of Michigan 13(8):181-210.
- Fowells, H. A. 1965. Silvics of forest trees of the United States. U.S.D.A. Agriculture Handbook No. 271.
- Geiger, R. 1965. The climate near the ground. Fourth edition. Harvard University Press, Cambridge, 611 pp.
- Gersmehl, P. 1973. Recent Appalachian vegetation history: A summary of two centuries of eyewitness descriptions. Unpublished manuscript. Concordia Teachers College.
- Gleason, H. A. 1923. The vegetational history of the middle west. Annals of the Association of American Geographers 12:39-85.

- Griffin, N. C. 1965. Germination and early survival of Picea rubens Sargent in experimental laboratory and field plantings. Master's thesis. The University of Tennessee, Knoxville.
- Hadley, J. B. and R. Goldsmith. 1963. Geology of the eastern Great Smoky Mountains, North Carolina and Tennessee. U. S. Geological Survey Professional Paper 349-B, pp. B1-B118.
- Harper, J. L. 1961. Approaches to the study of plant competition. In F. L. Milthorpe, ed., Mechanisms in Biological Competition. Symposia of the Society for Experimental Biology 15:1-39.
- Lafond, A. and Yvon Laflamme. 1968. Relative concentrations of iron and manganese: A factor affecting jack pine regeneration and jack pine-black spruce succession. In C. T. Youngberg and C. B. Davey, eds., Tree Growth and Forest Soils. Oregon State University Press, Corvallis, Oregon.
- Mark, A. F. 1958. The ecology of the Southern Appalachian grass balds. Ecological Monographs 28:293-336.
- McCracken, R. J., R. E. Shanks, and E. E. C. Clebsch. 1962. Soil morphology and genesis at higher elevations of the Great Smoky Mountains. Soil Science Society Proceedings 26:384-388.
- Meyer, B. S., D. B. Anderson, R. H. Bohning, and D. G. Fratianne. 1973. Introduction to Plant Physiology. D. Van Nostrand Company, New York. 565 pp.
- Mitin, V. V. 1971. The water-soluble inhibitors of seed germination from beech (Fagus silvatica L.) autumn leaves. In A. M. Grodzinsky, ed., Physiological-Biochemical Basis of Plant Interactions in Phytocenoses 2:22-25. Naukova Dumka, Kiev.
- Moore, B. 1917. Some factors influencing the reproduction of red spruce, balsam fir and white pine. Journal of Forestry 15(7):827-853.
- _____. 1926. Influence of certain soil and light conditions on the establishment of reproduction in northeastern conifers. Ecology 7(2):191-220.
- Muller, C. H. 1974. Allelopathy in the environmental complex. In B. R. Strain and W. D. Billings, eds.,

Vegetation and Environment. Handbook of Vegetation Science 6:73-85.

- Murphy, L. S. 1917. The red spruce--its growth and management. U.S.D.A. Bulletin 544, 100 pp.
- Oh, K. C. 1964. The sampling, pattern, and survival of the higher elevation beech in the Great Smoky Mountains. Ph.D. dissertation. The University of Tennessee, Knoxville.
- Oosting, H. J. 1956. The Study of Plant Communities. Second edition. W. H. Freeman and Company, San Francisco. 440 pp.
- Oosting, H. J. and W. D. Billings. 1951. A comparison of virgin spruce-fir forest in the northern and southern Appalachian system. Ecology 32:84-103.
- Pearl, I. A. 1967. The Chemistry of Lignin. Marcel Dekker, Inc., New York. 339 pp.
- Peterson, E. B. 1965. Inhibition of black spruce primary roots by a water-soluble substance in Kalmia angustifolia. Forest Science 11(4):473-479.
- Pinchot, G. 1898. The Adirondack spruce. The Critic Company, New York. 157 pp.
- Radford, A. E., H. E. Ahles, and C. R. Bell. 1968. Manual of the vascular flora of the Carolinas. University of North Carolina Press, Chapel Hill, North Carolina. 1183 pp.
- Radford, S. W. 1968. Factors involved in the maintenance of the grassy balds of the Great Smoky Mountains National Park. Master's thesis. The University of Tennessee, Knoxville.
- Ramseur, G. S. 1960. The vascular flora of the high mountain communities of the southern Appalachians. Journal of the Elisha Mitchell Scientific Society 76:82-112.
- _____. 1976. Secondary succession in the spruce-fir forest of the Great Smoky Mountains National Park. National Park Service Southeast Regional Uplands Field Research Laboratory, Management Report No. 7, 35 pp.

- Ribereau-Gayon, P. 1972. Plant Phenolics. Hafner Publishing Company, New York. 254 pp.
- Rice, E. L. 1974. Allelopathy. Academic Press, New York. 353 pp.
- Robinson, R. and H. Smith. 1955. Anthocyanins of the leaf of the copper beech (Fagus sylvatica) and the fruit of the cultivated strawberry (Fragaria virginiana). Nature 175:634.
- Robinson, T. 1967. The organic constituents of higher plants. Burgess, Minneapolis. 319 pp.
- Russell, N. H. 1953. The beech gaps of the Great Smoky Mountains. Ecology 34:366-374.
- Safford, L. O. 1974. PICEA A. Dietr. Spruce. In Seeds of woody plants of the United States. U.S.D.A. Agriculture Handbook 450:587-597.
- Schofield, W. B. 1960. The ecotone between spruce-fir and deciduous forest in the Great Smoky Mountains. Ph.D. dissertation. Duke University.
- Shanks, R. E. 1954. Climates of the Great Smoky Mountains. Ecology 35:354-361.
- . 1956. Altitudinal and microclimatic relationships of soil temperature under natural vegetation. Ecology 37:1-7.
- Smallshaw, J. 1953. Some precipitation-altitude studies of the Tennessee Valley Authority. Transactions of the American Geophysical Union 34:583-588.
- Stephens, L. A. 1969. A comparison of climatic elements at four elevations in the Great Smoky Mountains. Master's thesis. The University of Tennessee, Knoxville.
- Thorntwaite, C. W. 1948. An approach toward a rational classification of climate. Geographical Review 38:55-94.
- Tinnin, R. O. 1972. Interference or competition. American Naturalist 106:672-675.
- Tissut, M. 1967. Etude spectrophotometrique et chromatographique des flavonols du hêtre (Fagus sylvatica L.). Phytochemistry 6:1291-1296.

- _____. 1968. Etude du cycle annuel des derives phenoliques de la feuille du hêtre Fagus sylvatica L. Physiologique Vegetale 6(4):351-365.
- Van Hook, Jr., R. I., E. G. Blaylock, E. H. Bondietti, C. W. Francis, J. W. Huckabee, D. E. Reichle, S. H. Sweeten, and J. D. Witherspoon. 1974. Radio-isotope techniques to evaluate the environmental behavior of Cadmium. In Comparative Studies of Food and Environmental Contamination. IAEA - SM-175/22.
- Westveld, M. 1926. Logging damage to advance spruce and fir reproduction. Journal of Forestry 24:579-582.
- _____. 1930. Spruce regeneration in eastern Canada and northeastern U. S. Forestry Chronicle 6:22-23.
- Whittaker, R. H. 1952. A study of summer foliage insect communities in the Great Smoky Mountains. Ecological Monographs 22:1-44.
- _____. 1956. Vegetation of the Great Smoky Mountains. Ecological Monographs 26:1-80.
- Winter, A. G. 1961. New physiological and biological aspects in the interrelationships between higher plants. In F. L. Milthorpe, ed., Mechanisms in Biological Competition. Symposia of the Society for Experimental Biology 15:1-39.
- Winter, A. G., and W. Bublitz. 1953. Uber die keim- und entwicklungshemmende Wirkung der Buchenstreu. Naturwissenschaften 40(15):416.
- Wolfe, J. A. 1967. Forest soil characteristics as related to vegetation and bedrock in the spruce-fir zone of the Great Smoky Mountains. Ph.D. dissertation. The University of Tennessee, Knoxville.

VITA

The author was born on July 6, 1952 in San Diego, California. The first 12 years of his education were completed in San Diego county schools, and in June of 1970, he graduated from Monte Vista High School. From September, 1970, to June, 1974, the author attended the University of California at Santa Barbara, and received the Bachelor of Arts degree in Botany. In September of 1974, the author entered The University of Tennessee in the Graduate Program in Ecology to begin work toward the Master of Science degree. During this period, the author has enjoyed the benefit of consecutive teaching and research assistantships in biology and ecology.