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I am submitting herewith a thesis written by Noel Bruce Pavlovic entitled "An Examination of the Seed Rain and Seed Bank and Evidence of Seed Exchange Between a Beech Gap and a Spruce Forest in the Great Smoky Mountains." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology.

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AN EXAMINATION OF THE SEED RAIN AND SEED BANK FOR EVIDENCE OF SEED EXCHANGE BETWEEN A BEECH GAP AND A SPRUCE FOREST IN THE GREAT SMOKY MOUNTAINS

A Thesis

Presented for the

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ABSTRACT

The vegetation, seed rain, and seed banks were examined in a beech gap and a spruce stand in the high elevation Smoky Mountains to quantify the seed exchanges between these two plant communities. This information is of interest because these beech gaps are believed to be slowly invaded by Picea rubens along the abrupt boundary between the stands.

Five transects of seed traps were set up perpendicular to the boundary, extending into each community. Sticky and gravity traps were placed at preset intervals along the transects to collect seed rain for one year. At each seed rain sample site a soil core was collected to examine viable seeds and vegetative propagules in the soil.

The vegetation analysis showed quantitative differences rather than compositional differences between the tree canopies of the beech gap and spruce stand. The beech gap was dominated by Fagus grandifolia, whereas the spruce stand was dominated by Picea rubens and Betula lutea. The shrub layer and herbaceous vegetation differed greatly between these two plant communities. Canopy transects across the boundary demonstrated a narrow ecotonal zone rather than a distinct boundary between the communities although from a distance the boundary appeared sharp.

The seed rain data showed substantial seed dispersal of Betula lutea and Picea rubens and minimal dispersal of Cacalia rugelia into

the beech gap from the spruce stand. Some seeds of Poa alsodes were able to disperse into the spruce stand from the beech gap. Evidence is presented showing that Eupatorium rugosum was dispersed from the Clingman's Dome Road into the beech gap and possibly into the spruce stand as well. The seed bank data confirmed the exchange of seeds of these species except for Cacalia rugelia.

The seed bank results agreed with other seed bank studies, in the absence of seeds of late successional woody species such as Fagus grandifolia and Picea rubens. In contrast with most seed bank studies, the seed banks in these communities had a high similarity with the overlying vegetation. Multivariate analytical techniques showed significant differences in the seed banks between these adjacent plant communities. Reciprocal averaging showed a beech gap seed bank species gradient which is highly correlated with sample core slope position. This seed bank gradient is probably in response to a moisture topographic gradient affecting the overlying herbaceous species populations.

The implications of the limited seed exchanges between these communities are discussed in terms of the possible invasion of the spruce stand vegetation into the beech gap. The potential role of seeds stored in the soil in succession and vegetation dynamics is discussed.

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INTRODUCTION

Plant ecologists have for a long time been interested in the origin and maintenance of the high elevation beech gaps in the Great Smoky Mountains National Park. These nearly pure stands of American beech form narrow ecotones with the adjacent spruce-fir vegetation (Whittaker 1956, Schofield 1960, and Fuller 1977). Schofield (1960) presented evidence that red spruce was invading the beech gaps.

Whittaker (1967) stated that such narrow ecotones can be found in some rare circumstances in natural vegetation; he believed, however, that life form differences, edaphic or geological discontinuities or historical events could account for the existence of distinct plant community boundaries. The studies by Wolfe (1967) clearly demonstrated that edaphic and geological discontinuities were lacking; consequently, life form differences and historical events probably account for the distinct boundaries.

Whittaker (1967), Schofield (1960), and Fuller (1977) all believed that the beech gaps originated during the Hypsithermal Period when plant communities were believed to have migrated upslope as a result of climatic change. Since the more recent climatic cooling it was believed the conditions have been favorable for red spruce invasion into the beech gaps.

Naturally occurring and man-made vegetation boundaries are important systems to study because the boundaries act as interfaces of

plant seed[1] exchange. Such seed exchange can have a profound influence on vegetation migration and vegetation recovery after a disturbance. Seeds dispersing to a currently unfavorable germination site may at some future time be located in a favorable site as a result of climatic change.

If propagules of a particular species are absent at a site, then dispersal becomes critical in order for that species to occur there. The dispersal of seed across manmade boundaries between two plant communities, e.g., old field and forest, has been documented by Kellman (1974). No known studies have examined seed exchange across naturally occurring forest boundaries between plant communities. The presence of buried viable seeds in the soil can affect the rate and direction of successional seres.

Egler (1954) coined the terms initial and relay floristics to describe the effects different life history strategies have on the process of succession. The initial floristics concept states that all species of the successional seres are present in the site at the initiation of the succession; some of the species, however, do not become dominant (in stature) until a later time in the succession. The relay floristics concept describes the differential dispersibility of plant species as the cause of the successions observed in nature. This differential dispersibility is a component of a species' life history strategy.

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[1]Seed is defined throughout the text as those sexually produced diaspores irrespective of their morphological structure.

Both the concepts of relay and initial floristics are supported by the presence of viable dormant seeds of early successional species and the absence of late successional species in the soil of forests and fields. Studies by Oosting and Humphreys (1940) and Donelan and Thompson (1980) demonstrated the existence of early successional seeds in the soil of advanced successional stages. Late successional seeds are usually lacking from the seed banks of early successional stages; consequently these species are usually absent from early successional stages and depend on dispersal mechanisms to invade.

The purpose of this study was to examine seed dispersal across a naturally occurring forested community boundary. It was hypothesized that significant differences in seed rain composition and densities would occur with increasing distance from the boundary. A beech gap and a spruce forest were chosen because of the narrow ecotone between the two communities and because they differ significantly in species composition.

The seed bank was sampled as well for evidence of seed dispersal across the boundary between the two communities. The seed bank was also examined to determine whether early successional seeds occur in the soil that could contribute to vegetation recovery after a disturbance. An analysis of community seed budgets (seed rain and seed bank data) could also give an indication of the role seeds play in the maintenance of these two contrasting communities, particularly in zones of Fraser fir disturbed by the balsam woolly aphid. The recent paleoecological literature was also reviewed for the insight it gives

in understanding the origins of the beech gaps in the high elevation Southern Appalachian Mountains.

CHAPTER I

LITERATURE REVIEW

Plants exhibit various strategies to disperse their seeds away from the parent plant (Van der Pijl 1972). Once dispersed, some species' seeds have the ability, via various dormancy mechanisms, to be incorporated into the soil (Grime 1979). In this section an examination of seed dispersal and seed bank literature will be made.

A very extensive literature exists concerning seed dispersal (Van der Pijl 1972). Many of the earlier studies were qualitative and concerned with biogeography or long distance dispersal rather than with the quantitative examination of dispersal (Ridley 1930).

Van der Pijl (1972) classified seed dispersal mechanisms into the following syndromes: anemochory (wind), hydrochory (water), myrmecochory (ants), icthyochory (fish), saurochory (reptiles), ornithochory (birds), mammaliochory (mammals), autochory (self dispersing) and barochory (weight). Following is a discussion of those syndromes of particular importance to this study.

The syndrome most easily quantified and most widely studied is anemochory. Many trees and members of the family Asteraceae exhibit wind dispersal strategies with the typical negative exponential relationship between seed density and distance from the seed source (Johnson 1979).

Many scientists have examined the seed dispersal of economically important species such as spruce, fir and hemlock (Randell 1974), sugar maple and yellow birch (Benzie 1959) and paper birch (Bjorkbom et al. 1965). These studies have examined seed dispersal into clearcuts. Herbaceous dispersal has been examined by Werner (1975) and Rabinowitz and Rapp (1979).

Burrows (1975) showed that obstructions would cause seeds to lose velocity and be deposited downwind from the obstruction. In a previous study he derived equations for the primary trajectories of pappus-bearing achenes on which later work was based (Burrows 1973).

Sheldon and Burrows (1973) demonstrated that dispersal of many members of the family Asteraceae is hampered by the pappus response to humidity and air turbulence; in some cases, however, air turbulence can enhance dispersal. Dispersal effectiveness not only depends on the size and shape of the pappus but also on environmental factors such as height of first release, wind speed, and humidity.

Dispersal by birds has been less frequently studied. Livingston (1972) clearly demonstrated the role American robins (Turdus migratorius) play in the dispersal and successful germination of Juniperus communis[2] and J. virginiana. Marks (1974) showed the existence of a large Prunus pensylvanica seed bank that was presumably the result of bird dispersal. Bird dispersed seeds would not be expected to be found at high densities near the source since the seeds would be expelled at

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[2]Nomenclature follows Fernald (1950) except for species of southern distribution, in which case Radford et al. (1968) was consulted.

some time after their consumption. Expulsion would most likely occur some distance away from the site of consumption.

Thompson and Willson (1978) found higher rates of fruit removal from fruit sources in areas with disturbed canopy relative to those under closed canopies. This suggests that birds possess habitat search images to facilitate the finding of fruit sources.

Thompson and Willson (1979) found three fruit dispersal strategies in Illinois: (1) synchronous ripening at peak fall bird migration, (2) asynchronous ripening in summer, presumably to avoid invertebrate damage, and (3) winter ripening of species that are assumed to be dispersed by winter resident birds. These studies demonstrate the highly evolved nature of ornithochorous dispersal strategies.

Plant species of interest to this study whose fruits are consumed by birds are Potentilla sp., Rubus sp., Prunus pensylvanica, Sorbus sp., and Amelanchier sp. (Martin, Zim, and Nelson 1951).

Information from wildlife biologists concerning the subject of mammal food habits has contributed to our knowledge of the role mammals play in seed dispersal. Mammals such as squirrels (Sciurus sp.) and chipmunks (Tamias sp.) can play a role in seed dispersal, particularly if they cache the fruits. Barnett (1977) examined the survival and germination of squirrel cached oak and hickory nuts. Smith (1970) proposed that pine squirrels (Sciurus sp.) and conifers have coevolved to benefit each other: the pine seeds are a food source for the squirrels, and the squirrels are the seed dispersers for the pines.

Janzen (1971) hypothesized that tree seed predation by animals would result in higher survival of seeds and germinants at a greater distance from the seed source. Dispersal densities would be least in these areas, making them less desirable feeding sites for animals. Recent work by Hubbell (1980) and Formann and Hahn (1980) has shown that in the tropics trees tend to be clumped in distribution. These findings suggest that seed predation does not necessarily explain the pattern and high diversity of tropical forests.

Certainly mammals can exert a great influence on the reproduction of large-seeded taxa such as Pinus, Picea, Quercus, Carya, and Fagus.

Myrmecochorous plants have been studied only recently in the temperate forest region. This syndrome is characterized by seeds having an oily eliaosome that is an attractive food source for ants. In order to secure this, the ants carried away the whole seed (Van der Pijl 1972). Beattie et al. (1979) have studied ant dispersal of Sanguinaria canadensis, Hepatica acutiloba and various Viola species. They demonstrated non-specificity of the ants to the seed species, as did Culver and Beattie (1978).

Pudlo et al. (1980) showed that bloodroot (Sanguinaria) seeds could be dispersed by ants for a distance of up to 12 m in sparse plant populations, but very short distances in dense populations. Trillium sp., Uvularia sp., Asarum canadense and Dicentra sp. are also ant dispersed (Van der Pijl 1972).

Having finished a brief examination of the diversity of dispersal mechanisms that exist at the plant autecological level, it

is now appropriate to examine seed dispersal at the plant community level.

Seed rain, defined as all of those seeds falling on the soil surface of a particular community, has been infrequently studied. Wagner (1965) examined seed rain in an irradiated scrub oak pine forest. All species trapped were wind dispersed and peak seed rain occurred in the fall and spring.

Brower and Davenport (1973) sampled seed rain in a mixed hardwood forest and found that spring samples represented wind-blown species from adjacent fields. Later samples represented forest species. Archibold (1980) found that the first year's seed rain after a fire was dominated by herbaceous species, in particular Epilobium angustifolium. Shrub seed was lacking from the rain.

Gant and Clebsch (1975) sampled seed rain in several stands of differing age and locality in Tennessee. They found that old fields received the greatest variety and number of herbaceous seeds whereas an old sassafras stand had the highest total seed count. Gant (1978) in a study of the mechanisms that maintained the Smoky Mountains heath balds from tree invasion, found that the majority of the seed rain was composed of seeds of Abies fraseri, Picea rubens, and Betula lenta and ericaceous shrubs. The tree seeds were from the surrounding forest and shrub seeds were from the bald vegetation. Seed rain was found to be least dense in the summer months.

Rabinowitz and Rapp (1980) examined the seed rain in a tall grass prairie. They found peaks during the months of June and July

and October and November. The seed rain was heterogeneous in spatial distribution as well.

Once a seed has fallen onto the soil it can be subject to one of several fates. The seeds may germinate and survive, germinate and die, remain dormant for a period, become incorporated into the soil, or be consumed by animals (Harper 1977). If plants are to maintain their populations, an excess of propagules must be produced which balances the usually high mortality incurred by many of the seeds. The stored population of viable seeds in the soil is the next topic of interest since these seeds can represent a source of new individuals after poor seed production years.

Much has been written concerning seed banks in numerous types of communities and successional stages (Champness and Morris 1948, Oosting and Humphreys 1940, and Van der Valk and Davis 1979). In this section those studies concerning seed banks of deciduous and coniferous forests will be discussed.

Table 1 presents a list of the seed densities found and the locations of the forest seed bank studies to date. The large variation of seed density occurring in coniferous or deciduous forests is apparent from this table. Such variation in part is likely the result of differing ages and histories of the stands as well as various degrees of isolation from early successional stages as seed sources. Generally higher densities of seeds may occur under deciduous forests, although successional pine stands approach the high densities of old fields and pastures.

Table 1. Summary of Forest Seed Bank Literature.

Location	Forest Type	Seed #/m^2	Source
Deciduous Forests			
Anderson Co., Tennessee, U.S.A.	White Oak	326	Dobberpuhl 1980
	Beech	500	
	Chestnut Oak	352	
	Tulip Poplar	709	
Campbell Co., Tennessee, U.S.A.	Tulip Poplar Hickory	1924	Dobberpuhl 1980
	Oak Maple	2131	
	Chestnut & White Oak	1126	
	Chestnut Oak	1275	
Durham, England	Oak Woodland	32	Donelan & Thompson 1980
GSMNP, U.S.A.	Second Growth Forest	265	Gant & Clebsch 1975
Norris Watershed, Tennessee, U.S.A.	Sassafras Stands	118	Gant & Clebsch 1975
New Brunswick, Canada	Beech/Maple	1950	Moore & Wein 1977
	Red Maple Clearcut	1390	
	Maple/Fir	1230	
Maine, U.S.A.	Sugar Maple	11	Olmstead & Curtis 1947
	Beech-Birch-Maple	65	
North Carolina, U.S.A.	Oak-Hickory	2361	Oosting & Humphreys 1940
Coniferous Forests			
Saskatchewan, Canada	Pine	100	Johnson 1975
	Black Spruce	0	
	White Spruce	0	

Table 1. (Continued)

Location	Forest Type	Seed #/m^2	Source
British Columbia, Canada	Douglas Fir	1016	Kellman 1970
New Brunswick, Canada	Mixed Conifer	206	Kellman 1974
	Seral Mixed Conifer	2612	
Harvard Forest, Mass., U.S.A.	5 Yr. Pine	4500	Livingston & Allessio 1965
	25 Yr. Pine	5010	
	47 Yr. Pine	1350	
	80 Yr. Pine	3350	
Miyajima Island, Japan	Japanese Red Pine	1459	Nakagoshi & Suzuki 1977
Chiba, Japan	Japanese Black Pine Seral	4430	Numata et al. 1964
Maine, U.S.A.	70 Yr. White Pine	161	Olmstead & Curtis 1947
	Red Pine	5	
	Spruce Fir	48	
North Carolina, U.S.A.	Seral Pine	8297	Oosting & Humphreys 1940
California, U.S.A.	Sugar Pine	697	Quick 1956
La Grande, Oregon, U.S.A.	Giant Fir & Shore Pine	421	Strickler & Edgarton 1976
	Giant Fir & Engelmann Spruce	1863	
	Giant Fir & Western Larch	3447	
Fraser, Colorado, U.S.A.	Engelmann Spruce & Subalpine Fir	53	Whipple 1978
	Lodgepole Pine	3	

These wide variations may be due to differences in the treatment and collection methods used by the various authors. Some, such as Olmstead and Curtis (1947), Quick (1956), and Whipple (1978) cut out soil sections with a knife. Most, however, have used a soil core to collect their samples: Oosting and Humphreys (1940), Kellman (1970 and 1974), Johnson (1975) and Moore and Wien (1977).

Most authors placed their soil samples directly on sterile soil in a greenhouse, and then identified and counted the germinants that emerged. Olmstead and Curtis (1947) air dried their samples, sieved them and identified and counted the seeds. Later they performed germination tests on the seeds. Johnson (1975), on the other hand, placed the samples on appropriate media in the greenhouse; when no more seedlings emerged by germination, he sieved the soil to identify the non-germinating seeds as well.

Moore and Wein (1977) treated their samples in the same manner as Johnson (1975) except that they tested the viability of non-germinating seeds with neotetrazolium chloride.

It is questionable whether greenhouse germination studies give a true picture of actual seed densities. Major and Pyott (1966) identified six difficulties in studying seed banks: (1) many species reproduce vegetatively, (2) greenhouse germination may be species selective, (3) seed populations may be aggregated around mother plant, (4) appropriate sample sizes are unknown, (5) depth distributions are unknown, and (6) seedlings are difficult to identify. Difficulties 2, 3 and 4 certainly would add to the variability of seed bank samples.

Examination and knowledge of the reproductive strategies of plants will aid in determining which plants can be expected to contribute to the seed bank. Studies such as the one by Marks (1974) on Prunus pensylvanica have provided an excellent insight into reproductive strategies. The ecological implications of a species' reproductive strategy can only be understood by examining the fates (predation, seed bank, seedling death) of the dispersed seeds. Making a distinction between germinants from seed and vegetative reproductive structures will aid in understanding plant life history strategies.

At our present state of knowledge concerning seed germination requirements, it would be difficult to provide all the conditions necessary for the complete germination of all species; consequently, the physical separation of seeds from the soil and subsequent germination and/or viability testing is the best technique to alleviate the problem. This technique is very time consuming; Hodgkinson et al. (1980) spent over 8 to 12 man hours per 100 grams of soil sample. Aggregation of seeds around the parent plant would increase variability among seed bank samples. Most studies have shown a high coefficient of variation for the species densities. Seeds dispersed by animals might not necessarily be aggregated around the parent plant.

Champness (1949) found that seventy 25 m^2 plots were required to obtain density estimates within 10% of the population mean. Two hundred samples (0.5 m^2 total) were required for the total density estimates in order for the common species to be within 10% of the population mean. Champness' samples were collected in grasslands;

different minimum sizes might be required for different community types.

Kellman (1978) found that seeds in tropical corn fields are clumped in distribution, whereas they are more evenly distributed in pastures. If seed populations are clumped in distribution it may be misleading to calculate mean seed bank densities.

Depth distributions of seeds are better known now than in the early 1960's thanks to the work of Major and Pyott (1966), Kellman (1970 and 1978), Strickler and Edgarton (1976), Moore and Wein (1977) and Dobberpuhl (1980). Generally the density of seeds declines with depth; Dobberpuhl, however, found that fewer germinants emerged from the litter layer and 0 to 5 cm depths than from the 5 to 10 cm depths.

Little is known about the rates of seed movement into the soil depths from the surface. Movement of seeds downward would require that the seeds sifted through the litter layer. Perhaps soil invertebrates and other animals would aid in this process. Presumably those seeds deeply buried are older than those seeds nearer to the soil surface.

The following texts made seedling identification much easier: Kummer (1951), Chanceller (1966), Maisenhelder (1969), and Muller (1978).

Forest seed bank studies indicate that the species composition of the seed bank is usually dissimilar from the species composition of the overlying vegetation (Oosting and Humphreys 1940, Numata et al. 1964, Kellman 1970 and 1974, Johnson 1975, Whipple 1978, and Donelan

and Thompson 1980). This trend is presumably the result of the qualities of forest tree seeds.

Dominant overstory species usually have large seeds to assure a competitive advantage of the species during germination and establishment (Harper et al. 1970 and Stebbins 1971). Large seeds contain a greater proportion of endosperm or food reserve than do small seeds. The high caloric content of such seeds makes them attractive as an animal food source (Gashwiler 1965, 1967 and 1970; Thompson 1978). Data from seed germination and seed burial studies suggest that large seeds have a short viability period compared to small seeds (Harrington 1972); consequently, the characteristically large seeds of late successional species are rarely found in viable conditions in the soil.

Small seeds have been found to have high viability and last up to 60 years or more in the soil (Harrington 1972; Kivilaan and Bandurski 1973). Salisbury (1942, 1974) showed that as one progresses from a disturbed habitat to a closed forest community, the average seed size of plant species present increases. Recently Cook (1980) has hypothesized that small seed size is an adaptation permitting the accumulation of a persistent seed bank. Small seeds would persist for a long time in part due to the greater physical difficulty they have in bursting the seed coat to germinate. As seed size decreases the ratio of seed coat thickness to embryo size increases, making it necessary for the embryo to exert a greater force to burst the seed coat. These observations suggest that those species represented in the seed bank in a forest are early successional species, for which seeds have long viability, small size, and, most likely, high dispersibility.

Studies of community seed budgets are rare. A seed budget can be defined as the inputs, storages and losses of seeds in a plant community. Only Kellman (1974), Cheke et al. (1979), Archibold (1979, 1980), and Rabinowitz (1981) and Rabinowitz and Rapp (1980) have attempted to examine plant community seed budgets; they have only looked at inputs and storages, however.

Kellman (1974) found that three years of seed rain in an old forest and a secondary successional site were insufficient to account for the large densities of seeds in the soil. He concluded that the seed bank represented many years' accumulation from the seed rain. He also found that seed rain of successional species rapidly declined with increasing distance into the old forest stand, but that secondary successional species seeds did occur in the rain and bank at distances up to 100 m into the stand. Kellman predicted that "inefficient movement of seed of secondary species through forest stands suggests that only those open sites contiguous to an established secondary community would receive appreciable migrant seed." Cheke et al. (1979) reached similar conclusions; they found, however, that some seeds of secondary species did disperse into the forest in considerable numbers at 150 m.

Archibold's data (1979 and 1980) show higher densities of many seeds raining on the site than occur in the soil bank; this result is not surprising, however, since he sampled the seed bank in April 1977 immediately after a fire. Seed rain samples were collected in 1978 and 1979, time enough for plants that emerged in the summer of 1977 to significantly add to the seed rain.

Rabinowitz and Rapp found that seed rain density was higher than the seed bank density in a tall grass prairie (71% reduction) (Rabinowitz 1981; Rabinowitz and Rapp 1980). The majority of the common rain species occurred in the seed bank, but many of the common elements in the bank were not detected in the seed rain.

It has been shown that plants have evolved a diversity of dispersal mechanisms by which future offspring are transported into many areas including potential safe sites. Such mechanisms can determine the fate of populations in environmental mosaics of various disturbance frequencies. The seed rain acts as the ultimate source of future plant generations (sexually recombined variants), by contributing either to the next seedling generation, or to a potential future generation following seed storage in the seed bank.

The seed bank has been shown to be composed chiefly of herbaceous and woody early successional species, reflecting the different reproductive strategies of contrasting life forms in nature. Understanding seed rain and seed bank dynamics at the species and community levels will enhance our understanding of the population dynamics of species and the dynamics of plant communities.

CHAPTER II

THE STUDY AREA

The study site was a beech gap and adjacent spruce-stand 1 km west of Newfound Gap in the Great Smoky Mountains National Park in Swain County, North Carolina. The site lies between the North Carolina-Tennessee state line (the Appalachian Trail) and the Clingman's Dome Road (Figure 1).

A schematic diagram of the study area is shown in Figure 2. The site faced south and elevation was 1582 to 1615 m and with aspects from 49° to 140°. The slope ranged from 13° to 35°.

I. GEOLOGY

The rocks making up the Great Smoky Mountains are late Precambrian nonfossiliferous sediments called the Ocoee Series, that were pebbly, sandy, and/or muddy (King et al. 1968). The mountains are the product of prolonged uplift and erosion since the initial rock deformation during the mid-Ordovician Period.

Steep slopes which are prone to landslides are indicative of the Anakeesta Formation underlying the study area. This formation is composed of small pebbled arkosic conglomerate graywacke. These rocks are fine to coarse grained feldspathic sandstone, slate, argillite, and phyllite (Hadley and Goldsmith 1963). Carbon and iron sulfide within these rocks give them their characteristic dark coloration.

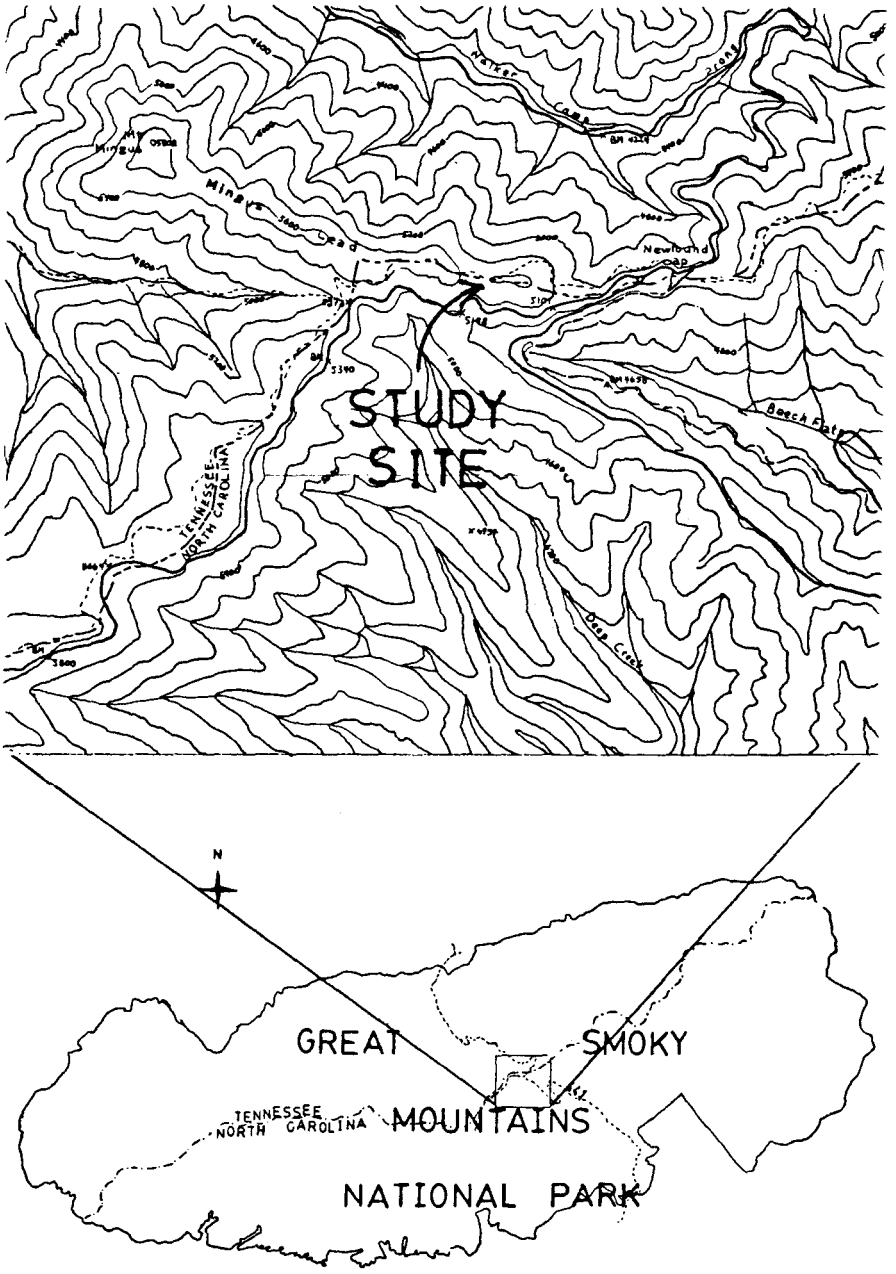


Figure 1. Location of Study Site in the Great Smoky Mountains National Park. The study site is 1 km west of Newfound Gap along the Clingman's Dome Road.

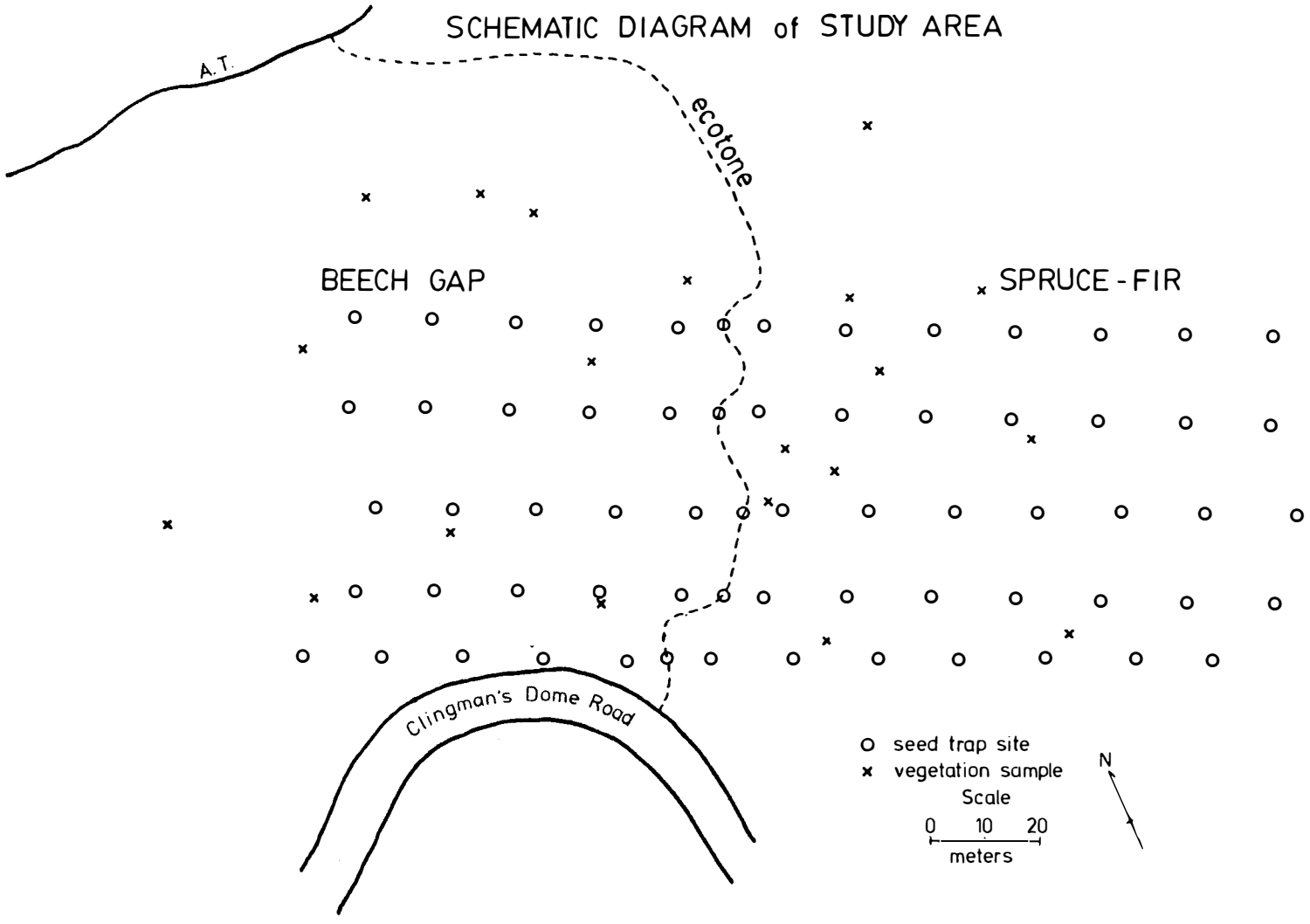


Figure 2. Schematic Diagram of Study Site.

II. SOILS

The study site contains soils of the Sol Brun Acide Group (McCracken et al. 1962) or under the Soil Conservation Survey's new classification system, Inceptisols classified as Dystrochrepts, Umbric Dystrochrepts, fine loamy, mixed, mesic permeable soils (Soil Survey Staff 1975). According to Buol et al. (1973) Inceptisols are immature soils with weakly expressed profiles closely resembling the parent material.

These soils lack an A_2 horizon and significant clay eluviation; they do, however, exhibit color differentiation between the horizons (McCracken et al. 1962). They suggested that soil creep helped maintain these soils at an undifferentiated state, whereas Wolfe (1967) also considered wind throw of the shallow rooted trees as contributing to the soil immaturity.

Wolfe (1967) reported that the minerology and texture of soils in beech gaps and spruce-fir forests were similar. This indicates that the abrupt vegetational changes between the two plant communities are not the result of parent material or edaphic changes.

Wolfe (1967) concluded chemical differences between the soils of the two communities were probably caused by the differing vegetation. Soils supporting spruce-fir stands contained a thick acidic litter layer producing an environment unfavorable to soil microfauna. Fast decay of the beech gap litter results from good aeration. Wolfe (1967) and McCracken et al. (1962) found that the eluviation of iron is more evident under the spruce-fir vegetation.

Beech gap and spruce-fir soils differ primarily in the litter and humus layers. Chiefly the texture, thickness, aeration, and pH of the litter layers differ.

III. CLIMATE

Shanks (1954) characterized the high elevation Smoky Mountains' climate as mesothermal, perhumid under the Thornthwaite classification system. In such a climate, precipitation exceeds potential evapotranspiration; consequently, plants are not under any water stress.

According to Stephens (1969) precipitation in the high Smokies can be classified as cyclonic or orographic. Orographic precipitation results from moist air being forced to higher and cooler altitudes, where the moisture condenses into rain size droplets. Cyclonic precipitation results from frontal systems passing through the area. Stephens found orographic precipitation occurred primarily during the summer and cyclonic primarily during the winter. Dense fog produced by orographic cooling was frequently observed in the study area.

Shanks (1954) reported an average precipitation of 226 cm at the Newfound Gap weather station. Figures 3 and 4 show, respectively, the monthly precipitation for 1979 and 1980. The monthly precipitation peaks in the winter and in July. July, September, and November 1979 were at least 8 cm above average in precipitation; 1980 was a drier year than 1979. The midsummer and late fall precipitation was below average in 1980.

Stephens (1969) reported an average of 148 day growing season at the Newfound Gap weather station. The average date of last frost

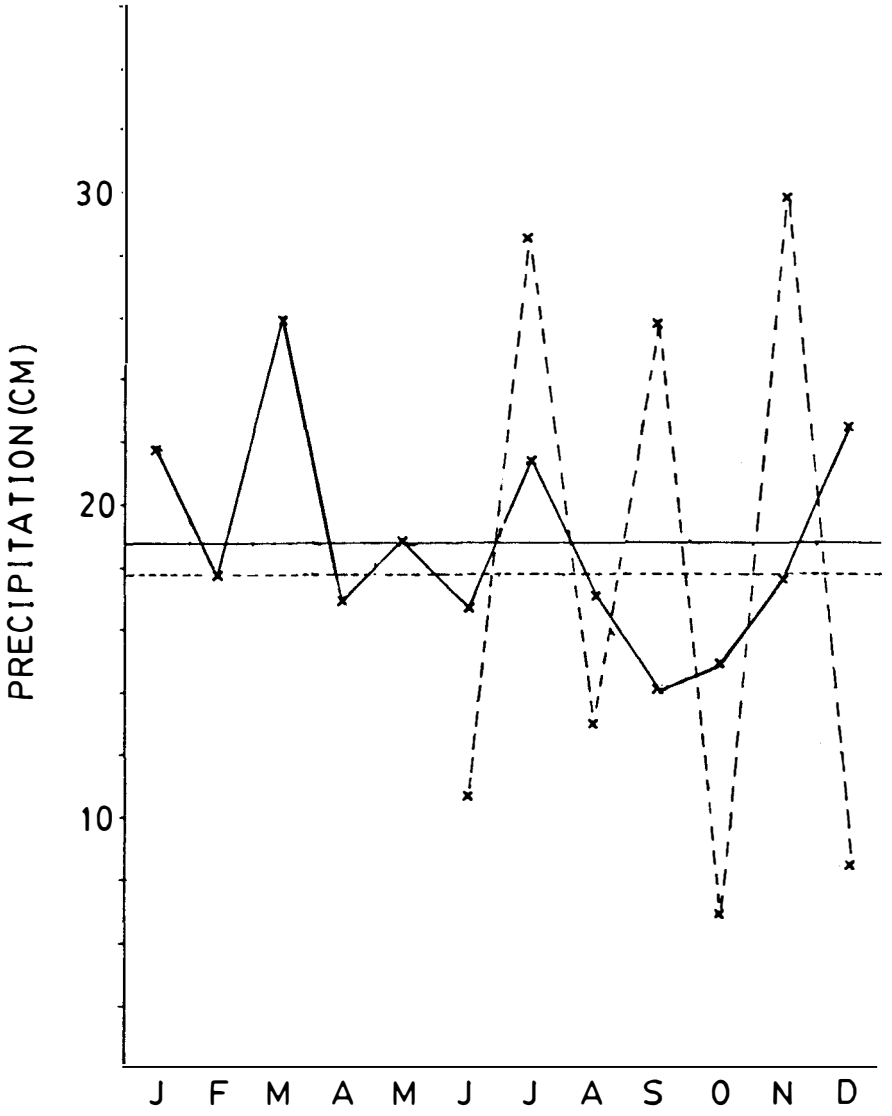


Figure 3. Mean Monthly Precipitation at Newfound Gap in 1979. Zigzag dashed line represents the monthly precipitation for 1979 (data before May unavailable). Zigzag solid line represents average monthly precipitation for the period of 1968-1977. Horizontal dashed line represents annual precipitation for 1979 divided by 12. Solid dashed line represents the average annual precipitation for the period of 1968-1977 divided by 12.

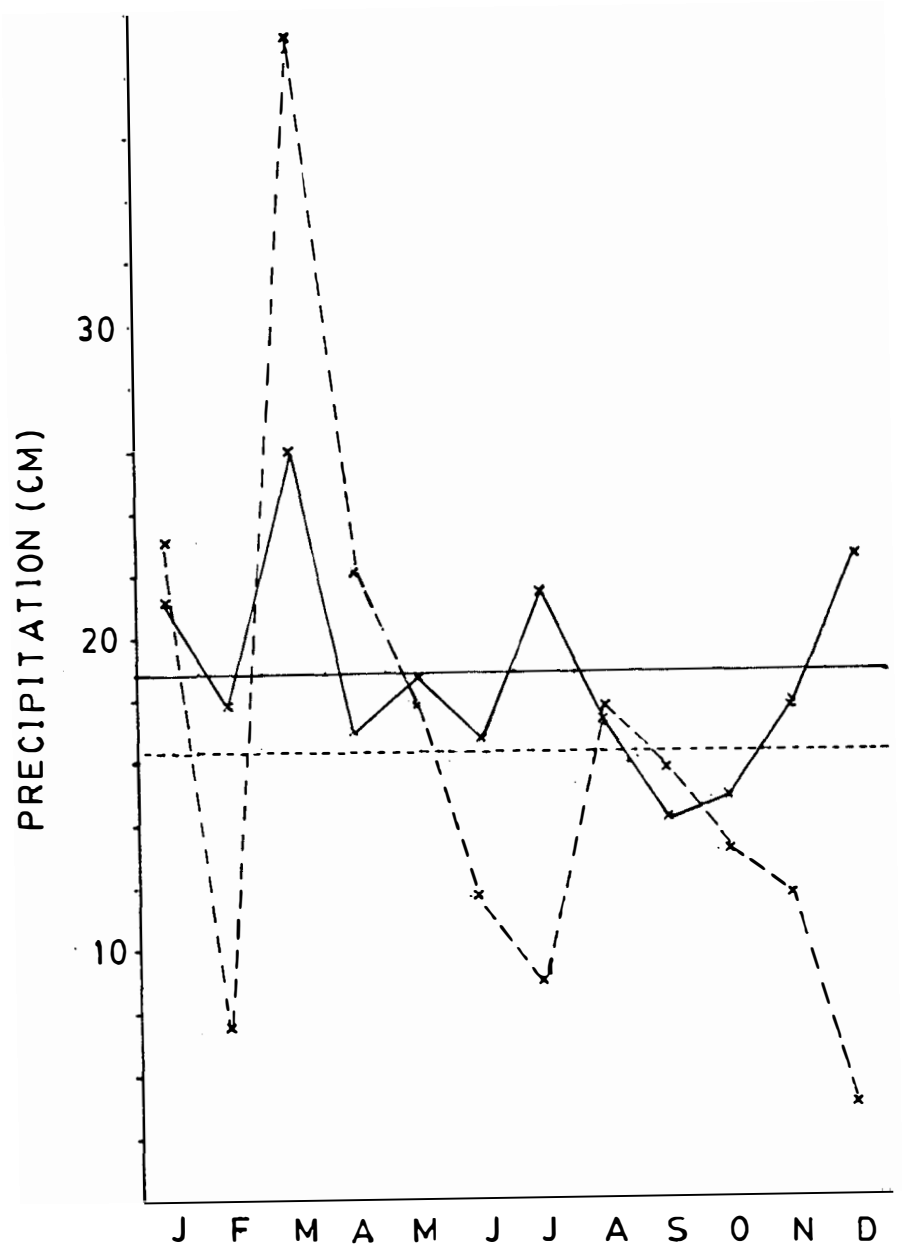


Figure 4. Mean Monthly Precipitation at Newfound Gap in 1980. Zigzag dashed line represents the monthly precipitation for 1980. Zigzag solid line represents average monthly precipitation for the period of 1968-1977. Horizontal dashed line represents the annual precipitation for 1980 divided by 12. Horizontal solid dashed line represents the average annual precipitation for the period of 1968-1977 divided by 12.

was May 9, and October 4 was the average first frost. Figure 5 gives the 10-day average maximum and minimum temperatures from the Newfound Gap weather station from May 1979 to December 1980. Of particular interest is the late frost on May 26 and 27, 1979; the minimum temperature was 28° F on both days.

IV. VEGETATION

Beech gaps, nearly pure stands of Fagus grandifolia, form very sharp boundaries with the adjacent spruce-fir vegetation (Russell, 1953). These plant communities have been studied for many years in an effort to understand their origin and maintenance. The actual area covered by beech gaps is quite small relative to other vegetation types in the Smokies.

Russell (1953) made a floristic survey of 13 beech gaps in the Smoky Mountains. Only Fagus grandifolia has a frequency of 100%. Other frequent species are Laportea canadensis, Poa alsodes, Rubus canadensis, Carex debilis, Carex artitecta, Stellaria pubera, Trillium erectum, Angelica triquinata, Luzula bulbosa and Prenanthes altissima. A total of 88 herbaceous species were found. Comparisons of the herbaceous vegetation found in beech gaps, spruce fir forests, and in disturbed sites showed many species in common among these communities.

Whittaker (1956) characterized beech gaps as having an overstory of stunted appearance with Fagus grandifolia trunks so covered with lichens as to make them unrecognizable by their bark. He considered the north facing gaps as extensions of the cove hardwood forests with Betula lutea and Aesculus octandra present. Characteristic herbs are



Figure 5. Ten Day Mean Minimum and Maximum Temperatures at Newfound Gap in 1979 and 1980.

Cacalia rugelia (previously named Senecia rugelia, Barkley and Cronquist 1974), Streptopus roseus and Rudbeckia laciniata. Whittaker considered the south facing gaps as intermediate vegetationally between the north facing gaps and the red oak-chestnut forests.

Crandall (1958) examined the ground vegetation in beech gaps. In gaps with high densities of Fagus grandifolia she defined two vegetation types: (1) Carex type and (2) Athyrium type. The Carex type occurred on level sites as are common at the ridge crest, while the fern type was found at steeper sites under the pure Fagus grandifolia canopy. In north facing stands with high densities of Betula lutea she found the Solidago site type.

Bratton (1975b) found a moisture gradient in the beech gap herbaceous layer. Carex sp. and Luzula sp. dominate at the dry end of the gradient while Impatiens pallida, Phacelia fimbriata, and other herbs are more common at the more mesic end of the gradient. The mesic end of the gradient occurred in north facing beech gaps and in low elevation sites in south facing beech gaps.

Since the early 1970's many beech gaps have been disturbed by rooting of the introduced European wild boar (Howe and Bratton 1976). These animals have mixed the litter layer with the A_{12} and B_2 horizons in many gaps (Bratton 1975a) and have reduced the herbaceous cover in some beech gaps to 5% of the expected undisturbed coverage (Bratton 1974). The data suggested that species such as Lilium superbum will become locally extinct as a result of the population's inability to regenerate after the disturbance. The hogs not only destroyed species they eat, but uprooted other herbs as well.

Oh (1964) examined the size class distribution and spatial patterns of the overstory species occurring in beech gaps. He found that Fagus grandifolia on north facing gaps had the same densities as south facing gaps; but it had significantly less basal areas on the north facing slopes. North facing slopes have more cove hardwood and spruce-fir species in the canopies, e.g., Betula lutea, Aesculus octandra, and Amelanchier laevis (Oh 1964; Bratton 1975b). Spatial distributions of Fagus grandifolia suggested that cyclic regeneration by root suckering occurs (Oh 1964).

Spruce-fir forests contain Abies fraseri, Acer pensylvanica, Amelanchier laevis, Betula lutea and Picea rubens in the overstory canopy (Russell 1953).

Oosting and Billings (1951) compared the southern Appalachian and northern Appalachian spruce-fir forests. They concluded that sufficient species composition and physiognomic similarity exists to consider the Southern Appalachian spruce-fir forests as part of the Boreal Forest; floristic and ecological differences exist, however, such that the two phases should be recognized: red spruce-fraser fir and red spruce-balsam fir.

Shrub species in spruce-fir forests include Viburnum alnifolium, Rubus canadensis, Vaccinium erythrocarpum, Sambucus pubens, Ribes rotundifolium and Rhododendron catawbiense (Oosting and Billings 1951).

Whittaker (1956) and Golden (1974) considered Betula lutea as an associate species with Picea rubens in red spruce forests. Although canopy composition was uniform, he did define five subtypes on

the basis of percent coverage by various specific undergrowth vegetation strata.

Crandall (1958) extensively examined the herbaceous floras under spruce-fir, spruce, and fir overstories in the Great Smoky Mountains National Park. Under the spruce canopy types she classified four types of ground cover: (1) Hyloconium-Vaccinium, (2) Viburnum-Vaccinium-Dryopteris, (3) Viburnum-Vaccinium-Lycopodium, and (4) Rhododendron.

The Hyloconium-Vaccinium type is dominated by Oxalis montana, mosses, liverworts and Vaccinium erythrocarpum. It occurs on steep southeast and northeast slopes. The Viburnum-Vaccinium-Dryopteris type is dominated by Cacalia rugelia, Dryopteris spinulosa, Vaccinium erythrocarpum and Viburnum alnifolium.

The Viburnum-Vaccinium-Lycopodium site type has low occurrences of ferns, Lycopodium lucidulum, Cacalia rugelia and Oxalis montana present in slight depressions. Most of the ground is bare with a shrub layer of Vaccinium erythrocarpum and Viburnum alnifolium. The fourth ground cover type is dominated by Rhododendron catawbiense, R. carolinianum and R. maximum.

Ramseur (1960) stated that Prunus pensylvanica communities are the major successional types in the spruce-fir region. These successional stands contained Rubus canadensis, Sambucus pubens, Diervilla sessilifolia, Betula lutea, Sorbus americana and a few other species. Common herbs were Eupatorium purpureum, Aster acuminatus, Carex brunnescens and Senecio aureus. Less common was Hieracium pilosella.

Some successional stages may exhibit high Rubus canadensis or Betula lutea cover. The Betula lutea-Prunus pensylvanica type is probably the second most common successional community compared to that discussed above. It contained those trees and shrubs mentioned above plus Vaccinium erythrocarpum, Viburnum alnifolium and Cornus alternifolia. Common herbs are Aster chlorlepis, Luzula acuminata, Eupatorium rugosum, Impatiens pallida, Cheloni lyoni and various ferns (Ramseur 1960).

The most recent destructive man caused disturbance has been the infestation of Abies fraseri by the balsam woolly aphid (Hay et al. 1978). Most fir trees die while standing (Pavlovic, personal observation); consequently the canopy opens up without the soil being disturbed, thus reducing the role seed banks would play in the succession on these sites. Hay et al. (1976) stated that Abies fraseri canopy death initiates release of advanced Abies fraseri seedlings except on south facing slopes where Sambucus, Rubus, Acer and Betula dominate.

Boner (1979) found the understory and the ground cover showed the most apparent changes in the spruce-fir forests after the balsam woolly aphid infestation. Vaccinium erythrocarpum and Viburnum alnifolium decreased in density after the canopy disturbance; Rubus canadensis, however, significantly increased in density. Prunus pensylvanica, Sorbus americana, and Sambucus pubens subsapling stems were found in higher densities in the disturbed sites than in the undisturbed sites. Oxalis montana initially increased in cover soon

after the disturbance, but declined as the succession proceeded, while ferns showed the opposite trend in coverage.

In the Great Smoky Mountains, sites disturbed by man--roadsides, trail shelters and so forth--contain herbaceous vegetation more characteristic of lower elevation agricultural land. Common plants in such localities include Potentilla canadensis, Rumex acetosella, Plantago major, Poa annua, Taraxacum officinale, Trifolium spp., Juncus tenuis, Rudbeckia laciniata, Monarda clinopoda, Blephilia hirsuta and Danthonia compressa (Lindsay and Bratton 1979).

CHAPTER III

METHODS

Below follows a summary of the data collection and analytical methods used to study the seed rain and seed bank pattern across the boundary between the beech gap and spruce stand.

I. VEGETATION DATA

The study site was divided into beech gap and spruce stand, with their boundary defined as the limit of continuous red spruce canopy. In order to map the boundary, a baseline transect was laid out roughly parallel to the boundary so that distances from the transect to the boundary could be measured. The transect also was used to construct a grid of squares (quadrats), 10 m on a side, from which sample plots were chosen.

In each community 10 circular plot centers were randomly selected from the quadrats defined by the baseline transect. The center of each quadrat was the center of a circular one-tenth acre (=0.04 ha) overstory plot and a one-hundredth acre (=0.004 ha) circular shrub layer plot. Four herbaceous quadrats (1 m^2) were arranged at the center of each circular plot.

Trees greater than 1 cm diameter at breast height (d.b.h.) were defined as overstory trees and trees and shrubs less than 1 cm d.b.h. and greater than 1 m tall were defined as shrubs. Overstory trees

were tallied by species and measured for d.b.h. Shrubs were tallied by species.

One of the four m^2 herb quadrats was sampled in July 1979 for density and coverage of the herbaceous species. Two herb sample plots were randomly chosen at each site for the spring herbaceous census in May 1980. The sample size increase from July to May was designed to reduce the sampling error in the plant population estimates.

In order to sample the vegetation change across the boundary, two transects 4 m wide were sampled perpendicular to the boundary. Each transect was centered at the boundary with a total length of 100 m. All trees and shrubs as previously defined were determined and counted in 10 m long segments.

II. SEED RAIN

Seed rain was sampled using two kinds of seed traps. Trap pairs consisting of sticky traps and gravity traps were placed along five transects perpendicular to the boundary. The transects were approximately 15 m apart. Along each transect, seed traps were placed at 0, 7.5, 22.5, 37.5, 52.5, and 67.5 m from the boundary (see Figure 2, page 21). In the spruce stand seed traps were extended to 82.5 and 97.5 m into a canopy gap resulting from Abies fraseri die off.

Sticky traps consisted of 10 by 20 cm metal lithographic plates elevated above the ground surface on a wooden dowel. A 10 by 25 cm aluminum foil sheet was laid on the plate to be coated with Bird Tanglefoot (Werner 1975). These traps were designed to collect

anemochorous seeds. They were effective even when wet, except for those times when they were covered by snow.

Gravity traps were constructed from two #10 cans by removing the ends and cutting the side of the resulting cylinder along its axis. The two cans were bent so that their edges could be taped together with duct tape to form a cylinder of 32 cm in diameter.

A screen of chicken wire was placed inside the cylinder to exclude frugivores. A compromise was made in mesh diameter so that Picea rubens cones and Aesculus octandra seeds would not be excluded; this mesh size, however, would probably permit vole and shrew entry. The collecting containers consisted of plastic bags paper clipped to the cylinder. Small perforations in the bottom of the bag permitted water drainage. On only one occasion during the year's collection was a plastic bag apparently chewed by an animal. A few traps were overturned during the year.

Seed traps were placed in the field on September 20, 1979, after testing of the sticky traps during the preceding July and August. Traps were examined and changed every 2 to 4 weeks. Sticky traps were not changed for the period of December 9, 1979 to April 1980. Gravity traps set up on December 9, 1979 were not collected until June 1980.[3]

In the lab, sticky traps were examined for seeds under a stereoscopic dissecting microscope. Any leaves or objects on the

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[3]Seed collection intervals: September 20, 1979 to September 30; September 30 to October 14; October 14 to October 27; October 27 to November 10; November 10 to December 9; December 9 to April 12, 1980; April 12 to May 24; May 24 to June 15; June 15 to July 20; July 20 to August 10; August 10 to September 6; September 6 to September 21, 1980.

surface were removed to determine if seeds were lodged underneath. Gravity trap contents were washed from the collecting bag into a white enamel tray to be examined for seeds under a stereoscopic dissecting microscope. Seed identifications were made by comparison with seeds collected in the field and with the use of seed guides such as Montgomery (1977). Dr. Paul Delcourt was helpful in conifer seed identification.

Directional seed traps were constructed to determine the direction from which the seeds were dispersing. In order to do this, sticky seed traps were placed vertically on 3 foot long wooden dowels. Each dowel had four traps, one facing upslope, one downslope, one into the beech gap and one into the spruce stand.

Shields were placed at the sides perpendicular to the sticky trap surface to prevent the collection of seeds coming at an acute angle with the sticky trap surface. The traps would, therefore, have a narrow trapping angle. Five such dowels were placed in the field in October 14, 1979. The traps were collected December 9, 1979.

Species from which more than 50 seeds were collected during each sampling period were tested for germination percentage. The procedures from Schopmeyer (1974) and Copeland (1978) were used in setting up the germination tests. Seeds were placed on two layers of germination blotters inside petri dishes. Petri dishes were placed in controlled growth chambers with an 8 hour light and 16 hour dark photoperiod. During the light period the temperature was kept at 30° C; in the dark period it was kept at 20° C. Germination counts were made over a 30-day period.

All seeds that did not germinate during the test period were tested for viability using the tetrazolium chloride method. The basis of the technique is that in the presence of biological reducing systems, the tetrazolium compound (colorless) is converted to a colored formazan (Altman 1976). In seed viability tests 2,3,5-triphenyl tetrazolium chloride is used. Moore (1958 and 1964) and I.S.T.A. (1976) give details concerning viability tests. Only completely stained embryos were considered to be viable.

III. SEED BANK

The seed bank was examined by removing 25 circular soil samples, each one adjacent to a seed rain site. Cores were not collected at the boundary or in the two farthest sampling distances in each transect in the spruce stand. Each core had a surface area of 0.08 m^2 and was 10 cm deep. All soil cores were collected December 1, 1979, placed in plastic bags and transported to the lab where they were stored in a cold room (1° C) until mid-February 1980.

At the TVA greenhouse at Norris, TN, the soil cores were placed in 6.5 by 24 by 62 cm flats over a layer of Promix Sterile Potting Soil. The collected soil samples were spread out to a 1.5 cm thickness on the sterile soil layer. The flats were randomly placed in the greenhouse to ensure greenhouse environmental effects did not impinge on any one set of samples.

Interspersed among the flats were six control flats to test for contaminants. Each flat contained Promix Sterile Potting Soil. These controls were judged ineffective because the vermiculite in the

Promix rose on watering thus disturbing the soil surface where germination would have taken place.

Preliminary results suggested that seed densities in the beech gap soil were high enough to examine seed depth distribution. In March 1980 a set of 10 soil samples randomly chosen from the previously sampled sites were collected from 0 to 3, 3 to 6, and 6 to 10 cm depths. Samples were taken immediately to the greenhouse to be set up as described above.

Colored toothpicks coded for week of emergence were placed in the flats adjacent to each seedling as it emerged. This was done for only the first 4 weeks. Thereafter seedlings were identified, recorded, and pulled up after identification had been made. The flats were watered when needed and a Hoagland's solution[4] was applied to the flats on July 1, 1980. The seed bank study was discontinued on July 29, 1980, after 21 weeks of examination.

Separation of the seed bank into a sexual component (seeds) and a vegetative reproductive component (stolons, tubers, corms, and so forth) was made to determine the relative importance of these different reproductive components in the populations. Since the seed bank is usually defined as including seeds and vegetative structures (Harper 1977) this aspect of the seed bank is not often examined. Germinants

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[4]The Hoagland's solution was prepared by mixing three different solutions containing the following quantities of nutrients (in ppm): (A) Ca-80.0, N-56.0; (B) K-117.6, N-35.1, P-15.5, Mg-24.9, SO_4^{2-}-33.1, Fe-10.0, Zn-0.03, Mn-0.03, B-0.3, Mo-0.005; (C) N-42.0, P-15.0, Na-4.6, Cl-7.1.

from seeds (as opposed to those young plants arising from vegetative propagules) were recognized by the presence of cotyledons.

IV. ENVIRONMENTAL VARIABLES

From each vegetation, seed rain and seed bank sampling site, several environmental variables were quantitied. Slope in degrees was measured using an Abney level, and aspect was determined with a compass. Elevation above the road in m was estimated from two data sets: (1) the slope (degrees) from one trap to the next and (2) the distance between traps. Distance to the ridgetop was similarly estimated. Distance from the sampling site to the community boundary has been defined previously. All environmental variables were used in correlations with ordination scores to be described later.

CHAPTER IV

ANALYTICAL METHODS

Various techniques have been developed to analyze vegetation data. Cluster techniques (Whittaker 1978b) and ordination techniques (Whittaker 1978a) were devised to respectively classify plant communities and examine vegetational gradients.

The former techniques were developed by researchers who belonged to the community concept school of vegetation. They believed that plant communities exist as clearly definable types which can be classified and mapped (McIntosh 1967). The latter group, the individualistic school, believed that plant populations are independently distributed across the landscape as a result of their individual environmental tolerances (Gleason 1926). Independent distributions result in continuous vegetation gradients such that mapping and classification of communities must be subjective.

These two views were a source of disagreement during the Botanical Congress in the early 1960's (Goodall 1963). As a result, confusion also arose as to the purpose of ordination and classification techniques in studying vegetational patterns. Many thought of these two techniques as being exclusive (McIntosh 1967). Others, such as Whittaker (1978a), considered these two techniques as compatible in that they illuminate different aspects of the same vegetation samples. Goodall (1963 and 1978) also considered ordination and classification

as complementary approaches. A combination of the two techniques were used by Robertson (1978), Hinkle (1978), Schmalzer (1978) and Stocum (1980). A similar approach is used here to study seed banks.

I. ORDINATION

Ordination is a technique used to arrange vegetation samples in a gradient in relationship to environmental gradients (Whittaker 1956). It involves the examination of trends in vegetation at three levels of observation; (1) environmental factors, (2) species populations, and (3) community characteristics (Whittaker 1967). Ordination attempts to simplify a data set (Pielou 1977) in hoping to yield an ecologically meaningful gradient of samples or species.

Ordination techniques assume some model defining how species populations are distributed along environmental gradients. Ordination techniques used by Gauch and Whittaker (Gauch et al. 1977) rely on the Gaussian distribution model of plant populations. Austin (1976) examined the results of several ordination techniques in response to artificial data sets having different species response curves. The species response models used were Gaussian distribution, beta functions, and ecological response. Austin found, for example, that reciprocal averaging works well with Gaussian distribution but poorly using the other species response models. Austin (1976 and 1980) has advocated developing meaningful and realistic species response models rather than further adding to the already diverse ordination techniques.

Two types of ordination techniques exist: direct and indirect. Direct gradient analysis involves the plotting of samples along known

environmental gradients to which species population changes can be related. Weighted averages is a direct ordination technique (Whittaker 1967). Indirect gradient analysis arranges samples into gradients based on similarity of floristic composition. Hopefully the major axis (or axes) of the ordination will be correlated with interpretable environmental variables. Polar ordination, principle components analysis, and reciprocal averaging are indirect techniques (Whittaker 1978a). Reciprocal averaging was used in this study.

Reciprocal averaging (hereafter abbreviated R.A.) or correspondence analysis is an eigenvector technique closely related to weighted averages ordination (Whittaker 1978c) and to principle components analysis (Hill 1973 and 1974). Hill (1973) introduced this technique to the ecological research community.

R.A. starts with a matrix (A) of a_{ij} elements specifying the species scores (rows) from different samples (columns). The algorithm involves successive iteration of the species scores using initial arbitrary sample scores (y_j) attempting to define the sample order along the vegetational gradient:

$$x_i = \sum_j a_{ij} y_j / a_i$$

and the sample scores using the species scores (x_i) derived from the previous iteration:

$$y_j = \sum_i a_{ij} x_i / a_j$$

After many iterations the result is a stable solution producing complementary ordinations of species and samples.

Gauch et al. (1977) compared R.A. with polar ordination and principle components analysis using simulated coenoclines and coenoplanes based on gaussian species distributions. R.A. was shown to exhibit less distortion and involution of the coenocline compared to the other techniques; reciprocal averaging on the other hand tends to produce second and greater axes that are quadratic or higher order functions of the first axis. This produces an arch distortion along high axes; consequently, higher axes are often uninterpretable by correlation with environmental variables.

Austin (1976) found an arch effect in his ordinations, but, like Robertson (1978) showed that such distortion did not preclude obtaining meaningful first axis ordinations. Recently Hill (1979) and Hill and Gauch (1980) have developed a modification of reciprocal averaging that mathematically removes the arch effect. This "detrended correspondence analysis" was not used in this study.

R.A. is also sensitive to outliers since they result in most samples being tightly clumped at one end of the ordination. It is necessary to remove such samples or species contributing to the outlier effect in order to obtain meaningful ordinations (Gauch 1977).

Whittaker (1978c) defined beta diversity or between-habitat diversity as the "degree of change in species composition in the samples taken along a coenocline." Gauch et al. (1977) showed R.A. to be insensitive to beta diversities up to 10 half changes; at high beta diversities, however, bending occurs along the second and third axes. At higher beta diversities the plot sequences along the first axis

can be distorted. R.A. was the least sensitive to high beta diversities among the ordination techniques examined.

In comparing R.A. with other ordination techniques, Gauch et al. (1977) found R.A. sensitive to plot disjunction. Those plots that have no species in common should be removed by ordinating the disjunct sets of plots separately. R.A. does give interpretable results with partial disjunctions in the data.

R.A. as an indirect ordination technique is advantageous since it is objective compared to direct ordination techniques in which the ecologist chooses the gradient end point samples. R.A. also produces simultaneous species and sample ordinations; other techniques do not. R.A. is less sensitive to disjunctions and high beta diversity compared to other techniques. The outlier problem is minor since it is easily solved.

R.A. was used in this study to examine the seed bank pattern across the boundary between the beech gap and spruce stand. In the manner of Peet (1980) the data set was further separated into beech gap seed bank and spruce seed bank. The seed bank pattern within each community could be examined in this manner. All matrices used contained seed density values per m^2. Ordiflex, an ordination computer program set (Gauch 1977) was used to perform reciprocal averaging.

II. CLUSTER ANALYSIS

Cluster analysis was used to determine whether groups observed in the ordinations are different enough to be classified as different

seed banks. Classification techniques group vegetation samples into clusters with similar species compositions.

Classifications can be hierarchical or reticulate; most ecological classifications have been hierarchical because these methods are simple and easy to understand (Pielou 1977). Classification techniques can be divisive or agglomerative. The former means that one large group is successively divided into smaller groups, whereas the latter means that samples are grouped on the basis of some measure of similarity. All classification techniques contain an element of subjectivity when one selects a level within the hierarchy of the cluster dendrogram that defines meaningful groups.

MINFO, a hierarchical agglomerative classification technique written in FORTRAN by Goldstein and Grigal (1972) was used. This algorithm is derived from Orloci's (1969) mutual information method. Robertson (1979) found, using simulated coenoplanes, that MINFO performed better at high beta diversities than did MDISP, another cluster program. On the average both techniques performed well.

The mutual information contained in the matrix A is defined as:

$$I_A = \sum_i \sum_{j \epsilon A} x_{ij} \ln \left\{ \frac{S_A x_{ij}}{\sum_i x_{ij} \sum_{j \epsilon A} x_{ij}} \right\}$$

where $S_A = \sum_i \sum_{j \epsilon A} x_{ij}$ is the value of the ith species from the jth sample. In this case x_{ij} is seed density per meter squared. "A" can refer to an individual sample or groups of samples. During each cycle of the program, pairs of samples or sample groups are grouped together when their clustering results in the minimum increase in the mutual

information value. When ties occur the algorithm has a random number generator to determine which sample or group is added to the previous group (Goldstein and Grigal 1972).

III. DISCRIMINANT FUNCTION ANALYSIS

Discriminant function analysis is a multivariate technique used to ascertain differences between two or more groups by finding a set of linear combinations of the variates giving the greatest separation between the group means (Pielou 1977).

The following statistical discussion relies heavily on Tatsuoka (1971). Discriminant analysis is essentially a multivariate analysis of variance where the object is to maximize the variance between the groups. This is accomplished by maximizing the following:

$$\frac{SS_b\ (Y)}{SS_w\ (Y)} = \frac{v'Bv}{v'Wv} \cong \lambda$$

This is the between groups sum of squares divided by the within groups sum of squares. B and W are, respectively, the between groups sum of squares cross products matrix and the within groups sum of squares cross products matrix. The ratio is maximized by the unknown transformation vector v.

By differentiating the above equation with respect to λ and v, it is possible to find a solution that maximizes the difference between the groups. The resulting eigenvector, v_i, contain weights deriving discriminant functions in the form:

$$Y_i = v_{i1}X_1 + v_{i2}X_2 + v_{i3}X_3 + \ldots + v_{ip}X_p$$

The K-1 discriminant functions optimally differentiate between the K groups. The first function represents the dimension along which the

maximum group differentiation occurs. The second function is inclined along the largest group separation not represented in the first function.

Each discriminant function is uncorrelated with the previous functions in order of increasing eigenvalues; consequently, it is possible to use the eigenvector weights (v_{ip}'s) corresponding to each predictor variable to determine those variables contributing most to the group separation on each discriminant axis. The standarized weights are calculated by multiplying each variable weight by its standard deviation from the corresponding diagonal element of the W matrix. The largest standardized weights correspond to the most important discriminating variables.

Discriminant analysis programs provide F statistics to determine whether significant differences exist between the groups. These F tests allow hypothesis testing when using discriminant analysis.

Discriminant analysis can also be used to classify samples. Discriminant analysis produces classification equations to be used in classifying either the samples used in deriving the functions or samples collected independently from the initial set of samples. Each observation is assigned to the group it has the highest probability of belonging to. Comparison of the known grouping with the expected grouping in the classification matrix aids in evaluating the effectiveness of the discriminant functions; consequently, the total percent correct classification is a measure of the success of discrimination between the groups (Klecka 1975).

To circumvent the circularity of the above approach of classifying the samples on the basis of discriminant functions derived from the same samples, a jackknife classification matrix has been used (Dixon and Brown 1977). This procedure classifies each case using discriminant functions derived from all other cases; the resulting classification matrix is consequently more conservative.

Plots of samples along the first two discriminant functions aid in determining the success of the discriminant analysis. Intermingling samples from different groups suggests unsuccessful discrimination. The distances between the group centroids also permits an evaluation of the success of the analysis (Klecka 1975).

The discriminant function equation reveals each discriminant transformed variable (Y_i) is defined as a linear combination of the predictor variable x_i to x_p. This is true, assuming that the predictor variables are multivariate normally distributed and that the group variance covariance matrices are equal. According to Pielou (1977) both of these assumptions were unlikely to be satisfied for ecological data. Klecka (1975) stated that in practice, the technique "is very robust and the assumptions need not be strongly adhered to."

Discriminant analysis has been used with structural environmental variables to examine small mammal niches by Dueser and Shugart (1979), Seagle (1980), and to examine herbaceous plant niches by Mann (1977). Schmalzer (1978) used discriminant analysis to show that the groups derived from cluster analysis could be distinguished on the basis of environmental variables. Goldstein and Grigal (1972) used discriminant analysis to compare cluster analysis techniques. Stocum (1980) used

discriminant analysis to choose less subjectively the level of dispersion in cluster analysis giving meaningful groups.

In this study discriminant analysis was used to objectively determine which level of mutual information seed bank groups defined by MINFO could be distinguished. The level of mutual information was determined by finding the number of groups (1,2,3,4) giving the highest percent correct classification. The highest percent correct classification reflected the greatest ability of the discriminant functions to distinguish among the groups. Discriminant analysis was also used to evaluate changes in the seed bank with increasing depth into the soil.

A stepwise discriminant analysis program BMDP7M was used in this study (Dixon and Brown 1977). Little trust was placed in the F tests since seed density most likely exhibits a poisson distribution.

IV. DIVERSITY

Diversity indices of the seed rain and seed banks were calculated to determine whether patterns of species richness and commonness occur across the plant communities' boundary. Peet (1974) cautioned that diversity indices quantify different aspects of the data and can be vague in their meaning.

Peet (1974) classified diversity indices into three categories: (1) richness, (2) heterogeneity, and (3) equitability. Species number or richness is simply the number of species present in the sample. This is the easiest index to understand; it is misleading, however, because it is dependent on sample size (Pielou 1977).

Heterogeneity indices quantify species richness and evenness. The Shannon-Wiener and Simpson indices are of this type. Equitability indices quantify the evenness of the species present.

Species richness and heterogeneity indices were calculated for each seed rain and seed bank sample site. A program using equations from Whittaker (1975), written by Anne Stocum and modified by the author was used to calculate the following indices.

1. Species number or richness

$$d = S$$

where S is the number of species in the sample. S was not divided by log A as is normally done to reduce sample size bias since all samples were of the same area (A).

2. Simpson's Index, measuring dominance concentration:

$$C = \sum_{i=1}^{S} p_i^2$$

where p is relative density.

3. Shannon-Wiener Index, measuring equitability:

$$H' = - \sum_{i=1}^{S} p_i \log p_i$$

V. GERMINATION VALUE

Germination value (Czabator 1962) was calculated using the following equation in a computer program written by this author:

$$GV = PV \times MDG$$

Peak value (PV) is the highest value of all the figures calculated in the following manner. For each day germinating seeds are

counted, the total cumulative percent germination is divided by the number of days since the beginning of the germination test. PV expresses the rate of germination because a quickly germinating sample will have a higher numerator than a slower sample on each count day. The result is a higher PV value for the former sample.

Mean daily germination (MDG) is the final total germination percent divided by the number of days of the test; consequently, MDG expresses the overall germination success.

Germination value expresses the germination rate and total germination of a seed sample and was calculated for all germination tests.

VI. JACCARD'S COEFFICIENT OF SIMILARITY

Jaccard's Coefficient of similarity was calculated to examine the similarity between the vegetation, the seed rain, and the seed banks of the two communities. This presence coefficient is defined as:

$$ISJ = \frac{c}{a + b + c} \times 100$$

where c is the number of species in common, a is the number of species unique to the first sample, and b is the number of species unique to the second sample (Muller-Dombois and Ellenberg 1974).

This index, rather than a more quantitative one, was used so comparisons could be made between the results reported here and those of Dobberpuhl (1980) from lower elevation sites in East Tennessee.

VII. DESCRIPTIVE STATISTICS

Descriptive statistics were calculated using programs from the Statistical Analysis System (SAS) (Helwig and Council 1979). Non-parametric statistics were calculated from programs provided by Statistical Package for the Social Sciences (SPSS) (Hull and Nie 1979).

CHAPTER V

THE VEGETATION

In order to understand the seed rain and seed bank data, it is necessary to examine the vegetation present in both communities. Table 2 summarizes the overstory vegetation using density, basal area, and importance values (relative density + relative basal area). The beech gap is clearly dominated by Fagus grandifolia with an average density two magnitudes greater and a basal area one magnitude greater than any other species. Picea rubens, Betula lutea, Amelanchier laevis and Aesculus octandra are of less importance in the canopy.

Picea rubens dominates the spruce stand, with Betula lutea being the next most important canopy tree. Amelanchier laevis occurs less frequently. Counts and d.b.h. measurements reveal this stand was once a spruce-fir community before the balsam woolly aphid killed the Abies fraseri trees.

Figure 6A and B shows the changes in importance values for the overstory and relative density for the understory across the boundary between the beech gap and spruce stand. Fagus grandifolia and Picea rubens intergrade with each other in a zone about 20 to 30 m wide. Aesculus octandra, Betula lutea, and Amelanchier laevis appear to be ecotonal in occurrence; only Amelanchier laevis, however, is limited to the ecotone.

Table 2. Beech Gap and Spruce Stand Overstory Vegetation.

Species	Beech Gap				Spruce Stand			
	D ± SE*	BA ± SE*	IV ± SE*	F*	D ± SE*	BA ± SE*	IV ± SE	F*
Fagus grandifolia	1787 ± 142	21.30 ± 2.55	173 ± 12	100	113 ± 52	1.38 ± 0.63	10 ± 4	57
Picea rubens	40 ± 23	0.01	6 ± 4	38	812 ± 152	35.80 ± 6.63	131 ± 10	100
Amelanchier laevis	34 ± 21	1.01 ± 0.68	5 ± 3	38	32 ± 14	1.46 ± 0.71	7 ± 3	57
Aesculus octandra	22 ± 10	0.94 ± 0.70	4 ± 2	50				
Betula lutea	19 ± 10	1.67 ± 1.62	6 ± 5	38	103 ± 53	6.05 ± 1.25	23 ± 7	100
Cornus alternifolia	15 ± 15	<0.01	<1	13				
Acer rubrum	6 ± 4	1.62 ± 1.62	5 ± 5	25	32 ± 15	0.03 ± 0.02	3 ± 1	57
Prunus serotina	6 ± 6	<0.01	<1	13				
Viburnum alnifolium	3 ± 3	<0.01	<1	13	169 ± 67	0.02 ± 0.01	13 ± 5	86
Abies fraseri	3 ± 3	0.01 ± 0.01	<1	13	39 ± 39	0.11 ± 0.11	2 ± 2	14
Acer pensylvanicum	3 ± 3	<0.01	<1	13	132 ± 60	0.05 ± 0.02	9 ± 4	86
Rubus canadensis					4 ± 4	<0.01	<1	14
Sorbus americana					35 ± 21	<0.01	3 ± 1	43
Abies fraseri dead					183 ± 57	10.72 ± 3.61		

*D ± SE = Density of stems per hectare ± 1 standard error. BA ± SE = basal area (m^2) of stems per hectare ± 1 standard error. IV ± SE = importance value (relative density ± relative basal area) ± 1 standard error. F = frequency of occurrence out of eight beech gap plots and seven spruce stand plots.

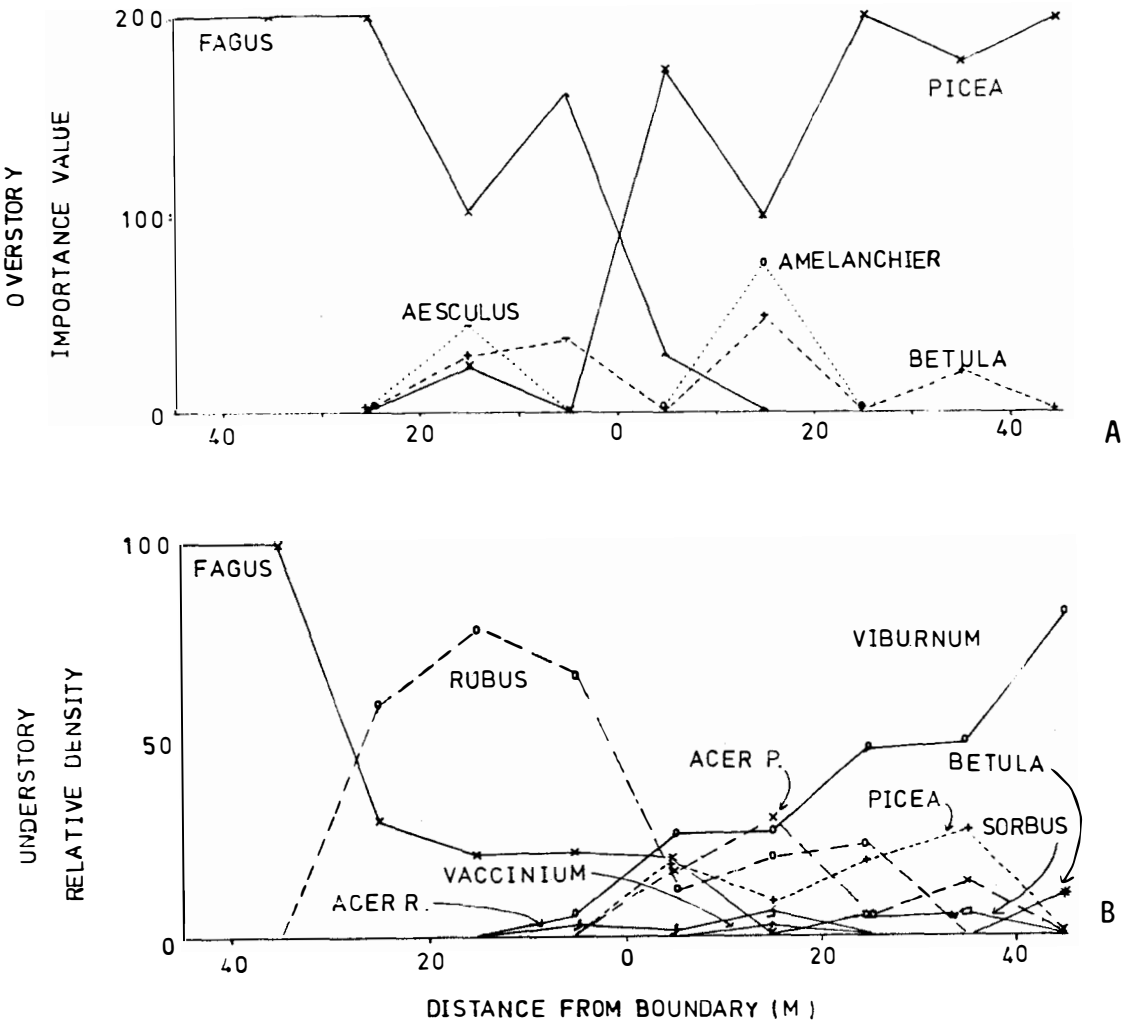


Figure 6. Overstory Importance Values and Understory Relative Density along Vegetation Transect.

A. Overstory Importance Value.

B. Understory Relative Density.

The understory also has a gradual intermixing of Picea rubens and Fagus grandifolia. Obviously the beech gap understory is dominated by Rubus canadensis and Fagus grandifolia. The spruce stand understory is characterized by the presence of several species, including Acer pensylvanicum, Acer rubrum, Viburnum alnifolium, Vaccinium erythrocarpum, Betula lutea, and Sorbus americana.

Figure 7A and B shows the diameter distribution of the four most common tree species at the study site: Picea rubens and Betula lutea and Fagus grandifolia and Abies fraseri.

Picea rubens shows gradual decline in numbers of stems from small to large d.b.h. Betula lutea had few small d.b.h. stems; its population was composed of trees of large diameters. Fagus grandifolia had high densities of young stems but did not grow to diameters greater than 40 cm d.b.h.

Abies fraseri size class distribution showed no living stems greater than 12 cm d.b.h. All stems greater than 12 cm d.b.h. were killed by the balsam woolly aphid infestation. It is not clear whether or not any Abies fraseri trees will be found in the smaller size classes in the future. The absence of any seed source suggested no further reproduction will occur until the present young trees bear seeds.

The beech gap understory (Table 3) is quite open with Rubus canadensis and Fagus grandifolia being the most common species. Rubus canadensis, however, forms a typical thicket at the site of a 83 cm d.b.h. senscent Acer rubrum. Other shrubs are infrequent and low in density.

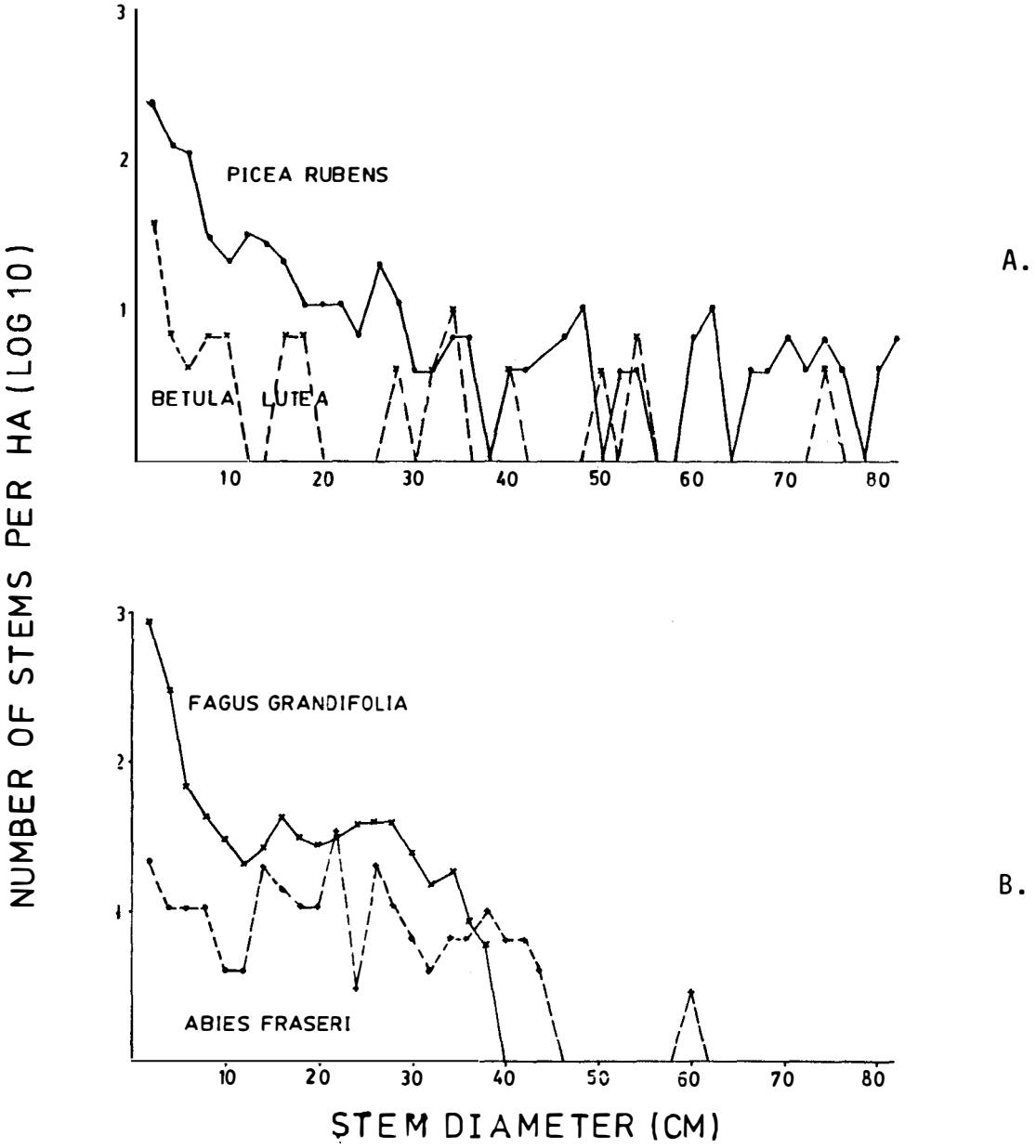


Figure 7. Size Class Distribution (2 cm Intervals) of Picea rubens, Betula lutea, Fagus grandifolia, and Abies fraseri.

A. Picea rubens and Betula lutea.

B. Fagus grandifolia and Abies fraseri.

Table 3. Beech Gap and Spruce Stand Shrub Vegetation.

Species	Beech Gap		Spruce Stand	
	Density/ha	Frequency (%)	Density/ha	Frequency (%)
Rubus canadensis	1738 ± 970	75	1306 ± 646	57
Fagus grandifolia	1007 ± 282	88	35 ± 35	14
Amelanchier laevis	213 ± 213	13		
Viburnum alnifolium	61 ± 61	13	2012 ± 433	100
Cornus alternifolia	31 ± 31	13		
Lilium arboreum	31 ± 30	13		
Abies fraseri	31 ± 30	13	71 ± 46	29
Betula lutea			529 ± 390	29
Picea rubens			494 ± 235	43
Vaccinium erythrocarpum			388 ± 309	43
Acer rubrum			318 ± 279	29
Sorbus americana			282 ± 244	29
Acer pensylvanica			141 ± 106	29
Prunus pensylvanica			106 ± 106	14

The spruce stand understory contains high densities and frequencies of Viburnum alnifolium, Rubus canadensis, and Vaccinium erythrocarpum. Betula lutea, Sorbus americana, and Prunus pensylvanica are present in the sample with the highest density of dead Abies fraseri. In the area of greatest canopy disturbance Rubus canadensis formed a nearly impenetrable thicket.

In May the beech gap herb layer (Table 4) was dominated by Claytonia virginica, Erythronium americanum and Phacelia fimbriata with patches of Carex intumscens and C. pensylvanica. In the spring it appears to be snow covered because of the dense coverage of Claytonia virginica flowers. Other herbs blooming at this time include Trillium erectum, Thalictrum dioicum, Stellaria pubera, and Houstonia serpyllifolia.

By July, the spring ephemeral herbs have died back; consequently, Laportea canadensis, ferns, Stachys clingmanii, Impatiens pallida, Angelica triquinata, and Solidago sp. are dominant. Other important herbs are Prenanthes altissima and Aster divaricatus. Epifagus virginiana, Allium tricoccum, Caulophyllum thalictroides, Polygonatum sp., Smilacina racemosa, and Hydrophyllum virginiana were observed in the beech gap, but were not present in the sample plots. The beech gap ground cover probably represents Crandall's Athyrium site type (1959).

The spruce stand herbaceous vegetation (Table 5) had less species richness than the beech gap. Oxalis montana, Cacalia rugelia, and various ferns were the most common herbs. The presence of Claytonia virginica and Erythronium americanum was due to an isolated island of beech gap herbs under the spruce canopy 15 m from the defined boundary.

Table 4. Beech Gap Herbaceous Vegetation.

Species	Density/m^2		Coverage (%)		IV (%)		Frequency (%)	
	May	July	May	July	May	July	May	July
Claytonia virginica	1176 ± 405		78 ± 17		142 ± 28		100	
Poa alsodes	55 ± 167	40 ± 88	3 ± 3	4 ± 9	6 ± 9	14 ± 4	60	91
Erythronium americanum	46 ± 40		9 ± 8		14 ± 12		90	
Houstonia serphyllifolia	45 ± 182		1 ± 2		3 ± 11		15	
Carex intumescens	26 ± 34	13 ± 26	2 ± 2	4 ± 8	3 ± 5	11 ± 8	55	36
Carex pensylvanica	34 ± 92		2 ± 5		3 ± 9		15	
Stellaria pubera	14 ± 22	6 ± 7	1 ± 1	<1	3 ± 4	4 ± 6	55	55
Phacelia fimbriata	10 ± 15		4 ± 9		8 ± 14		50	
Solidago sp.	10 ± 10	7 ± 8	2 ± 2	4 ± 6	3 ± 3	11 ± 15	80	73
Prenanthes altissima	6 ± 10	3 ± 4	4 ± 11	1 ± 1	3 ± 7	5 ± 6	65	55
Stachys climgmanii	4 ± 8	14 ± 18	1 ± 1	12 ± 19	1 ± 2	26 ± 42	40	55
Angelica triquinata	4 ± 5	6 ± 13	2 ± 4	7 ± 16	3 ± 6	10 ± 21	60	45
Luzula echinata	4 ± 16	<1	1 ± 2	<1	<1	1	10	10
Impatiens pallida	3 ± 6	3 ± 4	<1	5 ± 8	1 ± 2	14 ± 25	30	36
Aster divaricatus	2 ± 4	3 ± 4	1 ± 1	1 ± 3	1 ± 2	6 ± 8	35	45
Lilium superbum	1 ± 3		1 ± 3		2 ± 6		15	
Trillium erectum	1 ± 2		1 ± 1		1 ± 2		15	
Rubus canadensis	1 ± 1	1 ± 2	1 ± 1	5 ± 8	1 ± 1	7 ± 12	25	36
Dentaria diphylla	1 ± 1		<1		<1		25	
Poaceae	<1		<1		<1		5	
Thalictrum dioicum	<1		<1		<1		5	
Rudbeckia laciniata	<1		<1		<1		5	
Fagus grandifolia	<1	1 ± 1	<1	4 ± 8	<1	6 ± 11	5	64
Pteridophytes	<1	3 ± 2	<1	24 ± 25	<1	26 ± 30	5	73
Laportea canadensis		19 ± 12		15 ± 11		33 ± 29		100
Cuscuta gronovii		<1		<1		<1		18
Smilax sp.		<1		<1		<1		10

Table 4. (Continued)

Species	Density/m^2		Coverage (%)		IV (%)		Frequency (%)	
	May	July	May	July	May	July	May	July
Eupatorium rugosum	<1	<1		<1		<1		10
Streptopus roseus	<1	<1	<1	<1	<1	<1	10	10
Viburnum alnifolium		<1		<1		<1		10

*Twenty plots were sampled in May 1980 and 11 in July 1979.

Table 5. Spruce Stand Herbaceous Vegetation.

Species	Density/m^2		Coverage (%)		IV (%)		Frequency (%)*	
	May	July	May	July	May	July	May	July
Oxalis montana	767 ± 726[+]	487 ± 720	25 ± 26	26 ± 27	117 ± 58	116 ± 186	89	67
Lycopodium lucidulum	8 ± 10	8 ± 15	1 ± 1	1 ± 1	7 ± 23	8 ± 17	44	50
Cacalia rugelia	7 ± 4	7 ± 5	14 ± 10	15 ± 11	24 ± 23	22 ± 20	83	83
Clintonia borealis	3 ± 8	2 ± 5	7 ± 21	5 ± 16	5 ± 14	3 ± 11	17	8
Vaccinium erythrocarpum	2 ± 3	1 ± 2	9 ± 25	6 ± 11	27 ± 57	4 ± 8	50	33
Pteridophytes	1 ± 2	1 ± 1	3 ± 4	15 ± 22	8 ± 10	16 ± 22	67	50
Carex pensylvanica	1 ± 4	1 ± 1	2 ± 7	<1	1 ± 4	<1	6	8
Claytonia virginica	1 ± 2		<1		<1		17	
Picea rubens	1 ± 1	1 ± 2	5 ± 13	5 ± 14	4 ± 9	8 ± 17	28	42
Erythronium americanum	<1		<1		<1		6	
Viburnum alnifolium	1 ± 1	1 ± 2	1 ± 1	6 ± 9	2 ± 7	11 ± 21	28	42
Rubus canadensis	<1		2 ± 5		3 ± 8		22	
Luzula echinata	<1		<1		<1		6	
Streptopus roseus	<1	<1	<1	<1	<1	<1	11	8
Abies fraseri	<1	<1	<1	2 ± 7	1 ± 2	2 ± 5	17	17
Prunus pensylvanica	<1		<1		<1		6	
Betula lutea	<1	<1	<1	<1	<1	1 ± 3	17	8
Trillium erectum	<1		<1		<1		6	
Acer pensylvanicum	<1		<1		<1		6	
Eupatorium rugosum		2 ± 5		<1		9 ± 30		17

*Twelve plots were sampled in July 1979 and 18 in May 1980.

[+]The values are the means ± the standard deviation.

Other spring blooming herbs occurred infrequently in the spruce stand.

The spruce stand along the lowest transect was devoid of vegetation, except for some Lycopodium lucidulum, Oxalis montana, and Vaccinium erythrocarpum; consequently, this site probably represented Crandall's (1959) Viburnum-Vaccinium-Lycopodium spruce site type. The remainder and majority of the ground cover represents Crandall's Viburnum-Vaccinium-Dryopteris site type.

CHAPTER VI

THE SEED RAIN

Seed rain data were collected for one year. Figure 8 illustrates the seed rain phenology. The seed rain peaks in the fall and in the spring. Seventy-one percent of all seed collected was Betula lutea and 15% was Claytonia virginica. Only 2% were Fagus grandifolia and 1% Picea rubens.

Solidago sp., Aster cordifolius, Betula lutea, Picea rubens, Fagus grandifolia, Cacalia rugelia, Viburnum alnifolium, Eupatorium rugosum, Prenanthes altissima, Impatiens pallida, and Angelica triquinata all disperse seeds in the fall.

Spring dispersing species include Claytonia virginica, Phacelia fimbriata, Carex pensylvanica, and Poa alsodes. Oxalis montana, Amelanchier laevis, Laportea canadensis, and Rubus canadensis disperse seeds during mid and late summer. The phenology diagram shows a continuous seed rain throughout the year; the data collection was not frequent enough, however, to examine dispersal period overlap between species.

Since most seeds of Betula lutea and Picea rubens dispersed during the autumn, it is probably incorrect that seeds of these species dispersed in fairly high numbers during the months of March, April, and May as Figure 8 suggests. Ice and snow prevented trap collection more frequently during this period.

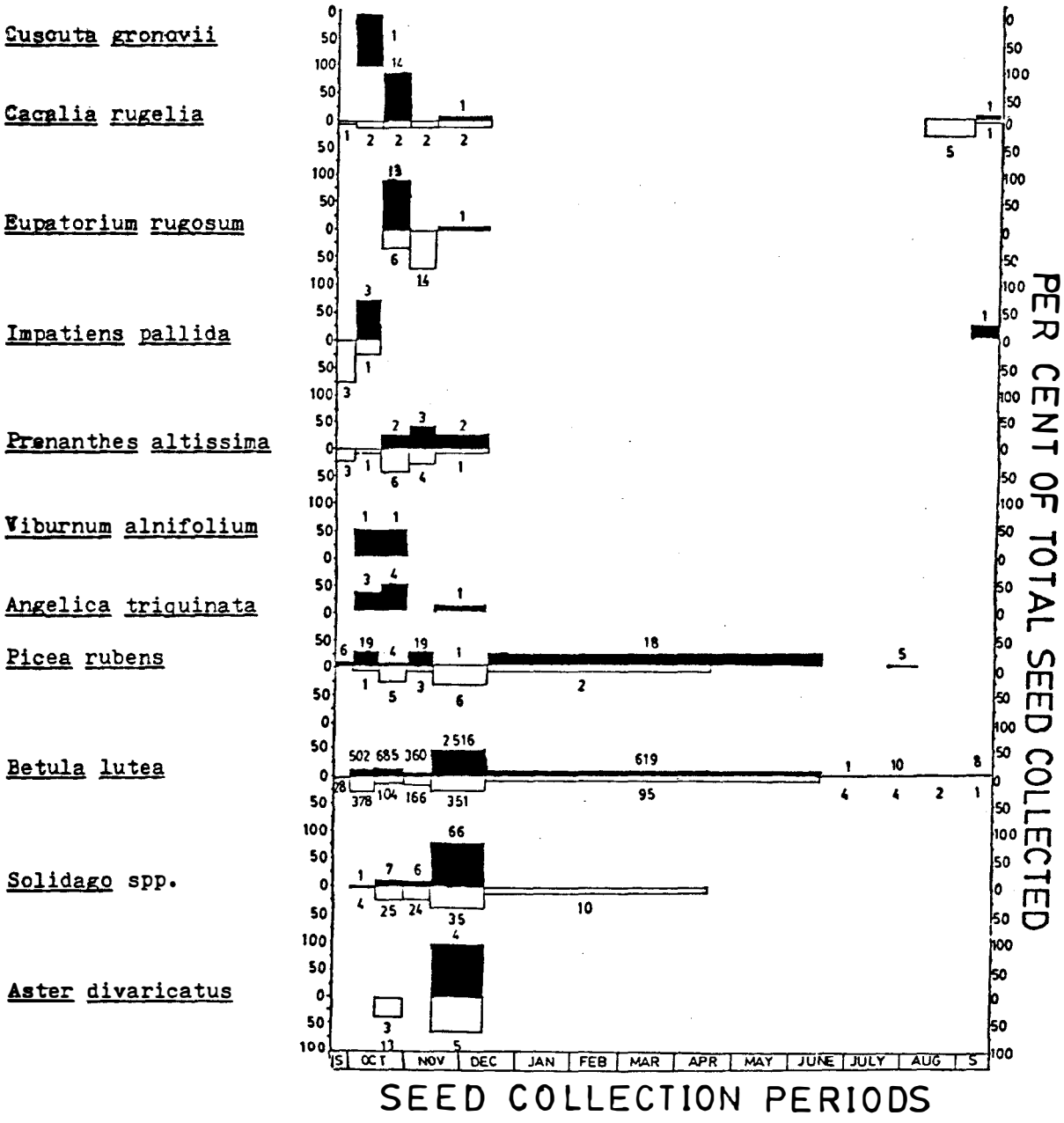


Figure 8. Seed Rain Phenology Summary. Bar height represents the proportion of all seeds of a species collected during a particular time period. Bar length represents the length of the seed rain collection period. Solid bars = gravity traps and open bars = sticky traps. Numbers above and below the respective bar type are the total number of seeds collected during that period.

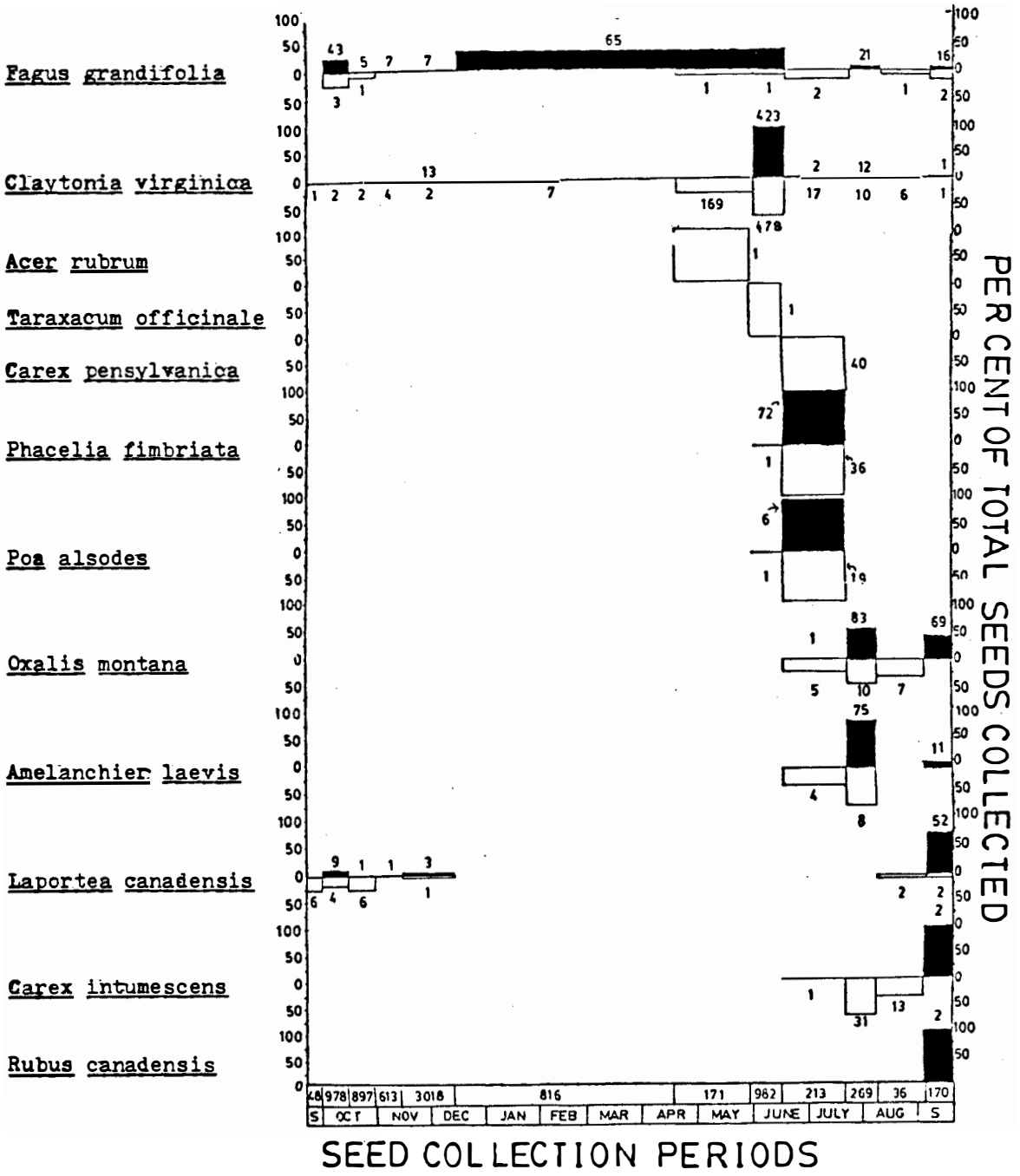


Figure 8. (Continued)

The occurrence of Claytonia virginica seed entering the traps in numbers throughout the year was the result of winds blowing seeds already dispersed into the leaf litter. Although the phenology diagram shows a total of 175 Fagus grandifolia nuts collected during the year, only two of them were found to be full; the majority were aborted. Unfortunately, the tetrazolium viability test was negative for viability; it was, however, suspected that the reagent had deteriorated at that time.

Table 6 summarized the seed rain by site and by trap type. The low frequency of most seeds prevented testing the hypothesis that significant changes in seed rain composition and density would occur with increasing distance from the boundary. Species common to both communities were Betula lutea, Picea rubens, Fagus grandifolia, Amelanchier laevis, Claytonia virginica, Poa alsodes, Eupatorium rugosum, and Cacalia rugelia. Of these, the following were not believed to be actually dispersing across the boundary: Amelanchier laevis, an ecotonal species, and Claytonia virginica and Fagus grandifolia since they had small populations within the spruce stand near the boundary.

Betula lutea and Picea rubens seeds dispersed from the spruce stand into the beech gap as did Cacalia rugelia. The presence of Poa alsodes seeds in the spruce stand indicates the seeds were dispersed from the beech gap where this species normally occurs. Eupatorium rugosum may have been dispersed from the beech gap into the spruce stand, but the higher density of this species in the spruce vegetation ($2/m^2$) than the beech gap ($1/m^2$) vegetation suggests likewise.

Table 6. Summary of the Beech Gap and the Spruce Stand Seed Rain by Seed Trap Type.

Species	Beech Gap* Density (#/m^2 + SE) Sticky	Beech Gap* Density (#/m^2 + SE) Gravity	Beech Gap* Frequency (%) Sticky	Beech Gap* Frequency (%) Gravity	Spruce Stand+ Density (#/m^2 + SE) Sticky	Spruce Stand+ Density (#/m^2 + SE) Gravity	Spruce Stand+ Frequency (%) Sticky	Spruce Stand+ Frequency (%) Gravity
Woody Species								
Betula lutea	732 ± 139	736 ± 166	100	100	858 ± 93	918 ± 111	100	100
Picea rubens	6 ± 4	7 ± 2	8	36	21 ± 5	18 ± 4	29	74
Fagus grandifolia	13 ± 5	53 ± 10	24	88		1 ± 1		5
Amelanchier laevis	2 ± 2		4		15 ± 13	34 ± 19	11	14
Viburnum alnifolium						1 ± 1		4
Rubus canadensis						1 ± 1		2
Acer rubrum	2 ± 2		4					
Herbaceous Species								
Claytonia virginica	1254 ± 192	211 ± 37	100	100	17 ± 14	18 ± 17	3	3
Solidago sp.	190 ± 107	43 ± 16	48	30				
Poa alsodes	85 ± 61	8	8		1 ± 1		3	
Carex pensylvanica	78 ± 78		4					
Phacelia fimbriata	72 ± 46	40 ± 40	16	4				
Laportea canadensis	56 ± 27	35 ± 8	32	68				
Eupatorium rugosum	37 ± 14	8 ± 5	32	16	1 ± 1		3	
Prenanthes altissima	23 ± 12	4 ± 2	20	16				
Oxalis montana					29 ± 8	51 ± 10	40	60
Aster divaricatus	15 ± 8	2 ± 1	16	12				
Impatiens pallida	8 ± 5	2 ± 1	4	12				
Cacalia rugelia	2 ± 2	1 ± 1	4	4	19 ± 11	1 ± 4	20	3
Carex intumscens	4 ± 3	37 ± 31	20	12				
Angelica triquinata		3 ± 2		12		1 ± 1		3
Cuscuta gronovii		1 ± 1		4				
Taraxacum officinale	2 ± 2		4					

*Sample size is 25.

+Sample size is 35.

The beech gap seed rain is dominated by Betula lutea, Claytonia virginica, and Solidago sp. while the spruce stand seed rain was dominated by Betula lutea and Oxalis montana.

On the average, 5 ± 2 species landed on beech gap sticky traps with a significantly lower number ($P=0.0001$, $T=6.6$, d.f.=58) of 2 ± 1 species per trap in the spruce stand. Beech gap sticky traps had a significantly higher Shannon-Wiener Index ($P=0.0001$, $T=7.3$, d.f.=58) of 0.41 ± 0.16 compared to 0.13 ± 0.12 for the spruce stand sticky traps. This trend occurred because the beech gap seed rain was more equitable. That is, it had two common species, Betula lutea and Claytonia virginica, whereas the spruce seed rain had only one common species, Betula lutea. Conversely, the spruce stand seed rain had a significantly higher Simpson's Index ($P=0.0001$, $T=8.0$, d.f.=58) than the beech gap since dominance measured by this index is inversely proportional to equitability. Similar diversity trends occurred in the gravity trap seed rain (see Appendix A).

Seed rain trap comparisons permits an assessment of the collection bias of each trap type. Generally, herbaceous seeds were more dense in sticky traps than in gravity traps; the converse was true for the tree seeds. Poisson distributions of most seed densities made statistical comparisons problematical.

Only Betula lutea had normally distributed seed rain densities; consequently, it was possible to demonstrate no significant difference between the densities collected by the two trap types ($P=0.91$, $T=-0.10$, d.f.=47). The following species were shown to have significantly different medians on the basis of the median test (Hull and Nie 1979):

Claytonia virginica (χ^2=15.68,P=0.001,N=50), Fagus grandifolia (χ^2=11.52,P=0.001,N=50), Laportea canadensis (χ^2=5.12,P-0.024,N=50), and Picea rubens (χ^2=6.65,P=0.01,N=50). Claytonia virginica had densities greater than the overall median for the sticky trap samples, whereas all the others had densities greater than the overall median for the gravity trap samples. The median test shows no significant differences between the two trap types in the spruce stand.

Since Betula lutea was the only species dispersing across the boundary in high densities, an examination of its dispersal seemed appropriate. Figure 9 shows the regression of the log density of Betula lutea as a function of seed trap distance from the boundary into the beech gap in meters. The F-max test (Sokal and Rolff 1969) demonstrated homogeniety of variances between the groups (P=0.05,F_{max}=17.3, d.f.=6,4). The overall regression is significant (P=0.001,F=21.88, d.f.=1,28,r=0.66). It is important to note that this regression includes empty seeds. This negative exponential density decrease with increasing distance from the seed source is the common dispersal function. Germination tests (Table 7) show that the percent germination for Betula lutea averaged 18% to 29% during the fall of 1979. The lower regression line in Figure 9 represents the density function with full seeds only. The percent germination used was 24% since no significant difference was found for seed traps 67.5 to 22.5 m (20%) and 0.0 to 7.5 m (28%) from the boundary.

The highest overall percent germination was 42% for seed collected October 14, 1979. This is significantly greater than (P=0.01,T=5.1,d.f.=5) the 23% germination of seeds collected October 27

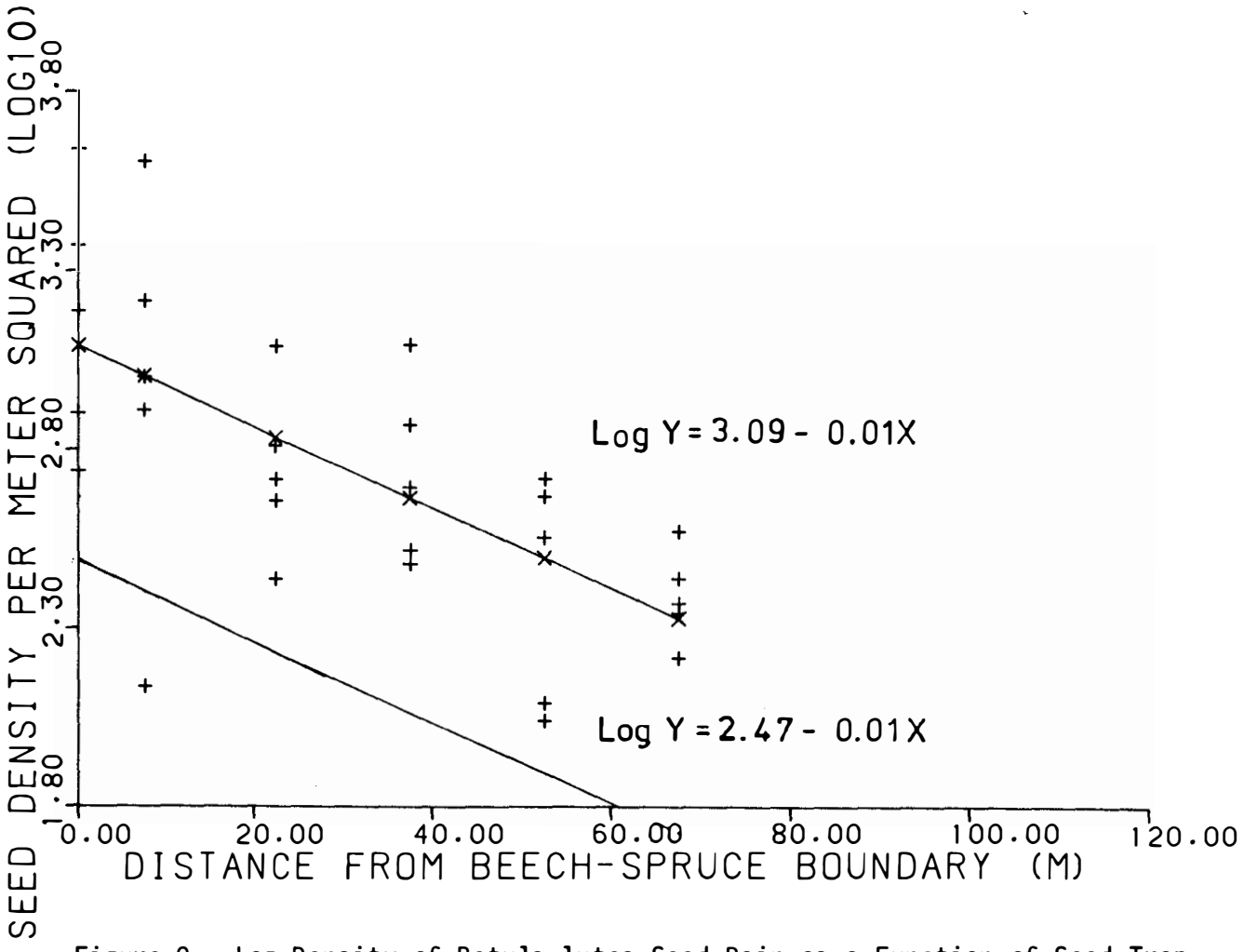


Figure 9. Log Density of Betula lutea Seed Rain as a Function of Seed Trap Distance from the Boundary into the Beech Gap. The regression equation is significant ($r = -0.66$, $F = 21.88$, d.f. = 1, 28, $P = 0.001$). The lower line represents the same line, taking into account the percent germination of the seeds.

Table 7. Summary of Betula lutea Germination and Viability Tests.

Date/ Location	Germination Test		Viability Test			
					%US*	
	%G	GV*	%S*	%PS*	%F*	%E*
October 14						
All sites	42 ± 6	3.06 ± 1.92				
October 27						
Beech Gap						
22.5 - 67.5 m	18	0.53				
0.0 - 7.5 m	19	0.53				
Spruce Stand						
7.5 - 22.5 m	26	0.81				
37.5 = 52.5 m	26	1.17				
67.5 - 97.5 m	27	0.84				
Average	23 ± 4	0.77 ± 0.27				
December 9						
Beech Gap						
22.5 - 67.5 m	22 ± 13	0.88 ± 0.91	3	4	2	69
0.0 - 7.5 m	36 ± 11	2.30 ± 1.21	2	1	5	57
Spruce Stand						
7.5 - 22.5 m	35 ± 10	1.95 ± 1.31	4	5	2	54
37.5 - 52.5 m	15 ± 12	0.62 ± 0.87	0	1	5	79
67.5 - 97.5 m	10 ± 8	0.24 ± 0.22	2	1	0	87
Average	24 ± 14	1.20 ± 1.19	2.2	2.4	2.8	69.2

*G = germination. GV = germination value. S = completely stained. PS = partially stained. US = unstained. F = full seeds with embryo. E = empty seeds without embryo.

and December 9. After correcting Betula seed rain for the percent of empty seeds, it was found that 19% of all full seeds were collected at the period ending October 14, 9% in the period ending October 27, and 36% in the period ending December 9. Dividing the number of full seeds per period by the number of days during the period gives a better indication of the rate of Betula lutea seed rain fall. Such calculations show 26 seeds per day were dispersed during September 30 to October 14, with slightly fewer seeds, 25 were dispersed during the November 10 to December 9 period. Seed rain rates between October 14 and November 10 were lower (14 and 9 seeds per day).

The germination values (Table 7) frequently parallel the germination percentages in magnitude; a few do, however, vary from the trends because germination value is a function of the speed of germination. For example, two samples collected October 27 show a final germination of 26%; one of these samples, however, has a germination value of 0.81 compared to 1.17 in the other. The high germination value in the latter results from more rapid germination than in the other sample. The germination value declines as autumn progresses from a high value of 3.06 on October 14, to 0.77 on October 27, to 1.20 by December 9.

Densities of Betula lutea decline with increasing distance from the seed source and the germination percent declines as the dispersal period progresses. The tetrazolium test (Table 7) indicates that the germination tests were low by approximately 2% (fully stained seeds) of all seeds.

Betula lutea seed rain was examined further by comparing the seed densities with distance, direction, and d.b.h. of the two nearest source trees. Correlations using all predictor variables on seed density and logarithm of seed density were not significant. It was assumed high variation would occur in this spruce stand data set resulting from wind direction differences, turbulence, and seed rain shadows. The data set was reduced in half by making the following assumptions.

Major winds were assumed to come from the north over the state line ridge crest in a southerly downslope direction. This was based on personal observation that winds and storms generally come from the west but are redirected to the south by the local topography. Directional seed traps along the boundary confirm that the major winds come from the ridge crest (see Figure 10). Although the directional densities are not significantly different, they suggest that winds come from the ridge crest, assuming that high seed densities reflect wind direction rather than the abundance of seed.

If the major winds do blow over the ridge crest and into the study area, then variation in the data can be eliminated by removing all sites upwind from the nearest source trees. The density of the seed rain on traps upwind from the nearest source tree would be a function of those trees occurring upwind from the trap, rather than the closer downwind seed sources.

All samples with the nearest and second nearest Betula lutea trees downwind or 90° to 270° from the trap were removed from the data set. Any samples with the two nearest trees less than 13 cm d.b.h.

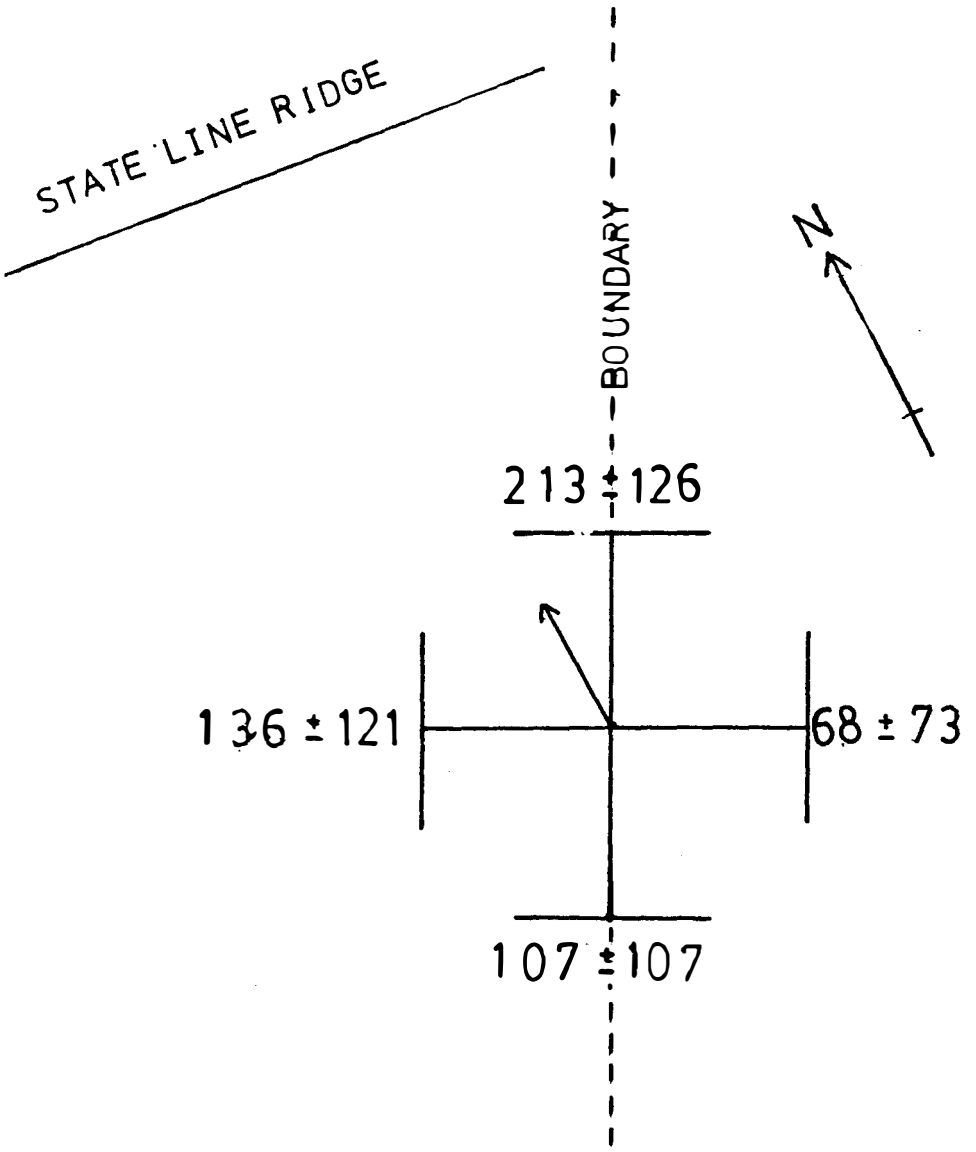


Figure 10. Directional Seed Trap Results. Values are mean densities per m^2 ($\pm$ SD) from five replicates in four directions. Arrow points in direction major winds are believed to originate.

were excluded because trees this size generally do not bear seed (Fowells 1965).

The above modifications resulted in a significant correlation between the log seed density and the distance and d.b.h. of the two nearest source trees (P-0.01,r-0.67). Much of the variance was explained by a high correlation (r=0.55) of the log seed density with the distance to the second closest tree (see Figure 11). The linear trends on these plots transforms into a negative exponential decrease in Betula lutea seed with increasing distance from the source tree on the arithmetic scale. Betula lutea seed dispersal in the spruce canopy demonstrates a similar pattern to that into the beech gap.

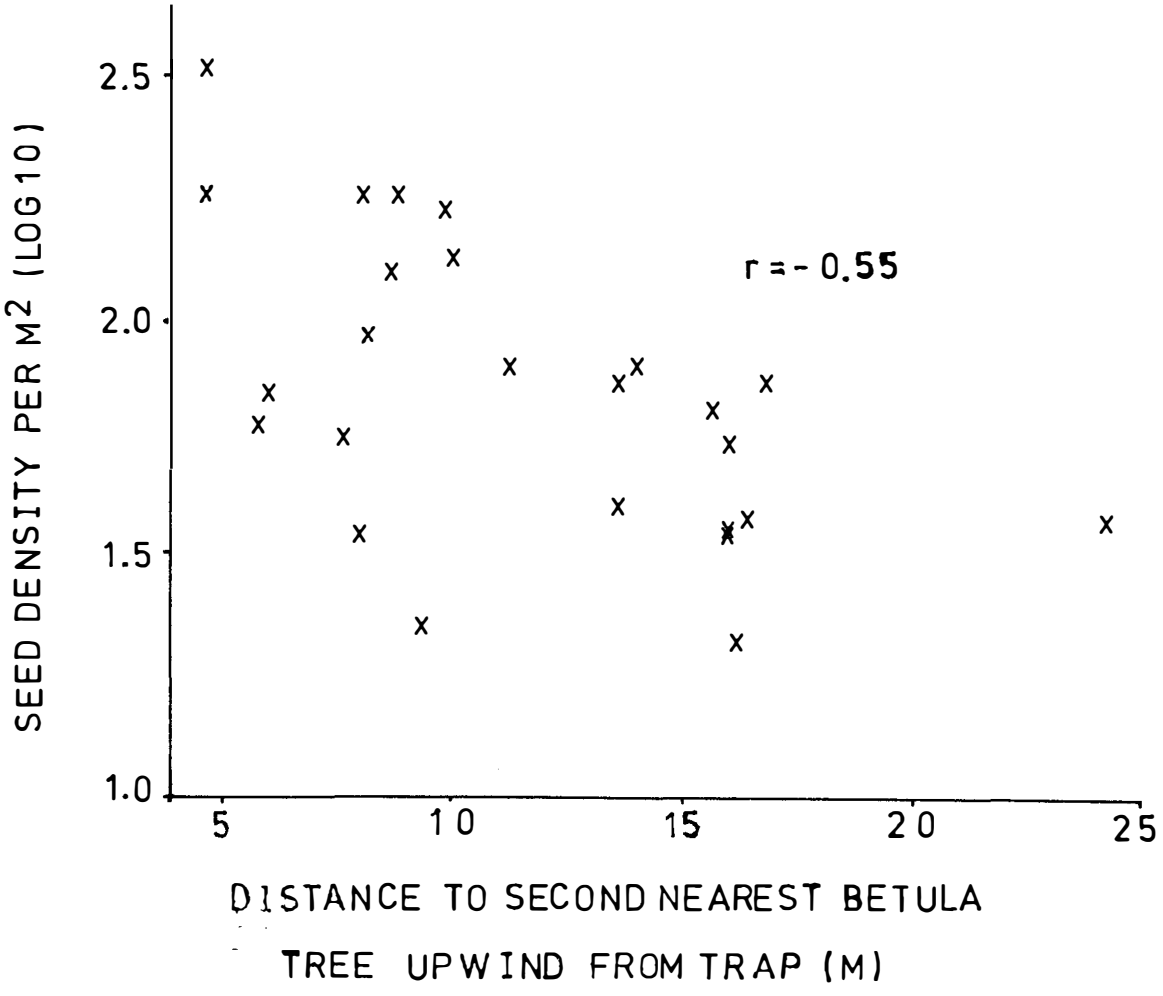


Figure 11. Scatter Diagram of Correlation between Log Density of Betula lutea and Distance to Second Nearest Tree.

CHAPTER VII

THE SEED BANK

A total of 8002 seedlings emerged from the seed bank samples with 6554 of these from the beech gap samples and 1448 from the spruce stand samples. The average number of seeds per beech gap sample (262 ± 389) was significantly greater than the number (58 ± 38) emerging from the spruce sample ($P=0.02, T=2.6, d.f.=48$).

The high average number of beech gap germinants is misleading because soil core #57 had a total of 1924 Potentilla simplex seedlings, an order of magnitude higher than all other plot totals! The recalculated average, 185 ± 113 is, however, still significantly greater than the average seed number per spruce sample ($P=0.001, T=5.3, d.f.=48$).

Greenhouse control flats contained three species: Betula lutea, Rubus canadensis, and Oxalis stricta. The first two were probably seeds splashed onto the controls from neighboring spruce soil flats during watering. Betula lutea and Rubus canadensis were not found at Norris, TN (Dobberpuhl 1980). Oxalis stricta plants grew in the greenhouse along the walls and under the benches; consequently, it is believed these plants were contaminants.

Other species that germinated in the flats include Andropogon scoparius seeds that were stored in a paper bag in the greenhouse. The seeds apparently dispersed onto the flats, where they germinated. Other species probably entered through the ventilation-cooling system.

Large fans blew air through a water cascade system to cool the greenhouse. Some seeds probably entered when the water was off and the fans were blowing. These other contaminants included Ulmus americana, Platanus occidentalis, and possibly Erechtites hieracifolia. Contaminants were excluded from the analysis. They comprised a small percent of the total seeds germinating.

Seed bank data calculated for the beech gap and spruce stand are summarized in Table 8. A significantly higher number of species germinated in the beech gap (13 ± 2) than in the spruce stand seed bank (6 ± 2) ($P=0.001, T=12.1, d.f.=48$).

Seed bank diversity index trends are similar to those for the seed rain. The beech gap seed bark had a significantly higher average Shannon-Wiener Index ($P=0.001, T=6.8, d.f.=98$) value (0.73 ± 0.17) than to the spruce stand index (0.50 ± 0.17). This results from the greater number of species in the beech gap with more equitable dominance relative to the spruce stand. Conversely the spruce stand seed bank had a significantly higher Simpson's index value (0.42 ± 0.18) than the beech gap seed bank (0.29 ± 0.13) ($P=0.0001, T=4.3, d.f.=98$). This was because the spruce stand seed bank was dominated by fewer species in contrast to the beech gap seed bank.

The beech gap seed bank was dominated by Claytonia virginica, Phacelia fimbriata, Carex intumescens, Eupatorium rugosum, Viola pallens, Betula lutea, Laportea canadensis, Houstonia serpyllifolia, Rubus canadensis, and Prenanthes altissima.

Some species occurring in high densities but in low frequency are Rumex acetosella, Barbarea vulgaris, and Potentilla simplex.

Table 8. Summary of the Beech Gap and Spruce Stand Seed Banks.

Species	Beech Gap				Spruce Stand			
	D ± SE	CV	F(%)	PCT	D ± SE	CV	F(%)	PCT
Potentilla simplex	963 ± 77	40	12	28.5	1 ± 1	800	8	0.1
Claytonia virginica	412 ± 62	75	96	12.2	22 ± 15	346	8	2.8
Carex intumescens	321 ± 143	223	72	9.5				
Eupatorium rugosum	286 ± 69	119	96	8.8	21 ± 6	153	60	2.7
Viola pallens	224 ± 148	331	56	6.6	75 ± 41	275	40	9.7
Rumex acetosella	219 ± 186	424	8	6.5				
Phacelia fimbriata	127 ± 49	192	64	3.8				
Betula lutea	125 ± 34	138	88	3.7	330 ± 53	81	100	42.7
Laportea canadensis	98 ± 29	148	84	2.9				
Houstonia serpyllifolia	97 ± 96	140	68	2.6	24 ± 18	383	8	3.1
Rubus canadensis	62 ± 11	86	84	1.8	162 ± 23	71	100	21.0
Prenanthes altissima	59 ± 32	269	40	1.7				
Barbarea vulgaris	52 ± 34	326	12	1.5				
Cuscuta gronovii	51 ± 25	242	35	1.5				
Poaceae	39 ± 39	500	8	1.2	4 ± 4	500		0.5
Solidago sp.	39 ± 13	170	56	1.2				
Stachys clingmanii	36 ± 8	117	60	1.1				
Blephilia hirsuta	36 ± 36	500	8	1.1				
Impatiens pallida	28 ± 14	254	32	0.8	3 ± 3	419	8	0.4
Erythronium americanum	21 ± 10	250	40	0.6	10 ± 10	500	8	1.3
Stellaria pubera	20 ± 9	224	28	0.6				
Dicentra cucullaria	13 ± 9	334	12	0.4				
Angelica triquinata	12 ± 6	249	28	0.4				
Diervilla sessilifolia	9 ± 9	500	8	0.3				
Oxalis montana					60 ± 19	158	76	7.8
Taraxacum officinale	8 ± 6	401	12	0.2				
Aster spp.	5 ± 2	252	12	0.08				
Viola sp.	5 ± 2	224	20	0.08				

Table 8. (Continued)

Species	Beech Gap D ± SE	CV	F(%)	PCT	Spruce Stand D ± SE	CV	F(%)	PCT
Dentaria diphylla	3 ± 1	288	12	0.08				
Luzula echinata	3 ± 2	406	8	0.08	3 ± 2	346		0.4
Oxydendrum arboreum	3 ± 2	300	12	0.08	1 ± 1	500		0.13
Carex pensylvanica	2 ± 1	234	16	0.06	26 ± 8	253	52	3.4
Hieracium paniculatum	2 ± 1	295	12	0.06	1 ± 1	500		0.13
Plantago major	2 ± 1	366	8	0.06				
Hypericum perforatum	2 ± 1	276	12	0.06				
Prunus pensylvanica	1 ± 1	500	4	0.03	16 ± 4	139	52	2.1
Polygonum erectum	1 ± 1	500		0.03				
Lactuca sp.	1 ± 1	500		0.03				
Sambucus pubens	1 ± 1	500		0.03	3 ± 1	218	20	0.4
Vaccinium erythrocarpum					2 ± 2	500		0.25
Cacalia rugelia					7 ± 3	211	24	0.9
Poa alsodes					1 ± 1	500	8	0.13
Erechtites hieracifolia					1 ± 1	500		0.13
Unidentified	3 ± 3	500		0.06				

*D ± SE = density per m^2 plus or minus the standard error of the mean. CV = coefficient of variation. F = frequency out of 25 samples per community. PCT = per cent of total seeds germinating.

The first and second were present in soil cores adjacent to the Clingman's Dome Road, so they represent species from disturbed sites. Other species present at disturbed sites include Taraxacum officinale, Blephilia hirsuta, Plantago major, and Polygonum erectum.

The spruce stand seed bank was dominated by Betula lutea, Rubus canadensis, Oxalis montana, and Eupatorium rugosum. Early successional species such as Prunus pensylvanica, Sambucus pubens, Hieracium paniculatum, and Potentilla simplex were also present.

Those species dispersing across the community boundary were Betula lutea, Eupatorium rugosum, Claytonia virginica, Erythronium americanum, Impatiens pallida, and Poa alsodes. The last four species were present in the seed bank adjacent to the boundary, especially at soil site #59. This site is located in an island of beech gap vegetation inside the spruce stand. One Impatiens pallida seed at site #10 is unlikely to have been naturally dispersed from the beech gap to deep inside the spruce stand. It is unlikely that Impatiens grows at the site so perhaps that seed was a contaminant.

Poa alsodes was present in core #18 and #46 near the ecotone suggesting some limited dispersal of this species. Low densities of Eupatorium rugosum in the spruce stand seed bank suggest that this species disperses from the beech gap where densities are higher. Betula lutea certainly disperses into the beech gap.

The absence of tree and shrub seeds in the seed banks is striking. Only early successional or understory species contribute to the seed bank; Betula lutea, Rubus canadensis, Diervilla sessilifolia, Prunus pensylvanica, Sambucus pubens, and Vaccinium erythrocarpum. Table 8

confirms the general observation that seed bank statistics have high coefficients of variation. In the beech gap only three species have coefficients of variation less than 100%: these are Potentilla simplex, Claytonia virginica, and Rubus canadensis. Only Betula lutea and Rubus canadensis have coefficients of variation less than 100% in the spruce stand. These results suggest species distributions are patchy in the seed bank which probably reflects the patchiness of the seed rain.

Figure 12 diagrams the species area curves from the study sites. Species area curves permit an evaluation of the success in sampling the most common species at a site. Unfortunately, species-area curves are biased by the sample size and the axes scales.

The three species area curves suggest that the number of samples collected were effective in sampling all the major species in the seed bank; particularly for the spruce stand seed bank. The two beech gap species-area curves demonstrate that the soil cores, influenced by the roadside vegetation did not alter the effectiveness of the number of samples required to represent the most common species. The cores influenced by the roadside vegetation only increased the total number of species collected. Sixteen soil cores would have been adequate for the beech gap seed bank and approximately 14 for the spruce stand seed bank.

I. RECIPROCAL AVERAGING

Discriminant analysis was ineffective in distinguishing the seed banks groups according to sample distance from the boundary; this means, therefore, that no significant changes occurred in the seed banks with

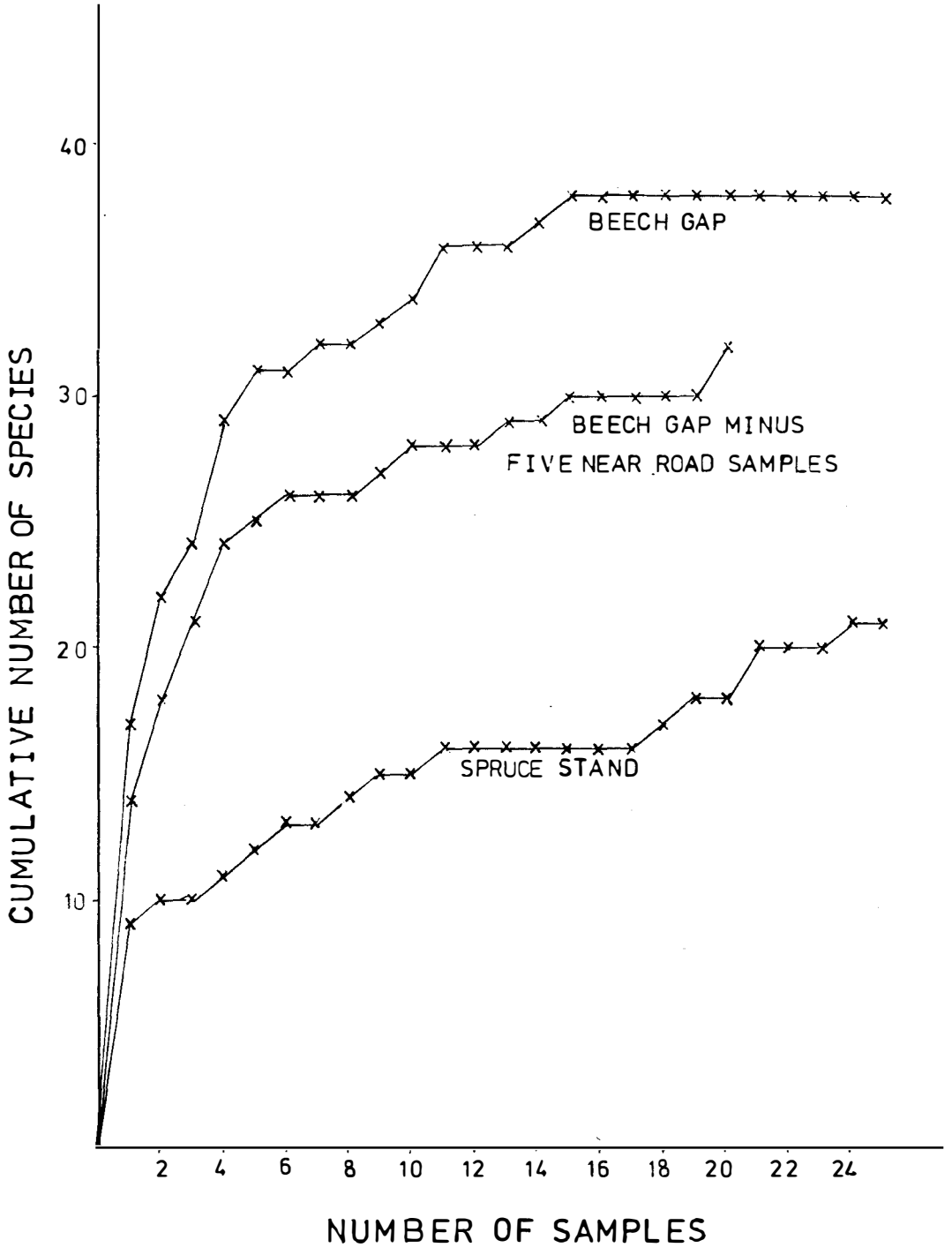


Figure 12. Seed Bank Species Area Curves.

increasing distance from the boundary. Reciprocal averaging was used to examine the patterns and gradients in the seed banks.

Plots of the first and second reciprocal averaging axes using all seed bank samples are shown in Figures 13 and 14. All species present in less than seven samples were deleted from the data matrix.

The seed bank samples are clustered into two groups with incomplete disjunction between them. The intermediate samples are those adjacent to the boundary, samples having a species in common with the other group of samples, or having intermediate densities of species occurring in both communities.

Examination of the species ordination and the primary data matrix demonstrates that the presence of Viola pallens, Eupatorium rugosum, Impatiens pallida, Houstonia serpyllifolia, and Claytonia virginica makes some spruce bank samples similar to the beech gap seed bank group. Conversely the presence of Carex pensylvanica, Prunus pensylvanica, and high densities of Rubus canadensis and Betula lutea makes some beech gap seed bank samples similar to the spruce seed bank group.

This ordination suggests a strong gradient along the first axis in the spruce stand seed bank and along the second axis in the beech gap seed bank. In order to interpret these gradients correlations between the different ordination axes and the environmental variables were calculated.

The highest Spearman correlation coefficient along the first ordination axis was with distance from soil core to the community boundary ($r=-0.83$) (Figure 15). This plot demonstrates that the

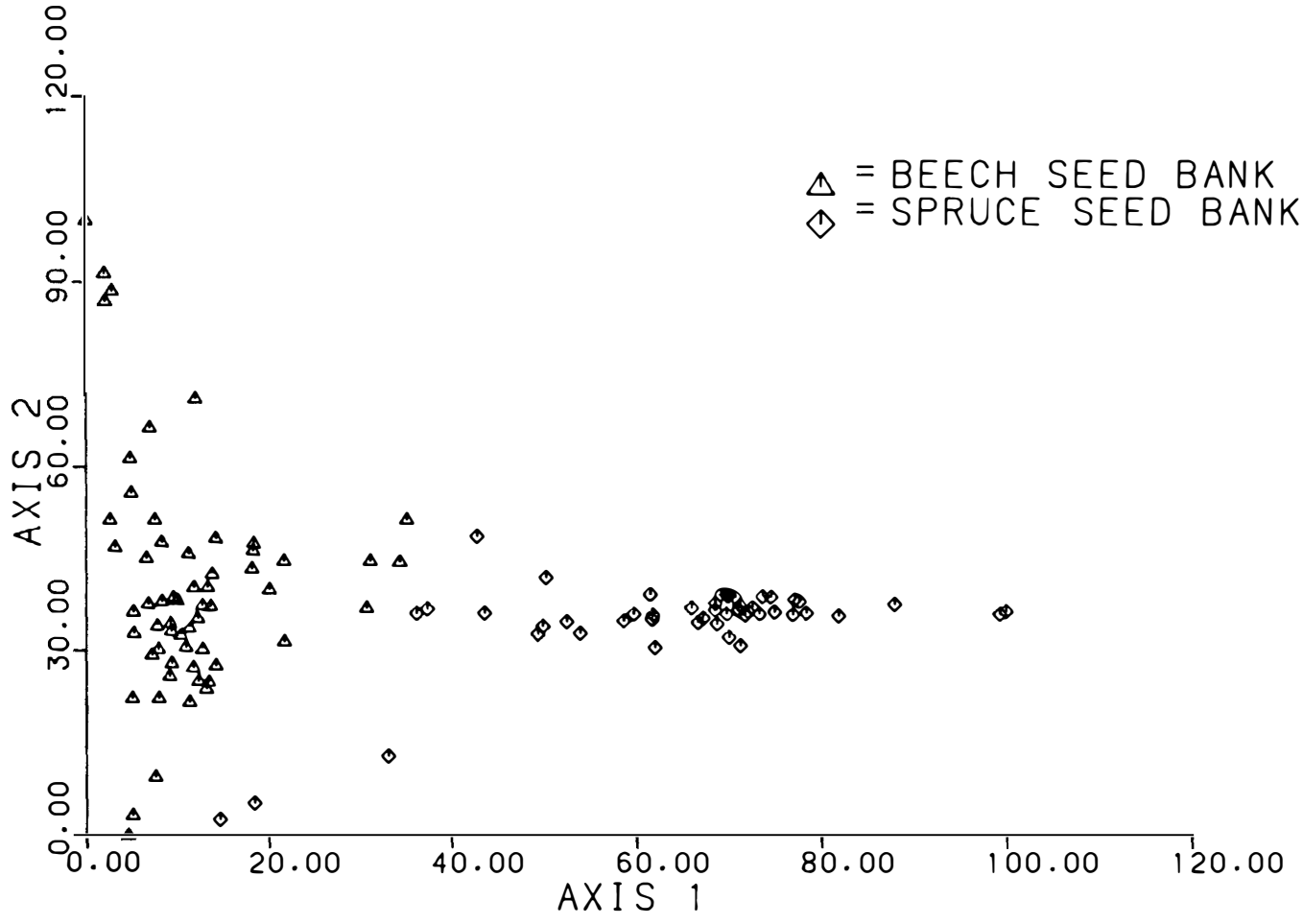


Figure 13. Plot of Beech Gap and Spruce Stand Seed Bank Samples on the First and Second Reciprocal Averaging Ordination Axes.

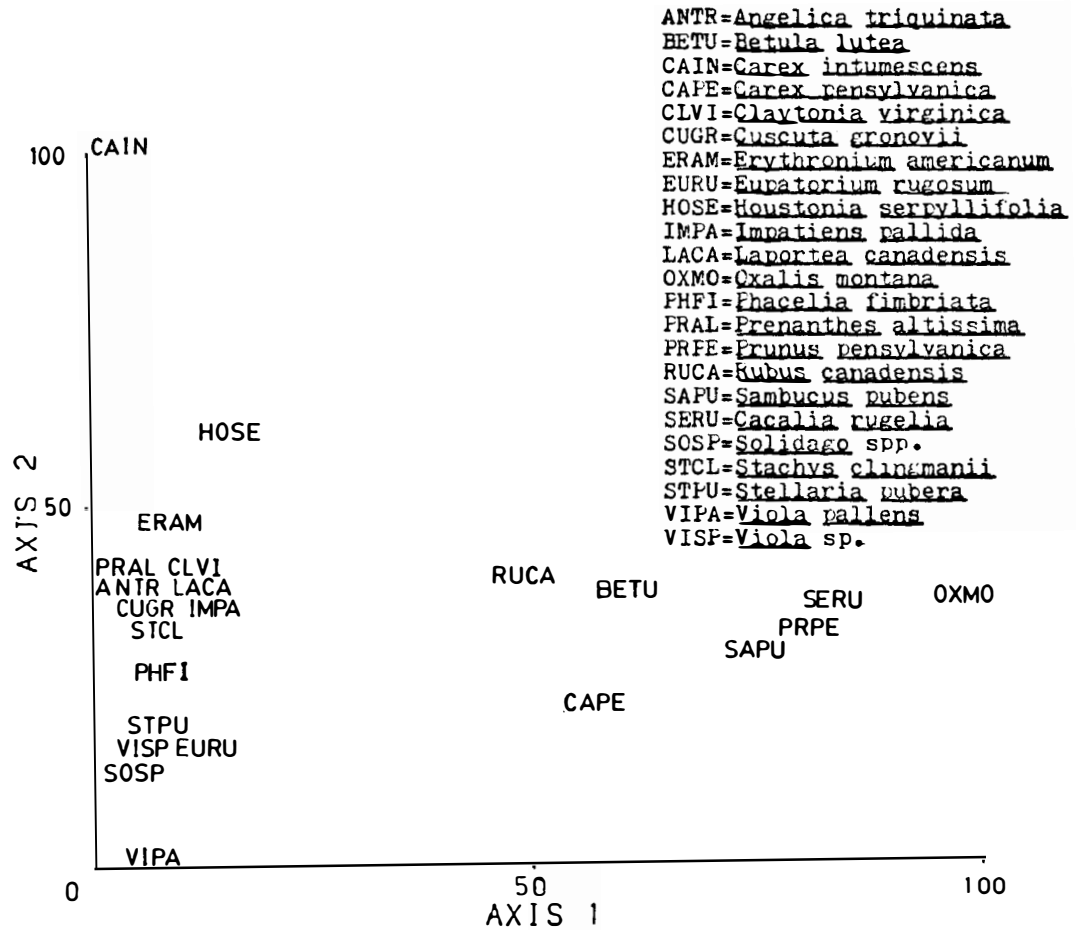


Figure 14. Plot of Beech Gap and Spruce Stand Seed Bank Species on the First and Second Reciprocal Averaging Ordination Axes.

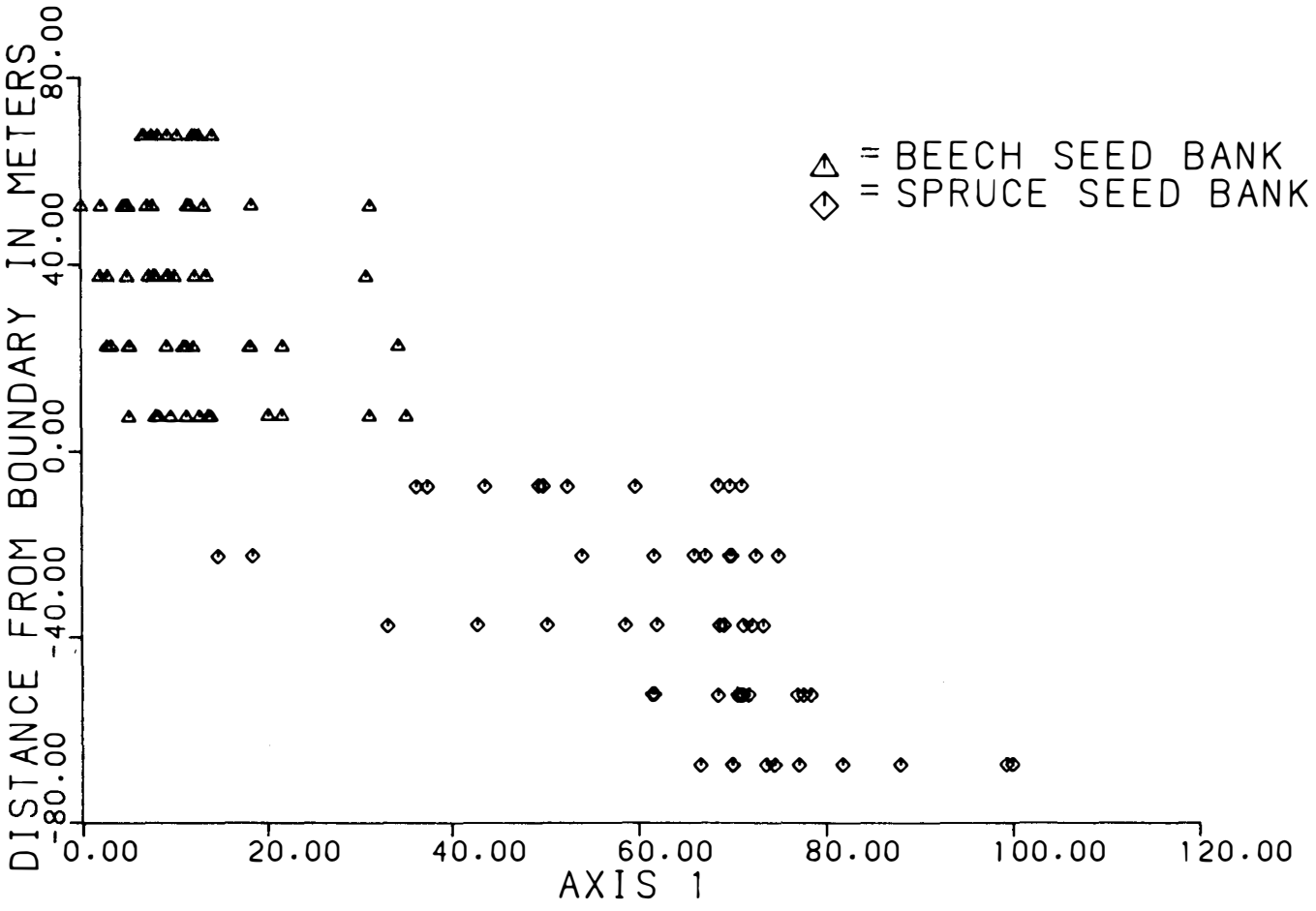


Figure 15. Plot of the Correlation between the First Reciprocal Averaging Ordination Axis and the Distance of the Sample from the Boundary (r = -0.83).

distance from the boundary is ineffective in separating the samples along the first axis of the ordination in the beech gap. Only weak separation of the spruce seed bank plots occurs along the first ordination axis by the distance from boundary measurement. Attempts to interpret the gradient along the first axis suggest that the major gradient is the result of ordinating the two partially disjunct seed banks together. This ordination suggests, however, that the two seed banks are quite different.

II. CLUSTER ANALYSIS AND DISCRIMINANT ANALYSIS

Cluster analysis (MINFO) was performed on the same data set used in the ordination, to determine if the two seed banks are dissimilar. Figure 16 shows the resulting dendrogram. The dendrogram shows two or three major groups.

Discriminant analysis was used to objectively choose the most meaningful groups. The analysis was performed on successively smaller groups at lower information levels to find the level giving the greatest discrimination. Discrimination was determined by the total percent correct classification.

The two group levels gave the most successful discrimination with a jackknife classification success of 85.5%! The three group level gave 83.6% correct classification. The F test was significant ($P<0.001, F_{23,86}=6.53, F_{24,66,.05}=1.70$). It is possible to discriminate with much success between the beech gap and spruce stand seed banks. One could choose the three group level; the third group, however, represents a special case of the beech gap vegetation, not an

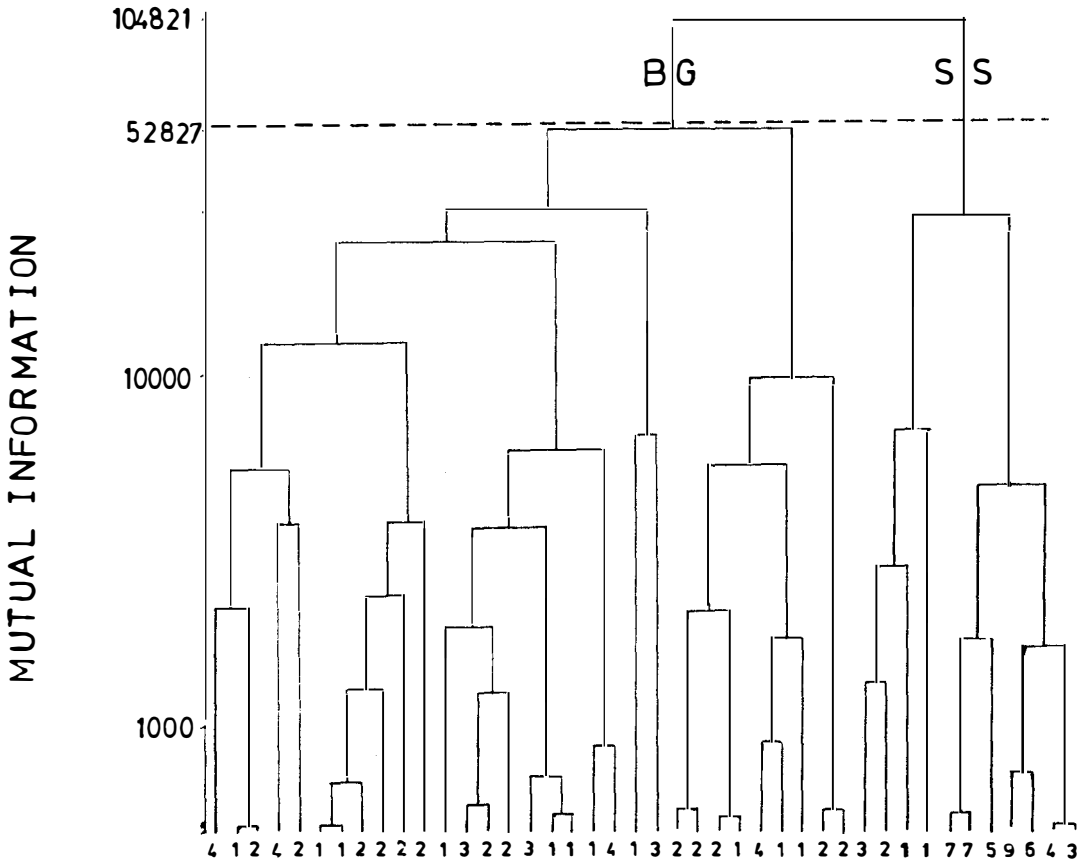


Figure 16. Dendogram from Cluster Analysis of the Seed Bank Samples. The two group level defines the beech gap and spruce stand seed banks.

intermediate between the beech gap and the spruce stand. The three group level was not selected for this reason.

Discriminant analysis correctly classified all the spruce stand seed bank samples, whereas the cluster analysis misclassified some of the spruce stand and some of the beech gap seed bank samples. Primary data matrix standardization in the discriminant analysis probably accounts for the difference; the data matrix used in MINFO is unstandardized.

III. RECIPROCAL AVERAGING REVISITED

Since the two seed banks can be distinguished, reciprocal averaging was continued to further examine in the manner of Peet (1980) the separate seed banks.

Figure 17 is the sample plot ordination of the beech gap seed bank with the deletion of all species present in less than four samples. The strong gradient of samples along the first axis had a high correlation with sample site elevation ($r=-0.80$, see Figure 18). Samples with high scores on the first axis were samples adjacent to the road; consequently, these samples contain several road disturbance species.

The species gradient in the beech gap is plotted in Figure 19. As in the initial ordination, Carex intumescens, Prenanthes altissima, and Houstonia serpyllifolia have highest densities at upper sites in the beech gap; Phacelia fimbriata, Barbarea vulgaris, Aster sp., Dicentra cucullaria, Dentaria diphylla, Impatiens pallida, and Viola pallens have highest densities in the lowest sites in the beech gap

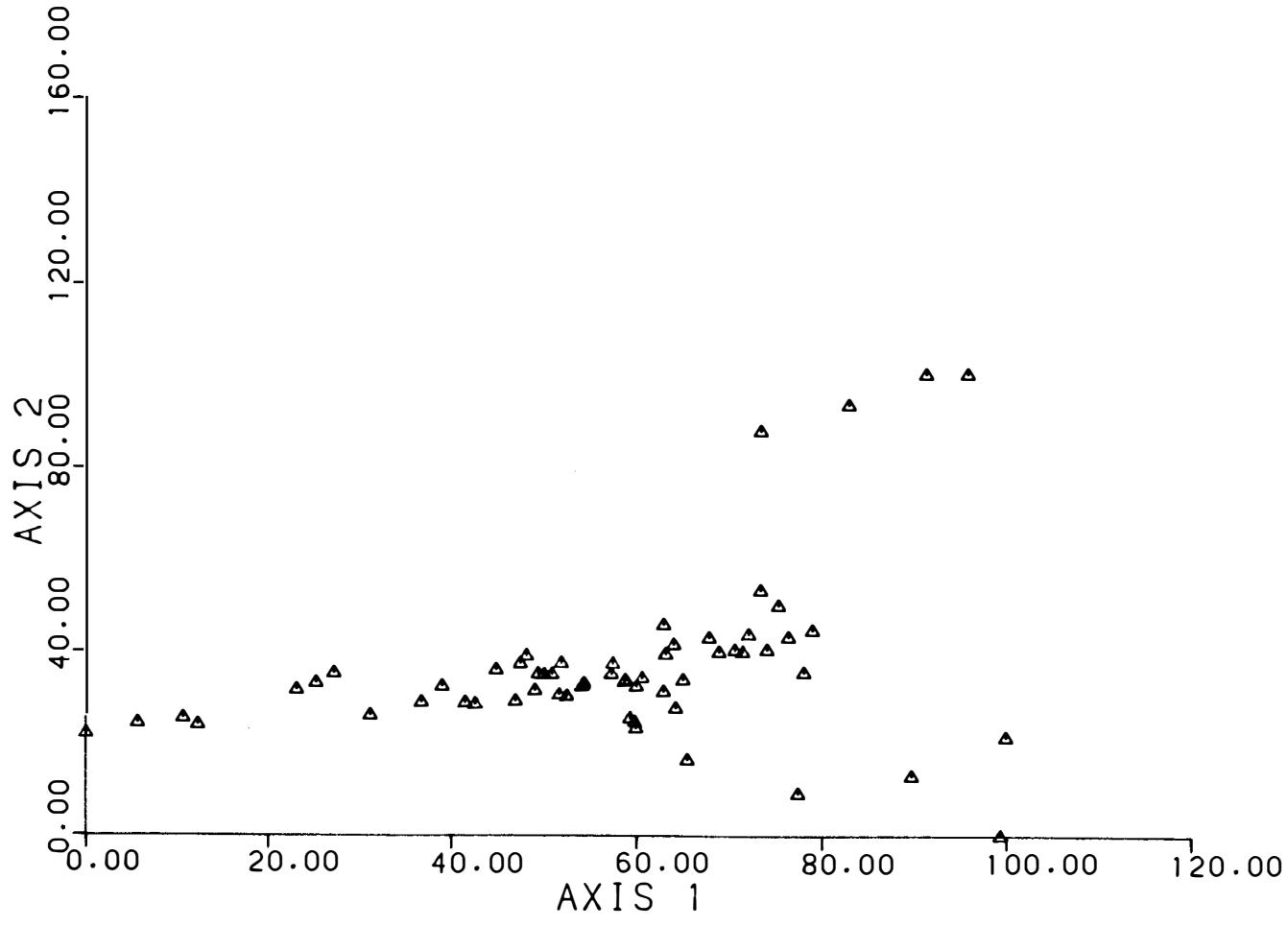


Figure 17. Plot of Beech Gap Seed Bank Sample Scores along the First and Second Reciprocal Averaging Ordination Axes.

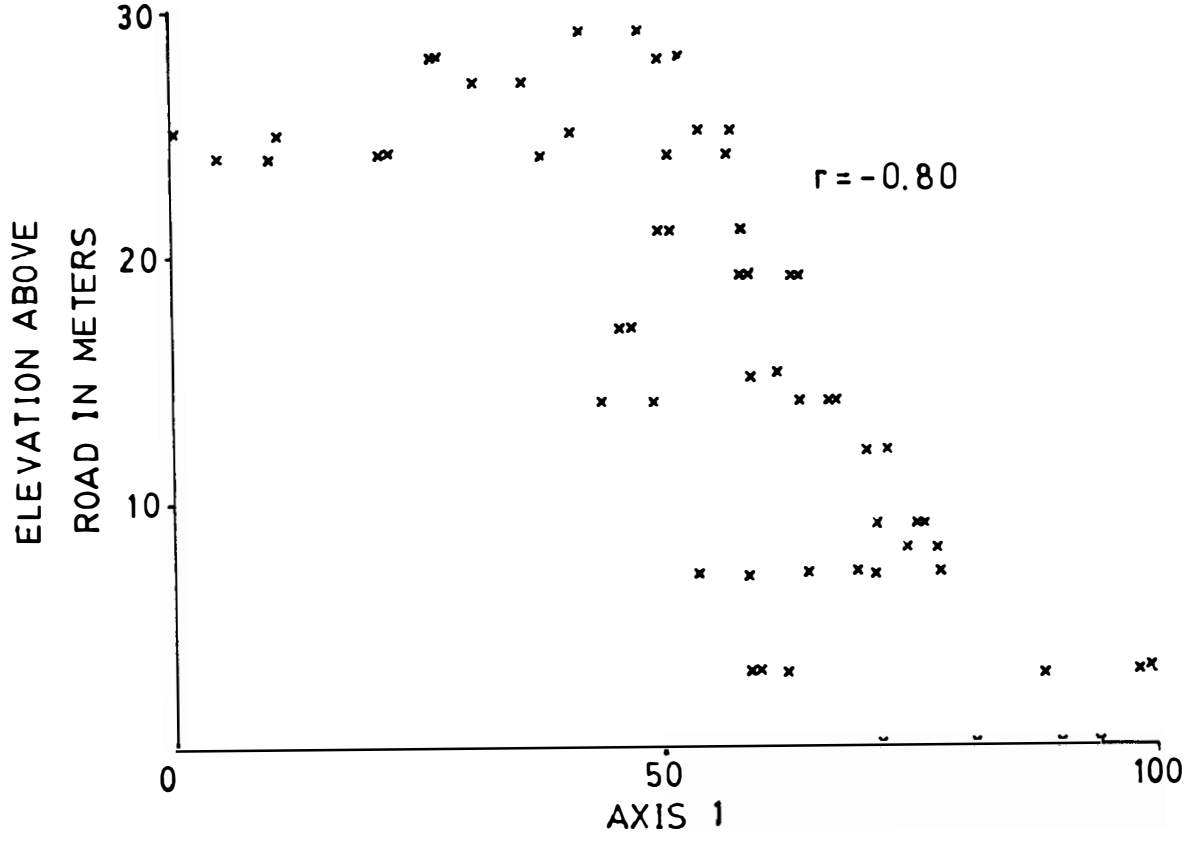


Figure 18. Scatter Diagram of the Correlation between the First Reciprocal Averaging Ordination Axis and the Sample Elevation above the Road.

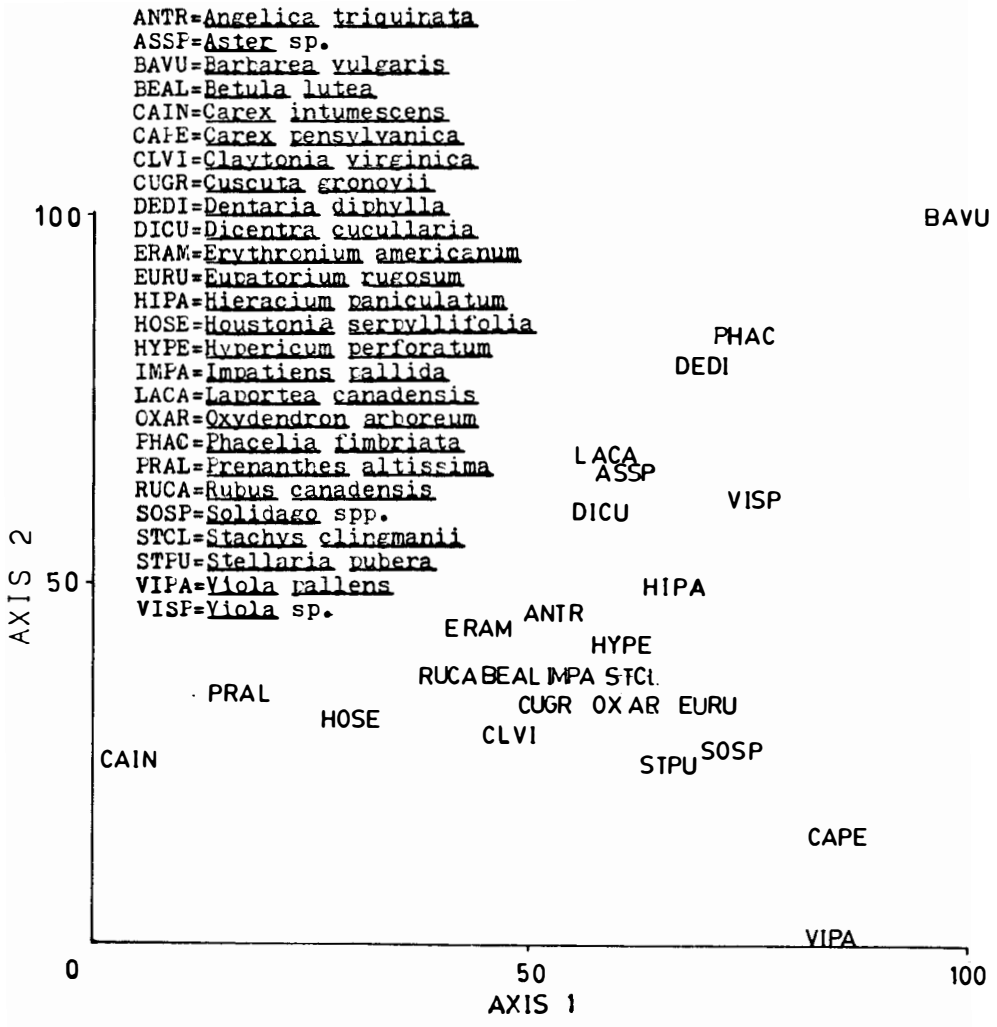


Figure 19. Plot of Beech Gap Seed Bank Species Scores along the First and Second Reciprocal Averaging Ordination Axes.

region. Species occupying the central position of the ordination such as Erythronium americanum, Claytonia virginica, Betula lutea, Eupatorium rugosum, and Laportea canadensis are present throughout the beech gap seed bank.

It is believed that this reflects a herbaceous species gradient with slope position which is probably the same species gradient Bratton (1975b and personal communication) observed in the beech gap herbaceous vegetation. Bratton believed this was due to a moisture gradient.

Reciprocal averaging of the spruce stand seed bank gave uninterpretable ordinations suggesting sufficient heterogeniety to make gradient analysis meaningless.

IV. SEED BANK DEPTH DISTRIBUTION

By March 1980 it was realized that the beech gap seed bank contained enough seeds to make it worthwhile to examine the seed depth distribution. Ten samples were collected. Table 9 shows the average number of seeds per m^2 that germinated at each depth sampled according to species.

A total of 3451 seeds germinated in samples, with 1777 in the top 3 cm of soil, 924 in the next 3 cm, and 750 seeds in the deepest 4 cm. Analysis of variance of the total number of seeds germinating at each depth sampled was not significant ($P=0.20, F_{2,27}=1.74$). The high variance within each depth accounted for the lack of significance.

High variance for most species at each depth accounted for the lack of any significant differences between depths. Kruskal-Wallis one-way analysis of variance test showed significant changes in seed

Table 9. Seed Densities per m^2 by Depth in the Beech Gap Seed Bank.

Species	0 - 3cm	3 - 6cm	6 - 10cm	Total
Claytonia virginica[a]	1180 ± 289*	244 ± 136	25 ± 2	1449 ± 345
Viola pallens	40 ± 37	254 ± 236	486 ± 460	780 ± 509
Eupatorium rugosum	291 ± 146	235 ± 82	146 ± 45	672 ± 241
Solidago sp.	126 ± 166	125 ± 106	8 ± 2	259 ± 131
Phacelia fimbriata	161 ± 75	25 ± 19	26 ± 15	212 ± 84
Carex intumescens	52 ± 21	44 ± 21	85 ± 33	181 ± 59
Rubus canadensis	44 ± 16	61 ± 20	60 ± 22	165 ± 43
Betula lutea[b]	74 ± 23	26 ± 12	9 ± 3	109 ± 25
Laportea canadensis[c]	72 ± 20	12 ± 5	8 ± 4	92 ± 26
Houstonia serpyllifolia	25 ± 17	42 ± 24	15 ± 10	82 ± 43
Stellaria pubera	41 ± 29	8 ± 6		49 ± 30
Impatiens pallida	36 ± 19	2 ± 2	2 ± 2	41 ± 20
Prenanthes altissima	25 ± 17	14 ± 11	1 ± 1	40 ± 28
Stachys clingmanii	4 ± 2	9 ± 5	16 ± 6	29 ± 9
Erythronium americanum	19 ± 10	6 ± 3	2 ± 2	28 ± 10
Viola sp.		10 ± 10	4 ± 3	14 ± 12
Angelica triquinata	6 ± 5	5 ± 5		11 ± 10
Cuscuta gronovii	1 ± 1	8 ± 4	1 ± 1	10 ± 6
Unknown 26		4 ± 3	5 ± 4	9 ± 4
Carex pensylvanica	8 ± 5			8 ± 5
Carex sp.			6 ± 6	6 ± 6
Poaceae		5 ± 5	1 ± 1	6 ± 5
Prunus pensylvanica	1 ± 1	1 ± 1	1 ± 1	4 ± 3
Taraxacum officinale	4 ± 3			4 ± 3
Gnaphalium sp.	4 ± 2			4 ± 2
Oxydendron arboreum	2 ± 2			2 ± 2
Hypericum perforatum			2 ± 2	2 ± 2
Dentaria diphylla		2 ± 2		2 ± 2
Rumex acetosella			1 ± 1	1 ± 1
Unknown 28		1 ± 1		1 ± 1
Dead	1 ± 1	7 ± 5	20 ± 7	29 ± 7
Totals	2217	1150	930	4301

[a]Significant Kruskal-Wallis Anova, P = 0.001.

[b]Significant Kruskal-Wallis Anova, P = 0.02.

[c]Significant Kruskal-Wallis Anova, P = -.02.

*The means ± the standard error of the mean from 10 replicates.

density with depth for Claytonia virginica ($P<0.001, \chi^2=19.3, N=30$), Betula lutea ($P<0.015, \chi^2=8.4, N=30$) and Laportea canadensis ($P=0.02, \chi^2=8.3, N=30$).

Discriminant analysis was used to test for significant differences in the seed bank with depth. Only species present at two or more of the depth classes were included in the analysis; rows of zeros would make the analysis invalid. The first 20 species in Table 9 were used.

F significant tests on the individual variables demonstrated significant differences in seed density with depth for Claytonia virginica, Betula lutea, Laportea canadensis and Phacelia fimbriata. All of these species except for Phacelia fimbriata were significant using the Kruskal-Wallis test. Perhaps some trust can be placed in the discriminant analysis F tests.

The model with the highest percent correct classification (70%) excluded Houstonia serpyllifolia and Rubus canadensis. This model was also significant in discriminating between the groups ($P=0.005, F_{34,22}=3.72, F_{30,22,.05}=1.98$). A significant difference exists between the upper and middle seed banks and between the upper and lower seed banks.

Group centroids and individual samples are plotted in Figure 20. Good separation of the upper seed bank from the other depths is demonstrated by this plot. No attempt was made to interpret the discriminant axes.

The following species occurred at highest densities in the upper 3 cm of the soil: Claytonia virginica, Eupatorium rugosum,

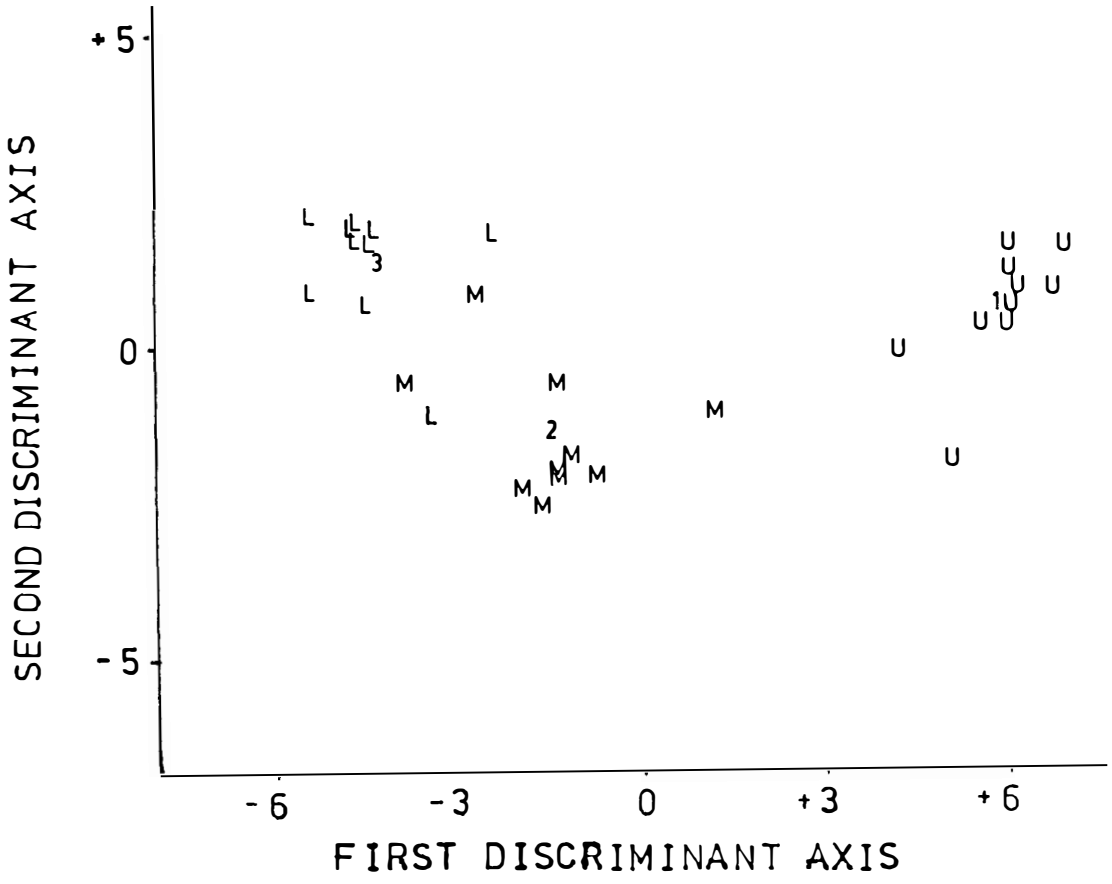


Figure 20. Discriminant Analysis of Seed Bank Depth Distribution. U = upper bank = 0-3 cm. M = middle bank = 3-6 cm. L = lower bank = 6-10 cm. Numbers are group centroids.

Solidago sp., Phacelia fimbriata, Betula lutea, Laportea canadensis, Stellaria pubera, Impatiens pallida, Prenanthes altissima, Erythronium americanum, Angelica triquinata, Carex intumescens, Taraxacum officinale, and Oxydendrum arboreum. The following species occurred at the highest densities in the middle 3 cm of the soil: Rubus canadensis, Viola sp., Cuscuta gronovii, Dentaria diphylla, and Poaceae. Those species occurring at the highest densities in the deepest stratum are Viola pallens, Stachys clingmanii, Carex pensylvanica, Hypericum perforatum, Rumex acetosella, and unknown 26. Presumably those species with highest densities at greater depths have been buried longer than those closer to the soil surface. Viola pallens is such a species since it was absent in the vegetation. Possibly the soil also acts as a sieve to filter seeds by size; smaller seeds could possibly move deeper into the soil.

V. PHENOLOGY OF EMERGENCE

Table 10 summarizes the weekly emergence of seedlings during the greenhouse germination period. More complete information can be found in Appendix B.

Many species emerged faster in the March seed bank than in the bank collected in December 1979. This difference may have resulted from a longer cold stratification of the March bank initiating faster germination. Or it could have been the result of a treatment effect, i.e., different placement in the greenhouse.

Early germinators are species likely to germinate early in the spring such as Erythronium americanum, Claytonia virginica, Stellaria

Table 10. Summary of Phenology of Emergence.

Periods	December Bank[a]	March Bank[b]
Week 1	Dicentra cucullaria	Claytonia virginica Cuscuta gronovii Erythronium americanum Impatiens pallida Prenanthes altissima Stellaria pubera
Week 2	Claytonia virginica Cuscuta gronovii Erythronium americanum Impatiens pallida Oxalis montana Potentilla simplex Prenanthes altissima Rumex acetosella Solidago spp. Stellaria pubera Taraxacum officinale	Angelica triquinata Carex intumescens Eupatorium rugosum Laportea canadensis Rumex acetosella Solidago spp. Stachys clingmanii Viola sp.
Week 3	Angelica triquinata Aster spp. Betula lutea Blephilia hirsuta Carex intumescens Laportea canadensis Luzula echinata Prunus pensylvanica Stachys clingmanii Viola sp.	Betula lutea Hypericum perforatum Rubus canadensis Taraxacum officinale Viola pallens
Week 4	Carex pensylvanica Diervilla sessilifolia Plantago major Sambucus pubens Viola pallens	Oxydendrum arboreum
Week 5	Cacalia rugelia Erechtites hieracifolia Eupatorium rugosum Hieracium paniculatum Houstonia serpyllifolia Hypericum perforatum	Carex pensylvanica Gnaphalium sp. Houstonia serpyllifolia Phacelia fimbriata unknown 26 unknown 28

Table 10. (Continued)

Periods	December Bank[a]	March Bank[b]
Week 5	Lactuca sp. Oxydendrum arboreum Phacelia fimbriata Poaceae Vaccinium erythrocarpum Unidentified	

[a]Week 1 = March 2 to March 7, 1980. Week 2 = March 7 to March 14, 1980. Week 3 = March 14 to March 21, 1980. Week 4 = March 21 to April 2, 1980. Week 5 = April 2 to July 29, 1980.

[b]Week 1 = March 14 to March 21, 1980. Week 2 = March 21 to April 2, 1980. Week 3 = April 2 to April 10, 1980. Week 4 = April 10 to April 20, 1980. Week 5 = April 20 to July 29, 1980.

pubera, Impatiens pallida and Cuscuta gronovii. Otherwise no other trends are apparent. It is not surprising that Phacelia fimbriata germinated in late June 1980 when most other species did not, since this is probably a time when seed in secondary dormancy over the winter germinate.

VI. VEGETATIVE REPRODUCTION

To understand the biology of the seed bank species, the sexual and vegetative reproductive components must be examined. The relative proportion of vegetative propagules to sexual propagules can give an indication of the predominant reproductive strategy for each species.

Table 11 illustrates the number of seeds and asexual propagules encountered in the soil. The percent of vegetative propagules is also calculated. Species exhibiting a preponderance of asexual propagules are Cacalia rugelia, Oxalis montana, Aster spp., Claytonia virginica, Trillium erectum and Medeola virginiana. The high degree of asexual reproduction in Aster spp., Trillium erectum and Medeola virginiana may be an artifact of the small sample size for these species.

The thick fibrous roots of Cacalia rugelia and the scaly rhizomes of Oxalis montana were the source of numerous vegetatively produced plants. Oxalis montana was notorious for its regrowth from pieces of the rhizome remaining in the soil after the above-ground portion of the plant had been removed during the greenhouse study. These two species are dominant in the spruce stand. It is interesting to speculate whether such reliance on vegetative reproduction has any

Table 11. Vegetative and Sexual Reproduction.

Species	# Seeds	# Asexual Plants	% Asexual
Angelica triquinata	24	5	17.2
Aster spp.	8	17	68.0
Cacalia rugelia	16	121	88.3
Claytonia virginica	1159	1852	61.5
Dentaria diphylla	5	3	37.5
Dicentra cucullaria	25	3	10.7
Erythronium americanum	100	77	43.5
Laportea canadensis	202	12	5.6
Medeola virginiana	0	3	100.0
Oxalis montana	115	2344	95.5
Prenanthes altissima	117	15	11.4
Rubus canadensis	448	5	1.1
Rumex acetosella	433	8	1.8
Solidago sp.	105	1	0.9
Stachys clingmanii	71	4	5.3
Stellaria pubera	39	7	15.2
Trillum erectum	0	1	100.0
Viola sp.	6	1	14.3

relationship to the type and frequency of disturbance in spruce and spruce-fir stands.

The asexual propagules of Erythronium americanum and Claytonia virginica are, respectively, bulbs and corms. The former were deeper in the soil than the latter.

One Rubus canadensis shoot came from a vegetative structure; this was, however, a biased representation because the tips of blackberry canes can produce new plants when covered by leaves or soil. Rubus canadensis does maintain a seed bank as well.

The presence of a substantial seed bank in the beech gap was not expected since most of the herbaceous plants are perennials! Species present in Table 10 but absent from Table 11 did not reproduce vegetatively. Most of the beech gap species may rely on sexual reproduction more than on vegetative reproduction to recruit new individuals. Two species not growing on the site but represented in the seed bank reproduced by numerous stolons; these were Viola pallens and Potentilla simplex.

CHAPTER VIII

THE VEGETATION, SEED RAIN AND SEED BANKS

In order to understand the dynamics of plant communities, it is useful to examine the density of seed inputs and seed storages. Such information can indicate whether seeds stored in the soil represent long term accumulations or annual storages.

Only two species (Table 12) were present in the vegetation, the seed rain and the seed bank: Betula lutea and Rubus canadensis. Rubus canadensis was lacking in the beech gap seed rain, but since only one seed was collected in the spruce stand, this is not surprising. Betula lutea was present in the seed rain at higher densities than in the seed bank, which suggests high mortality or rapid germination of these seeds. The correlation between the seed bank density and seed rain density for each sample site was 0.88 in the beech gap and 0.60 in the spruce stand.

Many species including Picea rubens, Fagus grandifolia, Amelanchier laevis, Acer rubrum, Viburnum alnifolium did not have viable seeds in the soil. The absence of Picea rubens in the seed bank is probably the result of a poor seed year, the consumption of seeds by mammals, and the short viability of the seeds of this species. According to Fowells (1965), good seed years occur every 3 to 8 years for Picea rubens. Fagus grandifolia was absent from the seed bank for the same reasons.

Table 12. Summary of Woody Vegetation, Seed Rain, and Seed Bank by Densities in Each Community.

Species	Beech Gap			Spruce Stand		
	Vegetation*	Rain	Bank	Vegetation*	Rain	Bank
Betula lutea	19	736	125	103	918	330
Picea rubens	40	7		812	21	
Amelanchier laevis	34	2		32	34	
Rubus canadensis	1738		62	1306	1	62
Acer rubrum	6	2		32		
Viburnum alnifolium	3			169	1	
Prunus pensylvanica			1	106		16
Abies fraseri	3			39		
Acer pensylvanicum	3			131		
Aesculus octandra	22					
Prunus serotina	6					
Cornus alternifolia	31					
Vaccinium erythrocarpum				388		2
Sorbus americana				282		
Diervilla sessilifolia			9			
Sambucus pubens			1			3
Fagus grandifolia	1787			113		
Oxydendrum arboreum			1			1

*The vegetation densities are number of stems per hectare. The seed rain and bank densities are the number of seeds per square meter.

Low densities of Acer rubrum seed rain explains the absence of seeds in the soil in spite of the fact that the seeds can remain viable over the winter (Fowells 1965). The only source of seeds is the senescent Acer rubrum high in the beech gap.

Amelanchier laevis pomes are a wildlife food source (Schopmeyer 1974; Martin, Zim and Nelson 1951); consequently, the absence of seeds in the soil perhaps can be explained by animal consumption. The collection of fruits in the gravity seed traps indicated that fruits reach the forest floor, with the possibility of a few being incorporated into the soil. Greenhouse conditions may have been unfavorable for germination. Schopmeyer (1974) stated that Amelanchier seeds require a period of 2 to 6 months to partially overcome the dormancy. No data exists concerning the frequency of large mast.

Viburnum alnifolium was also collected in the seed rain traps but was absent in the seed bank. Numerous immature red fruits observed in the summer of 1980 were reduced to a few black fruits by fall. Either animal consumption or fruit abortion may account for this loss of fruits. Perhaps the actual number of fruits reaching the forest floor are few. The absence of germinants in the greenhouse study could be caused by the difficulty in germinating seeds of this genus; they require warm stratifications for radicle growth and cold stratification to break epicotyl dormancy (Schopmeyer 1974). According to Schopmeyer, good seed crops occur every 3 to 4 years.

Some species present in the vegetation were only found in the seed bank: Prunus pensylvanica and Vaccinium erythrocarpum. The

absence of Prunus pensylvanica in the seed rain was likely due to the young age of the individuals present at the site. Seed present in the soil were probably from bird droppings. Those seeds arriving in this manner would only germinate if enough light was present as in a canopy opening.

The lack of Vaccinium erythrocarpum fruits in the seed rain was surprising considering the frequent occurrence of this shrub in the spruce stand. The moderately low stature of the species and the low dispersibility of the berries by abiotic means probably accounted for the absence of fruits in the seed traps. Ripe fruits were observed on the plants in the fall of 1979. The presence of seeds of this species in the soil confirms the deposition of seeds into the soil.

Species present in the vegetation but absent from the seed rain and seed bank include Viburnum alnifolium, Aesculus octandra, Prunus serotina, Cornus alternifolia, and Fagus grandifolia in the beech gap, Sorbus americana in the spruce stand, and Abies fraseri, and Acer pensylvanicum in both stands.

Abies fraseri does not have fruiting individuals in the study area because they have been killed by the balsam woolly aphid. The absence of Acer pensylvanicum is related to the low occurrence of this species and the small size of the trees present, particularly in the beech gap. The absence of seed rain and seed banks of Aesculus octandra, Viburnum alnifolium, Prunus serotina and Cornus alternifolia is due in part to the low frequency and density of these species in the vegetation. Empty capsules of Aesculus octandra were observed under a tree in late September 1979. Seed production does occur; it

is dubious, however, that such seeds would ever have a chance to become buried in the soil due to their large size and high caloric content.

Diervilla sessilifolia, Sambucus pubens and Oxydendrum arboreum contributed to the seed bank, but were absent in the vegetation. Diervilla sessilifolia is a common species along the Clingman's Dome Road; consequently, this author inferred that seeds can disperse upslope into the beech gap and spruce stand. Sambucus pubens produces red fruits characteristic of ornithochorous species (Pijl 1972), suggesting that seeds in the soil arrive indirectly by birds or by other animals.

Oxydendrum arboreum possibly disperses into the site; it is not clear, however, whether this species represents a contaminant from the greenhouse since Dobberpuhl (1980) noted its presence in the vegetation at Norris, TN. Stupka (1964) stated that Oxydendrum arboreum occurs up to 5000 ft elevation in the Smokies. This is almost as high as the study site.

All woody plant seeds present in the seed rain and seed bank occurred in lower density in the seed rain than in the seed bank. The seed bank is therefore probably the accumulation of seeds over many years of seed rain. Betula lutea, as previously mentioned, is the only exception to this observation.

Table 13 summarizes the density of herbaceous plants in the vegetation, seeds in the rain, and seeds in the soil. Only two species were present in both communities as plants, seed rain, and seed banks: Eupatorium rugosum and Claytonia virginica. As stated before, Claytonia virginica was present in the spruce stand in an

Table 13. Summary of the Plant or Seed Density in the Beech Gap and Spruce Stand Vegetation, Seed Rain and Seed Bank.

Species	Beech Gap			Spruce Stand		
	V*	R*	B*	V*	R*	B*
Claytonia virginica	1175	1254	412	<1	18	22
Eupatorium rugosum	<1	37	286	2	1	21
Aster sp.	3	15	5			
Phacelia fimbriata	10	72	127			
Impatiens pallida	3	8	28			3
Prenanthes altissima	6	23	59			
Angelica triquinata	6	3	12		1	
Carex intumescens	34	4	321			
Solidago sp.	10	190	39			
Laportea canadensis	19	56	98			
Cuscuta gronovii	<1	1	51			
Carex pensylvanica	26	78	2	<1		26
Oxalis montana				767	51	60
Cacalia rugelia		2		7	19	7
Erythronium americanum	46		21	1		10
Dentaria diphylla	1		3			
Stachys clingmanii	14		36			
Houstonia serpyllifolia	45		88			24
Stellaria pubera	14		20			
Poa alsodes	55	85			1	1
Luzula echinata	4		3	<1		3
Trillium erectum	1			<1		
Thalictrum dioicum	<1					
Rudbeckia laciniata	<1					
Lilium superbum	1					
Smilax sp.	<1					
Streptopus roseus	1			<1		
Clintonia borealis	1					
Taraxacum officinale		2	8			
Viola pallens			224			75
Rumex acetosella			219			
Potentilla simplex			963			1
Barbarea vulgaris			52			
Dicentra cucullaria			13			
Viola sp.			5			
Hieracium paniculatum			2			
Plantago major			2			
Hypericum perforatum			2			
Polygonum erectum			1			
Lactuca sp.			1			
Blephilia hirsuta			36			
Erechtites hieracifolia						1

*V = vegetation density. R = seed rain density. B = seed bank density.

island of beech gap vegetation. Claytonia virginica was the only herbaceous species with greater densities in the seed rain than in the seed bank. The seed rain and seed bank of this species were highly correlated ($r=0.51$, $P=0.008$ for test $Ho:r=0$).

Eupatorium rugosum seeds occurred in higher densities in the beech gap than in the spruce stand, in spite of the greater occurrence of Eupatorium in the spruce stand vegetation. Figure 21 gives the densities of Eupatorium rugosum seeds in the seed rain and seed bank at each site. The seed rain distribution suggests the seed source is probably near the Clingman's Dome Road where the highest seed densities occur. The seed bank site densities also suggest the seeds are from near the road in the region of the ravine in the beech gap. It is unclear whether Eupatorium arrived in the spruce stand from the road or from the beech gap. The data suggest perhaps that dispersal does occur across the boundary between the two plant communities. High densities of Eupatorium rugosum plants do grow along the Clingman's Dome Road.

Many of the herbs present in the beech gap produced seed rain and had seed populations in the soil; Aster sp., Phacelia fimbriata, Impatiens pallida, Prenanthes altissima, Angelica triquinata, Carex intumescens, Laportea canadensis, Cuscuta gronovii, and Carex pensylvanica. Only Solidago sp. and Carex pensylvanica had higher densities of seeds in the rain than in the seed bank. Some of the Solidago seeds were smaller than others suggesting they were aborted. The high density of Carex pensylvanica seed rain was the result of many seeds collected in one gravity trap.

SEED RAIN

0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
150	0	0	50	0	0	0	0	0	0	0	0	0
50	200	100	50	0	0	0	50	0	0	0	0	0
0	100	100	125	0	0	0	0	0	0	0	0	0

SEED BANK

94	19	44	12	19	44	6	19	0	0
56	31	25	75	113	6	25	6	0	0
112	50	88	31	69	12	6	63	6	6
169	256	544	281	75	38	6	0	0	0
444	656	100	0	169	6	0	6	0	0

Beech Gap Spruce Stand

Figure 21. Distribution of Eupatorium rugosum in the Seed Rain and Seed Bank. Values are densities of seeds per meter squared.

Plants, seed rain, and seed banks were present in the spruce stand for Oxalis montana and Cacalia rugelia. Cacalia rugelia seed densities were greater in the seed rain than in the seed bank. This suggests the seeds have low germination, short period of viability, high mortality, or readily germinate once dispersed. The total number of seeds collected in the seed rain were few (31) in spite of the large number of seeds produced by each plant and their high density in the vegetation. Perhaps the size of the seeds and the wetness of the environment prevent effective dispersal of this species.

The following herbs contributed to the seed bank but were absent from the seed rain; Dentaria diphylla, Stellaria pubera, Stachys clingmanii, and Luzula echinata. This was probably the result of the low occurrence of these plants in the beech gap and the large size of their seeds. Erythronium americana seeds were not collected since the seeds produced are quite large (Montgomery 1977) and the plants are low in stature. Houstonia serpyllifolia seeds were not trapped since this plant grows prostrate on the soil surface.

It was difficult to explain the absence of Poa alsodes seeds in the beech gap seed bank, particularly because the plants and seed rain were quite dense. Perhaps unfavorable greenhouse conditions prevented germination in the flats.

Species present on the site but absent from the seed bank and rain were uncommon species in both communities. These species include Trillium erectum, Thalictrum dioicum, Rudbeckia laciniata, Lilium superbum, Smilax sp., Streptopus roseus, and Clintonia borealis.

Many species present only in the seed bank were collected in sites adjacent to the Clingman's Dome Road, e.g., Rumex acetosella, Barbarea vulgaris, Plantago major, Polygonum erectum, Blephilia hirsuta, Hieracium paniculatum, Hypericum perforatum, and Lactuca sp. These species were present in the roadside vegetation.

Viola pallens and Potentilla simplex were absent in the vegetation; they, however, had infrequent but high seed bank densities. The presence of Potentilla simplex seeds at the Rubus canadensis thicket (trap site #57) suggests the seeds were transported by birds. Perhaps, on the other hand, Potentilla simplex plants were present in the vegetation when a previous disturbance opened the canopy which allowed the present senescent Acer rubrum to be released from competition. Viola pallens seeds occurred at the highest densities in the deeper soil sections suggesting they had been buried for quite some time. Perhaps a similar trend would have been observed for Potentilla simplex as well.

Table 14 shows high similarities within each community according to Jaccard's Index of Similarity (Mueller-Dombois and Ellenberg, 1974). Low similarities between the seed rain and seed banks occurred because many species in the vegetation were present in the seed bank but absent from the seed rain. High similarities between the vegetation and the seed rain were found because few species present in the seed rain were not present on the sampling sites. Similarities between the vegetation and the seed bank were quite high, also.

The similarity between the beech gap seed bank and the beech gap vegetation would have been higher if weedy road species present in

Table 14. Similarity Between the Vegetation, Seed Rain, and Seed Banks Within and Between the Communities.

Community	Source	Beech Gap			Spruce Stand		
		Vegetation	S. Rain	S. Bank	Vegetation	S. Rain	S. Bank
Beech Gap	Vegetation	---	45%	38%*	40%	---	---
	Seed Rain	---	---	34%	---	36%	---
	Seed Bank	---	---	---	---	---	37%
Spruce Stand	Vegetation	40%	---	---	---	40%	43%
	Seed Rain	---	36%	---	---	---	29%
	Seed Bank	---	---	37%	---	---	---

*The exclusion of roadside species results in a Jaccard's coefficient of similarity of 56%.

the seed bank had been considered present in the vegetation. Actually these species were present in the vegetation but sample plots were absent in these areas. Altering the calculations to recognize this gave a higher similarity index between the beech gap seed bank and the beech gap vegetation (56%).

Even though the vegetation, the seed bank, and seed rains were very similar between the two plant communities, significant quantitative differences did exist. Similarity indices take into account the presence of species but do not incorporate quantitative differences.

The seed rain and seed banks of these two plant communities had a high degree of similarity with the vegetation which contrasts with most of the seed rain and seed bank studies. Dobberpuhl (1980) had similarity indices of 4.5 to 21% in comparisons between vegetation and seed banks.

This is not to say that some species did not occur in the inputs and storages that were absent from the vegetation, but that those species formed a minor part of the seed rain inputs and storages. The most common plants were also the most common components of the seed rain and the seed banks. The only exceptions were Potentilla simplex and Viola pallens.

Species absent in the seed rain tended to be the uncommon species, prostrate species, or species predominantly dispersed by birds. Species absent from the seed bank tended to be uncommon herbaceous species or woody perennials except for secondary successional species.

CHAPTER IX

DISCUSSION

I. DISPERSAL ACROSS BOUNDARIES

The vegetation data collected demonstrated the contrasting species assemblages and dominants characterizing the beech gap and spruce stand communities. Without such contrasting compositions, it would have been impossible to examine seed exchange across the boundaries between the plant communities.

The seed rain clearly demonstrated the dispersal of Picea rubens and Betula lutea seeds into the beech gap. Their dispersal most likely occurred because of their wind dispersed seeds and their release from in the canopy. The demonstration of a negative exponential decrease in Betula lutea seed rain into the beech gap was indicative of dispersal from the spruce stand.

The presence of Betula lutea in the beech gap may have contributed to the seed rain in the beech gap: the dispersal curve, however, suggests its contribution was minimal. Perhaps the late frosts on May 26 and 27, 1979 during the flowering season (Fowells 1965) significantly damaged the developing embryos in unprotected trees outside of the Picea rubens canopy. Brown and shriveled leaf ends of Betula lutea and Fagus grandifolia observed in 1979 were presumably the result of these late frosts.

Cacalia rugelia appeared to have minimal dispersal deep into the beech gap (traps #50 and #51); the absence of Cacalia seeds closer to the boundary suggested that these seeds might have been dispersed unusually far. If major winds blow downslope, the seeds could have arrived from the strip of spruce vegetation along the ridge crest (see Figure 2, page 21).

The presence of Poa alsodes in the spruce stand seed rain and seed bank near the boundary suggests that this species can disperse into the spruce stand.

The occurrence of Eupatorium rugosum in the seed rain and seed bank needs explanation particularly since it occurs in low density in the vegetation. These seeds possibly originated from (1) plants in the community, (2) buried seeds from plants once from the community, and/or (3) from plants outside of the community.

Eupatorium rugosum plants occurred in a slightly higher density in the spruce stand compared to the beech gap; but higher densities of seeds in the seed rain and banks occurred in the beech gap (see Figure 21, page 112). This supports the suggestion that seeds in the beech gap have dispersed from populations along the Clingman's Dome Road. Otherwise the seed densities should be expected to be higher in the spruce stand.

It is not clear, however, whether the seeds present in the spruce stand seed rain and banks represent the combined input from the Clingman's Dome Road and the plants in the spruce stand or solely from the plants in the vegetation.

There was little evidence for appreciable herbaceous seed exchange between these two plant communities. Kellman (1974) found seeds from the adjacent secondary community at distances up to 100 m into the forest. Cheke et al. (1979) found seeds dispersing up to 150 m into a tropical forest. These studies suggested dispersal into forests can occur; the distances would, however, be affected by the wind direction and speed and the turbulence inside the forest.

Major winds at the study site probably blow downslope from the state line ridge where major storms and clouds originate. Such winds blowing in this manner would blow parallel to the boundary. This would reduce the seed exchange between the plant communities.

Sheldon and Burrows (1973) demonstrated that wind turbulence could affect the dispersal of pappus haired seeds. The presence of a dense shrub layer in the spruce stand could have reduced the distance wind could transport seeds. Tree boles would also reduce wind speed.

In an environment of high frequency of orographic precipitation, it would be expected that the effectiveness of dispersal of pappus bearing seeds would be reduced by the hygroscopic properties of pappus hairs. Perhaps seeds of Eupatorium rugosum along the road have a higher chance of dispersing since greater wind velocity in the unforested areas may dry pappus hairs more quickly.

The species studied that rely on wind dispersal were Eupatorium rugosum, Aster divaricatus, Solidago sp., Cacalia rugelia, Acer rubrum, Acer pensylvanicum, Betula lutea, Picea rubens, Hieracium paniculatum, and Diervilla sessilifolia.

Many of the seeds are animal dispersed such as Prunus pensylvanica, Sambucus pubens, Sorbus americana, Rubus canadensis, Potentilla simplex (?), and Amelanchier laevis. These species would be found where plants were not available, but they would not occur in a predictable manner.

The beech gap herbs may possess several dispersal mechanisms. Some such as Claytonia virginica and Trillium erectum are probably myrmecochorous. Seeds of Claytonia are also dispersed by leaf litter movement as well. Many herbs are essentially barochorous, including Phacelia fimbriata, and Impatiens pallida (also autochorous). These are probably not dispersed very far. It is unknown if myremecochory occurs at these elevations; Cole (1940) did find genera of ants at these elevations (Lasius, Crematogaster, and Aphaenogaster) which Beattie and Culver (1981) implicate as seed dispersing.

Seed production variation in response to yearly climatic fluctuations is also important in examining dispersal. Greater seed exchange between these communities could be expected in years favorable for large seed crop production and favorable for dispersal (drier for anemochorous plants).

The year 1980 was probably a more favorable year for seed production because the summer was drier than in 1979 when near record precipitation occurred. Also there was no late May frost to damage young leaves and flowers of the trees and spring flora. Such 1980 conditions resulted in the production of some full Fagus grandifolia seeds and a good Amelanchier laevis pome crop.

While Picea rubens and Betula lutea seeds moved into the beech gap from the spruce stand, few herbaceous species and seeds dispersed across the boundary. These observations make it interesting to speculate that the tree canopy can migrate faster than the herbaceous flora as a result of environmental change and the greater tree seed dispersibility. This would not be true, however if the successful germination and establishment of those tree seeds were infrequent. The herbaceous flora might have time enough to keep up with the advancing overstory vegetation migration. Clearly dispersal in space and time must be understood in vegetation migration and dynamics.

The overstory and understory vegetation transects did not suggest that either plant community is migrating in any particular direction. The presence of isolated small Picea rubens trees in the beech gap is evidence for red spruce invasion into the beech gap: no young Fagus grandifolia stems were observed deep inside the spruce stand. The island of Claytonia and Erythronium americanum 15 m inside the spruce stand under the Picea rubens canopy suggested that the red spruce has migrated into the beech gap and formed an overstory. It does not seem likely that these two herbs would be migrating into a coniferous stand as the seed dispersal study supports. Also the lack of deciduous canopy fluctuations in the spruce stand would be unfavorable for these species. Schemske (1977) has accumulated evidence that Claytonia virginica flowering phenology and life history are influenced by the development of the canopy in the spring. A study of Claytonia virginica seed survival and germination would help answer this question.

II. SUCCESSION AND REGENERATION

The seed banks of these two plant communities contrasted greatly as to species composition and total seed densities. These differences were likely due to distinct herb layer since most of the seeds in the soil were of herbaceous origin.

The overall density of seeds per m^2 in the beech gap was 2518 seeds. This density is quite high for most seed banks examined under deciduous forests (see Table 1, page 11). Only Oosting and Humphreys (1940) found a comparable density of seeds in the soil of an oak-hickory forest. A total of 773 seeds per m^2 was found in the spruce stand which compares quite well with most coniferous seed banks.

In agreement with all previous seed bank studies, these banks lacked seeds from overstory species except for Betula lutea. This finding was likely due to the particular life history strategies that trees have evolved which maintain and perpetuate their species. To paraphrase Grime (1979), these genera (Fagus, Aesculus, Amelanchier, and Picea) lacking in the seed bank depend on their seeds being digested by animals with a few seeds lost in transit to a storage or feeding site. Those lost seeds will hopefully survive to germinate and become established.

Most surprising is that the seed bank of both communities was very similar to the overlying community composition. The beech gap seed bank had a Jaccard Index of similarity of 38% with the overstory vegetation. The spruce stand seed bank had a value of 43%. Most seed bank studies have found high densities and frequencies of early

successional species. Only Rubus canadensis, Eupatorium rugosum, and Prunus pensylvanica had high densities and frequencies of seeds in the soils. Potentilla simplex had high densities of seeds in the beech gap but its frequency was low. Other early successional species such as Sambucus pubens, Hypericum perforatum, Lactuca sp., Diervilla sessilifolia, and Hieracium paniculatum had low densities and frequencies. Only the spruce stand seed bank conformed to other seed banks studied by having the most important and common species being early successional.

Large populations of weedy successional species were absent in these seed banks except for samples removed adjacent to the Clingman's Dome Road. This result can be explained by one observation: in the Great Smoky Mountains National Park, large scale man-made disturbance is rare, so that weedy successional seed sources are lacking. A major mosaic of man-made disturbance does not occur here. The nearest early weedy successional seed source of any kind is the narrow disturbed strip along the Clingman's Dome Road and Highway 441. These disturbed areas are fairly static.

Ramseur stated that Prunus pensylvanica is the most common secondary successional community followed by its later stage, the Prunus pensylvanica-Betula lutea community. These communities are dominated by Prunus pensylvanica, Sorbus americana, Betula lutea, Sambucus pubens, Eupatorium rugosum, Diervilla sessilifolia, Viburnum alnifolium, and Amelanchier laevis.

High densities of Betula lutea, Rubus canadensis, Prunus pensylvanica, and Eupatorium rugosum seeds in the spruce stand suggest

that a vegetation cover should develop rapidly following a disturbance, e.g., windthrow. The low density of Sambucus pubens did not detract from its potential role in disturbance recovery.

Little information exists concerning disturbance and succession in beech gaps. Russell (1953) noted a bad windstorm that blew down trees and limbs in a beech gap. Oh (1964) proposed that the patterns of Fagus grandifolia in the beech gap suggest cyclic regeneration by root suckering which prevented Picea rubens from invading. Clebsch and DeSelm (personal communication) have observed Fagus grandifolia seedlings in beech gaps twice in 25 years; however, their survival is unknown.

Disturbances observed during this study included the blowing down of large Fagus limbs and a canopy opening resulting from the slow death of an Acer rubrum tree. The understory under the tree included a dense thicket of Rubus canadensis. Successional species present in the seed bank included Betula lutea, Eupatorium rugosum, and Potentilla simplex. Low densities and occurrence of Prunus pensylvanica and Sambucus pubens indicated that these species might occur given a major canopy opening.

Comparison of the total number of seeds that germinated relative to the number of reproductive propagules that emerged shows some interesting trends. The major herbaceous species in the spruce stand relied mostly on asexual reproduction; some seed, however, is produced each year. These species are Cacalia rugelia and Oxalis montana. On the other hand, Rubus canadensis, the major shrub species,

maintained a large seed bank but is able to reproduce by cane burial in the soil.

Most of the herbaceous species in the beech gap had a higher proportion of their reproduction in seeds rather than in asexual means. Claytonia virginica and Erythronium americana had approximately equal numbers of seeds and asexual reproductive organs (bulbs and corms) suggesting that these two species may reproduce by both means more or less equally.

Most of the commonly occurring species in both communities were perennials. The only exception is Impatiens pallida. The ability to regenerate asexually ensures the continued survival of these plant populations during extreme environmental periods when sexual reproduction may be limited. Some level of sexual reproduction ensures continued variability in the plant population genotype upon which natural selection may act on (Grime 1979). The occurrence of buried viable seed banks of most herbaceous species ensures that after some disturbance, genetically variable individuals will be available for future generations. According to Templeton and Levin (1979) these seed bank seedlings will ensure some degree of genetic stability over time.

Species relying most on buried roots, corms, and bulbs for successful reproduction were those that are most likely to become locally extinct from wild bear rooting in the Great Smoky Mountains National Park. Bratton (1974 and 1975a) stated that observed food items include Claytonia virginica, Lilium superbum, Stachys clingmanii,

Stellaria pubera, Laportea canadensis, Impatiens pallida, Dentaria diphylla, and Polygonatum pubescens. Other herbs and ferns are also damaged by wild boar rooting.

Of these species, Lilium superbum, Dentaria diphylla, and Polygonatum pubescens lacked an appreciable seed bank; these species would, therefore, most likely become extinct. The other perennial species maintaining some seed bank would probably persist for several years until their seed bank had been depleted. This study confirmed the results of Bratton (1974, 1975a) in suggesting that many species would become locally extinct since they lack a seed bank. These species would not have seed populations that could germinate and become established to replace the populations decimated by the boar.

III. ORIGIN AND MAINTENANCE OF BEECH GAPS

Various researchers have speculated on the origin and maintenance of the high elevation beech gaps in the Great Smoky Mountains National Park. Much new evidence has come to light in the last several years that bears on this topic.

Whittaker (1956) proposed the hypothesis that the beech gaps originated during the post glacial hypsithermal period. The post glacial hypsithermal period is defined as that period from 10,000 to 2000 years BP when the thermal maximum temperature was 2°-3° C higher than today (Deevey and Flint 1957). An historical explanation seemed likely since the abrupt boundary between the two communities could not be explained by bedrock differences, topographic discontinuities, or disturbance differences (Whittaker 1967 and Wolfe 1967).

Whittaker (1956) hypothesized that spruce and fir occurred at lower elevations in the Smokies during the Pleistocene glaciation. The subsequent hypsithermal period eliminated these species from elevations up to 5600 ft. This would have eliminated spruce and fir from sites south of Clingman's Dome and Miry Ridge. Beech, mixed beech and red and white oak-chestnut would have migrated upslope to fill the gap. These barochorous species would have migrated upslope by root suckering (Fagus) or by animal dispersal of seeds.

At the end of the hypsithermal, when the earth's climate cooled, spruce and fir would have migrated downslope again to their present limit of 4500 ft; further migration to the southwest would have been hindered by the nearly pure stands of beech. Schofield (1960) and Fuller (1977) also believed the beech gaps originated during the hypsithermal period.

Since the early 1970's a wealth of paleobotanical information has been collected concerning Pleistocene and Holocene vegetation migrations in the southeast. Most sites southeast of Tennessee show a gradual warming trend since the end of the Pleistocene (Delcourt and Delcourt 1977; Delcourt 1980; Delcourt et al. 1981; Watts 1971, 1975, and 1980); work in Tennessee, however, at Shady Valley by Barclay (1957) and on the Cumberland Plateau by Delcourt (1979) suggests a warmer and drier period (the hypsithermal) between the Pleistocene and the climate of the last several thousand years.

Recently Delcourt and Delcourt (1979) have developed maps of the vegetation of eastern North America for the last 40,000 years. These maps are based on the palynological records from sites across the

region. The maps illustrate their ideas concerning vegetation movements for the time period examined. In expanding on their ideas Delcourt (1979) presents the following ideas: (1) deciduous forest species were located in refugia along the southward flowing rivers entering the Gulf of Mexico during the height of glaciation, (2) minor refugia may have also occurred on south facing slopes in the Great Smoky Mountains, (3) deciduous taxa migrated northward to where they are found today as the glaciers and spruce and jack pine retreated northward, and (4) American beech probably reached these latitudes around 12,000 years ago. A final important conclusion of this is that plant communities are dynamic and that those observed today were created as the great Laurantide ice sheet receded at the end of the Pleistocene.

Unfortunately, the Whittaker hypothesis will probably never be conclusively confirmed; the palynological evidence, however, makes this hypothesized origin of beech gaps plausible. Perhaps easier to understand and to examine experimentally is the maintenance of the beech gaps and the slowness of the red spruce invasion into them.

Schofield (1960) presented evidence that red spruce is invading the beech gaps. His evidence consisted of the observation that young spruces grow in proximity of the boundary. He believed that patches of spruce become established in the beech gap and by population growth, coalesce with the neighboring red spruce stand.

Schofield (1960) believed red spruce could only slowly invade the beech gaps because their seedlings could not survive in the deciduous leaf litter and its microclimate. Oh (1964) saw evidence

for the cyclic regeneration of beech from its distribution pattern. He detected a mosaic of large tree clumps (mature sites) and dense small tree clumps (regeneration patches). He observed that red spruce is capable of invading what he called the subarea where the beech regeneration mosaic pattern is least developed. These subareas are often on or near the boundary. He concluded that red spruce is probably not a part of the normal regeneration complex in the beech gaps.

Fuller (1977) tested the hypothesis that some "interference mechanism caused by the dominance of beech was preventing red spruce from invading the beech gaps." Fuller discovered that spring diurnal soil temperature variation was greater in the beech gap than in the spruce stand. This delayed and reduced red spruce germination. He found that beech litter contained possible allelochemical inhibitors.

Red spruce seed loss by predation was shown to be higher in the beech gap than in the spruce stand. Fuller also observed that some beech mortality was due to damping off of the germinating seeds in the beech gap. He suggested that the deciduous leaf litter layer prevents successful germination by acting as a barrier to radicle growth into the mineral soil. Fuller concluded that a combination of all these factors hampers the invasion of red spruce.

Wolfe (1967) found that the only soil differences between beech gaps and spruce fir are the result of the vegetation. He only found differences in the litter and humus layers. The lower pH under the spruce stand caused cheluviation of iron into lower layers. This does not occur in the beech gap soil. The texture and surface of the coniferous and deciduous litter layer are significantly different.

Fuller found soil temperature differences and moisture content differences between the soils.

It is possible with our present knowledge to theoretically explain the lack of invasion of either community species group into the other, on the basis of litter differences alone, excluding biotic factors.

Successful invasion depends on the successful dispersal of propagules into the site and their landing at a safe site. Harper (1977) defines the safe site as that environment with the appropriate conditions for successful germination and establishment where predators, competitors, and allelochemics are absent. This is a subset of Grubb's (1977) regeneration niche defined as the differing seed production, dispersal mechanisms, germination and establishment requirements, and plant development strategies that separates plants having the same nutritional and environmental requirements as adults.

Factors important in determining safe sites have been examined experimentally. Harper and Benton (1966) demonstrated that water tension significantly affects seed germination success. They also showed that seed shape, size, and how it is placed on the substrate can determine what conditions are favorable for germination. Harper et al. (1965) showed that the soil microtopography has a profound importance in determining which species can successfully germinate where. Peart (1979) demonstrated the role seed shape plays in the dispersal of seeds to specific microsites.

Other factors of importance would be the amount and quality of light (Wesson and Waring 1969), soil and litter chemistry, presence of competitors, and the presence of seed consumers.

It is easy to cite any of these factors as preventing the successful invasion of specific species, it is more difficult to demonstrate which factors are important. The work of Fuller (1977) is a fine example of a study designed to examine the factors important in the successful or unsuccessful recruitment of plant populations.

The study area provides an excellent field laboratory in which to investigate the factors important in the successful recruitment of plant populations by seeds. Studies of the requirements for successful seed germination of herbaceous species could be easily performed since the herbs might be less likely to exhibit large fluctuations of seed production from year to year compared to trees. Studies concerning the lack of successful germination of invading foreign seeds would contribute to our understanding of the maintenance of plant communities and the migration of plant community boundaries.

CHAPTER X

CONCLUSION

The main objective of this study was to determine if seed exchange occurs across the boundary between beech gaps and spruce stands by quantifying any seed rain changes with increasing distance from the boundary. The viable seed bank was sampled for evidence of seed exchange and to determine the potential role buried viable seed might play in the vegetation dynamics and gap-phase succession of the area.

Vegetation sampling demonstrated that the canopy of the beech gap and spruce stand differ quantitatively in the importance of species in common to both. Overstory transects demonstrated the existence of a narrow ecotone between the two plant communities where Picea rubens and Fagus grandifolia intergrade and where Amelanchier laevis is found.

The beech gap lacks an appreciable shrub layer with only Fagus grandifolia and Rubus canadensis being common. The spruce stand, however, has a dense shrub layer dominated by Rubus canadensis, Viburnum alnifolium, Betula lutea, and Vaccinium erythrocarpum.

The most obvious difference is found in the herbaceous flora. The spruce stand is dominated by Oxalis montana and Cacalia rugelia, whereas the beech gap contains a rich mesic woodland flora of Claytonia virginica, Erythronium americanum, Impatiens pallida, Aster

divaricatus, Poa alsodes, Carex intumescens and Phacelia fimbriata.

The seed rain study established that Betula lutea and Picea rubens seeds disperse from the spruce stand to the beech gap. Betula lutea showed a negative exponential decrease in density with increasing distance into the beech gap. Only Cacalia rugelia and Poa alsodes appear to be dispersing from their respective habitat (spruce stand and beech gap) into the adjacent community. Evidence is presented for the dispersal of Eupatorium rugosum into the beech gap from the Clingman's Dome Road; it is, however, uncertain whether those seeds present in the spruce stand originate from the road also.

From the seed bank data, it was inferred that seeds of Betula lutea (from the spruce stand) and Poa alsodes (from the beech gap) disperse across the boundary. The density pattern of Eupatorium rugosum seeds in the soil throughout the study site suggests that dispersal is occurring from the Clingman's Dome Road.

The seed banks of both communities contained seeds of early successional species such as Betula lutea, Eupatorium rugosum, Prunus pensylvanica, Sambucus pubens, and Potentilla simplex. The presence of these seeds would probably ensure vegetation recovery after a disturbance.

As with other seed bank studies, it was found that the seed bank lacked seeds of woody species. In contrast to other studies, however, these seed banks showed a high similarity with the overlying vegetation, particularly with the herbaceous vegetation. This

similarity is the result of the absence of major disturbed weedy seed source areas.

Reciprocal averaging, cluster analysis, and discriminant analysis were all effective in distinguishing the beech gap seed bank from the spruce stand seed bank. Reciprocal averaging demonstrated a vegetation gradient in the beech gap seed bank that is highly correlated with the sample slope position. This seed bank gradient is presumed to be caused by a herbaceous vegetation gradient where plant populations are responding to a moisture gradient. Reciprocal averaging gave uninterpretable gradients in the spruce stand seed bank.

Evidence of Betula lutea and Picea rubens seed dispersal into the beech gap suggests that the spruce stand has the potential to invade the beech gap, albeit slowly in light of Fuller's (1977) results and the erratic seed crops likely at these elevations. Lack of herbaceous species seed exchange is likely caused by the prevailing wind direction, reduced wind speed, frequent orographic precipitation, the low number of species exhibiting anemochorous dispersal and their low stature. These results suggest that herbaceous plant migration may be slow. Perhaps the high elevation beech gaps will resist encroachment from Picea rubens for a long time.

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APPENDICES

APPENDIX A

SUMMARY OF CALCULATED DIVERSITY INDICES

Table 15. Diversity Comparisons Between Beech Gap and Spruce Stand Seed Rain for Each Trap Type.

	Sticky Trap			Gravity Trap		
Diversity Indices	Beech G.		Spruce S.	Beech G.		Spruce S.
Species Richness	5 ± 2[A]	*	2 ± 1	5 ± 2	*	3 ± 1
Simpson's Index	0.48 ± 0.16	*	0.83 ± 0.15	0.48 ± 0.13	*	0.79 ± 0.18
Shannon-Wiener Index	0.41 ± 0.17	*	0.13 ± 0.12	0.43 ± 0.12	*	0.17 ± 0.13

[A]Mean ± standard deviation. *Significant difference at P = 0.0001 between the seed rain from the two plant communities.

APPENDIX B

PHENOLOGY OF SEEDING EMERGENCE

Table 16. Proportions of Germinants by Species Emerging per Period from the December Seed Bank.

Species	Weeks[a] 1	2	3	4	5	Totals
Angelica triquinata	4%(1)[b]	29%(7)	33%(8)	17%(4)	17%(4)	24
Aster spp.			62%(5)	25%(2)	13%(1)	8
Barbarea vulgaris		67%(53)	14%(11)	18%(14)	1%(1)	79
Betula lutea	1%(6)	2%(15)	50%(453)	30%(273)	17%(149)	898
Blephilia hirsuta		17%(12)	56%(40)	7%(5)	21%(15)	72
Cacalia rugelia		13%(2)	13%(2)	13%(2)	62%(10)	16
Carex intumescens	1%(3)	6%(38)	40%(258)	35%(223)	19%(120)	624
Carex pensylvanica			35%(17)	37%(18)	28%(14)	49
Claytonia virginica	25%(217)	45%(388)	20%(175)	4%(37)	6%(50)	867
Cuscuta gronovii	13%(9)	54%(13)	27%(19)		6%(4)	70
Dentaria diphylla		40%(2)	40%(2)		20%(1)	5
Dicentra cucullaria	60%(15)	28%(7)	12%(3)			25
Diervilla sessilifolia					100%(16)	16
Erechtites hieracifolia					100%(1)	1
Erythronium americanum	34%(21)	59%(36)	7%(4)			61
Eupatorium rugosum	1%(7)	17%(102)	22%(133)	27%(162)	33%(199)	603
Hieracium paniculatum					100%(6)	6
Houstonia serpyllifolia		1% (1)	23%(44)	33%(63)	43%(83)	191
Hypericum perforatum					100%(2)	2
Impatiens pallida	3%(2)	54%(33)	39%(24)	2%(1)	2%(1)	61
Lactuca sp.					100%(1)	1
Laportea candensis	3%(7)	24%(49)	33%(67)	17%(35)	18%(37)	202
Luzula echinata			42%(5)	33%(4)	25%(3)	12

Table 16. (Continued)

Species	Weeks[a] 1	2	3	4	5	Totals
Oxalis montana	3%(4)	47%(54)	19%(22)	19%(22)	11%(13)	115
Oxydendrum arboreum				34%(4)	66%(8)	12
Phacelia fimbriata					100%(252)	252
Plantago major				100%(1)		1
Poa alsodes					100%(1)	1
Poaceae					100%(78)	78
Polygonum erectum		100%(1)[b]				1
Potentilla simplex			58%(1119)	7%(129)	35%(678)	1926
Prenanthes altissima	16%(19)	67%(78)	9%(10)	1%(1)	7%(9)	117
Prunus pensylvanica		6%(2)	72%(23)	19%(6)	3%(1)	32
Rubus canadensis	1%(2)	5%(23)	43%(194)	43%(191)	8%(38)	448
Rumex acetosella		79%(342)	15%(63)	2%(10)	4%(18)	433
Sambucus pubens				86%(6)	14%(1)	7
Solidago spp.	6%(6)	45%(47)	26%(27)	10%(11)	13%(14)	105
Stachys clingmanii	4%(3)	28%(20)	49%(35)	11%(8)	7%(5)	71
Stellaria pubera	21%(8)	62%(24)	8%(3)		10%(4)	39
Taraxacum officinale		64%(9)	7%(1)	14%(2)	14%(4)	14
Vaccinium erythrocarpum					100%(5)	5
Viola pallens		5%(29)	27%(162)	48%(289)	20%(121)	601
Viola sp.	7%(1)	20%(3)	40%(6)	7%(1)	26%(4)	15
Unidentified					100%(6)	6

[a]The weeks are defined at the bottom of Table 10 on page 100.

[b]The percentages are the proportion of all the seeds germinating during each week. The numbers in parentheses are the actual numbers of germinants that emerged during the week.

Table 17. Proportions of Germinants by Species Emerging per Period from the March Seed Bank.

Species	Weeks 1	2	3	4	5	Totals
Angelica triquinata	11%(1)	67%(6)	11%(1)		11%(1)	9
Betula lutea	7%(6)	28%(24)	45%(39)	6%(5)	15%(13)	87
Carex intumescens	9%(13)	39%(57)	25%(36)	11%(16)	16%(23)	145
Carex pensylvanica					100%(11)	11
Claytonia virginica	42%(487)	41%(478)	14%(166)	2%(23)	1%(5)	1159
Cuscuta gronovii	38%(3)	12%(1)	12%(1)	12%(1)	25%(2)	8
Dentaria diphylla	50%(1)			50%(1)		2
Erythronium americanum	50%(11)	50%(11)				22
Eupatorium rugosum	3%(16)	31%(168)	27%(148)	9%(47)	30%(159)	538
Gnaphalium sp.					100%(3)	3
Houstonia serpyllifolia		2%(1)	32%(21)	15%(10)	52%(34)	66
Hypericum perforatum			100%(2)			2
Impatiens pallida	52%(17)	45%(15)	3%(1)			33
Laportea canadensis	22%(16)	47%(35)	11%(8)	14%(10)	7%(5)	74
Oxydendrum arboreum				100%(2)		2
Phacelia fimbriata				1%(1)	99%(170)	171
Poaceae				40%(2)	60%(3)	5
Prenanthes altissima	59%(19)	31%(10)	6%(2)	3%(1)		32
Prunus pensylvanica	33%(1)	33%(1)	33%(1)			3
Rubus canadensis	10%(13)	30%(40)	46%(61)	8%(10)	6%(8)	132
Rumex acetosella		100%(1)				1
Solidago spp.	14%(28)	70%(146)	12%(24)	1%(3)	3%(6)	207

Table 17. (Continued)

Species	Weeks 1	2	3	4	5	Totals
Stachys clingmanii	22%(5)	52%(12)	22%(5)	4%(1)		23
Stellaria pubera	41%(16)	33%(13)	10%(4)	5%(2)	10%(4)	39
Taraxacum officinale		33%(1)	67%(2)			3
Viola pallens	1%(1)	25%(158)	45%(283)	4%(23)	25%(159)	624
Viola sp.		82%(9)	18%(2)			11
Unknown 26				14%(1)	86%(6)	7
Unknown 28					100%(1)[b]	1
Dead	30%(7)	65%(15)	4%(1)			23

[a]The weeks are defined at the bottom of Table 10 on page 100.

[b]The percentages are the proportion of all the seeds germinating during each week. The numbers in parentheses are the actual numbers of germinants that emerged during the week.

VITA

Noel Bruce Pavlovic was born February 21, 1955 at Bellefonte, Pennsylvania. He attended public schools in Morgantown, West Virginia. He spent his senior year in high school at Campbelltown, New South Wales, Australia as a Rotary International High School Exchange Student. While in Australia, he attended Hurlstone Agricultural High School where he received his Higher School Certificate. In March 1974, he received his High School Diploma by passing the West Virginia G.E.D. Test.

After four years attending Earlham College, in Richmond, Indiana, he received his A.B. in biology with Honors in June 1978. He also received the Millard Markle Award for field biology. While at Earlham College, he was active in the Joseph Moore Museum as a curator for the teaching and seed collections.

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