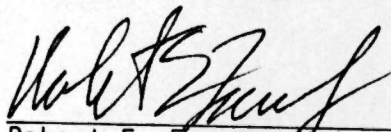
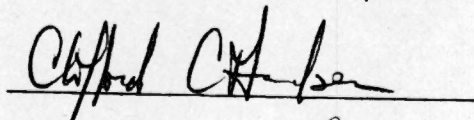


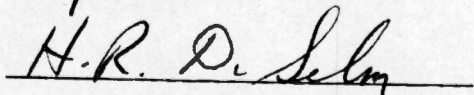
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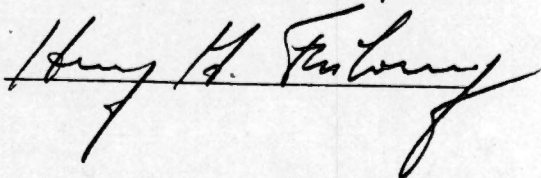
I am submitting herewith a thesis written by June M. Dobberpuhl entitled "Seed Banks of Forest Soils in East Tennessee." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology.


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IN EAST TENNESSEE

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

June M. Dobberpuhl
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ABSTRACT

The objectives of this study were to examine viable seed banks of forest soils in East Tennessee and to evaluate the potential of the forest topsoil as a source of propagules for use in the revegetation of surface mine sites. Four high elevation sites (800-1000 m), typical of areas being surface mined, were located in Campbell County in the Cumberland Mountains. Four low elevation sites (300-400 m) were located in Anderson County in the Tennessee Valley. At each of these sites, soil samples were collected in the spring and summer of 1978. The samples were incubated in a greenhouse and emergent germinants were identified. The standing vegetation was sampled at each site, and its composition was compared to that of the seed bank.

The results showed that there were large quantities of buried viable propagules in the soils, with germinants ranging from 300 to over 2,000 seedlings/m². A grand total of 199 species germinated from all soil collections, including 170 species from the spring samples and 113 species from the summer samples.

Over twice as many germinants emerged from the spring soil collections as from the summer sets. Significantly greater numbers germinated from the high elevation soils than from the low elevation soils with the spring collection. Sites differed greatly from one another in terms of the numbers and species composition of the germinants. Significantly fewer numbers emerged from the litter than from the 0-5 cm and the 5-10 cm depths.

At all sites, the species composition of the seed bank was very different from that of the vegetation. The species which were among

the most abundant germinants are typically found in early successional environments. On the other hand, most of the species composing the vegetation were apparently absent from the seed bank and tended to germinate from the litter layer. The fact that many of the early successional species germinated in the largest numbers from the 5-10 cm soil depth is evidence in support of the long-term storage of their seeds in the soil. Possible roles of such dormant seeds in the succession of plant communities were considered.

The implications of the buried seed populations in terms of the revegetation of disturbed areas were discussed. Although there is great potential within the topsoil to initiate revegetation, further studies are needed to assess its usefulness in surface mine reclamation and post-logging regeneration.

TABLE OF CONTENTS

CHAPTER	PAGE
I. INTRODUCTION.	1
II. REVIEW OF SELECTED LITERATURE	5
Characteristics of Plant Populations.	5
The Viability of Buried Seeds	11
Studies of Seed Banks	14
III. PROBLEMS IN DETERMINING BURIED SEED NUMBERS	33
IV. METHODS	36
General Summary	36
Site Selection and Characterization	38
Vegetation and Soil Sampling.	39
Seed Germination Studies.	42
V. DATA ANALYSIS	48
Vegetation.	48
Germination Studies	48
Relationships of the Seed Banks to the Vegetation	51
VI. CHARACTERISTICS OF THE STUDY SITES.	52
Site Characteristics, Geology, and Land Use	52
Site Soil and Vegetation Descriptions	54
VII. RESULTS OF THE GERMINATION STUDIES.	64
Total Germination and Its Relationship to Elevation, Site, Soil Depth, and Time of Sampling.	64
Total Numbers of Species and Their Relationship to Elevation, Site, Soil Depth, and Time of Sampling	69
Floristic Composition of the Buried Viable Seed Populations at the Eight Study Sites.	72
Species Diversity and the Index of Similarity	84
Ferns and Bryophytes.	88
VIII. SPECIES--AREA CURVES.	92
IX. PATTERNS OF GERMINATION	97
General	97
Germination Characteristics of Important Species.	99
Effects of Soil Depth on Germination Behavior	105
X. COMPARISONS OF SITE VEGETATION WITH BURIED SEED BANKS	109
General Comparisons and Similarity Indices.	109
Comparisons Between the Buried Seed Populations and the Site Vegetation	111

CHAPTER	PAGE
Summary	120
XI. DISCUSSION.	122
The Biology of Buried Seed Populations.	122
Applications in Surface Mine Reclamation and Forest Regeneration.	126
XII. SUMMARY AND CONCLUSIONS	132
LITERATURE CITED	136
APPENDICES	147
A. DESCRIPTION OF THE STUDY AREA.	148
B. COMPOSITION OF THE VEGETATION AT THE STUDY SITES	156
C. FLORISTIC COMPOSITION OF THE BURIED VIABLE SEED POPULATIONS. .	181
D. SEED GERMINATION FROM DIFFERENT SOIL DEPTHS.	215
VITA	219

LIST OF TABLES

TABLE	PAGE
1. Information on Studies of Buried Seed Populations	16
2. Summary of Site Characteristics, Including Slope Angle, Elevation, Aspect, and Bedrock.	53
3. Summary of Soil Characteristics at the Study Sites.	55
4. Total Numbers of Germinants from the Soil Collections	65
5. Analysis of Variance of the Numbers of Germinants	66
6. Results of Student's Test of Differences in Mean Numbers of Germinants Between Soil Depths Within Sites	68
7. Total Numbers of Germinating Species.	70
8. Importance Values of the Germinating Species.	73
9. Species Germinating in Greatest Abundance	82
10. Species Diversity of the Germinants	85
11. Indices of Species Similarity of Germinants Among the Different Sites (Spring Collection)	86
12. Indices of Species Similarity of Germinants Among the Different Sites (Summer Collection)	87
13. Similarities of Germinating Species Between the Spring and Summer Samples.	89
14. Numbers of Plants and Numbers of Species Which Were Early Germinants.	98
15. Times of Maximum Germination of Selected Species.	100
16. Species Germination from Different Soil Depths.	107
17. Species Similarity Between the Standing Vegetation and the Viable Seed Bank.	110
18. Composition of the Canopy and Understory at Site 1 (Clear Creek).	157
19. Composition of the Groundcover at Site 1 (Clear Creek).	158

TABLE	PAGE
20. Composition of the Canopy and Understory at Site 2 (Greenbelt Cove)	160
21. Composition of the Groundcover at Site 2 (Greenbelt Cove) . .	161
22. Composition of the Canopy and Understory at Site 3 (River Bluff).	163
23. Composition of the Groundcover at Site 3 (River Bluff). . . .	164
24. Composition of the Canopy and Understory at Site 4 (State Park)	166
25. Composition of the Groundcover at Site 4 (State Park)	167
26. Composition of the Canopy and Understory at Site 5 (Cross Mountain)	169
27. Composition of the Groundcover at Site 5 (Cross Mountain) . .	170
28. Composition of the Canopy and Understory at Site 6 (Hatmaker Knob)	172
29. Composition of the Groundcover at Site 6 (Hatmaker Knob). . .	173
30. Composition of the Canopy and Understory at Site 7 (Big Bruce Ridge).	175
31. Composition of the Groundcover at Site 7 (Big Bruce Ridge). .	176
32. Composition of the Canopy and Understory at Site 8 (Wheeler Creek Cove)	178
33. Composition of the Groundcover at Site 8 (Wheeler Creek Cove)	179
34. Floristic Composition of the Buried Viable Seed Population at Site 1	182
35. Floristic Composition of the Buried Viable Seed Population at Site 2	186
36. Floristic Composition of the Buried Viable Seed Population at Site 3	190
37. Floristic Composition of the Buried Viable Seed Population at Site 4	193
38. Floristic Composition of the Buried Viable Seed Population at Site 5	197

TABLE	PAGE
39. Floristic Composition of the Buried Viable Seed Population at Site 6	201
40. Floristic Composition of the Buried Viable Seed Population at Site 7	206
41. Floristic Composition of the Buried Viable Seed Population at Site 8,	211
42. Overall Summary of Species Germination from Different Soil Depths.	216

LIST OF FIGURES

FIGURE		PAGE
1.	Map of the Region of East Tennessee Where the Study Sites Were Located.	37
2.	Locations of the Four Low Elevation Study Sites in the Area of Norris in Anderson County, Tennessee	40
3.	Locations of the Four High Elevation Study Sites in the Cumberland Mountains in Campbell County, Tennessee.	41
4.	Cumulative Species Numbers of Germinants from the Spring Collection of Sites 1 to 4.	93
5.	Cumulative Species Numbers of Germinants from the Spring Collection of Sites 5 to 8.	94
6.	Cumulative Species Numbers of Germinants from the Summer Collection of Sites 1 to 4.	95
7.	Cumulative Species Numbers of Germinants from the Summer Collection of Sites 5 to 8.	96
8.	Cumulative Germination of Species-- <u>Hydrangea arborescens</u> , <u>Rubus allegheniensis</u> , <u>Houstonia purpurea</u>	101
9.	Cumulative Germination of Species-- <u>Gramineae</u> spp., <u>Eupatorium rugosum</u> , <u>Liriodendron tulipifera</u>	102
10.	Cumulative Germination of Species-- <u>Erechtites hieracifolia</u> , <u>Eupatorium serotinum</u> , <u>Phytolacca americana</u>	103
11.	Cumulative Germination of Species-- <u>Panicum commutatum</u> , <u>Poa pratensis</u> , <u>Oxydendrum arboreum</u>	104

CHAPTER I

INTRODUCTION

Forest ecosystems are periodically subject to disturbances, of both human and natural origins, including cultivation, logging, fire, wind, and disease. Although effects vary depending on the type of vegetation and site characteristics, a major event, such as clear-cutting for timber or agriculture, will disrupt ecosystem functions. However, if no further disturbing forces occur, dense stands of fast-growing, early successional species may appear almost immediately (Marks and Bormann 1972).

The revegetating species may originate from the growth of germinating, buried seeds and of other underground plant propagules or by transport of seed dispersed by wind and animals following the disturbance. A common example of revegetation is the rapid growth of early successional herbs on recently abandoned farmlands.

The role of buried seeds and other underground propagules in revegetating disturbed sites is easily overlooked, a situation perpetrated by an "out of sight--out of mind" attitude. However, most land which supports vegetation will hold a reservoir of accumulated seeds derived from the sexually reproductive plants of the area and incoming disseminules of certain adaptive species. The germination of these seeds may lead to the rapid revegetation of the site.

Revegetation following logging operations may depend to a considerable extent upon the germination of seeds buried in the soil.

The degree to which forest ecosystems are disturbed by logging activities varies from clear-cutting to the selective harvests of certain species.

The size of canopy openings and the degree of soil disturbance which result from logging schemes alter the speed and pattern of revegetation from buried and dispersed propagules. Therefore, knowledge of the size and composition of buried propagule populations, and the relationship of different types of disturbances to revegetation rates, may be very important in developing sound forestry management practices. In other words, the seed bank (which includes seeds and vegetative propagules) should be considered a natural resource.

Coal mining is an activity which usually drastically changes the landscape. The surface of the land is left covered by spoil materials which vary greatly from site to site, and revegetation may be a slow process. These materials may consist of a mixture of shale fragments, coal chips, soil, and rock debris. Properties of the spoil which make it adverse to plant growth may include: unfavorable pH value of the parent material, derived directly or derived as a result of weathering and the oxidation of pyrites; high concentrations of available heavy metals such as iron, manganese, copper, and zinc; absence of humus; coarse structure with low water retention capacity, or compacted material with poor aeration, as in the case of spoil banks; and high spoil surface temperatures during the summer. Because of the heterogeneity of the spoil material, invasion and subsequent plant succession may vary considerably within a given area (Barnhisel and Massey 1969; Meyer 1973).

Previously, the topsoil, which is the storage compartment of revegetating propagules and is capable of providing the environment favorable for seedling growth, was typically removed and buried during mining operations. Rehabilitation of the sites was commonly begun by planting species different from those species composing the original vegetation.

However, recent surface mining regulations (PL-95) encourage the use of native species in revegetation. In addition, the topsoil which is removed during mining activities must be stored and spread on top of the spoil after other operations cease. The topsoil may not only contribute to the revegetation scheme through the germination from buried seeds but will serve as a medium for the planting of desirable native species. These measures should aid in the recovery and eventual development of stable plant communities on the land.

The objective of this study was to examine viable seed banks of forest soils in East Tennessee. Four high elevation sites (800-1000 m), typical of areas being surface mined, were located in Campbell County in the Cumberland Mountains. Four low elevation sites (300-400 m) were located in Anderson County in the Tennessee Valley. At each of these sites, soil samples were collected and the densities and species composition of buried viable propagules (including seeds and various organs of vegetative reproduction such as roots, bulbs, and cormes) were determined. The standing vegetation was sampled at each site, and its composition was compared to that of the seed bank. The results should aid in the prediction of the potential of forest topsoil as a revegetation medium after site disturbances such as surface mining or logging.

The study should contribute to knowledge of the role of buried seeds in the dynamics of plant communities. As potential resources for the revegetation of disturbed lands, the buried seed populations may influence the type of vegetation growing on a site, and because they represent the accumulation of viable propagules, their study should enhance the understanding of the successional history of the land.

CHAPTER II

REVIEW OF SELECTED LITERATURE

Characteristics of Plant Populations

Plant populations, like those of most other organisms, are composed of individuals of different ages. However, in most cases it is difficult to study age classes of plants, because considerable differences in vigor and in importance in the population may exist among plants of the same age. Therefore, individuals in a plant population may be classified in terms of their distribution in various "age states." Some individuals are present in a dormant condition as viable seeds in the soil. Others may be in a pre-reproductive, vegetative state initiated by the germination of seed. Plants in this juvenile stage are weakly developed, a condition which may persist for years if light and nutrient resources are in low supply. Another part of the population is producing seeds while the final group consists of post-reproductive, vegetative individuals. It is a characteristic of plants that individuals in the purely vegetative states may be increasing the numbers of individuals in the population through asexual reproduction.

Plant populations may include viable propagules in the soil consisting of dormant seeds and various vegetative forms such as stolons and rhizomes. All of these forms together represent the "seed bank," a term which may be somewhat misleading since it includes vegetative propagules in addition to seeds. However, this is the terminology

which has been accepted in the literature and will be adhered to here (Harper 1977).

In a plant community, the number of underground propagules may greatly exceed the number of individuals in the standing vegetation. The populations of certain species may consist only of viable seeds, some of which remain dormant and viable for many years. Alternatively, accumulated viable seeds may be entirely absent in other species. There may be several reasons for this, including lack of seed-bearing individuals, inability of individuals to produce viable seeds, rapid germination of seeds resulting in no accumulation, and often, in conjunction with this, a short period of seed viability, or high rates of animal predation (Rabotnov 1969).

Most seeds are physiologically dormant when they enter the soil, and some require a period of afterripening before they will germinate. Depending upon the species, a proportion of the seed population may germinate when favorable light, water, temperature, and nutrient conditions prevail. Harper (1977) designated this group the population's "current" account while long-term dormant seeds become part of the "deposit" account.

The most deeply buried seeds are not likely to germinate until they are brought up to or near the surface, perhaps through the action of a burrowing animal. However, the frequency of such events is unknown and is difficult to assess. It is likely that most of the seeds will die and decay in situ unless some outside force, such as cultivation for agriculture, disturbs the soil (Harper 1977).

It has been shown that loss of viability occurs most rapidly in those seeds with little initial dormancy or in those seeds with shallow placement. Seeds of a particular species which accumulate

at depths of 10 to 15 cm may maintain dormancy for longer periods than seeds of the same species with more shallow placement. However, if seeds remain deeply buried beyond their period of natural dormancy, they may germinate in situ, and the embryo will decay when emergence cannot occur. Such events would lead to rapid losses in the numbers of buried seeds (Horng and Leu 1978; Kellman 1978; Stoller and Wax 1973, 1974; Williams 1978).

The soil surface functions as a sieve determining the proportion of the seed population which will germinate and the proportion which will be subject to further dormancy. Many characteristics of the environment, including temperature, moisture levels, light intensity and spectral composition, and the effects of surrounding vegetation, influence germination (Harper and White 1970).

Dormancy in a seed population may be an adaptive strategy allowing plants to minimize environmental stress. Seed germination and early seedling growth are the most vulnerable phases in the plant life cycle. Selection should occur for those mechanisms that stimulate germination under the conditions most favorable for survival. The accumulation of viable seeds in the soil and the environmental regulation of germination represent adaptive strategies which increase the chances of a given genotype germinating under optimal conditions (Angevine and Chabot 1979).

Several adaptive mechanisms have been recognized as a result of studies dealing primarily with species of early successional habitats. For instance, Wesson and Wareing (1967) suggested that weed seed burial induced a light requirement for the germination of some species. Taylorson (1970) found that the light sensitivity

appeared to be mediated by the phytochrome system. This response may be affected by other environmental factors, especially moisture levels (Stoller and Wax 1973). A light requirement for germination implies certain ecological conditions. The forest canopy may inhibit the germination of buried seeds of early successional species. The chances of survival of such species would be greater in a forest clearing than under the shade of a dense or mature canopy.

Buried seeds of early successional species apparently are able to respond to environmental disturbances in other ways. A disturbance of the forest canopy will alter the local environment. When a tree is uprooted, some buried seeds are brought to the surface of the soil; there they experience unfiltered light, higher temperatures during the growing season, greater fluctuations in daily temperature, low CO₂ concentrations, and possibly high levels of potassium and nitrate ions. The germination of early successional herbaceous species and some woody species has been shown to be enhanced by these factors (Marks and Bormann 1972; Bazzaz 1979).

Some species have evolved other adaptive mechanisms such as seed polymorphism. Somatic polymorphism of seeds is common in certain families such as the Chenopodiaceae, Compositae, Cruciferae, and Gramineae. In species of Atriplex and Chenopodium, in the Chenopodiaceae, polymorphism seems to be the rule.¹ Individual plants of Chenopodium album produce both large brown and small black seeds. The brown seeds are able to germinate at once while the black ones are innately dormant (Harper, Lovell, and Moore 1970).

¹All binomial Latin names follow those used by the authors in the citation.

Germination characteristics may differ even among seeds which are phenotypically similar. Thompson (1973) found that great variation existed among the germination rates of seeds from different capsules on a given plant, although the amount of variation among progeny occurred within a limited range for each parent plant. Thus, within a given habitat, a species may show more than one germination pattern.

Angevine and Chabot (1979) recognized two adaptive syndromes of seed germination which they called avoidance and tolerance strategies. A tolerant species would typically be one of mature communities, able to germinate under shaded, highly competitive circumstances. In oak (Quercus spp.), the embryo is dependent upon the large reserve of endosperm to survive the initial stages of seedling development. Large-seeded tree species, such as the oaks and buckeye (Aesculus octandra), have hypogeal germination where the young seedling remains independent of the necessity for photosynthesis. In contrast, most small-seeded tree and early successional herbaceous species have epigeal germination (Bazzaz 1979).

However, the photosynthetic advantages of epigeal germination have associated costs. In response to the physical stresses of drought or cold and the biotic stresses associated with the vegetation at the site, the small-seeded species have evolved avoidance strategies of germination. The species may be capable of prolonged seed survival in the soil, where dormancy could be broken by factors such as light, fire, or, alternatively, widespread dispersion into more favorable environments (Angevine and Chabot 1979). These ideas have received support by Werner (1979), who contends that species with small seeds and limited dispersal abilities tend to have great longevity.

Apparently some species, particularly wind-dispersed members of the Compositae and bird-dispersed species such as pin cherry (Prunus pennsylvanica) and sumac (Rhus spp.), may have the further advantage of both widespread dispersal and long-term dormancy.

Several investigators have viewed the population dynamics of the seed bank as distinct from the rest of the life cycle of plants. Schafer and Chilcote (1969) have presented a model which divides the total buried seed population into four additive components. (1) P_{ex} are the exogenous, or environmentally induced, dormant seeds, which would be expected to germinate under favorable conditions. (2) P_{en} are the endogenous or innately dormant seeds which require internal physiological changes before they will germinate; they may not germinate even if the environmental conditions are optimum. (3) D_g are seeds which germinate in the soil and consequently decay. (4) D_n are the nonviable portion of the ungerminated seeds. The number of seeds in each of these categories will vary with the plant community under study. However, little is known about the magnitudes of the controlling factors under natural conditions.

Cohen (1966) modelled the factors affecting the size of the seed bank of annual plants to arrive at optimal strategies. The factors used included the number of seeds expected to be produced per seedling, the fraction of the total accumulated seeds which decay each year, and the probability of successful reproduction. Several preferred strategies were reached. For example, in an environment where there is a high probability of failure, the ability of the seeds

to survive a long time in the soil and to maintain a low germination rate would comprise an optimal strategy except under extremely favorable conditions, when high germination should occur. Conversely, where the probability of successful germination is high, an optimal strategy would include a high germination fraction with less emphasis on storage in the soil. The model predicted that there should be a strong positive correlation between the fraction of seeds which germinate each year and the fraction which decays. In addition, in a highly uncertain environment, the fraction of the seeds remaining dormant in a given year should be correlated with the probability of the seedlings growing to reproductive size.

Models such as those of Schafer and Chilcote, and of Cohen, assume that seeds do in fact remain dormant and viable in the soil for substantial periods of time. However, until recent years, reliable evidence concerning the lifespan of all but a few species of seeds was lacking although some people have long been interested in this topic.

The Viability of Buried Seeds

Studies of seed viability fall into two groups: (1) records of germination of dry-stored or herbarium seed and (2) records of seeds which supposedly have been dormant in undisturbed soil over a period of time. The earliest complete information of stored seeds was compiled by de Candolle and later extended by Becquerel (Ewart 1908 and Crocker 1938). Ewart tested the germination of seed samples of 46 species or varieties after storage in an herbarium and found that many specimens which were over 100 years old germinated. In contrast,

results of germination tests carried out by the British Association between 1840 and 1857 indicated that seeds remain viable in dry storage for only short periods of time, on the order of three to eight years. A few of the 220 species which they studied were typical farm weeds. In both these tests and those of Ewart, the longest-lived species produced hard seeds and were in the families Leguminosae and Malvaceae (Brenchley 1918).

Despite the usefulness of such studies, it must be recognized that the conditions of seeds existing in dry storage are different from those of seeds buried in the soil. The soil environment is highly variable, and seeds are subject to fluctuating temperatures and moisture and oxygen levels. Recognizing this, several early investigators did examine the viability of seeds stored in soil.

Although numerous dubious claims have been made, viable seeds of Nelumbo nucifera dug up from Manchurian peat have been reliably dated at 150-250 years old (Exell 1931 and Harper 1977). Other studies have been reported by Harper (1977). For instance, the use of radio-carbon techniques with Chenopodium album and Spergula arvensis indicate that their seeds may remain viable in the soil for 1600 years.

Peter (1894) collected soil samples from forests with known histories at depths of 8, 16, and 25 cm. Seeds present in these samples were allowed to germinate and the seedlings were later identified. The seedlings which emerged from old forest samples were composed of species characteristic of that habitat. However, samples from younger forests yielded species of the prairies and fields which had earlier been the predominant vegetation types. Some of the most abundant species germinating included Juncus bufonius, Ranunculus

repens, Plantago major, Gnaphalium uliginosum, Chenopodium polyspermum, and Rubus idaeus, all typical of early successional environments.

Peter concluded that the presence of these viable seeds in the soil indicated that they may have been stored there for more than 50 years.

The first systematic attempt to study the longevity of seeds buried in the soil was begun by Beal in 1879 at East Lansing, Michigan. Seeds of 23 species of plants commonly growing in the vicinity were used. Twenty lots of 50 seeds of each species were mixed with moistened sand in unstoppered jars and were buried slanting downward three feet below the ground surface. A bottle was dug up every five years for the first 35 years of the experiment and every tenth year thereafter. The results of viability tests on the seeds were reported in the literature (Beal 1884, 1904, 1905, 1911; Darlington 1922, 1931, 1941, 1951).

The 90-year period of the experiment was reported by Kivilaan and Bandurski (1973). Although three species (Rumex crispus, Oenothera biennis, and Verbascum blattaria) had germinated at the 80-year period (Darlington and Steinbauer 1961), only one, V. blattaria, had viable seed (20% germination) after 90 years. No other species germinated.

Another study of the viability of buried seeds was initiated by Duvel in 1902. Lots of 100 or 200 seeds of 107 species of crop and weed species were mixed with soil in flower pots and buried at 20, 55, and 105 cm below the soil surface. The lots were periodically removed and the species tested for germination. Of the 107 species buried in 1902, 36 remained viable after 39 years, most of them typical of early successional environments (Duvel 1902; Toole and Brown 1946).

Before the investigations of Beal and Duvel were reported, there was some skepticism concerning the ability of seeds, particularly small ones, to remain viable for long periods of time (Ewart 1908). It was reasoned that only large, hard-seeded species would have the necessary food reserves and mechanical resistance to survive in an unpredictable environment. However, the work of Beal and Duvel suggested that small seeds, especially those of early successional species, may be among the most long-lived (Crocker 1938 and Goss 1924).

Studies of Seed Banks

Arable lands. The role of buried, viable seeds in plant population dynamics was not recognized until several British workers began examining the weeds of arable lands. Brenchley's (1918) work represents the first thorough attempt to enumerate the buried seed populations of arable lands, and numerous related studies have appeared since then (Brenchley and Warrington 1930, 1933, 1936, 1945; Chippendale and Milton 1932; Čepil 1946a, 1946b; Champness and Morris 1948; Champness 1949; Dore and Raymond 1942; Barton 1962; Rampton and Ching 1966, 1970; Robinson and Kust 1962; Roberts 1968; Roberts and Stokes 1965; Roberts and Feast 1972; Roberts and Ricketts 1979; Horng and Leu 1978; Williams 1978; Stoller and Wax 1973, 1974; Taylorson 1970; Kropáč 1966; Kellman 1974b, 1978).

The general procedure used to enumerate viable seeds in these studies included the collection of soil samples in the field and the storage of them under conditions suitable for germination. In some cases, the soil was sifted and sieved to reduce its volume, remove undesirable rocks and vegetative matter, and to concentrate the seeds.

As the seedlings emerged they were identified and removed. Summaries of the buried seed populations for some of the papers cited above, dealing with agricultural soils, along with the results from studies in other habitats, are presented in Table 1.

In 1918, Brenchley concluded that the floristic composition of the buried seed banks is closely related to the vegetational history of the land. The soil of land once cultivated, and then planted to grass for over 50 years, contained many viable weed seeds of species typical of those invading arable land. Brenchley noted that in old pastures, there was a tendency for the buried weed seeds to be concentrated in the lower soil depths while in recently cultivated fields there were more seeds near the surface. This seems reasonable since the seeds at the surface are in a better position to germinate than those buried more deeply. Therefore, the deeply buried seeds represent accumulation over a longer period of time, possibly since the last disturbance. In one pasture which had been cultivated ten years before, 4200 seeds/m², comprised mainly of arable weed species, were found. On the older pastures the numbers gradually declined, presumably the result of the decay of accumulated seeds.

Brenchley and Warrington (1930) studied the buried seed population in a field which had been planted in winter wheat since 1843. During a three year period, 47 species germinated from the samples they had collected, amounting to a seed population of about 39,000/m². However, poppy (Papaver spp.) made up about 70% (almost 28,000 seeds/m²) of all the seedlings recorded.

Most of the species showed a definite periodicity in their timing of germination over the year, with the greatest numbers emerging

Table 1. Information on studies of buried seed populations.

Location	Vegetation	Number of Seeds Per Sq. Meter	Depth of Sampling	Source
Great Britain (Rothamsted)	Permanent wheat	39,100	15cm	Brenchley & Warington (1930)
Great Britain (Woburn)	Permanent wheat	28,800	15cm	Brenchley & Warington (1933)
Great Britain (Welsh Plant Breeding Stat.)	Native pasture	23,500	15cm	Chippendale & Milton (1934)
	Formerly arable grassland	62,300		
	Managed for hay	38,000		
Great Britain (Grassland Improvement Stat.)	Newly sown grassland	4900-18,800	16cm	Champness & Morris (1948) & Champness (1949)
Quebec, Canada	Permanent pastures	2300-7300	2.5cm	Dore & Raymond (1942)
Great Britain (Vegetable Research Stat.)	Vegetable crops	1200-66,000	10-15cm	Roberts (1968) and Roberts & Ricketts (1979)
Belize Valley, British Honduras	Pastures	5200	4.2cm	Kellman (1974b, 1978)
		12,960	10cm	
	Cultivated fields	7600	4.2cm	
		9800	10cm	

Table 1 (Continued)

Location	Vegetation	Number of Seeds Per Sq. Meter	Depth of Sampling	Source
Great Plains, USA	Mixed prairie	300-800	1.25cm	Lipert & Hopkins (1950)
	Revegetating, previously cultivated lands	20,000		
California, USA	Bunchgrass sites: Ungrazed	8,200	5cm	Major & Pyott (1966)
	Grazed	12,300		
Wyoming, USA	Sagebrush-grass	60-1150	5cm	Beauchamp et al. (1975)
	Greasewood	30-780		
	Saltbush	138-1900		
Rio Puerco Basin, West Central New Mexico	Alkali sacaton shrub canopy	70-680	1.3cm	Knipe & Springfield (1972)
	Barren sites	0-50		
Mojave Desert, Nevada, USA	Shrub canopy	2400-7700	2cm	Nelson & Chew (1977)
	Exposed areas	230-570		
North central Iowa, USA	Prairie glacial marshes	22,500-24,400	0-5cm	van der Valk & Davis (1978, 1979)
		14,100	10-15cm	
		2880	20-25cm	
		1140	30-35cm	

Table 1 (Continued)

Location	Vegetation	Number of Seeds Per Sq. Meter	Depth of Sampling	Source
Trenton, New Jersey, USA	Freshwater tidal marsh	6400-32,400	10cm	Leck & Graveline (1979)
Durham, North Carolina, USA	Successional Series: Cultivated field	7000	14cm, excluding	Oosting & Humphreys (1940)
	1-yr field	13,600	litter to	
	2-yr field	4400	fermentation	
	5-yr field	7000	zone	
	15-yr pine stand	6600		
	33-yr pine stand	8300		
	58-yr pine stand	725		
	85-yr pine stand	4300		
	112-yr pine stand	1500		
	Oak-hickory forest	1200		
Orono, Maine, USA	Forest stands:		Duff, humus, Olmsted & Curtis (1947)	
	70-yr white pine	173	& top layer	
	80-yr white pine	0	of mineral	
	30-yr spruce-fir	48	soil	
	24-yr red pine	5		
	50-yr beech-birch-maple	38		
	110-yr beech-birch-maple	91		
	150-yr sugar maple	11		
Harvard Forest, Massachusetts, USA	Stages in old field succession:		11cm, including	Livingston & Allesio (1968)
	1-yr horseweed field	2500	litter	
	2-yr goldenrod field	4600	& humus	
	8-yr broomsedge field	1260		

Table 1 (Continued)

Location	Vegetation	Number of Seeds Per Sq. Meter	Depth of Sampling	Source
Urbana, Illinois, USA	5-yr white pine stand	4500	5cm	Raynal & Bazzaz (1973)
	25-yr white pine	5010		
	47-yr white pine	1350		
	80-yr white pine	3350		
	60-yr cultivated fields from 2 original vegeta- tion types:			
	1) Deciduous Forest Soil			
	Spring	2,074		
	Fall	825		
	2) Tall Grass Prairie Soil			
	Spring	511		
	Fall	527		
LaGrande, Oregon, USA	Mixed Conifer Stands:		Litter 0-2cm 2-4cm	Strickler & Edgerton (1976)
	Fir-pine	145		
		126		
		83		
	Fir-spruce-tamarack	720		
		453		
		298		
	Hemlock-spruce	1433		
		845		
		209		

Table 1 (Continued)

Location	Vegetation	Number of Seeds Per Sq. Meter	Depth of Sampling	Source
New Brunswick, Canada	Deciduous Forests:		Organic soil	Moore & Wein (1977)
			Mineral soil	Wein (1977)
	Birch-beech	3050	0-6cm	
		350	0-6cm	
	Maple (clear-cut 5 yrs before)	1290	0-10cm	
		100	0-6cm	
	Spruce	370	0-10cm	
		0	0-6cm	
	spruce (clear-cut 30 yrs. before)	130	0-6cm	
		50	0-6cm	
Haney, British Columbia	Tamarack bog	320	10cm	
	Treeless bog	0	10cm	
	Douglas Fir-hemlock	845	0-5cm	Kellman (1970)
	Old-growth coniferous forest	171	5-10cm	Kellman (1974a)
		205	10cm, including litter	
East Great Slave Lake, N.W.T.	Secondary community	2610		
	Subarctic Forests	0	10cm	Johnson (1975)
Fraser, Colorado, USA	Subalpine Forests:			Whipple (1978)
	Mesic spruce-fir	52.8	5cm, including litter	
	Dry lodgepole pine	3.2		

during the fall and winter. In addition, many species displayed a natural period of dormancy, during which time they would not emerge even if placed under conditions suitable for continuous germination. This is in contrast to seeds which remain viable in the soil for long periods, in a state of dormancy induced by conditions unfavorable for germination. Such seeds would be likely to germinate immediately if placed in a favorable environment.

Chepil (1946a, 1946b) studied the viability of lots of seeds of weed species buried in cultivated soil. He found that the lifespans of six of the 58 species studied were one year or less, while 18 species had seeds which did not live beyond three years. The majority of the species with longer seed lifespans were those commonly recognized as serious agricultural weeds. With most species, the ratio of the total number of seeds germinating to those initially present in the soil was very low, indicating low viability at the outset or appreciable death during storage.

The relationship between weed seedling emergence and buried seed populations was further illuminated by Roberts and Ricketts (1979). Using sieving and flotation techniques to extract the seed, the emergence of seedlings from prepared seedbeds was compared with the total number of viable seeds present in the soil to a depth of 10 cm. Although the numbers varied with the species, under adequate moisture conditions, only 3% to 6% of the total number of seeds emerged, while under drought conditions the percentages were even lower. The authors suggested that data of this sort would be useful in predicting potential weed floras at a given locality.

The persistence of arable weed seeds in the soil and the variation among species, in terms of the number of seeds produced per plant and the period of natural seed dormancy, would be expected to account for differences in composition between the buried seed flora and the standing vegetation. Although few such comparisons have been done for cultivated crops, several studies have been reported for pastures and grasslands.

Generally, investigators have found that the species composition of buried seed populations in pastures and grasslands was dissimilar from that of the standing herbage. Lippert and Hopkins (1950), working in the Great Plains, found that perennial grasslands had a paucity of buried seeds (300-800/m²) compared with the soils of disturbed lands. However, the species composition of the buried seeds was similar at both sites. Blake (1935) studied the germination requirements of native grassland species and found that viable seed of few of those species germinated under natural conditions. Major and Pyott (1966) suggested that the presence of seeds of weedy species in the soil of native grassland may have reflected the disturbance of those areas during the "dust storms" of the 1930's.

Dore and Raymond (1942) studied pastures in Quebec and found a similar lack of correlation between the buried seed flora and the herbage. At one site, five species made up 63% of all the seeds but less than 7% of the plant cover. On the other hand, of the five most common plants, only one was well represented in the seed flora. The authors found that much of the seed of the desirable forage species was brought in by grazing cattle. Those seeds able to withstand the

animals' digestive tracts would be deposited near the surface of the soil where germination would be likely.

Chippendale and Milton (1934) showed that pastures bore viable seeds of arable weeds 68 years after the last cultivation. Champness and Morris (1948) found that, in general, soils which were acid or waterlogged tended to have the largest accumulation of seeds.

Kellman (1974b) studied agricultural soils in British Honduras and found that the composition of the buried seed populations was in poor correspondence with the vegetation. He concluded that the factors determining the size and composition of the buried seed populations were complex and involved the effects of field age, usage, and soil conditions.

To summarize the studies of buried seed populations of arable lands, it must be emphasized that they encompass a variety of habitats and degrees of disturbance. However, a few general conclusions are apparent. Most importantly, the buried seed populations are very large, usually several tens of thousands per square meter. In addition, the vegetational history of the land may often be read from the various strata of the seed bank. The long-term accumulation of weed seeds in the soil of arable lands commonly results in a poor correspondence in species composition between the underground populations and herbage cover, particularly for perennial grasslands.

Species vary greatly in their seed viability and periodicity of germination. Those with long survival capabilities may remain viable and dormant in the soil at even shallow depths while seeds on the surface will tend to germinate. Most of the seeds eventually decay if not brought to the soil surface, by cultivation, for example.

Arid lands. Several studies of the soil seed reserves of arid shrub communities in the western United States have been published (Knipe and Springfield 1972; Young and Evans 1975; Nelson and Chew 1977; Beauchamp et al. 1975; Keeley 1977; Howard and Samuel 1979).

In the first three of these studies it was found that viable seed reserves and successful seedling establishment were much greater in areas under shrubs than in the interspaces between shrubs. Knipe and Springfield (1972) found that although many alkali sacaton (Sporobolus airoides) seeds reach the barren areas between shrubs, the harsh environmental effects of wind, animal predation, and unfavorable moisture-temperature relations prevent many of the seeds from germinating. Young and Evans (1975) reported that unfavorable conditions may induce dormancy in downy brome (Bromus tectorum) seeds which land in the exposed areas. Seed reserves under shrubs in the Mojave Desert were five times as large as those in exposed areas, although the numbers in all soils were considerably affected by the activities of rodents (Nelson and Chew 1977).

Wetlands. The seed banks of several wetlands have been examined. Milton (1939) found that the species composing the vegetation of salt marshes had low buried seed populations and that most reproduction was by asexual means.

These results contrast considerably with those from studies of freshwater marshes. The species composition of the standing vegetation and buried seeds were similar for areas studied in freshwater tidal marshes in New Jersey (Leck and Graveline 1979). The seed populations of prairie glacial marshes in Iowa were found to be

enormous, probably the largest figures thus far published. Germination densities were as high as 255,000 seeds/m². When drawdown and submerged conditions were simulated on soil samples in the greenhouse, the species which germinated were the same ones which would be expected to emerge under comparable conditions in the marsh (van der Valk and Davis 1976, 1978).

An interesting attempt was made to reconstruct the vegetational history of the prairie marsh based on the species of buried seeds present in successional layers of the soil. The seed bank was probably a crucial factor enabling the marsh to regenerate and respond to the recurring cycles of drawdown and high water levels (van der Valk and Davis 1979).

Forests. Numerous studies have dealt with the buried viable seeds of forest soils, beginning with the early work of Peter (1894), discussed above. Oosting and Humphreys (1940) sampled soils from the stands of a successional series after old-field abandonment on the North Carolina Piedmont. The succession proceeded from annuals (Leptilon canadense, Aster spp., and Ambrosia artemisiifolia) to perennial grasses (dominated by Andropogon sp.) after five years, followed by pines after 15 years, and finally hardwoods after about 200 years. It was expected that a study of a series such as this would provide information about the changes in the composition and viability of buried seed populations with each passing stage. The numbers of seeds germinating from the mineral soil were generally an order of magnitude or more below those reported from arable lands (Table 1, page 16). They varied from a high of 13,600 seeds/m² at

the one-year abandoned fields to a low of 725/m² at the 58-year pine stands. The five-year Andropogon fields had 7,000 seeds/m² in the soils (Table 1, page 16).

A total of 127 species germinated, of which 18 were old-field herbs which appeared in every age class through 85 years or more. The greatest number of species occurred in soils from the five-year fields. In addition, it was found that over 90% of the germinants in the old field age classes were of species found growing in successional younger fields. Not only did these species appear in the greatest number of age classes, but they made up the largest percentage of the total species in every age class except the oak-hickory stand. There was a rapid decrease in the buried viable seeds of these species with each succeeding age class of pine forest, followed by an increase in the oak-hickory stands. The authors suggested that the latter phenomenon may have been due to the opening up of hardwood stands following disturbance, allowing the growth of some early successional species.

The results of analyses of variance performed on the numbers of germinants of the different species showed that the greatest differences occurred between wooded and open sites. The general lack of correlation between the standing vegetation and the germinants, and the decreasing numbers of germinants with increasing stand age, provided strong evidence in support of the existence of buried seeds, the viabilities of which declined with age.

Oosting and Humphreys (1940) thought it unlikely that most seeds of early successional species which germinated from forest soils could have sifted down through the litter and fermentation layers to

reach the mineral soil. Billings (1938) showed that these species were most likely to germinate from mineral soil. Seeds present in the plowed horizon of the soil during cultivation could later become incorporated into the developing A1 and A2 horizons as succession continued. If these seeds retained their viability, they might germinate when environmental conditions became favorable.

The rates of vertical movement of seeds through the soil are unknown. Seeds landing on the forest floor must first sift down through the litter layers before they can be incorporated into the mineral soil. Movement of seeds through the soil depths is certainly aided by burrowing soil invertebrates and by rodents burying seed caches. According to Harper (1977), movement of seeds through the profile of loose-textured soil has been simulated under laboratory conditions.

A tendency for the number of viable seeds to decrease with increasing soil depth has been reported (Numata et al. 1964; Kellman 1970; Strickler and Edgerton 1976; Moore and Wein 1977), although this factor was not considered in many of the other studies. Presumably, those seeds which are buried more deeply are more likely to be older than seeds at more shallow depths and therefore are less likely to be viable.

However, there is evidence that seed longevity of some weed species increases with depth of storage. Seeds buried at shallow depths would exist in a more variable environment, in terms of temperature, moisture and oxygen levels, and light, conditions more conducive to germination (Chepil 1946a; Rampton and Ching 1966).

Since the study by Oosting and Humphreys was published in 1940, many other investigations of the seed banks of old field successional series and forest soils have been conducted (Olmsted and Curtis 1947; Quick 1956; Clark and Boyce 1964; Numata et al. 1964; Livingston and Allesio 1968; Kellman 1970, 1974a; Raynal and Bazzaz 1973; Wendell 1972; Johnson 1975; Marquis 1975; Strickler and Edgerton 1976; Moore and Wein 1977; Whipple 1978). The locations and estimated buried viable seed populations of a number of these studies are listed in Table 1, page 16.

The studies varied considerably in terms of the techniques used and the size of the soil samples collected. In addition, they involved local forest stands distributed over a wide geographical range of the continental United States and adjacent Canada. Because of the scattered nature of these studies, few conclusive interpretations of buried seed populations can be made. However, several tentative generalizations do emerge.

A general lack of correlation between the standing vegetation and the buried seed populations was shown in a number of studies (Olmsted and Curtis 1947; Livingston and Allesio 1968; Kellman 1970, 1974a; Moore and Wein 1977; Whipple 1978). Livingston and Allesio (1968) examined the seed bank of a successional series from a field abandoned one year to an 80-year-old pine stand in New England. They found that early successional species were the most abundant germinants, dominating all samples except those of the mature pine forest. In addition, 45% of the seedlings were of species not present in the standing vegetation of the sites from which the soils were collected.

Generally, the results of these studies agree with those of Oosting and Humphreys (1940) in that early successional fields and young forests had large seed populations, and the numbers declined with increasing stand age (Quick 1956; Livingston and Allesio 1968; Kellman 1974a; Marquis 1975). However, Johnson (1975) considered such a conclusion to be premature because of the paucity of reliable studies. Moore and Wein (1977) agreed and suggested that the populations of viable seeds decrease only when stands are quite old, on the order of 200 years. The results of their studies of the seed banks of undisturbed and clear-cut forests and bog communities suggested that vegetation type rather than age was the more important factor. They noted that the largest seed banks were present in the soils of deciduous-dominated sites, with smaller numbers in conifer forest soils, while the smallest seed banks were present at organic soil sites.

The buried seed populations of forest soils ranged from a few hundred (Kellman 1974a) to several thousand (Oosting and Humphreys 1940) per square meter, with some exceptions. Olmsted and Curtis (1947) screened, sorted, and counted the seeds of forest soils in Maine and then placed the seeds in environments suitable for germination. The former counting method yielded 122 to 2850 seeds/m² while the extremely low densities of 5 to 173 seeds/m² germinated.

Johnson (1975) was unable to obtain any germinants from soil collected from subarctic forests in the region of Great Slave Lake, although some nonviable seeds were present. He proposed that his results might indicate a general poleward decline in the number of buried viable seeds. Coincident with the shorter growing seasons of

higher latitudes is a greater decline in the number of herbaceous species relative to woody species. Herbaceous plants seem to be more adapted to preservation as viable seeds than do woody species. In addition, shorter growing seasons may promote the emergence of shorter germination times in some northerly species, with less investment in long-term seed preservation. Johnson's ideas are supported by the fact that other workers in northern parts of the United States have not only found low numbers of viable seeds but also relatively high proportions of nonviable seeds in the soil. Coniferous seeds in particular seem to be characterized by short-term viability (Haig 1932; Olmsted and Curtis 1947; Moore and Wein 1977).

However, the large populations of buried seeds in forest soils of more temperate regions emphasize the importance of an understanding of seed dynamics to plant population studies. Several studies of seed budgets have been done at the level of specific sites. Kellman (1974a) presented the first attempt to monitor seed budgets in secondary and primary communities in British Columbia. His study showed that most of the seed trapped in a forest stand included species characteristic of that community, although a proportion of foreign species also arrived. Seed of secondary species was trapped to distances of up to 100 m within a forest located adjacent to a secondary community.

Wagner (1965) trapped incoming seed in an irradiated forest stand where the buried seed population had been destroyed. Most of the dispersed species were early successional annuals. The distances of dispersal into the forest were similar to those measured by Kellman.

Naylor (1973) attempted to estimate the rates of germination of seed accumulated in the soil. He sprayed florescent paint on the inflorescences of Alopecurus myosuroides and then recorded the proportion of each year's seed production which emerged with the next seedling population. His study indicated that about 80% of the seedlings emerging during a given year had come from seeds dispersed the previous season, with only 20% derived from older populations.

Few attempts have been made to measure all of the population factors, including seed immigration, emigration, death rate, and germination rate for a single species or cohort during its incorporation into the soil. The detailed studies of the life history of the winter annual, Leavenworthia stylosa, by Baskin and Baskin (1971, 1972, 1978) represent some of the most thorough work which has been done.

The authors found, from germination experiments in the laboratory and greenhouse, that not all seeds of L. stylosa germinate in the autumn of the year in which they are dispersed. Soil samples to a depth of 3.5 cm were kept in a greenhouse and produced germinants of the species for each of the next seven years without augmentation by immigration.

The accumulation of seed banks in the soil may have implications for the genetic structure and evolutionary survival of plant populations. The mechanisms regulating seed germination prevent the entire reproductive capacity of a species from being depleted within a given habitat unless the probability for survival is maximal. The plant population may therefore avoid the bottleneck effect of bad years (Harper and White 1971; Hamrick 1979).

The buried seed population essentially provides a genetic pool from which the population may withdraw resources for future generations. The seed pool provides for an overlapping of generations and age classes characteristic of most animal species. The genetic "memory" encompassed within the seed pool may retard the loss of genetic variability and delay inbreeding, with the result that generations are not synchronous. This phenomenon may be particularly important for annual species which endure severe fluctuations in population size from year to year. The seed pool, by reducing the necessity for a plant population to evolve a genetic response to random or cyclical environmental fluctuations, increases the fitness certainty of the population (Solbrig 1979; Templeton and Levin 1979).

Epling et al. (1960) emphasized the importance of buried seed pools to the genetic stability of plant populations. They found that the effective breeding group of the desert annual, Linanthus parryae, was much larger than the surface population would suggest. This factor, in conjunction with localized pollen and seed dispersal, appeared to be responsible for the extreme stability of small populations over time.

Baskin and Baskin (1978) concluded that knowledge of the buried seed population would be valuable for conserving rare plant species. Preservation of the species should account for all aspects of its life history. The size of designated natural areas may incorporate knowledge of the seed pool.

CHAPTER III

PROBLEMS IN DETERMINING BURIED SEED NUMBERS

Several difficulties are involved with the methods used to estimate buried seed numbers. First, in most of the published investigations, viable seeds were allowed to germinate in the greenhouse from stored soil samples. Since species vary in their germination requirements, the greenhouse provides a selective environment, favorable for the germination of some species but not others. It follows that the studies must extend for long periods of time, perhaps two or three years, in order to obtain the maximum numbers of germinants possible. Seedlings of some species may be difficult to identify, particularly when they are grown under the artificial conditions of a greenhouse.

Alternative procedures have been employed. Olmsted and Curtis (1947) used sieves to concentrate the seeds and then sorted and counted those recovered. These seeds were later tested for their germination capabilities. In other cases the soil material was sieved and the seeds were extracted by flotation in concentrated salt solutions, after which they were tested for viability with tetrazolium staining or by germination (Quick 1956; Malone 1967).

These seed isolation procedures all have the disadvantage of being extremely laborious and requiring a great deal of time to perform. It may be difficult to recognize the seeds and separate them from the soil particles in which they are embedded so that potentially viable seeds may be overlooked (Quick 1956). Tetrazolium viability staining

is not regarded as a consistently reliable method. In addition, it is possible that the chemicals used to extract the seeds are detrimental to the viability and germination properties of some species (Kropač 1966). The seedling emergence method, on the other hand, is easily set up, provided there is adequate greenhouse space, and an optimal environment for the germination of as many species as possible is provided.

Perhaps the most problematic aspect of seed germination studies at the present time is the determination of the numbers and sizes of soil samples to be collected. No thorough investigation has been conducted in this regard. Individual sample sizes have ranged from 0.0008 m^2 (Milton 1939) to 0.09 m^2 of soil surface area and to varying depths (Olmsted and Curtis 1947). The number of samples collected in a given vegetation type has varied depending on the size of the individual cores. However, the total area sampled in a given vegetation type has usually been less than 0.5 m^2 (Major and Pyott 1966).

Buried seeds tend to remain aggregated around the parent plant and to disperse only short distances. This leads to a clumped distribution of seeds in the soil, a factor which may preclude the possibility of obtaining an adequate number of samples.

Champness (1949) has discussed the problems of obtaining the necessary number of samples to give a pre-determined degree of accuracy of the average density of seeds. She found that in order to get density estimates within 10% of the population mean, 70 samples

would be required for all of the species together, while 200 samples of size 24 cm² would be necessary for even the most common species.

It is unlikely that more than a few of the published buried-seed studies have been based on adequate sample numbers. It may be overly presumptuous to regard most of the results as more than estimates of species presence rather than as estimates of seed densities (Whipple 1978).

The distribution of viable seeds often varies with depth of burial in the soil (Harper 1977). However, studies differ considerably in the depth to which samples have been taken, some not even mentioning this factor, while in others the soil was carefully separated into strata.

Finally, a few other considerations must be taken into account when examining buried seed populations. If all vegetative propagules are removed from the soil samples, the potential of the perennial plants for revegetation will be underestimated. In addition, different soil types, textures, and porosities may affect the capacities of some seeds to germinate, and therefore their effects need to be considered (Champness and Morris 1948; Major and Pyott 1966).

CHAPTER IV

METHODS

General Summary

Four low elevation sites were located in the vicinity of Norris in Anderson County and four high elevation sites in the Cumberland Mountains of Campbell County (Figure 1). All sites had stands of second-growth, deciduous forest. The areas selected in Campbell County were typical of those which are surface-mined for coal. These four study sites were located on land owned by Koppers Company of Pittsburgh, Pennsylvania.

The standing vegetation at each site was sampled using nested quadrats. Diameter at breast height was measured for canopy species located in the quadrats, and the densities of understory and groundcover species were recorded from subplots and microplots, respectively.

In order to estimate buried seed populations, soil samples were collected at each site and were incubated in flats in a greenhouse where viable propagules present in the soil were allowed to germinate. Emergent seedlings were removed from the flats when they could be identified.

In the data analysis, the densities and species composition of the buried propagules in the soil from the different sites were determined. Patterns of germination of the most abundant emergent species were identified. The relationships of the species composition of the seed bank to that of the standing vegetation were examined.

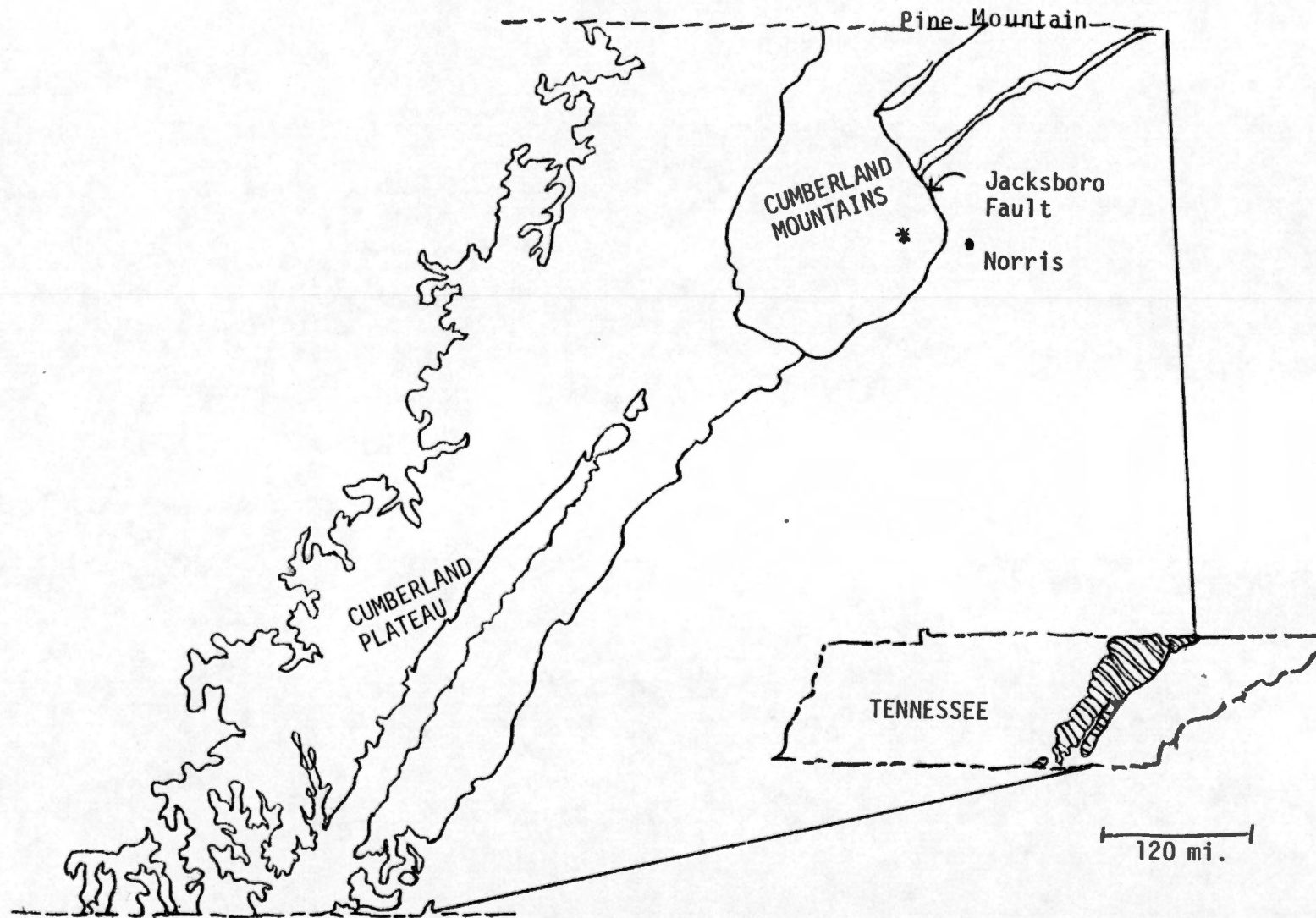


Figure 1. Map of the region of East Tennessee where the study sites were located. (* represents the area of Massengale Mountain where the four high elevation sites were located.) The four low elevation sites were located in the Norris area.

Site Selection and Characterization

A detailed description of the study area is presented in Appendix A. The characteristics of the area described include the location, climate, physiography and geology, soils, vegetation, and human history.

The high and low elevations were chosen for study in order to detect possible differences in the composition and quantities of buried seed populations between the elevations. The objective was to examine differences in storage capacities of the soils from the different elevations and sites, in addition to investigating the distributions of species predominant at either elevation, or common to both.

Sites were chosen so as to represent four different slope aspects at each elevation. At Site 6 on Massengale Mountain, however, the available area for study was considerably reduced by adjacent mining activities. Therefore, one-half of the sampling at that site was completed at a location across an intervening gap (Grave's Gap), where the aspect differed by 90 degrees. No attempt was made to treat separately the data from this site according to aspect. Obtaining an adequate number of samples for the seed germination tests from each site was considered more important than a satisfactory representation of each aspect. Slope gradient, recorded as the average of three readings, was measured in percent with an Abney level. Aspect was recorded as the average of three compass readings and elevation was found using U.S. Geological Survey-Tennessee Valley Authority (TVA) 7.5' quadrangle maps. TVA aerial photos for the Norris sites were used to determine past land use. The locations of the four low elevation study

sites are presented in Figure 2 and those of the four high elevation sites in Figure 3.

Vegetation and Soil Sampling

The plant communities at the eight study sites were sampled between 15 July and 15 September 1978.

The sampling design included recording woody and herbaceous species in quadrats spaced regularly along a transect line. At each site, three quadrats (four at the divided site on Massengale Mountain) 10 x 30 m and spaced 30 m apart, were used to record overstory species (≥ 2.5 cm diameter at breast height (dbh)). Six 4 m² subplots were nested in the quadrat, their location determined using a random numbers table. In each subplot, the stems of saplings and shrubs (< 2.5 cm dbh and > 1 m high) and woody vines were counted. Within each of the six subplots, a 1 m² microplot was located in one corner. Herbaceous species were counted in each of the microplots, including the number of plants of each species present and an estimate of the percent species cover.

Soil profiles were examined in holes dug to at least 10 cm deep into the second layer of mineral soil. Horizon development was described and samples were collected from the top one or two layers of mineral soil, depending upon the thickness of the layers. Moist soil colors were described using Munsell color charts. Soil pH was determined in a 1:1 soil-water suspension with an Orion Research Digital Ionalyzer (Model 701A), and the results were compared with those from a Beckman Zeromatic pH meter. Particle size distribution was determined by the hydrometer method using the procedure described by

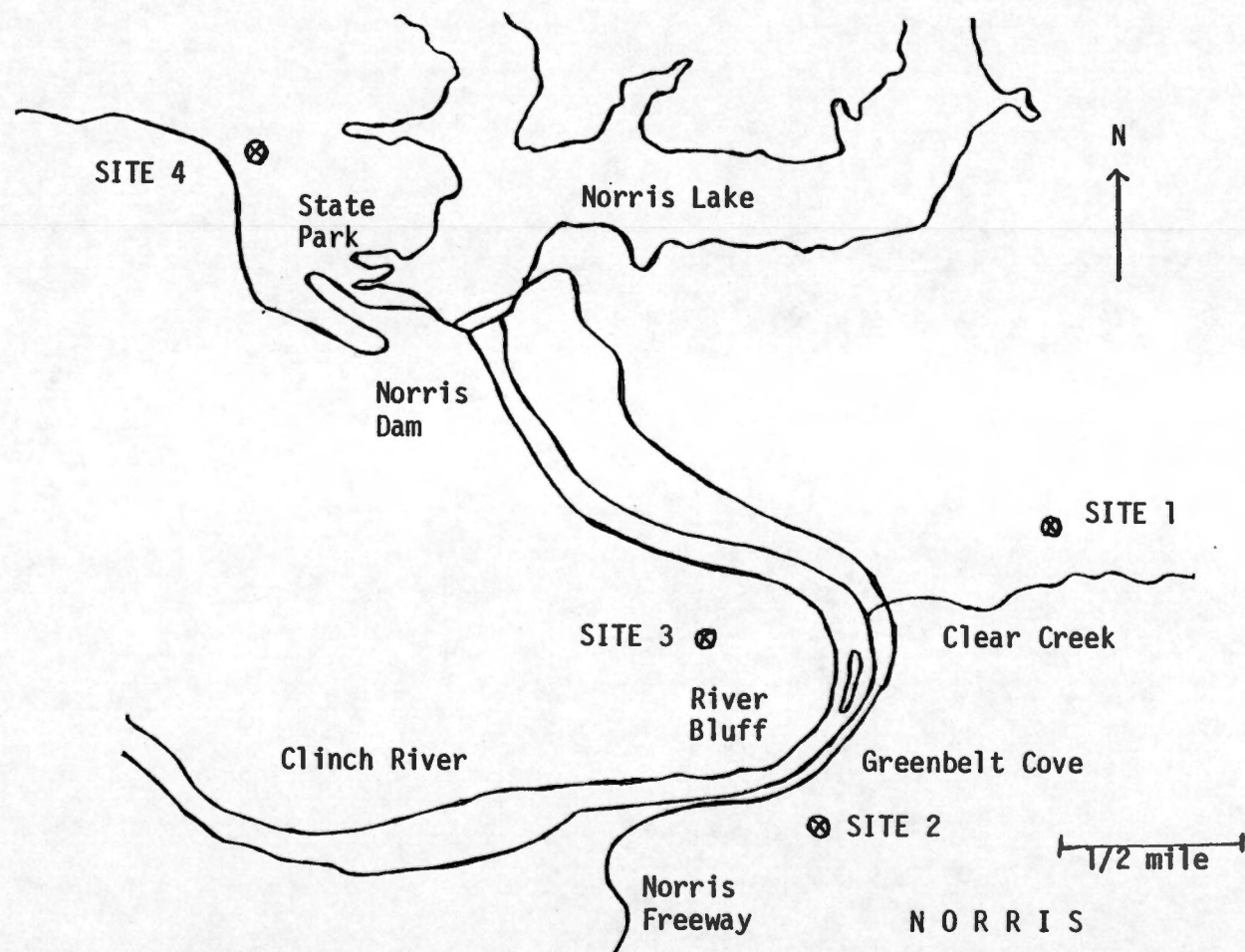


Figure 2. Locations of the four low elevation study sites in the area of Norris in Anderson County, Tennessee.

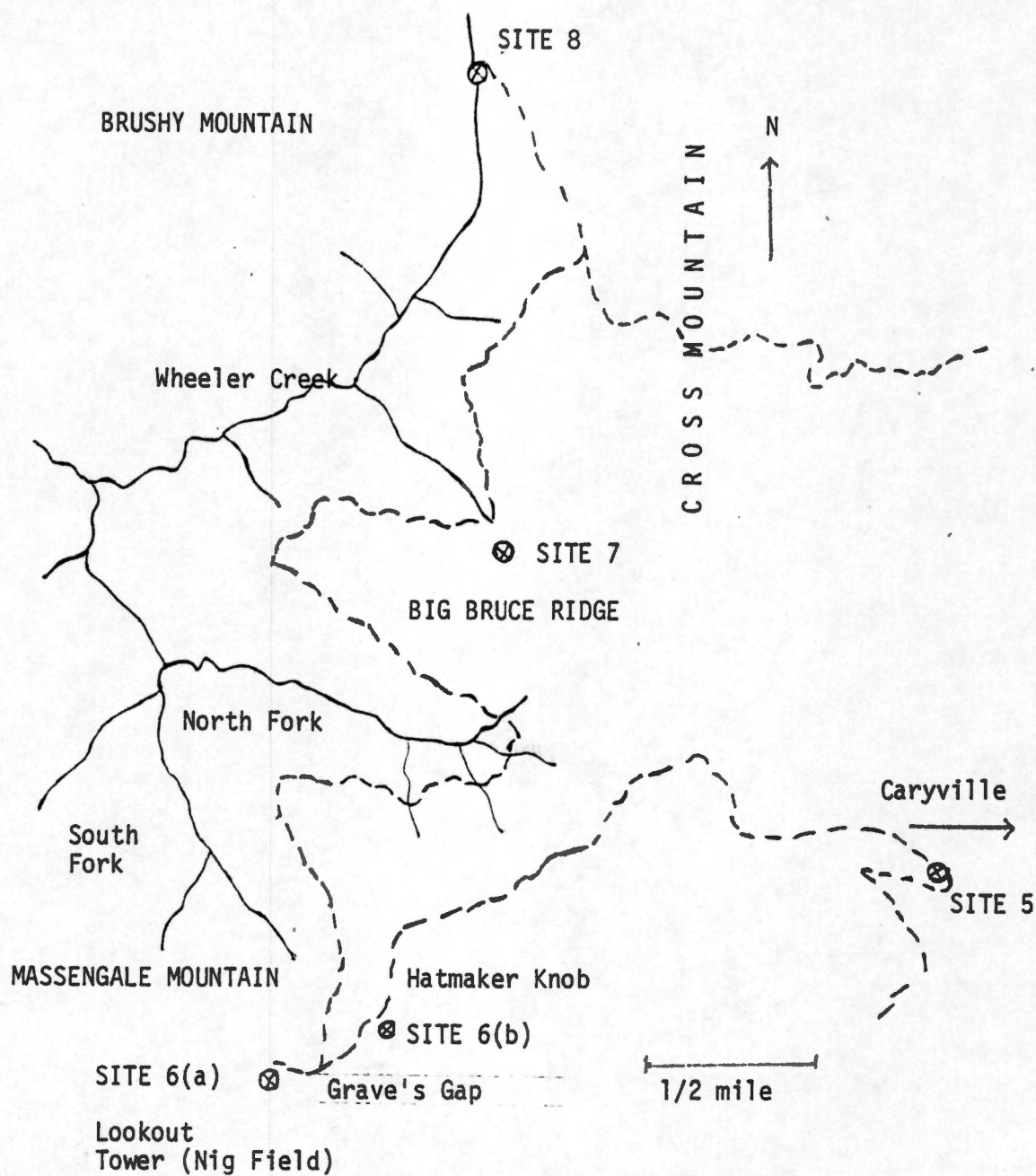


Figure 3. Locations of the four high elevation study sites in the Cumberland Mountains in Campbell County, Tennessee. (- - - represents roadways, most of which follow along surface mine highwalls.)

Foth et al. (1976). It should be mentioned that the silt fraction of the soil samples may have been consistently underestimated because the procedure used assumes that all the silt particles will have settled out of the suspension after two hours. This point has been contested, and Day (1956) recommended allowing 12 hours to complete the settling procedure.

Seed Germination Studies

Soil samples for the greenhouse germination tests were collected in the spring and summer of 1978. It was originally intended that additional samples would be collected in the fall, but the carryover of the spring and summer samples beyond the latter seasons precluded the availability of greenhouse space for another set of samples.

The original set of spring samples was collected in April 1978. Unfortunately, on the night of 27 April 1978, the greenhouse, where most of the samples were stored, was vandalized and all but several of the experimental flats were destroyed.

Another set of samples was collected during the first week of May 1978 and greenhouse incubation was begun on 10 and 11 May. Emerging seedlings from these samples were recorded until the first week of December 1978.

A summer set of soil samples was collected on 26 and 27 July 1978. Emergent germinants were recorded through May 1979.

At each site, ten 0.1 m^2 plots (32 x 32 cm) were located approximately 30 m apart along a transect. Thus, the total surface area sampled at each site was 1 m^2 and at all sites 8 m^2 . A shortage of greenhouse space necessitated the collection of only six samples at each site for the summer collection.

The samples were collected by placing a wooden frame on the ground and removing the inside soil layers by cutting along the inner edge of the frame. The successive soil layers, including the litter, were carefully removed so as to minimize contamination of lower layers. Soil subsamples, composed of one layer, were collected in polyethylene bags at each plot. Included in the subsamples was an approximation of the material contained in each of three layers: (1) the litter layer; (2) 0-5 cm topsoil; and (3) 5-10 cm topsoil. These layers were designated A, B, and C, respectively. The subsamples were placed in cold storage at 3C for a week. All facilities used in this study, including the greenhouse space, were provided by the Forestry Division of the Tennessee Valley Authority at Norris, Tennessee.

After one week of cold storage, the soil samples were moved to two greenhouses, both of which were necessary to accommodate the large number of samples. Since the objective of this study was to obtain an estimate of the total density of underground propagules as potential sources of revegetating material, isolation of seeds from rhizomes and other vegetative organs was not desirable. Therefore, the soil was not sieved. Instead, rocks and large roots were removed by hand. Many small rhizomes, etc., undoubtedly remained in the samples. Whole leaves and other large pieces in the litter layer were cut up using scissors.

The different layers from a soil sample were each spread over METRO MIX 200 in 50 x 25 x 6 cm plastic greenhouse flats which had perforated bottoms. METRO MIX 200 is a commercial potting medium which contains a blend of composted pine bark, vermiculite, sphagnum peat moss, perlite, and granite sand. It includes a starter nutrient charge in slow release form and is supplemented with essential trace elements.

The pH range of the product was 5.8 to 6.5, and the waterholding capacity in a volume to volume ratio was approximately 80%.²

The soil samples were layered 1.0 to 1.5 cm deep over the surface of the METRO MIX to bring the contents level with the sides of the flat. In order to spread the samples this thinly, most of the collection bags containing the B and C layers had to be divided between two flats because of their large volume.

The flats were placed on greenhouse benches so that the same order of layers was repeated from sample to sample (e.g., for sample no. 1, the flat order was 1A, 1B1, 1B2, 1C1, 1C2; for sample no. 2, it was 2A, 2B1, 2B2, 2C1, 2C2, etc.). The samples from the different sites were arranged randomly so as to minimize variability induced by greenhouse conditions. This was accomplished by setting up a random arrangement of eight samples, one from each of the sites, on a single bench. This pattern was repeated at the 10 bench locations. Two control flats, containing METRO MIX only, were placed among the sample flats on each bench.

The samples were kept under natural photoperiod throughout the duration of the experiment, except during January and February 1979. The samples remaining at that time had been collected in the summer and had essentially ceased to produce seedlings. When the light was increased to 16 hours/day, a number of new germinants emerged.

²Personal communication to Andrew White (Graduate Program in Ecology, The University of Tennessee, Knoxville) from Mr. Dennis Kirven, Product Manager, TERR-LITE Horticultural and Agricultural Products, 20 June 1977.

Watering of the samples was done as often as was necessary to maintain field capacity, usually once a day except during the heat of midsummer when two waterings were supplied. A small amount of complete and modified Hoagland's solution was applied every other week three times in late June and July when some of the germinants showed evidence of deficiencies.³

The two greenhouses used for the spring samples differed in the germinating environments they provided. The first greenhouse, where most (70%) of the spring samples were placed, was initially ventilated by a large fan. This broke down in the middle of the summer and was not repaired while the experiment was in progress. Consequently, it became very warm inside this greenhouse in July and August. During those months, daytime temperatures typically ranged from 32C to 35C and went as high as 43C. Temperatures during the night generally ranged from 18C to 24C. To reduce temperatures by promoting circulation, the plastic sheet sides of the greenhouse were raised up. This obviously increased the chances for contamination of the flats by wind-dispersed seed, but it was assumed that the control flats would provide an adequate record of such occurrences. This greenhouse was unheated in winter, but this was probably not a very important factor for this study since the samples were removed and disposed of in early December after the first frost.

³The nutrient solution was composed of three different solutions (A, B, and C) with 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.

All of the summer samples and 30% of the spring samples were incubated in the second greenhouse, which was temperature-controlled by an air conditioner in the summer and was heated in cool weather. During the summer, daytime temperatures ranged from 24C to 27C and nighttime temperatures ranged from 18C to 21C. In winter, temperatures averaged 18C but ranged from a nighttime low of 16C to a daytime high of 27C.

The first germinants emerged from the soil samples one week after incubation in the greenhouse was begun. The new germinants were counted each week for the first four weeks of the experiment. Thereafter, time of emergence was not recorded and all germinants were totaled irrespective of time of emergence. When the seedlings were identified, they were removed from the flats. Otherwise, a colored toothpick was placed into the soil next to the plant, which was allowed to grow until it was identifiable. In cases where numerous seedlings in a flat were obviously of one species, only a few were left to grow. When the seedlings were removed, care was taken to extract all of the root and other underground storage organs along with the emergent seedlings. However, when germinants had to be left in the flats until they flowered, the complete removal of the roots of these larger plants would have been severely disruptive to the rest of the sample. In such cases, a pruning scissors and a knife were used to carefully dig and cut out the main part of the root. This procedure kept resprouting to a minimum, and when the latter did occur, it usually was easily recognized and could be verified by checking the data sheets to see if the species had previously emerged. Specimens of the germinating species were pressed and a voucher collection is stored at

The University of Tennessee, Knoxville. Plant nomenclature from this experiment follows Radford et al. (1976), unless otherwise indicated.

In August, seedlings of some species did start appearing in the control flats in the greenhouse on which the sides had been raised. From then on, whenever those species occurred in the experimental flats, they were not counted as part of the data. The species germinating in the control flats included Oxalis dillennii, O. corniculata, Gnaphalium spp., Erigeron annuus, E. canadensis, Mollugo verticillata, Digitaria spp., Sonchus asper, Erechtites hieracifolia, and Oenothera biennis. This problem did not occur in the temperature-controlled greenhouse.

Although most of the species which emerged were angiosperms, a number of bryophytes and ferns appeared in some of the flats. They occurred irregularly and mostly in humid locations in the temperature-controlled greenhouse. Specimens were identified at least to the level of genus. They were not included in the data analysis, but their presence was recorded as percent cover in the flats where they occurred.

CHAPTER V

DATA ANALYSIS

Vegetation

Vegetation data for the seedling and sapling layers were recorded on computer forms and keypunched at The University of Tennessee Computing Center. These data were submitted to a Fortran computer program written by Virginia Patterson, The University of Tennessee Computing Center, and modified by Ross C. Hinkle, Graduate Program in Ecology. The program calculates, for each plot, absolute density, relative density (RD), absolute basal area, relative basal area (RBA), an importance value ($IV = RD + RBA$), and diameter distributions of canopy and understory species on the plot. The analysis was conducted at The University of Tennessee Computing Center, utilizing the IBM 360/65-370/148 and DEC-10 Model 1080 computers.

The vegetation data for the groundcover were reduced using a hand calculator. The average number of plants per square meter and the average percent cover were calculated for each species recorded in the microplots at each site.

Germination Studies

The greenhouse germination data were keypunched at the TVA, Office of Natural Resources, Computer Systems Development Branch. The data analyses were performed there using the IBM 370/165 and at The University of Tennessee Computing Center. Descriptive statistics and some analyses have used the Statistical Analysis System (SAS) (Barr et al. 1979).

The analyses were conducted for the spring and summer data sets separately. The average densities of the seedlings germinating at each site were computed on a per square meter basis. This was done for the litter layer and for each of the soil depths separately and then computed for each of the three sampling depths combined. Coefficients of variation were computed for the average number of plants germinating from the soil from each site. The total numbers of germinating species were calculated for each of the above categories. Nonparametric statistics were used to test for associations between the densities of seedlings and the number of species germinating from each site collection. Species diversity of the germinants was calculated using the Shannon-Weiner Index (Pielou 1975).

The analysis of variance (ANOVA) was performed for the number of plants, testing for the following effects:

<u>Source of Variation</u>	<u>Degrees of Freedom</u>	
	<u>Spring</u>	<u>Summer</u>
Elevation	1	1
Site (Elevation)	6	6
Layer	2	2
Layer x Elevation	2	2
Layer x Site (Elev)	12	12
<u>Among Samples</u>	<u>216</u>	<u>120</u>
<u>Total</u>	<u>239</u>	<u>143</u>

Within this format, the error term (among samples) included the variability due to the soil samples and to different locations within the greenhouses. The experiment was designed so as to minimize the effects of the greenhouses. Nevertheless, microenvironmental variations did exist. For instance, nearly all of the mosses and ferns which appeared in the flats did so in a particularly humid corner near an

air-conditioning unit in one of the greenhouses. Therefore, the ANOVA was repeated, using the bench location as a separate effect. However, the results showed that it was not a significant source of variation at $P = 0.05$.

Student's Test was used to compare the mean numbers of germinants among soil depths within sites. Student's Test was also used to test for differences in the numbers of germinants between the spring and summer samples, on the bases of sites, layers within sites, and elevations. The Jaccard Index of Similarity was used to compare the species composition of the different sites between and within the spring and summer samples (Mueller-Dombois and Ellenberg 1974).

Species-area curves were drawn in order to illustrate the increase in numbers of species with increasing sample area. Such curves may be useful in determining the appropriate sample size for seed germination studies.

The germination patterns of individual species were examined. The average numbers of germinants per square meter, the percent of the total number of germinants, and the sample frequency were calculated for each species at each site. Coefficients of variation were computed for the important species at each site. Each of the more abundant species was examined for its pattern of germination over time. The ANOVA was performed for approximately 30 species using the same format as for the total numbers of germinants described above. Species were described in terms of their tendencies to germinate from certain soil depths or site collections.

Relationships of the Seed Banks to the Vegetation

The composition of the vegetation at each site was compared with that of the buried seed population. Student's Test was used to test for differences in the densities of germinants in the flats and plant densities of the groundcover. The Jaccard Index of Similarity was used to compare the species composition of the vegetation with that of the seed bank.

CHAPTER VI

CHARACTERISTICS OF THE STUDY SITES

Site Characteristics, Geology, and Land Use

A summary of the field characteristics at each site appears in Table 2. All sites except two were located on slopes. The exceptions were the river bluff site (no. 3), situated at the top of a northeast-facing bluff overlooking the Clinch River, and the Norris Dam State Park site (no. 4), located on a relatively flat hilltop.

All of the Anderson County sites had forest stands which were at least 47 years old. None of the area had been logged extensively since the TVA acquired the land in 1933. TVA aerial photographs reveal that all but one of the sites was under forest cover in 1935. Therefore, the present stands at these sites must be 65 or more years old. The river bluff site (no. 3) was a cultivated field until 1933, but the photographs show that by 1935, it had begun to revert to forest.

Much of the land in the vicinity of the high elevation sites was under lease to surface mine operators, and mining activities in the area were extensive. Each of the study sites was located within 500 m of active or abandoned mines. Part of Site 6 was located in an area known as Nig Field, which apparently had been under pasture at one time. An old fencerow and charred tree stumps were present, indicating that the forest was burned when it was converted to pasture.

Table 2. Summary of site characteristics, including slope angle, elevation, aspect, and bedrock.

Site Number	County	Site Locale	Slope Angle (Degrees)	Elevation (m)	Aspect	Bedrock*
1	Anderson	Clear Creek	20-22	333	S	Dolomite
2	Anderson	Greenbelt Cove	28-38	330	W	Dolomite
3	Anderson	River Bluff	10-17	330	NE	Dolomite
4	Anderson	State Park	5-10	375	Hilltop	Dolomite
5	Campbell	Cross Mountain	11-15	850	NE	Vowell Mountain Formation
6	Campbell	Hatmaker Knob	14-24	960	SE & NE	Cross Mountain Formation
7	Campbell	Big Bruce Ridge (Cove)	10-20	800	N	Vowell Mountain Formation
8	Campbell	Wheeler Creek Cove	23-26	750	W	Redoak Formation

*See Appendix A for a brief discussion of the geology.

Site Soil and Vegetation Descriptions

Soils. A summary of the physical description of the soil present at each site is presented in Table 3. Most of the soils of forested slopes at the study sites were shallow and rocky. In Table 3, the soil horizon beneath the A1 horizon (mineral soil layer 2) was not identified because the holes which were dug were not deep enough to examine lower layers. Therefore, the mineral soil layer 2 could have been the A2, B1, or a transitional layer. The interest in this study was to obtain soil from the depths corresponding to those from which the samples for the seed germination studies were taken. The information given in Table 3 merely indicates the main soil features at the sites. It should be noted that the samples from Site 3 were taken from a plow layer which was only beginning to show horizon differentiation. This was the site which was farmland when the TVA acquired it in 1933.

Most of the soils were sandy loams or loams and acid. The lowest pH value of 3.6 was recorded for the A1 horizon at Cross Mountain.

Vegetation. This section presents descriptions of the floristic composition of the standing vegetation at each site, as summarized in Tables 18-33 in Appendix B. For each species in the canopy, the relative density (RD), the relative basal area (RBA), and an importance value (IV), are presented in the tables. Relative densities (RD) are presented for saplings, shrubs, and woody vines recorded in the understory. The average cover and frequency are presented for the species recorded in the groundcover. The species are categorized according to their densities of occurrence, from less than one plant/m² to more than five

Table 3. Summary of soil characteristics at the study sites.

Site	Depth of Litter (cm)	Depth of Organic Layer (cm)	Al Horizon				Mineral Soil Layer 2				Percent Stoniness
			Depth (cm)	Color	pH	Texture Class	Depth (cm)	Color	pH	Texture Class	
1	2	1	2	gray brown	5.2	sandy loam	> 12	lt. gray brown	4.9	sandy loam	30
2	2	1	1	very dk. brown	5.0	sandy loam	> 10	dk. gray brown	4.4	loam	30
3	2	2	10 (plow layer)	dk. reddish brown	4.6	loam					15
4	2	2	8	dk. brown	4.7	loamy sand	> 5	reddish brown	4.6	loam	30
5	3	2	5	dk. brown	3.6	sandy loam	> 10	dk. yellowish brown	4.1	sandy loam	10
6	2	2	7	dk. brown	4.5	loamy sand	> 13	dk. yellowish brown	4.5	sandy loam	5
7	2	2	7	dk. brown	5.4	loamy sand	> 12	yellowish brown	5.4	sandy loam	5
8	3	2	6	yellowish brown	4.8	sandy loam	> 8	light yellowish brown	4.7	loam	20

plants/m². A summary of the groundcover vegetation at each site is presented as the total number of species, the average number of plants/m² for all species, and the average total cover.

The information contained in the tables in Appendix B is summarized in the following descriptions of the vegetation present at each site.

Site 1. The forest at Site 1 was located on a southern slope above Clear Creek at 335 m elevation in Anderson County. White oak (Quercus alba) was the dominant canopy species, accounting for 42% of the total canopy importance value. Mockernut hickory (Carya tomentosa) was the codominant species. Associated canopy species included sugar maple (Acer saccharum), sourwood (Oxydendrum arboreum), southern red oak (Quercus falcata), and shortleaf pine (Pinus echinata) (Appendix B, Table 18).

In the understory, red maple (Acer rubrum), dogwood (Cornus florida), blackgum (Nyssa sylvatica), and sourwood were the important sapling species. Virginia creeper (Parthenocissus quinquefolia) was the common vine counted in this layer.

In the groundcover layer, the 47 species recorded represented an average total cover of 37% and an average of 35 plants/m². Most of the species of groundcover plants were rather sparsely distributed over the forest floor. Unidentified species of the genus Desmodium were the most common plants, accounting for 35% of the total estimated cover. Seedlings of red maple, dogwood, and sassafras (Sassafras albidum) each occurred with a frequency of 50% or greater and at a density of one to five plants/m² (Appendix B, Table 19).

The underlying bedrock at Site 1 was dolomite. Soils were derived in residuum and partly from colluvial materials. Soil textures were sandy loam overlying loam, and both layers were acid.

Site 2. Site 2 was located at 330 m elevation along a western slope at Greenbelt Cove in Anderson County. Beech (Fagus grandifolia) was clearly the dominant canopy species, accounting for over half of the total importance value. Associated species included sugar maple, dogwood, and red oak (Quercus rubra) (Appendix B, Table 20).

Sugar maple was by far the most abundant species in the understory, followed by beech which occurred in considerably fewer numbers. Other understory species, present in very low densities, included red maple, pignut hickory (Carya glabra), dogwood, cucumber magnolia (Magnolia acuminata), and hop hornbeam (Ostrya virginiana) (Appendix B, Table 20).

In the groundcover layer, 50 species were present, amounting to an average total cover of 23% and an average of 15 plants/m². As in the understory layer, sugar maple was the most abundant groundcover species, with a frequency of 83%. In contrast, beech seedlings were present with a frequency of only 6%, accounting for less than 1% ground cover. Other woody species, which were generally represented by rather low frequencies, included red maple, tulip poplar (Liriodendron tulipifera), hop hornbeam, white ash (Fraxinus americana), redbud (Cercis canadensis), and rhododendron (Rhododendron sp.) (Appendix B, Table 21).

The herbaceous plants at Site 2 made up a rather sparse cover. Some of the common species included Polystichum acrostichoides,

Hexastylis arifolia, Polygonatum biflorum, Taenidia integerrima, and various grasses.

The loamy soils of this site were underlain by dolomitic bedrock and developed in residuum and partly from colluvial materials. The texture of the A1 horizon was sandy loam with pH 5.0 and that of the underlying layer of mineral soil was loam with pH 4.4.

Site 3. Site 3 was located at 330 m elevation on the top of a northeast-facing bluff overlooking the Clinch River in Anderson County. Chestnut oak (Quercus prinus) was the dominant canopy species with black oak (Q. velutina) as codominant. Associated species included white oak, mockernut hickory, red hickory (Carya ovalis), and sugar maple (Appendix B, Table 22).

The understory was characterized by an abundance of sugar maple saplings, accounting for over 50% of the stem density of this layer. Red maple was also fairly common in this layer. In contrast, the dominant canopy oak and hickory species were only poorly or not at all represented in the understory.

This pattern was repeated in the groundcover layer, where red maple and sugar maple were among the most abundant and most frequent of both woody and nonwoody species. Oak and hickory seedlings were present in very low numbers (Appendix B, Table 22).

In the groundcover layer, a total of 32 species was counted with an average total cover of 21% and an average of 19 plants/m². Virginia creeper was the most abundant species. The total cover was low at this site, but some of the other common species included Chimaphila maculata, Anisostichus capreolata, Rhus radicans, Vitis spp.,

dogwood, cucumber magnolia, and sassafras (Appendix B, Table 23).

The bedrock underlying the river bluff site was dolomite. The soil showed only initial horizon development but evidently had been plowed in recent times. As the TVA photographs show, this site was farmland before 1933. Therefore, at the time of the study, the forest stand was just over 45 years of age. The texture of the soil was sandy loam overlying loam, and pH values for the two horizons were 4.5 and 4.6, respectively.

Site 4. The forest at Site 4, located at 375 m elevation near the western boundary of Norris Dam State Park in Anderson County, was dominated by tulip poplar. Associated species included red maple, red hickory, and black oak. The most abundant understory species included black gum, ironwood (Carpinus caroliniana), and dogwood (Appendix B, Table 24).

In the groundcover layer, a total of 32 species was counted, amounting to an average total cover of 25.4% and average density of 21 plants/m². The most abundant woody seedlings included red maple, dogwood, sassafras, and tulip poplar. Several woody vines, including poison ivy (Rhus radicans), greenbriar (Smilax glauca), and Virginia creeper were common in the groundcover layer. Some of the representative herbaceous species were Chimaphila maculata, Galium circaezans, and Uvularia perfoliata (Appendix B, Table 25).

The underlying bedrock was dolomite and soil was derived from residual and colluvial materials. The texture of the A1 horizon was loamy sand and that of the underlying layer was loam. The layers had pH values of 4.7 and 4.6, respectively.

Site 5. Site 5 was located in Campbell County on Cross Mountain on a northeast exposure at elevation 850 m. The dominant canopy species was tulip poplar, and the codominant was shagbark hickory (Carya ovata). Associated species included red oak, sugar maple, cucumber magnolia, red hickory, and hop hornbeam (Appendix B, Table 26).

Sugar maple was the most abundant species in the understory layer, making up more than half of the stems counted. Other species, in order of decreasing abundance, included tulip poplar, dogwood, white basswood (Tilia heterophylla), white ash, black locust (Robinia pseudo-acacia), and cucumber magnolia. The woody vine, frost grape (Vitis vulpina), was present in small numbers (Appendix B, Table 26).

A total of 38 species was counted in the groundcover layer, with an average total cover of 62.3% and an average of 38 plants/m² (Appendix B, Table 27). In contrast to Sites 1 to 4, woody species were much less abundant in the groundcover layer of Site 5. Sugar maple and white ash seedlings were the most common.

The herbaceous species with the greatest density and frequency values was Aster divaricatus, while the species with the greatest cover was Laportea canadensis. Other common species included Viola canadensis, Impatiens spp., Tiarella cordifolia, Hepatica acutiloba, and Amphicarpa bracteata.

The geologic beds underlying Site 5 were of the Cross Mountain Formation. This group is represented by three intervals of shale containing minor sandstones and coal. The soils at the site were very acid. With pH values of 3.6 and 4.1, both the A1 horizon and the second layer of mineral soil were sandy loams.

Site 6. Site 6 was located on two slopes, separated by Grave's Gap on Massengale Mountain, in Campbell County at elevation 960 m. One of the sampled slopes had a northeast exposure and the other had a southeast exposure. The latter slope had apparently been part of a pasture before it was abandoned. Both it and the other slope had apparently been burned at some time, as evidence by the presence of charred stumps. Two 30 x 10 m quadrats were sampled on each slope, and the data from all four quadrats were analyzed together.

The dominant canopy species was red oak with sugar maple as codominant. Associated species included black walnut (Juglans nigra), tulip poplar, sourwood, pignut hickory, black locust, white oak, and bitternut hickory (Carya cordiformis) (Appendix B, Table 28).

Sassafras and sugar maple were the most abundant woody understory species. Low densities of a number of other species were present. These included red maple, pignut hickory, black cherry (Prunus serotina), bitternut hickory, and others. Shrub species present included Rubus spp. and elderberry (Sambucus canadensis). Among the vine species were virgin's bower (Clematis virginiana), greenbriar, and summer grape (Vitis aestivalis) (Appendix B, Table 28).

In the groundcover layer, a total of 66 species was counted with an average total cover of 57.9% and an average of 56 plants/m². The most abundant species were herbaceous plants and woody vines. The former group included Panicum boscii, Sedum ternatum, Solidago curtsii, Amphicarpa bracteata, Aster cordifolius, Fragaria virginiana, and Spigelia marilandica. The common vines included virgin's bower, greenbriar, and summer grape (Appendix B, Table 29).

The geologic beds underlying Site 6 were of the Cross Mountain Formation, which is represented by three intervals of shale containing minor sandstones and coal. The soil of the A1 horizon was loamy sand with pH 4.5 and that of the second layer of mineral soil was sandy loam with pH 4.5.

Site 7. Site 7 was located on a northern slope of a cove above Wheeler Creek along Big Bruce Ridge in Campbell County. The elevation was about 800 m. The dominant canopy species at this site were chestnut oak and white oak. Associated species included pignut hickory, red maple, dogwood, blackgum, and shagbark hickory (Appendix B, Table 30).

The most common species in the understory were sugar maple, dogwood, and red maple. Other tree species were red, chestnut, and white oak, blackgum, cucumber magnolia, tulip poplar, and witch hazel (Hamemalis virginiana). One shrub, the juneberry (Amelanchier arborea) and one vine, greenbriar (Smilax rotundifolia) were recorded (Appendix B, Table 30).

In the groundcover layer, a total of 65 species occurred, with an average total cover of 45.9% and an average of 37 plants/m². Sugar maple seedlings accounted for more average cover than any other species. Red maple was the only other woody species which had a density of one or more plants/m². Poison ivy was a common vine in the ground layer. The most common herbaceous species included Thalictrum thalictroides, Dryopteris marginalis, Eupatorium purpureum, Muhlenbergia tenuiflora, and Solidago arguta (Appendix B, Table 31).

Site 7 was underlain by geologic beds of the Vowell Mountain Formation. Capped by sandstone beds, this formation is represented by three intervals of shale containing minor sandstones and coal. The soils of the A1 horizon were loamy sands of pH 5.4 underlain by sandy loam with pH 4.7.

Site 8. Site 8 was located on a western slope at elevation 750 m along Wheeler Creek on Cross Mountain in Campbell County. Chestnut oak was the dominant canopy species, accounting for 50% of the total importance value. Associated species included red, black, and white oak, pignut hickory, and blackgum (Appendix B, Table 32).

Blackgum and red maple comprised over 70% of the total density of understory species. Other tree species present included sourwood, pignut hickory, sassafras, red, chestnut, and black oak, and dogwood. The shrub species present was blueberry (Vaccinium vacillans) (Appendix B, Table 32).

In the groundcover layer, a total of 37 species was counted, with an average total cover of 30.1% and an average of 26 plants/m². The most common species included both woody and herbaceous plants. Included in the former group were red maple, chestnut oak, sassafras, and Rhododendron spp. The common herbaceous species included Aster divaricatus, Chimaphila maculata, Mitchella repens, and Solidago arguta. Several vines were present, including greenbriar (Smilax spp.) and poison ivy (Appendix B, Table 33).

The geologic beds underlying the site were of the Redoak Formation, which is represented by three sandstones and coal strata. The soil of the A1 horizon at the site was sandy loam with pH 4.8 underlain by a loamy soil with pH 4.7.

CHAPTER VII

RESULTS OF THE GERMINATION STUDIES

Total Germination and Its Relationship to Elevation, Site, Soil Depth, and Time of Sampling

Table 4 presents the mean numbers of germinants emerging per square meter of soil surface from the litter layer and two mineral soil layers from each of the eight study sites for the spring and summer collections. There was high variability in the numbers of germinants emerging among the samples collected at any one site, resulting in large standard errors and coefficients of variation for the mean numbers of germinants.

Table 5 presents the results of analyses of variance of the numbers of seedlings germinating from the spring and summer collections. All effects, including elevation, site, layer (i.e., soil depth), and the interactions (layer * elevation and layer * site), were highly significant with the spring collection. Significant sources of variation in the summer collection included site, layer, and the interaction layer * site.

The effect of elevation on the numbers of germinants was significant with the spring samples. Nearly four times as many seedlings (1619 plants/m² versus 474 plants/m²) germinated from the high elevation soils as from the low elevation spring collection soils. The effect of elevation was not significant with the summer collected samples.

Table 4. Total numbers of germinants from the soil collections.

Study Sites	Collection Depth			Total	Coefficient of Variation (Percent)
	Litter	0-5 cm	5-10 cm		
Spring Collection (10 Replications)					
1	48±7 ^a	140±20	138±32	326±28	28
2	42±5	207±40	251±33	500±74	47
3	61±6	162±34	129±25	352±51	46
4	62±20	268±50	389±72	709±129	57
5	335±111	756±212	851±183 ^b	1942±473 ^b	77
6	227±55 ^b	924±269	980±345	2131±615	91
7	229±66	404±77	493±90	1126±192	54
8	107±20	435±93	733±110	1275±188	59
Summer Collection (6 Replications)					
1	30±5	178±51	163±46	372±96	63
2	20±8	303±71	485±140	808±206	62
3	22±5	180±50	138±37	340±69	50
4	20±5	248±71	278±75	547±136	61
5	33±13	228±73	222±85 ^b	483±154 ^b	78
6	65±29 ^b	462±97	547±108	1073±204	47
7	105±30	517±114	610±156	1232±260	52
8	43±19	273±55	415±120	732±120	59

^aMean (±standard error) number of germinants/m².

^bSpring and summer sample means are significantly different (P = 0.05).

Table 5. Analysis of variance of the numbers of germinants.

Source of Variation	df	Mean Square	F Value
Spring Collection (10 Replications)			
Elevation	1	87287.21	**
Site (Elevation)*	6	4585.25	**
Layer	2	27833.45	**
Layer x Elevation	2	7145.70	**
Layer x Site (Elevation)	12	9508.11	**
Between Samples	216	1409.95	
Total	239		
Summer Collection (6 Replications)			
Elevation	1	5280.45	NS
Site (Elevation)*	6	1595.33	**
Layer	2	13473.84	**
Layer x Elevation	2	657.51	NS
Layer x Site (Elevation)	12	934.60	**
Between Samples	120	281.62	
Total	143		

*All site means were significantly different using Duncan's Multiple Range Test at $P = 0.05$.

**Significant at $P = 0.01$.

The effect of site was a significant source of variation in the spring collection. All site means were significantly different using Duncan's Multiple Range Test ($P = 0.05$) (Snedecor and Cochran 1978). The greatest number of seedlings emerged from the Site 6 soils (2131 plants/m²) and the fewest from Site 1 soils (326 plants/m²). The other sites, listed in order of decreasing numbers of germinants, were Sites 5, 8, 7, 4, 2, 3, and 1. The soils producing the greatest numbers of germinants were from the high elevations.

The effect of site was a significant source of variation in the summer collection. All site means were significantly different using Duncan's Multiple Range Test ($P = 0.05$). The greatest number of seedlings emerged from Site 7 soils (1232 plants/m²) and the fewest from Site 3 soils (340 plants/m²). The other sites, listed in order of decreasing numbers of germinants, were Sites 6, 2, 8, 4, 5, and 1. It was of interest to determine if there was a relationship between the spring and summer collections in terms of the rank order of the different sites for the numbers of germinants. When Spearman's Rank Correlation Coefficient was calculated, no significant association was found ($r_s = 0.571$; $P = 0.05$).

The pattern of germination from the different soil layers was similar with the collections from all eight sites from both the spring and summer sets. The mean number of germinants from the litter layer was significantly lower than the numbers from the other soil depths with nearly all sites from both the spring and summer samples. No significant differences were found in the average numbers of germinants emerging between the 0-5 cm and 5-10 cm depths in either the spring or summer collections (Table 6).

Table 6. Results of Student's Test of differences in mean numbers of germinants between soil depths within sites.^a

Site	Sample Time					
	Layers A and B ^b		Layers A and C		Layers B and C	
	Spring	Summer	Spring	Summer	Spring	Summer
1	0.001	0.01	0.05	0.01	NS	NS
2	0.001	0.01	0.001	0.01	NS	NS
3	0.01	0.01	0.05	0.01	NS	NS
4	0.01	0.01	0.001	0.01	NS	NS
5	NS	0.05	0.05	NS	NS	NS
6	0.05	0.01	0.05	0.01	NS	NS
7	NS	0.01	0.05	0.01	NS	NS
8	0.01	0.01	0.05	0.01	NS	NS

^aPresented in the table are the probabilities of significant differences between means.

^bSoil layers A, B, and C refer to the litter, 0-5 cm, and 5-10 cm depths, respectively.

A grand total of 8,371 germinants (1047 plants/m²) emerged from the spring soil collections, and 3,352 (698 plants/m²) germinated from the summer set. More seedlings germinated from the spring than from the summer collections from all locations except Sites 1, 2, and 7. However, the differences in value between the mean numbers of germinants in the two sets of samples were not significant ($P = 0.05$), except with Site 5.

When the numbers of germinants emerging from the soils from the two elevations were compared between the spring and summer samples, the differences were not significant with the low elevation soils (Student's Test, $P = 0.05$). However, the differences between the spring and summer collections with the high elevation collections were significant (Student's Test, $P = 0.05$). An average of 1619 plants/m² germinated from the spring high elevation soil, but only 880 plants/m² germinated from the summer high elevation samples.

Total Numbers of Species and Their Relationship to Elevation, Site, Soil Depth, and Time of Sampling

The total numbers of species and the numbers emerging from each soil depth at the eight study sites and the average numbers germinating from each elevation are presented in Table 7. The numbers of germinating species in the spring collection ranged from 54 (Site 3) to 95 (Site 8). Soils from sites which produced larger numbers of germinating plants usually produced larger numbers of species, as indicated by the computation of a significant value of Spearman's Rank Correlation Coefficient ($r_s = 0.785$; $P = 0.05$).

Table 7. Total numbers of germinating species.

Study Sites	Litter	0-5 cm	5-10 cm	Total
Spring Collection (10 Replications)				
1	20	43	47	65
2	19	47	58	73
3	17	34	32	54
4	<u>24</u>	<u>51</u>	<u>67</u>	<u>84</u>
	$\bar{x} =$	$\bar{x} =$	$\bar{x} =$	$\bar{x} =$
	20±1.5	44±3.6	51±6.3	69±6.3
5	37	54	56	75
6	37	64	67	90
7	46	56	50	87
8	<u>36</u>	<u>67</u>	<u>71</u>	<u>95</u>
	$\bar{x} =$	$\bar{x} =$	$\bar{x} =$	$\bar{x} =$
	39±2.3	60±3.1	61±1.8	87±4.3
Summer Collection (6 Replications)				
1	9	29	30	43
2	8	23	30	39
3	7	24	23	36
4	<u>12</u>	<u>27</u>	<u>33</u>	<u>47</u>
	$\bar{x} =$	$\bar{x} =$	$\bar{x} =$	$\bar{x} =$
	9±1.1	26±1.4	29±2.1	41±2.4
5	13	29	29	43
6	15	45	54	73
7	17	38	42	53
8	<u>16</u>	<u>25</u>	<u>26</u>	<u>40</u>
	$\bar{x} =$	$\bar{x} =$	$\bar{x} =$	$\bar{x} =$
	22±0.9	34±9.5	38±6.4	52±7.5

$\bar{x}$ (±standard error) refers to the mean number of species germinating from each elevation.

The numbers of germinating species in the summer collection ranged from 36 (Site 3) to 73 (Site 6). In this case, the correlation between the numbers of species and the numbers of plants was not significant ($r_s = 0.589$; $P = 0.05$). In addition, the correlation between the numbers of species emerging from the different sites comprising the spring and summer samples was not significant ($r_s = 0.5774$; $P = 0.05$).

A grand total of 199 species germinated from all soil collections, including 170 species from the spring samples and 113 species from the summer samples. These included the following breakdown by growth form of those plants which could be identified to the species level: trees - 24; shrubs - 9; woody vines - 7; perennial herbs - 112; annuals - 37; and biennials - 2. These numbers included 41 species of monocots. A total of 129 genera and 53 families were recognized among the germinants.

Table 7 presents the numbers of species germinating from each soil layer from each of the eight study sites. The pattern of species distribution follows that for the numbers of plants; the litter layer produced the fewest numbers of species, followed by the 0-5 cm and 5-10 cm layers. However, compared to the relative numbers of plants produced by that layer, the numbers of species emerging from the litter layers of the different soils were large. For instance, when the spring collection results from all the sites were combined, 78% of the total number of species emerged from the 5-10 cm depth while 56% emerged from the litter layer. Thus, although significantly fewer seedlings germinated from the litter, the numbers of species represented were large compared to the lower soil layers.

Floristic Composition of the Buried Viable Seed Populations at the Eight Study Sites

The floristic compositions of the buried viable seed populations of the litter layer and the upper 10 cm of the forest soil for the eight study sites are summarized in Appendix C, Tables 34 to 41. In those tables, the frequency, density per square meter ($\pm$ standard error), and the species relative density are presented for the species germinating from the spring and summer soil collections. Each species germinating from the soils from a given site received an importance value ($IV = \text{frequency} \times \text{number of plants/m}^2$). Summarizing the species data with an importance value is useful because it accounts for species frequency and abundance. Therefore, although some species germinated in large numbers, an accompanying low frequency value would result in a moderate importance value. Table 8 presents the importance values calculated for each species from the spring and summer soil collections from each of the eight sites. The major features of the buried seed populations are summarized in this section, based on the information contained in Table 8.

The analysis of variance was performed on many of the species which were among the most abundant germinants, following the design used with total number of plants (Table 5, page 66). Of interest were the tendencies of individual species to germinate in greater quantities from one elevation or certain sites or soil depths than from others.

The species composition of the germinants varied greatly with site. However, general patterns and some similarities were apparent. Most of the species germinated in only very small quantities. However, some species were prominent germinants at most, or at least several, of

Table 8. Importance values of the germinating species.^a

Species	1		2		3		4		5		6		7		8	
	SP ^b	SU	SP	SU	SP	SU	SP	SU	SP	SU	SP	SU	SP	SU	SP	SU
<i>Acalypha rhomboidea</i>			0.8	1.2		0.5	0.4				0.3	0.2			0.1	
<i>A. virginica</i>		0.3	0.6	19.1						0.3					0.2	
<i>Acalypha</i> spp.																0.2
<i>Acer rubrum</i>	0.4				1.6		3.2		0.1				0.1			
<i>A. saccharum</i>													0.1			
<i>Agrostis hyemalis</i>													0.1			
<i>A. perennans</i>									2.0		0.3	0.1				
<i>A. stolonifera</i>											2.2	3.8			0.2	
<i>Ailanthus altissima</i>			0.3	1.2	0.3											
<i>Ambrosia artemisiifolia</i>							1.4	2.3			1.2					0.3
<i>Amphicarpa bracteata</i>					0.3		0.2				0.4					
<i>Andropogon virginicus</i>	2.0	3.5	9.1	10.8	5.4	0.3	9.0	1.0	0.4		0.1	2.5	0.1	2.3	1.6	
<i>Anisostichus capreolata</i>	0.9															
<i>Antennaria plantaginifolia</i>				1.0			1.4		0.3					0.3		
<i>Aralia racemosa</i>			0.1						0.1					0.4		
<i>Aster acuminata</i>															0.4	
<i>A. cordifolius</i>			3.2						0.1		0.3				5.2	0.3
<i>A. divaricatus</i>									1.5		0.3		87.2			
<i>A. lateriflorus</i>			0.1						0.1	0.5	0.3	0.1	0.3	2.0		
<i>Aster patens</i>					0.1											
<i>A. pilosus</i>					0.2				6.5		0.3	0.1	7.5	3.0	2.6	
<i>A. puniceus</i>											0.3					
<i>A. umbellatus</i>													0.1			
<i>Aster</i> spp.		0.5	3.0		0.1		4.2	0.3	56.0	1.7	2.0	7.5	3.0	27.0	16.8	8.7
<i>Asteraceae</i> spp.			0.1		0.1										0.1	
<i>Betula lenta</i>							0.1		58.5			1.0		19.1	0.6	0.3
<i>B. lutea</i>									4.6							
<i>Campanula divaricata</i>										2.6	19.4	0.3	0.3			

Table 8 (Continued)

Species	1		2		3		4		5		6		7		8	
	SP	SU	SP	SU	SP	SU	SP	SU	SP	SU	SP	SU	SP	SU	SP	SU
<i>Carex debilis</i>								0.5						0.3		
<i>C. nigromarginata</i>	0.2	33.0	4.8			0.5		1.2								
<i>C. oxylepis</i>													0.8			
<i>C. pensylvanica</i>							0.1									
<i>C. platyphylla</i>	3.2				0.1		0.2		0.6							
<i>C. virescens</i>	1.4		2.9	0.3			1.0		3.0		0.1				0.4	
<i>Carex</i> spp.	3.0	2.3	6.9		0.4		11.7		0.3		0.4		0.3	0.9	6.0	0.3
<i>Caryophyllaceae</i> spp.											0.2				0.1	
<i>Ceanothus americanus</i>	0.1															
<i>Cercis canadensis</i>	11.4	0.3	16.0	11.4	2.1	0.3		0.3							0.1	
<i>Chenopodium ambrosioides</i>														0.3		
<i>Chrysanthemum leucanthemum</i>							0.1									
<i>Claytonia virginica</i>		0.2	3.3													
<i>Clematis dioscoreifolia</i>											0.2					
<i>Clematis virginiana</i>									0.1			0.5		0.7		1.7
<i>Collinsonia canadensis</i>								2.2								
<i>Convolvulus sepium</i>											0.1					
<i>Cyperus lancastris</i>			0.1		0.1		0.2									
<i>C. odoratus</i>														0.1		
<i>C. pseudovegetus</i>							1.5									
<i>Danthonia spicata</i>						0.9	1.0		0.5	0.3	0.3	3.0				
<i>Desmodium</i> spp.	0.1						0.3									
<i>Digitaria ischaemum</i>			0.2		0.1		0.1		0.1				0.1			
<i>D. sanguinalis</i>	0.1							0.5						0.5		
<i>Digitaria</i> spp.																
<i>Dioscorea villosa</i>											1.8					
<i>Duchesnea indica</i>											0.3					
<i>Eleocharis obtusa</i>		0.3							9.5							

Table 8 (Continued)

Species	1		2		3		4		5		6		7		8	
	SP ^b	SU	SP	SU	SP	SU	SP	SU	SP	SU	SP	SU	SP	SU	SP	SU
<i>Eleusine indica</i>							0.1		0.1							
<i>Epigaea repens</i>		0.3				0.3				1.2						
<i>Epilobium coloratum</i>									2.4					2.3	0.1	
<i>E. intermedia</i>													0.1			
<i>Eragrostis</i> sp.							0.6						0.9		0.1	
<i>Erechtites hieracifolia</i>	6.6	5.0	6.0	5.4	3.0	0.9	55.0	53.0	36.9	23.3	17.9	8.7	39.9	63.0	44.0	58.0
<i>Erianthus alopecuroides</i>							0.1									
<i>Erianthus</i> sp.							0.1									
<i>Erigeron annuus</i>		1.0	0.4	1.0	0.1	0.3		1.0	0.1			18.5	0.1	0.3		0.3
<i>E. canadensis</i>			0.1		0.4				1.0		0.8		1.2		0.3	
<i>E. strigosus</i>							0.1									
<i>Erigeron</i> spp.	1.6		1.3				1.6		10.0		5.4	1.7	1.2	0.3	1.6	
<i>Eupatorium purpureum</i>					0.1		0.8	1.0	1.0		70.0	18.1	26.4	0.7	2.6	4.3
<i>E. rugosum</i>	0.1	0.3	0.1				0.5	1.7	108	0.5	82.2	47.3	4.0	47.0	33.6	16.8
<i>E. serotinum</i>	0.2	1.0	0.1		0.8	0.3	29.6	29.1	104	0.9	0.8		31.5	100	15.3	11.4
<i>E. sessifolium</i>											2.6		1.6		0.6	
<i>Festuca obtusa</i>							0.1		0.1				0.2		0.2	
<i>Fimbristylis autumnalis</i>			0.1													
<i>Fragaria virginiana</i>							0.8	0.3			3.2	0.5	1.5		12.5	
<i>Fragaria</i> spp.	0.4				0.1					1.0	0.8	1.4			5.5	
<i>Fraxinus americana</i>									0.2							
<i>F. pennsylvanica</i>									0.4							
<i>Galinsoga ciliata</i>							0.2									
<i>Galium circaeazans</i>		0.3						0.3								
<i>G. obtusum</i>	0.2															
<i>G. pilosum</i>	0.2															
<i>G. triflorum</i>	0.1								0.4		10.1	4.3		9.9	1.8	
<i>Galium</i> spp.	0.1															
<i>Gnaphalium obtusifolium</i>	1.6		0.1		0.1		1.5		0.1		0.2		0.4		0.1	

Table 8 (Continued)

Species	1		2		3		4		5		6		7		8	
	SP	SU	SP	SU	SP	SU	SP	SU	SP	SU	SP	SU	SP	SU	SP	SU
<i>Gnaphalium purpureum</i>	1.8	0.3	0.1		0.4	3.3	1.0	0.5		0.3			0.2			
<i>Gnaphalium</i> spp.	1.6	2.5	5.5	0.5		1.0	7.0		0.4	0.3	2.0	1.0	0.1	0.3	0.4	
<i>Goodyera repens</i>													0.6			
Gramineae spp.	0.8	0.3	0.6		0.1		0.8	1.0	268	4.0	28.0	5.0	33.6	30.0	31.2	4.0
<i>Hedeoma pulegioides</i>			0.2				0.3	2.5			13.6	0.3				
<i>Helianthus microcephalus</i>							0.1				1.0		9.6		0.1	
<i>H. strumosus</i>									0.1							
<i>Helianthus</i> spp.											1.5	0.3	6.0			
<i>Heuchera americana</i>			0.2	0.5												
<i>Hexastylis virginica</i>								0.3								
<i>Hieracium paniculatum</i>										1.4	3.2	1.7	3.0			
<i>Houstonia purpurea</i>		8.0	1.0	1.7		4.3	0.6			65.0	123	93.0	74.2		249	52.3
<i>Hydrangea arborescens</i>	1.2	15.4	33.6	393				0.3	434	12.5	415	133	104	222	128	40.2
<i>Hydrophyllum virginianum</i>									5.4					7.6		
<i>Hypericum mutilum</i>								1.0			0.1	0.3				
<i>H. punctatum</i>		0.3		0.3	0.1	0.3				2.0						
<i>Hypericum</i> spp.		0.3	0.1		0.1										0.8	
<i>Juncus interior</i> ^C	0.6		3.0		0.3		0.2			2.3	1.2	0.3	41.6		0.1	
<i>Juncus</i> spp.	0.1				0.1		1.2				1.4		0.4			
<i>Lactuca</i> sp.	2.0	0.3	0.9		1.0	0.3	4.0		1.6		2.0	1.2	1.5	3.5	0.4	2.5
<i>Lespedeza intermedia</i>							0.1									
<i>Lindernia anagallis</i>													1.6			
<i>Liriodendron tulipifera</i>	47.7	27.0	18.4	30.7	49.0	50.0	24.8	35.7	53.0	0.3	12.6	25.0	8.0	57.0	2.4	38.0
<i>Lobelia inflata</i>	0.1	2.2	1.2	4.3		1.4	0.1	22.5	3.3		0.6	16.5	1.6	38.6	38.8	0.3
<i>L. siphilitica</i>															0.5	

Table 8 (Continued)

Species	1		2		3		4		5		6		7		8	
	SPb	SU	SP	SU	SP	SU	SP	SU	SP	SU	SP	SU	SP	SU	SP	SU
<i>Lolium multiflorum</i>															0.3	
<i>Ludwigia microcarpa</i>											0.1					
<i>Lysimachia ciliata</i>											0.1		21.8			
<i>L. quadrifolia</i>									0.3							
<i>Mikania scandens</i>											0.1					
<i>Mimulus alatus</i>	0.1															
<i>Mollugo verticillata</i>							0.1		0.1							
<i>Monarda clinopodia</i>							0.1		6.0		0.1	13.9			1.8	1.7
<i>Morus rubra</i>			32.0	12.1	29.7	32.0	0.4									
<i>Muhlenbergia tenuiflora</i>															0.2	
<i>M. schreberi</i>	0.1	0.3														
<i>Oenothera biennis</i>	0.3	1.7	0.1	0.3	0.1		2.1		2.8	0.3	0.1		0.8	0.5	4.8	
<i>O. grandis</i>															0.2	
<i>O. stricta</i>			1.6	0.3							2.7	4.0	0.3	2.3	0.4	
<i>Oxalis</i> spp.							0.2				0.1					
<i>Oxydendrum arboreum</i>	14.4	1.0	0.1	17.6	22.1		1.8		0.1	1.0	40.0	0.3	0.7		1.2	
<i>Panicum commutatum</i>	6.0	78.4	0.3	4.3	3.0	20.1	7.3	5.5		4.3	3.3	15.5		1.0	3.4	26.8
<i>P. dichotomum</i>	9.6	1.4			11.6	1.1	0.2	12.5		3.7	3.6	1.7	39.6		1.2	
<i>P. gattingeri</i>							0.1									
<i>P. lanuginosum</i>			0.8				0.4				2.4		0.6		3.2	
<i>Panicum</i> spp.	0.4						14.4	0.3	3.8		0.1		1.2		1.2	
<i>Paronychia canadensis</i>											1.2		0.1		0.2	
<i>Parthenocissus quinquefolia</i>					0.1				2.4				0.1	1.0		
<i>Paulownia tomentosa</i>	4.0	8.0	7.7	0.3	4.5	3.5	5.0	4.8	18.9		0.1		0.1		0.1	
<i>Phleum pratense</i>														0.3	0.1	0.3
<i>Physalis pubescens</i>														0.2		

Table 8 (Continued)

Species	1		2		3		4		5		6		7		8	
	SP	SU	SP	SU	SP	SU	SP	SU	SP	SU	SP	SU	SP	SU	SP	SU
<i>Phytolacca americana</i>	2.4	1.0	3.0	17.5	42.7	16.6	9.0	18.3	16.8	11.4	19.8	20.1	6.5	15.4	14.7	18.3
<i>Pilea pumila</i>			0.1	0.3					1.6			2.0				0.5
<i>Plantago major</i>									0.2							
<i>Platanus occidentalis</i>	0.1		7.0													
<i>Poa cuspidata</i>											0.3				0.1	
<i>P. pratensis</i>			0.6	1.7							1.0	49.8	0.1		0.4	95.5
<i>Polygonum scandens</i>											1.6					
<i>Portulaca oleracea</i>													0.3		0.2	
<i>Potentilla canadensis</i>		1.0	1.2		0.2	0.3			0.5	0.3	1.2	0.3	0.5		7.0	0.9
<i>Potentilla simplex</i>							1.0				0.2				0.1	1.7
<i>Potentilla</i> spp.	0.1														0.1	
<i>Quercus alba</i>													0.1			
<i>Ranunculus carolinianus</i>											0.5			3.3		
<i>Rhododendron</i> sp.									0.3							
<i>Rhus copallina</i>	5.4		0.1		1.6		6.0	0.3								
<i>R. glabra</i>	0.1	0.3	0.4		0.3		26.4	23.4							0.4	
<i>Rhus</i> spp.					0.4											
<i>Robinia pseudoacacia</i>					2.0				0.4		0.4		0.1		0.2	51.5
<i>Rubus allegheniensis</i>	0.4		0.8		0.1	0.3	26.0	1.7	63.7	27.4	158	73.0	88.8	8.7	82.4	2.9
<i>R. argutus</i>	2.4	0.5	3.0	31.4	6.0	5.0	12.0	10.0	0.5	5.0	15.2	5.0	10.6		0.2	
<i>R. hispidus</i>	0.1		0.1				0.1								0.1	
<i>R. idaeus</i>				2.6		0.3		2.3		14.2		0.5	6.9		1.5	1.7
<i>R. occidentalis</i>	0.3		0.4				1.8		2.0		0.4					
<i>Rubus</i> spp.			0.1					0.3	0.2		0.1	0.3				0.5
<i>Rudbeckia hirta</i>															0.3	
<i>Rynchospora globularis</i>	0.1															
<i>Salix alba</i>	0.2										0.1	0.3	0.4		0.1	

Table 8 (Continued)

Species	1		2		3		4		5		6		7		8	
	SP ^b	SU	SP	SU	SP	SU	SP	SU	SP	SU	SP	SU	SP	SU	SP	SU
<i>S. nigra</i>													0.1		0.6	
<i>Sambucus canadensis</i>			0.2						0.1		0.1	0.9		0.3		
<i>Sanicula</i> spp. ^d											0.1	2.6		23.5	0.2	
<i>Sassafras albidum</i>	0.1		0.4	1.7	0.1	2.5	3.5	1.0		0.3	0.4			0.3	0.1	
<i>Scirpus</i> sp.		0.3												0.3		
<i>Scutellaria elliptica</i>			0.5				0.1	0.5			0.2					
<i>Scrophularia marilandica</i>											0.1					
<i>Sedum ternatum</i>									23.1							
<i>Setaria viridis</i>	0.1															
<i>Silene stellata</i>											0.2					
<i>Smilax glauca</i>							0.1	0.5	0.1	1.7	0.1	0.9	0.4			
<i>Solanum americanum</i>					0.5	6.3	0.1				0.1		0.1			
<i>S. carolinense</i>		0.9				3.1										
<i>S. nigrum</i>							0.1				0.1	0.3				
<i>Solidago altissima</i>	0.3								3.6		0.4		0.1		1.6	
<i>S. arguta</i>													0.4			
<i>S. caesia</i>	0.1	0.3							0.6		9.0	2.6	1.8	4.0	1.2	0.3
<i>Solidago</i> spp.	0.8		1.5	0.3		0.3	0.4		1.0	0.3	4.8	0.3	3.5	2.5	0.8	1.0
<i>Sonchus asper</i>							0.1		0.2				0.1		0.2	
<i>Sphenopholis nitida</i>										0.3						
<i>Stellaria media</i>			2.2						0.6		4.4			1.7		0.3
<i>S. pubera</i>									0.2				0.1			
<i>Streptopus roseus</i>												0.3				
<i>Taraxacum officinale</i>			1.8			0.3	0.1		0.1		0.3	2.0	0.4	2.3	0.1	3.5
<i>Taraxacum</i> sp.		0.3							0.1			2.6				
<i>Thalictrum thalictroides</i>	0.3								0.2		0.4	0.3		1.2	0.4	
<i>Tiarella cordifolia</i>		1.7		4.3										4.3		

Table 8 (Continued)

Species	1		2		3		4		5		6		7		8	
	SP ^b	SU	SP	SU	SP	SU	SP	SU	SP	SU	SP	SU	SP	SU	SP	SU
<i>Tradescantia ohienensis</i>											1.9					
<i>Trifolium repens</i>			0.2										0.1			
<i>Triosteum angustifolium</i>									1.0		0.3		0.4			
<i>Typha latifolia</i>	2.0		1.4		0.1		0.1		18.9				0.1	1.0	2.8	0.3
<i>Ulmus alata</i>	0.1		1.2	0.9				0.3								
<i>U. americana</i>		0.3	0.1		0.1		0.1	0.3								
<i>U. rubra</i>			0.2				0.1									
<i>Vaccinium</i> sp.									0.9		0.3		1.0			
<i>Verbascum thapsus</i>	1.0	0.3	5.0	0.3	0.2		37.1	62.3			0.4	0.3			6.0	0.3
<i>Verbena urticifolia</i>							0.2	0.3							0.1	
<i>Veronica peregrina</i>					0.2								1.0		0.3	
<i>Vicia</i> sp.											0.2	1.2				
<i>Viola palmata</i>			0.3												0.3	
<i>V. papilionacea</i>			0.3	0.3					15.4		24.8	5.6	12.5	0.5	69.3	
<i>Viola</i> spp.	0.9				0.3		0.1	0.3	2.4		12.6	28.8	2.7	6.0	18.9	
<i>Vitis aestivalis</i>	0.9				0.3		0.2					0.5	0.2		0.4	3.9
<i>V. Baileyana</i>			0.1			1.0	0.1	0.3	0.2		2.1	0.9	2.4		1.0	
<i>V. rotundifolia</i>				1.0	0.1											
<i>V. vulpina</i>	0.1	0.01	0.4	5.0	0.1	1.0	0.6		0.7	0.3	2.7	3.3	0.2	5.6	1.2	9.0
<i>Vitis</i> spp.					0.1				0.1		0.6				1.6	

^aImportance Value (IV) = frequency x number plants/m².

^bSP = Spring collection; SU = Summer collection.

^cNomenclature follows Gleason (1952).

^d*Sanicula* sp. may actually have been *Ranunculus carolinianus*.

the sites. These most numerous species comprised the majority of the germinants. They included Hydrangea arborescens, Houstonia purpurea, Rubus allegheniensis, R. argutus, Eupatorium purpureum, E. rugosum, E. serotinum, Erechtites hieracifolia, Liriodendron tulipifera, Phytolacca americana, and Lobelia inflata. Despite their significance in the buried seed populations at many of the sites, each of these species germinated heavily from only several sites. In addition, certain other species were particularly important germinants but only from the soil from one site. These included species such as Betula lenta from Site 5 spring soils, Robinia pseudo-acacia and Poa pratensis from Site 8 summer soils, Aster divaricatus from Site 7 summer soils, and Juncus interior from Site 7 spring soils. Nearly all of the major species germinated in greater numbers from the spring than the summer samples although this varied with the species and the site locations. The percentage of the total number of plants accounted for by each of the most abundant species is presented in Table 9.

Many species tended to germinate from either the high- or the low-elevation soils. High elevation species generally had higher importance values than those from the low elevation, as would be expected given their greater numbers.

Many of the most important germinants from the low elevation soils were woody species. These included Liriodendron tulipifera, Cercis canadensis, Morus rubra, Rhus coppalina, R. glabra, Oxydendrum arboreum, and Paulownia tomentosa. Liriodendron was one of the most important germinants from both low- and high-elevation sites. It generally germinated in large numbers from the spring collection of the low elevation soils but from the summer collection of the high

Table 9. Species germinating in greatest abundance.^a

Spring Collection (%) ^b	Summer Collection (%)
A. Species making up more than 10% of the total number of plants.	
Hydrangea arborescens (15.4)	Hydrangea arborescens (16.1)
B. Species making up between 2% and 10% of the total number of plants.	
Rubus allegheniensis (7.7)	Houstonia purpurea (6.6)
Houstonia purpurea (6.5)	Panicum commutatum (5.1)
Gramineae spp. (5.4)	Liriodendron tulipifera (5.0)
Eupatorium rugosum (3.6)	Rubus allegheniensis (4.5)
Liriodendron tulipifera (3.3)	Erechtites hieracifolia (4.3)
Erechtites hieracifolia (3.0)	Lobelia inflata (4.2)
Eupatorium serotinum (2.6)	Poa pratensis (3.3)
Phytolacca americana (2.1)	Rubus argutus (3.2)
	Phytolacca americana (3.1)
	Eupatorium serotinum (2.9)
	E. rugosum (2.5)
	Lysimachia ciliata (2.3)
C. Species making up 1% to 2% of the total number of plants.	
Eupatorium purpureum (1.9)	Aster divaricatus (1.9)
Rubus argutus (1.9)	Verbascum thapsus (1.9)
Viola papilionacea (1.9)	Aster spp. (1.2)
Lobelia inflata (1.8)	Rubus idaeus (1.2)
Panicum dichotomum (1.7)	Panicum dichotomum (1.1)
Juncus interior (1.5)	Vitis vulpina (1.1)
Aster spp. (1.4)	
Galium triflorum (1.4)	
Oxydendrum arboreum (1.3)	
Campanula divaricata (1.2)	
Paulownia tomentosa (1.2)	
Duchesnea indica (1.1)	
Verbascum thapsus (1.1)	

^aBased on the results from all eight study sites combined.

^b(%) refers to the percent of the total number of plants which that species represents.

elevation soils. Several other woody species, which produced few germinants, but were restricted to the low elevation soils, included Acer rubrum, Platanus occidentalis, Ailanthus altissima, and Ulmus alata.

Although woody species were important germinants from the low elevation soils, many herbaceous species also emerged, and several of them accounted for high importance values. These included Erechtites hieracifolia, Phytolacca americana, Panicum commutatum, P. dichotomum, and Verbascum thapsus. In general, there was a correspondence between important germinants comprising the spring and the summer samples at the low elevation soils.

The most ubiquitous species germinating from the high elevation soils was the shrub, Hydrangea arborescens. It germinated in very large numbers from soils from Sites 5, 6, and 7. In contrast, it was absent from or germinated in very small quantities from the low elevation soils except from Site 2 soil. Only 60 of the 1289 Hydrangea plants which germinated from the spring samples were from low elevation soils. In the case of Site 2, however, Hydrangea germinated in enormous numbers from the summer soils when compared to the other important species.

Other than Hydrangea arborescens, herbaceous species were usually the most important germinants from high elevation soils. These species included Eupatorium purpureum, E. rugosum, E. serotinum, Houstonia purpurea, Erechtites hieracifolia, Phytolacca americana, and several grasses. Rubus allegheniensis was an important germinant from all of the high elevation soils. There was a general correspondence of the most important species in the spring and summer collections from most

of the sites. Liriodendron was an important germinant from Site 5 spring and Site 7 summer soils although few other woody species also germinated in large numbers. Several woody species, which generally germinated in small numbers, were more or less restricted to high elevation soils. These included Betula lenta, B. lutea, Fraxinus americana, Salix alba, S. nigra, and Ulmus americana.

Species Diversity and the Index of Similarity

Species diversity values of the spring and summer collections are presented in Table 10. Diversity was calculated using the Shannon-Weiner Index. The resulting values ranged from a high of 2.16 at Site 5 from the spring set to a low of 0.98 at Site 2 from the summer set. The low diversity values may be explained by the fact that the Shannon Index includes an evenness component (Odum 1971). In the results, the apportionment of the germinants among the species was not equitable. Instead, a few species comprised most of the germinants from the soils of any one site. Large numbers of seedlings from a few species lead to low diversity values.

Tables 11 and 12 present arrays of the indices of similarity between the eight different sites for the species of germinants, using Jaccard's Index of Similarity (Mueller-Dombois and Ellenberg 1974). Used alone, similarity indices are of minimal value in the quantitative sense. However, they can serve as descriptive tools to help elucidate vegetation patterns. According to Mueller-Dombois and Ellenberg (1974), the Jaccard IS tends to underestimate the similarity of plant groups. They suggest that communities may be part of the same association if the IS value is "more than 25 percent, but less than 50 percent (based

Table 10. Species diversity of the germinants.

Study Sites	Species Diversity (H) ^a	
	Spring	Summer
1	1.57	1.25
2	1.58	0.98
3	1.33	1.29
4	1.57	1.42
5	2.16	1.27
6	1.34	1.67
7	1.47	1.22
8	1.40	1.08

^aShannon-Weiner Index of Diversity (Pielou 1975):
 $H = - \sum \frac{n_i}{N} \log \frac{n_i}{N}$, where n_i = number of individuals of a given species,
 and N = total number of species.

Table 11. Indices of species similarity of germinants among the different sites (Spring Collection).^a

Site	Site							
	1	2	3	4	5	6	7	8
1		31.4	31.4	27.4	21.7	23.0	21.6	25.0
2			30.9	33.1	27.6	26.4	27.0	31.3
3				30.2	21.7	20.0	24.8	24.2
4					24.2	27.9	27.6	29.7
5						24.1	28.6	29.6
6							31.1	33.1
7								33.8

^aThe numbers presented were calculations of Jaccard's Index of Similarity (IS_j): $IS_j = \frac{C}{A+B-C} \times 100$, where A = the number of species from the first set; B = the number of species from the second set; and C = the number of species common to sets A and B.

Table 12. Indices of species similarity of germinants among the different sites (Summer Collection).^a

Site	Site							
	1	2	3	4	5	6	7	8
1		26.2	36.2	28.6	22.9	18.4	17.1	20.3
2			31.6	22.9	20.6	17.9	21.1	23.4
3				25.8	29.5	21.1	15.6	22.6
4					21.6	22.4	19.0	22.5
5						26.1	17.1	20.3
6							24.8	29.9
7								29.2

^aSee Table 11 for calculation of the Jaccard Index of Similarity.

on presence only)" (page 228). The term "association" refers to vegetation units which are floristically defined by associated as well as dominant species.

Given these constraints, not very much information can be derived from the IS values presented here. In the spring samples, most of the values were slightly above 25% while they appeared to be lower overall in the summer samples. This discrepancy was probably due to the lower numbers of germinants and species in the summer sets. One general conclusion which does emerge, however, is that the similarities of sites within elevations tended to be greater than of those between elevations. Sites at low elevations tended to have species compositions most similar to other low elevation sites, and high elevation sites tended to be most similar to other high elevation sites.

Species similarities between the spring and summer samples had a Jaccard Index of Similarity which ranged from a low of 13.6% from Site 5 to a high of 32.1% from Site 2 (Table 13). The values calculated from Site 5 and Site 6 (17%) were particularly low, suggesting a rather pronounced difference in the types of species which would germinate from soil collected during different seasons of the year. In general, the species similarities between the spring and summer samples collected from one site were not greater, and were often less, than the similarities between different sites, particularly when the latter occurred within the same elevation band.

Ferns and Bryophytes

Nine species of ferns emerged from the soil samples collected during the spring and summer. The germination of these plants seemed

Table 13. Similarities of germinating species between the spring and summer samples.^a

Site	Number of Species Spring	Number of Species Summer	Number in Common	Percent Spring Sample in Both	Percent Summer Sample in Both	IS _J (Percent)
1	65	43	21	32.3	48.8	24.1
2	73	39	27	37.0	71.1	32.1
3	54	36	30	37.0	55.6	28.6
4	84	47	27	32.1	58.7	26.2
5	75	43	14	18.7	33.3	13.6
6	90	73	38	42.2	52.8	30.7
7	87	52	20	23.3	38.5	17.0
8	95	40	26	27.7	66.7	24.3

^aSee Table 11 for calculation of Jaccard Index of Similarity.

to depend upon the warm, moist conditions of the temperature-regulated greenhouse; no ferns emerged from the soil samples placed in the other unregulated greenhouse where the summer temperatures were very high. Therefore, the ferns emerged from most of the summer samples and only those of the spring set which were stored in the first greenhouse. Few ferns germinated from the litter layer, although comparable numbers emerged from the two soil depths. More ferns emerged from the low-elevation soils than from the high-elevation soils. The most abundant species was the Christmas fern (Polystichum acrostichoides). The other species emerged in variable numbers and there seemed to be no relationships between the species and the site from which soil was collected.

The ferns were:

1. Adiantum pedatum L.
2. Asplenium platyneuron (L.) Oakes
3. Cystopteris protrusa (Weatherby) Blasdel
4. Dennstaedtia punctilobula (Michaux) Moore
5. Lygodium palmatum (Bernh.) Sartz.
6. Osmunda cinnamomea L.
7. Pellaea atropurpurea (L.) Link
8. Polystichum acrostichoides (Michaux) Schott
9. Thelypteris hexagonoptera (Michaux) Weatherby

Most of the soil samples which were stored in the humid greenhouse eventually became covered with mosses. Since the entire summer collection was kept in that greenhouse nearly all the soil layers from all the samples developed a rich moss cover. Nine species were identified. Several liverworts appeared in some of the flats, but no

attempt was made to identify them. The following species of mosses were collected (after Crum et al. 1973):

1. Ditrichum pallidum (Hedw.) Hampe
2. Fissiden osmundoides (Hedw.)
3. Funaria flavicans Michx.
4. Leptodictyum riparium (Hedw.) Warnst.
5. Philonotis spp.
6. Physcomitrium pyriforme Hedw.
7. Polytrichum juniperinum Michx.
8. Trematodon longicollis Michx.
9. Weissia controversa Hedw. var. controversa

CHAPTER VIII

SPECIES--AREA CURVES

An attempt was made to estimate the number of soil samples needed from each site to adequately characterize the seed bank populations. Figures 4 to 7 show the cumulative species totals with the addition of each soil sample for the eight sites from both the spring and summer collections. The figures are presented so that the first sample was the one with the largest number of species germinating. Thus, the graphs do not correspond to the order in which the samples were collected and would therefore lead to underestimates of the numbers of samples necessary.

Given these precautions, it can be seen that the numbers of samples collected at each site were not entirely adequate. However, for most sites, the slope of the curve begins to decrease after eight samples, indicating only small increases in the number of species with additional samples. It is likely that most of the abundant species were included in 10 samples. This would lead to the recommendation that at least one square meter of surface be sampled within a forest stand. The 0.6 m² sampled at each site during the summer may not have taken into account all of the major species and probably led to an inadequate characterization of the seed bank.

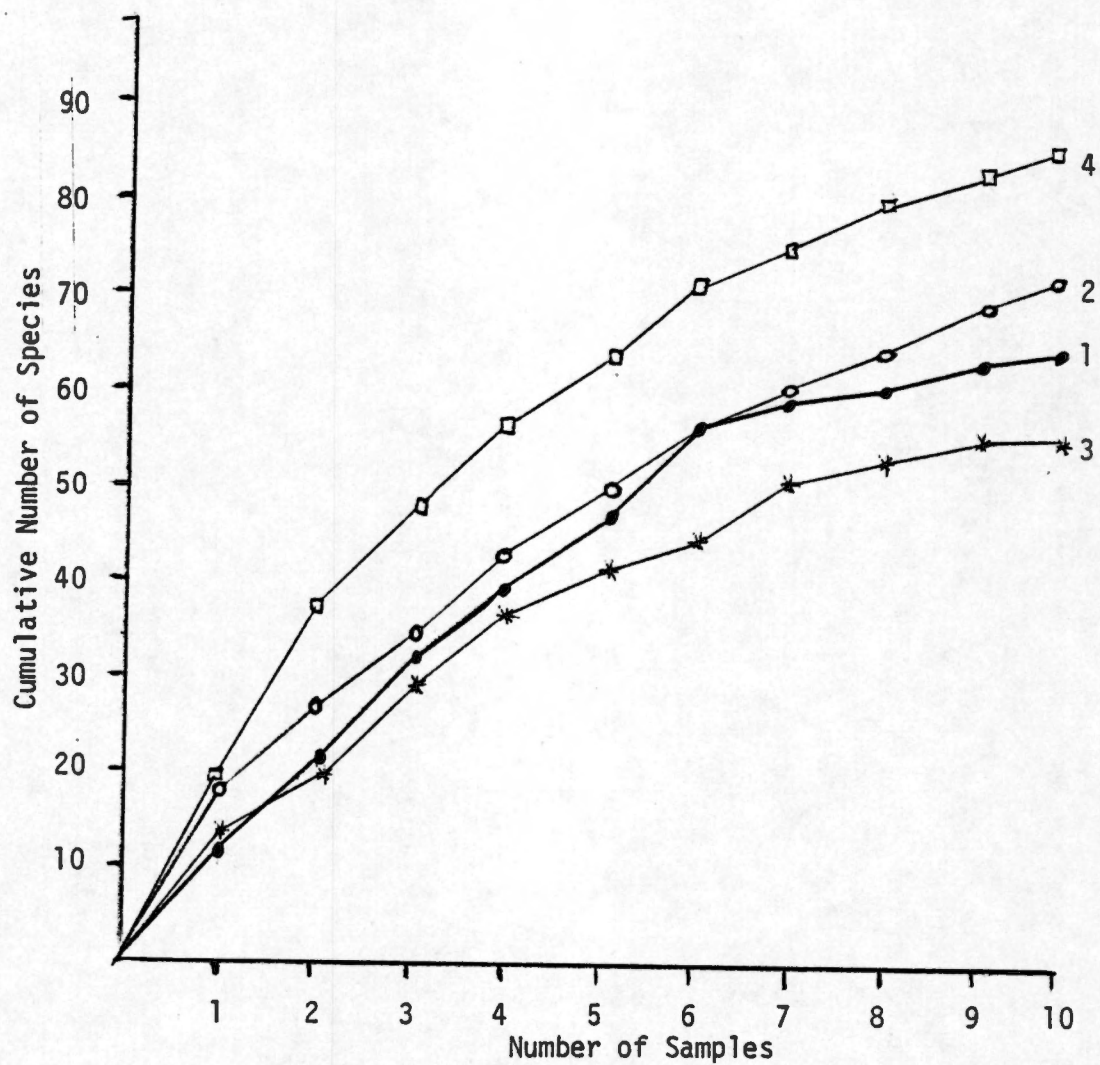


Figure 4. Cumulative species numbers of germinants from the spring collection of Sites 1 to 4. (● = Site 1; ○ = Site 2; * = Site 3; □ = Site 4)

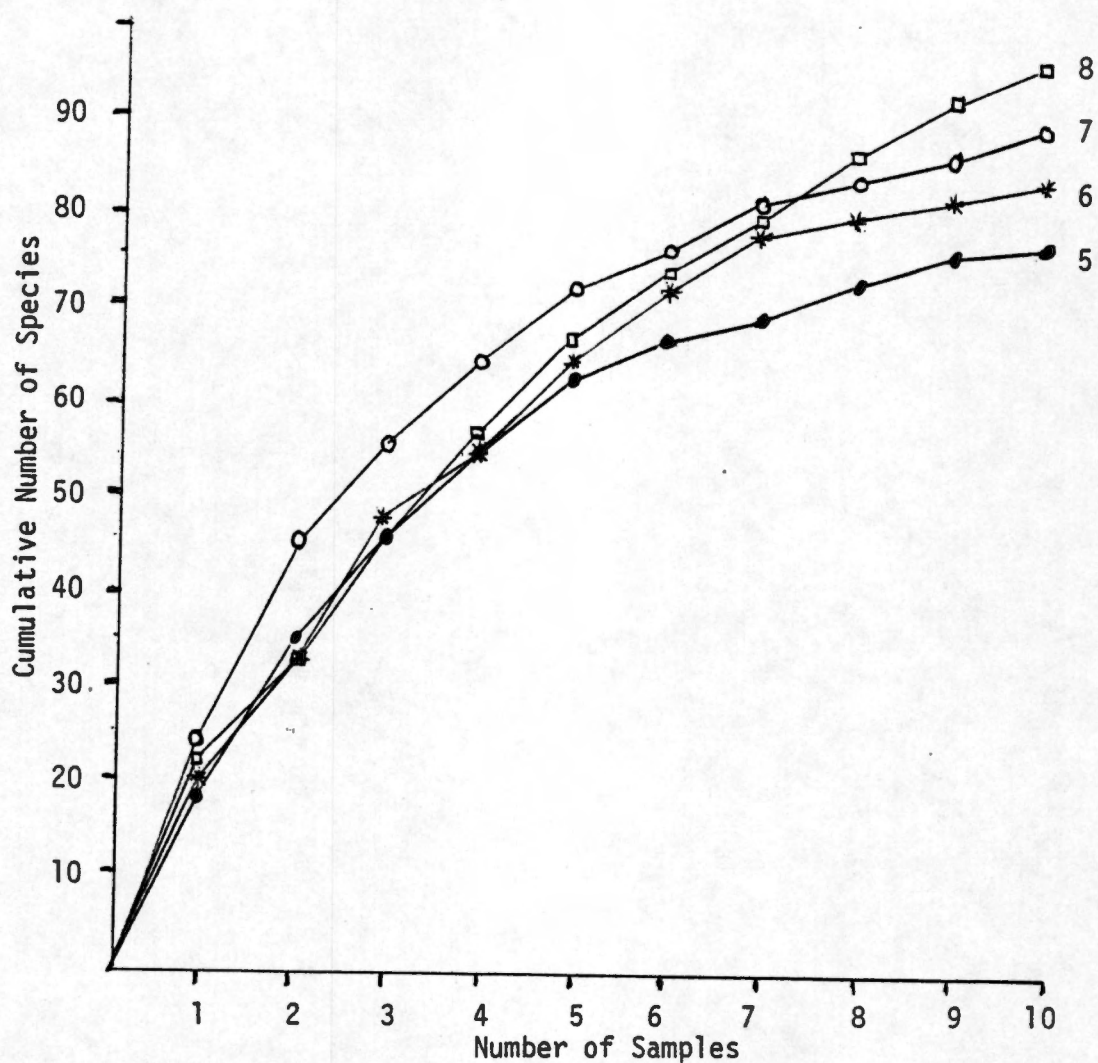


Figure 5. Cumulative species numbers of germinants from the spring collection of Sites 5 to 8. (• = Site 5; o = Site 6; * = Site 7; □ = Site 8)

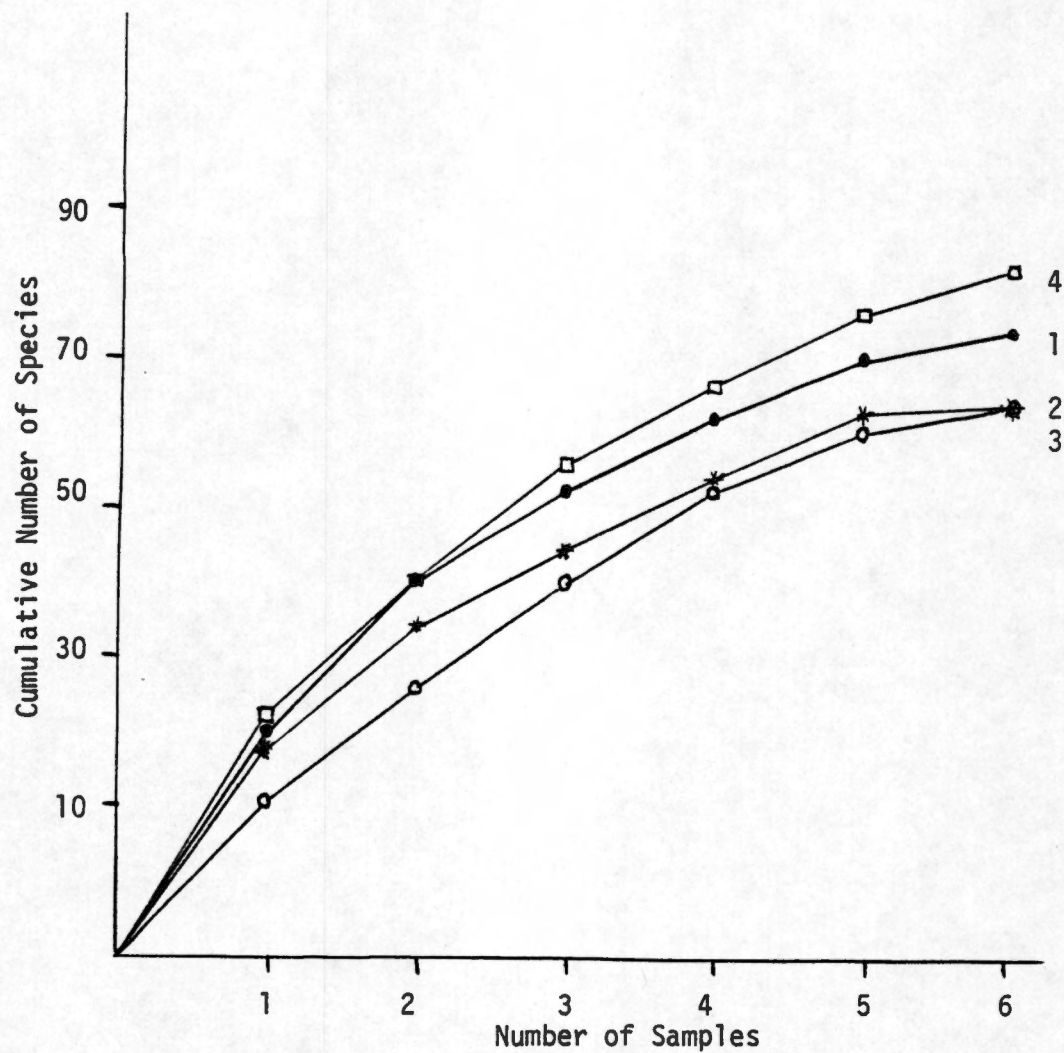


Figure 6. Cumulative species numbers of germinants from the summer collection of Sites 1 to 4. (● = Site 1; ○ = Site 2; * = Site 3; □ = Site 4)

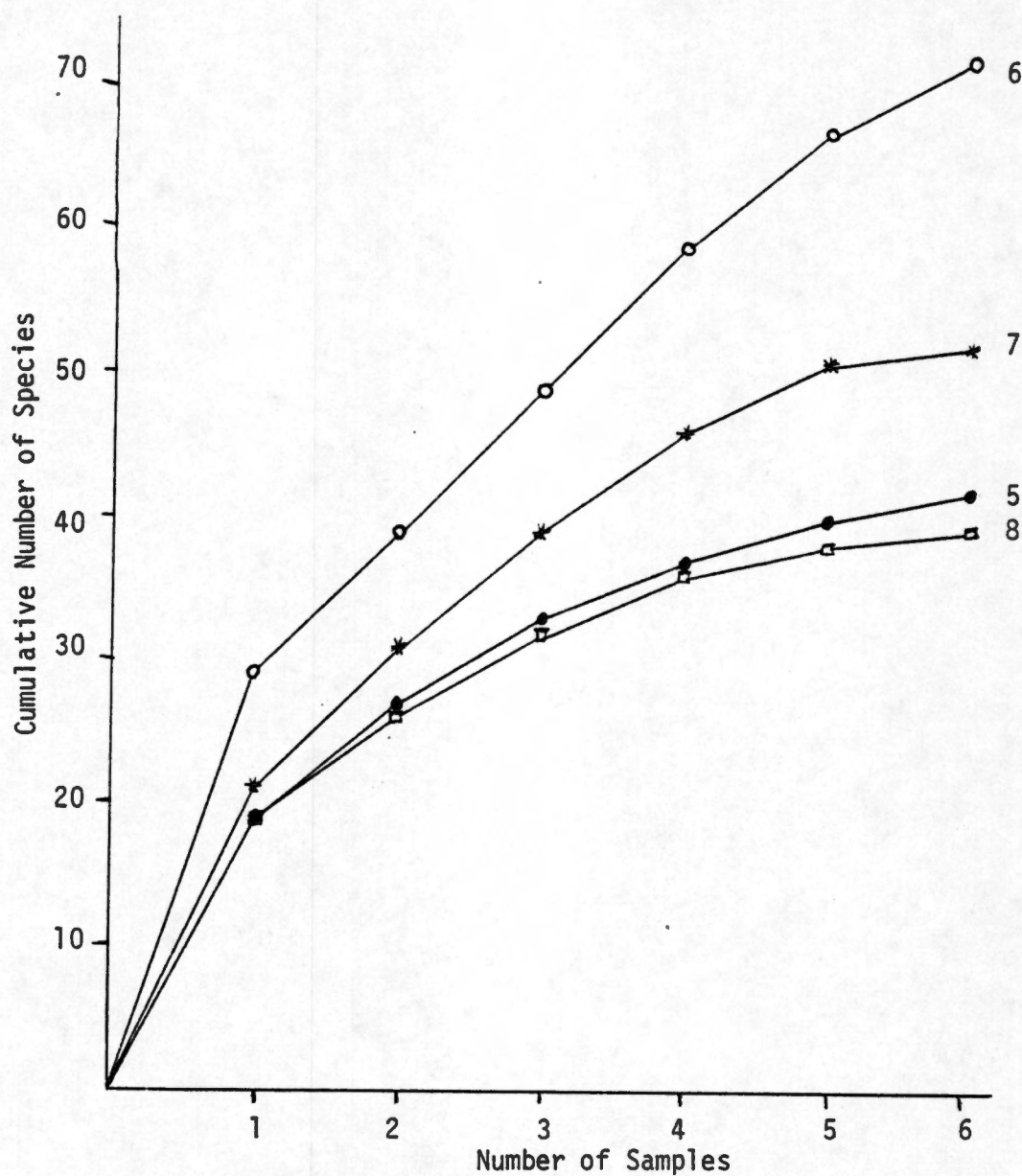


Figure 7. Cumulative species numbers of germinants from the summer collection of Sites 5 to 8. (● = Site 5; ○ = Site 6; * = Site 7; □ = Site 8)

CHAPTER IX

PATTERNS OF GERMINATION

General

Knowledge of the patterns of germination over time is of practical interest. In a surface mine operation, where topsoil is replaced as part of the revegetation scheme, it will be desirable to be able to estimate the densities of species which grow and may become prominent later. The greenhouse studies provide an estimate of the potential for such natural revegetation.

Table 14 presents a summary of the number of seedlings and the number of species germinating during the first two weeks after the soil was placed in the greenhouse. These are the cumulative results for all of the soil samples collected at each site.

In nearly every case, maximum germination in the soil from each site occurred during the second week in the greenhouse. With the eight site collections of the spring sample, between 37% and 55% of all the seedlings which eventually did emerge had done so by the end of the second week. Similarly, with the summer samples, between 36% and 72% of all the germinants had appeared after two weeks.

This section presents a discussion of the individual patterns of germination of some of the most abundant species which emerged from either of the spring or summer sets, in addition to the results of other species of interest. Generally, the patterns of emergence of a species from the spring and summer collections were very similar. Therefore,

Table 14. Numbers of plants and numbers of species which were early germinants.^a

Site	Number of Plants		Number of Species	
	Week #1	Week #2	Week #1	Week #2
Germinants from Spring Soil Collection				
1	31	104	14	33
2	46	205	17	44
3	4	146	3	32
4	55	306	17	58
5	110	787	24	59
6	189	945	33	63
7	79	346	19	53
8	71	472	25	74
Germinants from Summer Soil Collection				
1	28	56	12	18
2	36	267	15	23
3	23	50	8	20
4	134	100	20	25
5	35	135	8	24
6	134	259	30	45
7	134	333	18	38
8	67	152	16	30

^aThese were the germinants emerging within the first two weeks after the soil was placed in the greenhouse.

the results from both sets are treated together and any deviations are noted.

In Table 15, the more abundant or otherwise significant species are listed according to their periods of maximum germination. Many of the species germinated in substantial numbers during times other than the weeks of maximum germination. However, the majority of the germinants of the species had emerged by the second or, less frequently, the third week. The category of "week 5+" refers to seedlings emerging after the fourth week of the experiment. Weekly counts of new germinants were done only through the first four weeks of the experiment. Later germinants were grouped. Thus, although for a species, the time of maximum germination is described as week 5+, emergence may have occurred during from two weeks to five months. In some, it may have taken place quickly, within one week. The individuals of species listed under "no peak time" usually emerged at a uniform rate over the entire period.

Germination Characteristics of Important Species

The pattern of seed germination in the soil samples varied with species (Figures 8 to 11). The patterns of some species, which show a second maximum of germination at the 5+ week mark, may be somewhat misleading since that time-period represents all recorded germination between four weeks and five months. However, the main interest is in determining the species most likely to establish immediately. In addition, knowledge of the germination characteristics of woody species, particularly trees and shrubs, is useful due to their desirability in revegetation.

Table 15. Times of maximum germination of selected species.^a

Weeks	Species	Species
1	Acer saccharum Collinsonia canadensis	
1 & 2	Erechtites hieracifolia Erigeron annuus Eupatorium purpureum E. rugosum E. serotinum Monarda clinopodia Panicum dichotomum	Phytolacca americana Salix alba Solidago caesia Ulmus alata U. rubra Verbascum thapsus
2	Agrostis stolonifera Aster cordifolius Betula lenta Cercis canadensis Danthonia spicata Duchesnea indica Erigeron canadensis Fragaria virginiana Fraxinus pennsylvanica Galium triflorum Hedeoma pulegioides Helianthus spp. Hydrangea arborescens Lobelia inflata	Morus rubra Panicum lanuginosum P. commutatum Paulownia tomentosa Ranunculus carolinianus Rhus copallina R. glabra Rubus argutus R. idaeus Sambucus canadensis Tiarella cordifolia Viola papilionacea Vitis vulpina
2 & 3	Ailanthus altissima Betula lenta Carex virescens Carex spp. Gnaphalium obtusifolium Liriodendron tulipifera	Morus rubra Platanus occidentalis Rubus allegheniensis Salix nigra Sassafras albidum
2,3,4	Gnaphalium purpureum Oenothera biennis	
2 & 5+ ^b	Houstonia purpurea	
No peak time of germination	Acer rubrum Aster divaricatus Campanula divaricata Panicum commutatum	Robinia pseudo-acacia Taraxacum officinale Ulmus americana

^aIncluded in the table are many of the more abundant or otherwise important species.

^bRefers to seedlings emerging any time after the fourth week of the experiment.

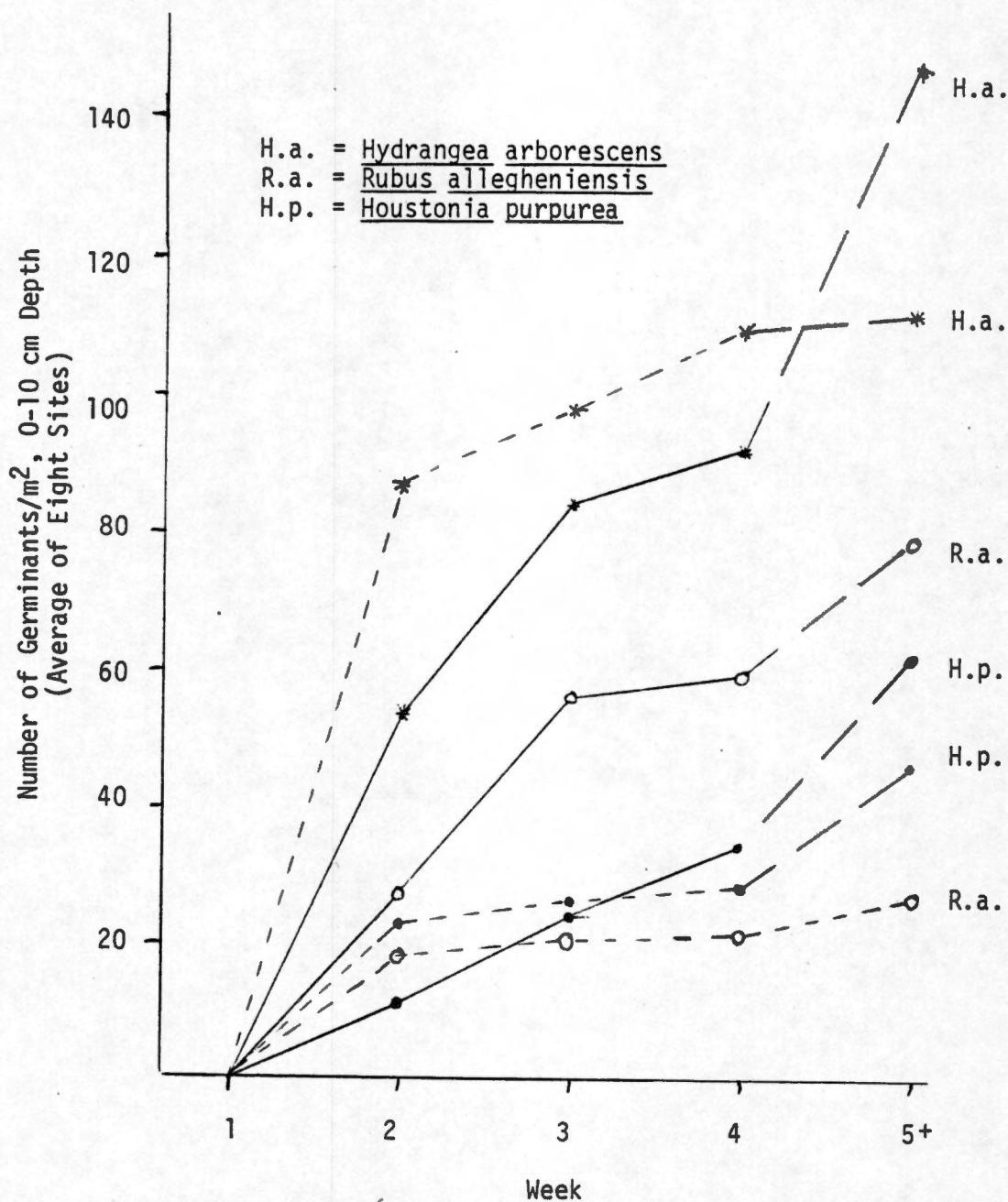


Figure 8. Cumulative germination of species--*Hydrangea arborescens*, *Rubus allegheniensis*, *Houstonia purpurea*. Results are presented for the first four weeks of greenhouse incubation and all weeks thereafter (week 5+) for the spring (solid lines) and summer (dashed lines) soil collections.

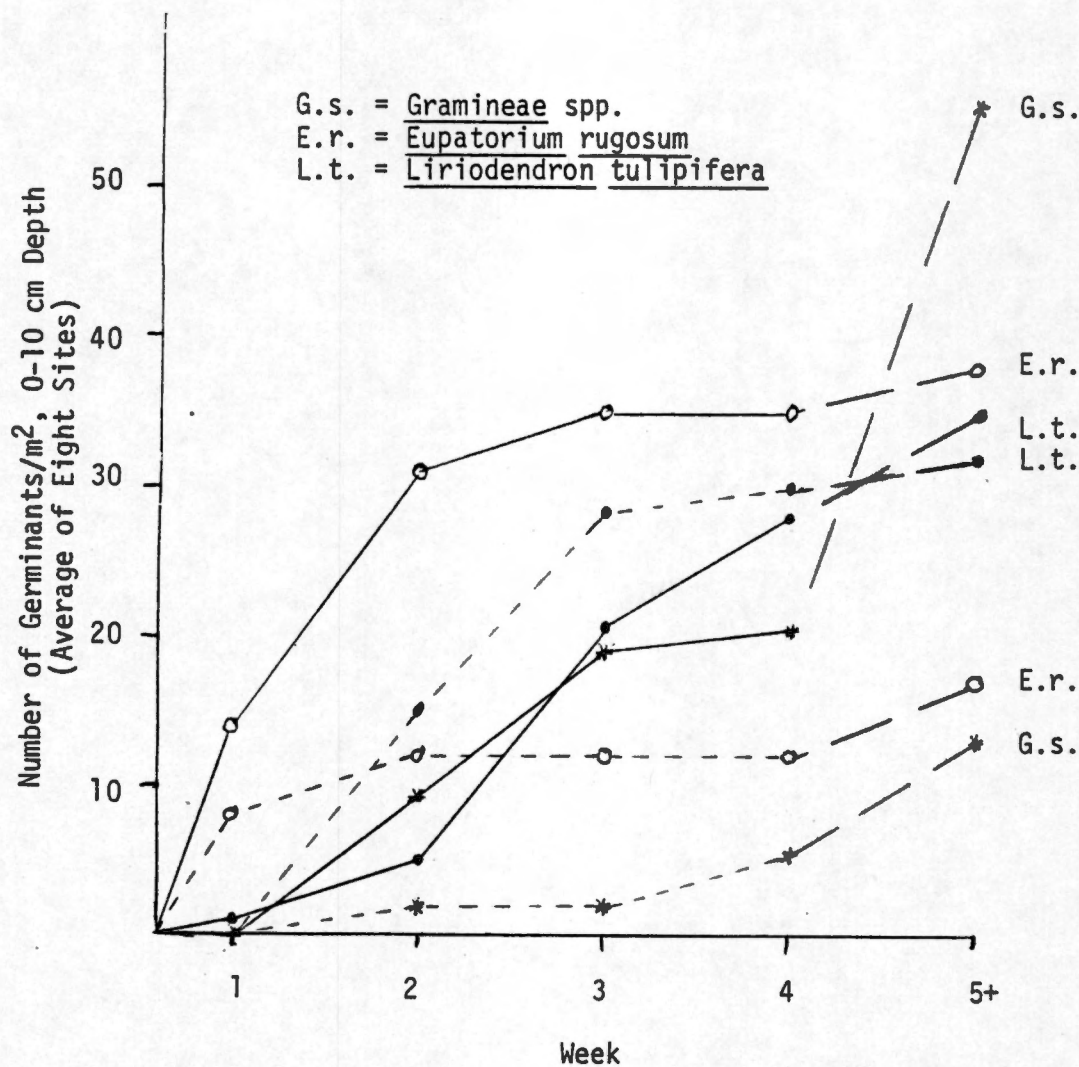


Figure 9. Cumulative germination of species--Gramineae spp., Eupatorium rugosum, Liriodendron tulipifera. Results are presented for the first four weeks of greenhouse incubation and all weeks thereafter (week 5+) for the spring (solid lines) and summer (dashed lines) soil collections.

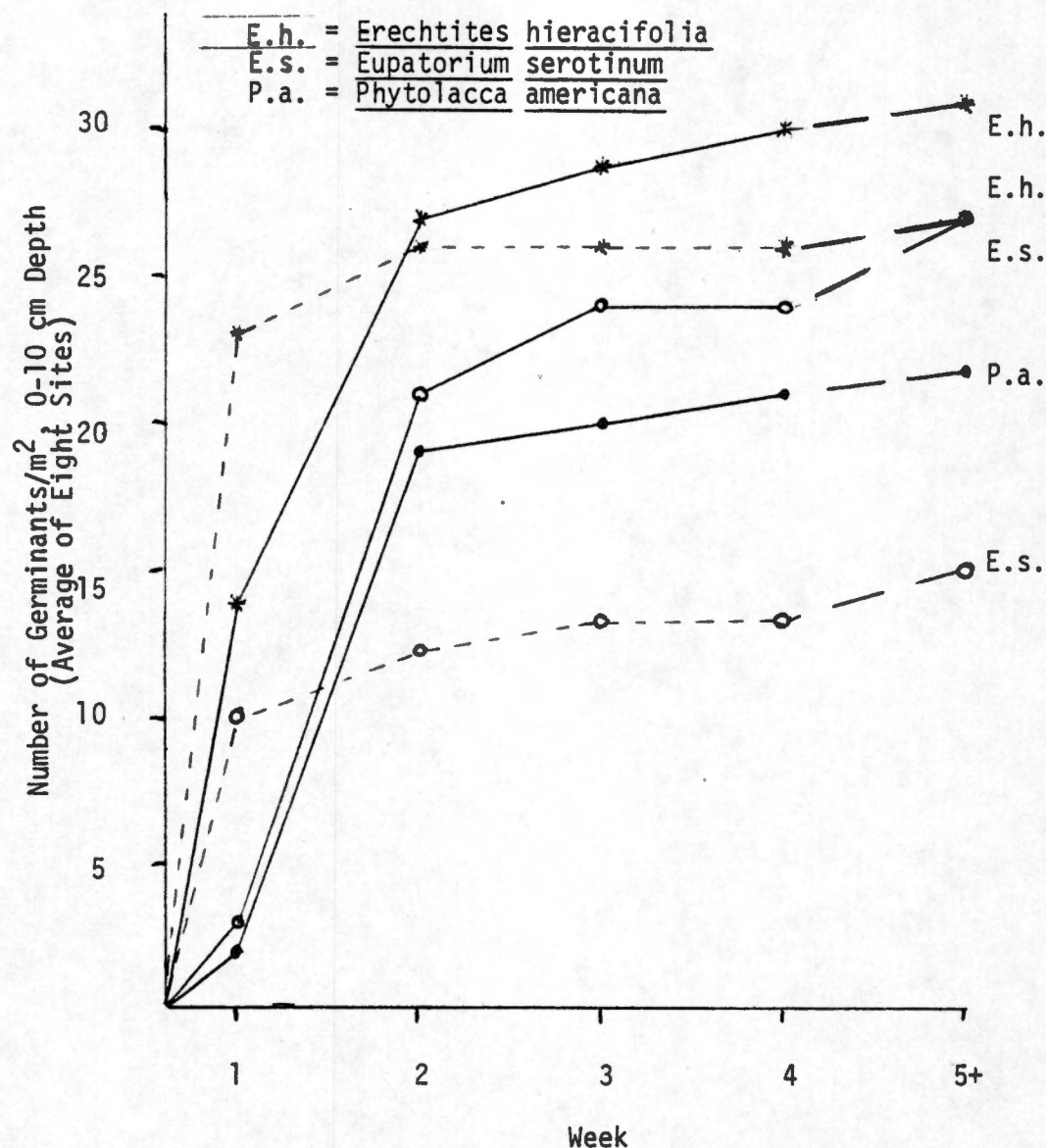


Figure 10. Cumulative germination of species--*Erechtites hieracifolia*, *Eupatorium serotinum*, *Phytolacca americana*. Results are presented for the first four weeks of greenhouse incubation and all weeks thereafter (week 5+) for the spring (solid lines) and summer (dashed lines) soil collections.

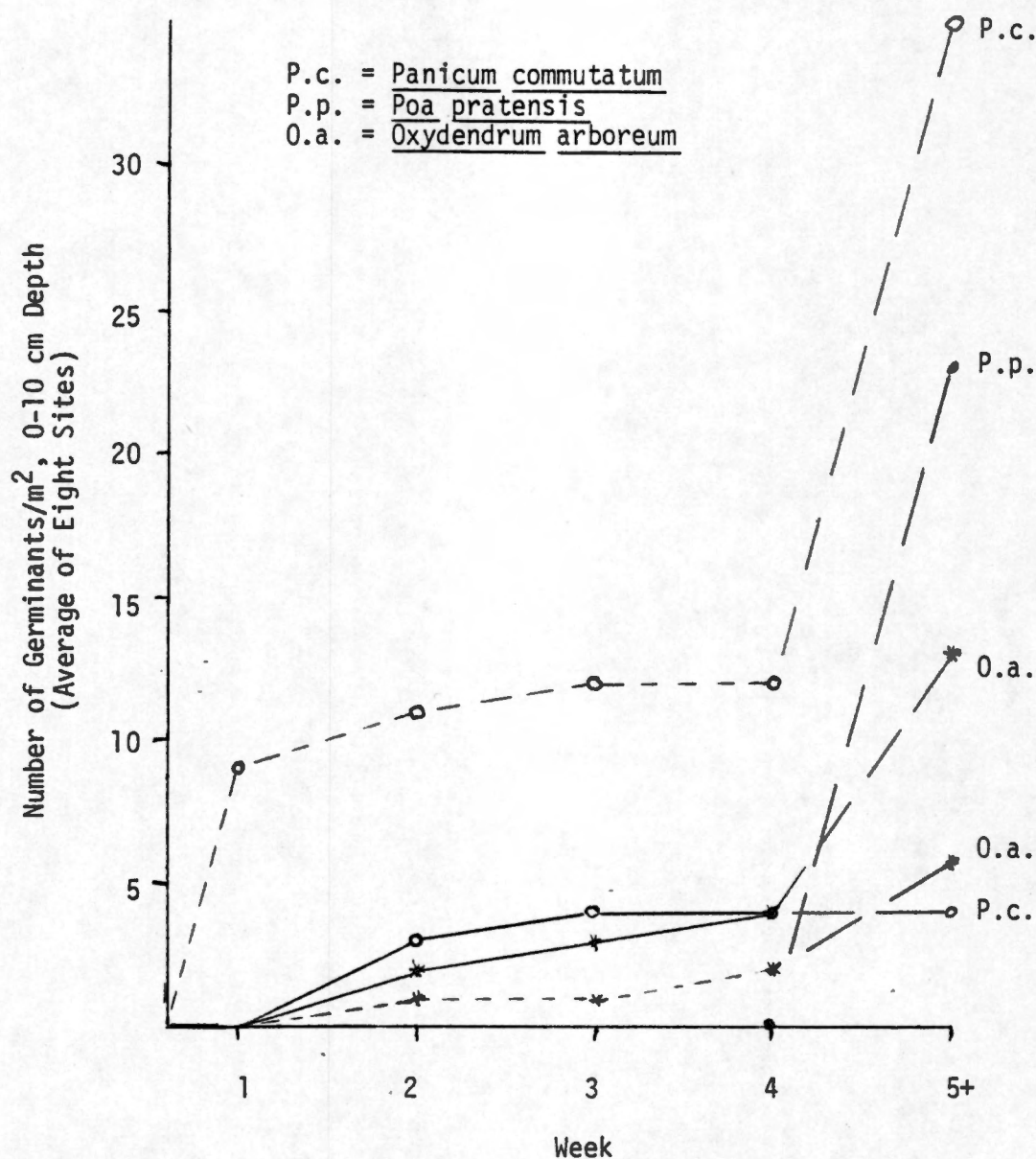


Figure 11. Cumulative germination of species--Panicum commutatum, Poa pratensis, Oxydendrum arboreum. Results are presented for the first four weeks of greenhouse incubation and all weeks thereafter (week 5+) for the spring (solid lines) and summer (dashed lines) soil collections.

Most of the abundant species from both the spring and summer collections had maximum germination times within the first two or three weeks after incubation of the soil samples in the greenhouse. For example, with Hydrangea arborescens, the most abundant species, 440 plants (35%) germinated within the first two weeks with the spring collection and 540 plants (77%) with the summer collection (Figure 8).

Different patterns were exhibited by some of the other species. Both Erechtites hieracifolia and Phytolacca americana (Figure 10) had maximum germination times during the first week of incubation. Houstonia purpurea (Figure 8), on the other hand, germinated at a fairly steady and even rate over the entire period of observation, although the largest seedling numbers emerged during the second and third weeks. The time of maximum germination of Liriodendron tulipifera seedlings (Figure 9) from the spring sample occurred during the third week of incubation. The patterns of germination for Poa pratensis (Figure 11) and many of the unidentified grass species (Figure 9) were such that most of the seedlings did not emerge until after four weeks in the greenhouse.

Effects of Soil Depth on Germination Behavior

Most of the species which germinated showed some influence of soil depth on the numbers of germinants. The results of analyses of variance of total numbers of plants on the individual species demonstrated that the effect of soil depth was a consistently significant factor. Generally, the fewest numbers emerged from the litter layer and there was an increase in the numbers with increasing soil depth. Often, however, the quantities germinating from the 0-5 and 5-10 cm

depths were similar, and sometimes the 0-5 cm layer contained the largest numbers. Although, overall, the largest numbers emerged from the 5-10 cm layer, the differences between it and the 0-5 cm layer were never significant for any of the sites.

For example, about twice as many germinants of Hydrangea arborescens emerged from each of the two soil depths as from the litter layer. Of a total of 541 seedlings of Houstonia purpurea, only 12 (2%) germinated from the litter layer, while 298 (55%) originated with the 5-10 cm layer. However, with Liriodendron tulipifera, greater numbers of germinants emerged from the top two layers, including the litter.

An abbreviated list of the species which tended to exhibit definite patterns of germination from one or more soil layers is presented in Table 16. A more extensive list is presented in Appendix D (Table 42). Despite variation, a majority of the species germinated from the same layers regardless of site location or date of sampling, an indication that viable seeds of those species did tend to accumulate at certain soil depths more so than in others.

Table 16. Species germination from different soil depths.^a

Species	Soil Layer		
	Litter	0-5 cm	5-10 cm
A. Spring samples.			
1. Species germinating in greatest numbers from the litter layer.			
<i>Acer rubrum</i>	80	15	5
<i>Fragaria</i> spp.	100	0	0
<i>Fraxinus americana</i>	100	0	0
<i>Ranunculus carolinianus</i>	67	0	33
<i>Sedum ternatum</i>	85	15	2
<i>Ulmus americana</i>	64	37	0
2. Species germinating in greatest numbers from the 0-5 cm layer.			
<i>Agrostis perennans</i>	0	100	0
<i>Amphicarpa bracteata</i>	0	100	0
<i>Betula lutea</i>	13	70	17
<i>Cercis canadensis</i>	2	62	36
<i>Danthonia spicata</i>	9	61	30
<i>Gnaphalium obtusifolium</i>	6	59	35
<i>Hieracium paniculatum</i>	4	77	19
<i>Lysimachia ciliata</i>	8	75	17
<i>Potentilla simplex</i>	33	77	0
3. Species germinating in greatest numbers from the 5-10 cm layer.			
<i>Acalypha rhomboidea</i>	0	9	91
<i>A. virginica</i>	0	24	76
<i>Ambrosia artemisiifolia</i>	0	23	77
<i>Cyperus pseudovegetus</i>	0	0	100
<i>Eupatorium sessifolium</i>	1	29	70
<i>Fragaria virginiana</i>	0	0	100
B. Summer samples.			
1. Species germinating in greatest numbers from the 0-5 cm layers.			
<i>Paulownia tomentosa</i>	18	53	29
<i>Vitis vulpina</i>	3	75	22
2. Species germinating in greatest numbers from the 5-10 cm layer.			
<i>Acalypha virginica</i>	6	13	81
<i>Aster divaricatus</i>	14	25	61
<i>Galium triflorum</i>	0	31	69
<i>Lobelia inflata</i>	0	25	75

Table 16 (Continued)

Species	Soil Layer		
	Litter	0-5 cm	5-10 cm
(2. Species germinating in greatest numbers from the 5-10 cm layer.)			
<i>Panicum commutatum</i>	2	38	60
<i>Rubus allegheniensis</i>	3	37	60
<i>Solanum carolinense</i>	0	0	100
<i>Verbena urticifolia</i>	0	0	100
<i>Vitis aestivalis</i>	0	0	100

^aThe numbers in the columns refer to the percentage of total germination originating from each depth over all eight sites.

CHAPTER X

COMPARISONS OF SITE VEGETATION WITH BURIED SEED BANKS

General Comparisons and Similarity Indices

At all eight sites, the species composition and numbers of the plants which germinated from the buried seed population were different from the composition of the standing vegetation. T-tests were used to compare the densities of plants in the vegetation (mean number of plants/m²) with the densities of the seed populations (mean number of plants/m² to a depth of 10 cm) at each site and at each elevation. In all cases, the results were significant ($P = 0.01$). The densities of the buried seed populations from both the spring and summer collections were always many times greater than the densities of the groundcover vegetation.

Spearman's Rank Correlation Coefficient was used to test for significant association between the average density of plants in the groundcover layer of the vegetation and the average density of germinants at a given site. The results were significant when the vegetation was compared with the spring germinants ($r_s = 0.691$; $P = 0.05$) but were not significant when the vegetation was compared with the summer sample ($r_s = 0.31$; $P = 0.05$). However, when the densities for the spring and summer samples were averaged for each site, the correlation with the vegetation was significant ($r_s = 0.762$; $P = 0.05$). These results suggest that there was some degree of positive association between the densities of the seed populations and the densities of the groundcover plants in the vegetation. In other words, there was a

tendency for higher densities of buried viable propagules to be associated with higher densities of groundcover species.

The species composition of the vegetation was compared with that of the buried seed population using Jaccard's Index of Similarity (IS_J) (Mueller-Dombois and Ellenberg 1974). (Refer to Table 11, page 86, for a discussion of the Index.)

Presented in Table 17 are the calculated IS_J values for comparisons between the standing and the seed populations from each of the spring and summer samples and from the spring and summer samples combined. In all cases, the composition of the standing vegetation included species from all three layers sampled, i.e., the herbaceous understory, the woody understory, and the canopy.

Table 17. Species similarity between the standing vegetation and the viable seed bank.^a

Site	Index of Similarity (%) ^b		
	Spring Collection	Summer Collection	Spring/Summer
1	10.2	11.1	14.1
2	5.9	6.6	6.3
3	11.9	7.0	10.4
4	10.1	11.3	8.7
5	14.3	4.5	12.4
6	21.1	19.0	20.5
7	16.1	15.1	13.3
8	6.9	5.0	7.5

^aIncluded in the standing vegetation were the species from the herbaceous understory, the woody understory, and the canopy.

^bThe calculated values are the Jaccard Index of Similarity. (See Table 11, page 86, for the Index formula and explanation.)

IS_j values of 25% and above indicate similar species composition of two populations (Mueller-Dombois and Ellenberg 1974). Therefore, there were no buried seed populations which could be considered similar to the standing vegetation. When the results from the spring and summer soil collections were combined, the IS_j values ranged from a low of 6.3% at Site 2 to a high of 20.5% at Site 6. The separate values for the spring and summer collections were similar to the combined values.

However, the IS_j values provide only a limited description of the populations being compared. An examination of the actual species which were common to the buried seed populations and the standing vegetation is illuminating. Specifically, the populations may appear to be more similar when the densities of the common species are investigated. Thus, if the species which were common were also the most abundant and accounted for large percentages of the total populations, the similarity may actually have been considerably greater than was suggested by the IS_j value.

Comparisons Between the Buried Seed Populations and the Site Vegetation

General. In this section, the comparisons between the seed banks and the standing vegetation are summarized for the eight sites, and individual species characteristics are discussed.

Several conclusions were apparent from an examination of the patterns of germination from the soils from the different sites. In general, the abundant woody species in the vegetation, including the oaks, hickories, blackgum, beech, red and sugar maple, dogwood, and sassafras, were uncommon in, and frequently absent from, the seed bank.

On the other hand, woody species were often among the most numerous germinants, particularly from the low elevation soils. However, these species were usually absent from the vegetation or were recorded only infrequently. The abundant woody species which germinated included Hydrangea arborescens, Cercis canadensis, Morus rubra, Rhus copallina, R. glabra, Rubus spp., and Paulownia tomentosa. Liriodendron tulipifera and Oxydendrum arboreum were two tree species for which germination from the seed bank generally reflected presence in the vegetation canopy.

The dissimilarity in species composition between the vegetation and the seed banks exemplified by the woody plants was equally pronounced for the herbaceous species. Typical herbaceous species of the vegetation included Panicum boscii, Hexastylis virginica, Polystichum acrostichoides, Chimaphila maculata, Uvularia perfoliata, Parthenocissus quinquefolia, Euonymus spp., Rhus radicans, Smilax glauca, Aster divarivatus, and Eupatorium purpureum. Most of these species did not germinate from the soil samples.

Among the herbaceous species which generally germinated in abundance were Houstonia purpurea, Phytolacca americana, Eupatorium rugosum, E. serotinum, Lobelia inflata, Erechtites hieracifolia, Panicum spp., and Verbascum thapsus. These species were usually absent from the vegetation.

The dissimilarity between the buried seed flora and the vegetation suggests that seed of the predominant species in the vegetation was not accumulating in appreciable quantities in the soil. On the other hand, the species, for which seed was stored in the soil, were usually absent from the vegetation. However, these species might be expected to

appear should the canopy open up and early successional conditions prevail. Most of the herbaceous and woody species predominant in the seed populations were typical early successional invaders.

Individual species comparisons. The dominant canopy species at most of the sites were several species of oaks and hickories. Generally, few saplings and seedlings of these species were present in the forest stands. Germination of these oaks and hickories from the soil samples may not have occurred because the samples were collected in the spring, before the time the nuts fall. The nut crop from the previous season had probably been removed and stored in caches by rodents. Most of the remaining seeds, particularly the acorns, would have lost their viability (Olson 1974). One white oak seedling did emerge from the litter at Site 7. However, the oak and hickory species were essentially absent from the buried viable seed populations of the study area.

Beech, blackgum, and dogwood were three other species which were often abundant in the vegetation but never germinated from the soil samples. Natural germination of most dogwood seeds occurs in the first spring after dispersal. The few seeds which do not germinate then will do so the following spring if they are still viable (Brinkman 1974b). It is possible that the soil samples were collected after the normal germination period of dogwood and that remaining viable seed may have entered secondary dormancy. However, it seems likely that some of these seeds would germinate under greenhouse conditions. The absence of dogwood germinants may actually have been the result of inadequate sampling.

Beech was the dominant canopy species at Site 2 and was present as both saplings and seedlings there. However, no germinants of the species emerged from any of the soil samples. According to Marquis (1975), American beech seeds normally germinate the year after seed dispersal and do not remain viable in the forest soil.

Evidence of the possible reasons that no blackgum seedlings germinated was not found. Germination of the species in the forest stands had clearly occurred in the recent past since there were abundant seedlings at several sites. Perhaps the soil was collected too late in the season for germination to occur, although reports of germination characteristics of this species were not found in the literature. The greenhouse conditions may not have been appropriate for germination. On the other hand, the soil sampling scheme may have been inadequate.

Redbud germinated only from low elevation soils, mostly from Sites 1 and 2 and from the 0-5 cm layer of soil. It was recorded as seedlings in the vegetation of Sites 1, 2, and 8, at low densities in all cases. Since seed-producing plants were not recorded at any of the sites, it seems likely that there was a reservoir of viable seeds in the soil although the duration of viability is unknown. The seed is eaten by birds which may have transported the seeds to the site shortly before the collections. However, the fact that buried seeds take some time to become incorporated into the soil suggests that they had probably been there for longer than one year.

A few sassafras seedlings germinated from the soils from every site. There seemed to be no relationship between the density of

individuals in the canopy and the number of germinants. Seedlings emerged from both the 0-5 cm and 5-10 cm depths in comparable numbers. Dispersal of fruits is aided by birds in the autumn (Bonner and Maisenhelder 1974). The fact that a few seeds germinated from the lowest sampling depth suggests that there is some storage of viable propagules in the soil. However, Wendell (1972) reported that seed viability is limited to one winter, and Sander and Clark (1971) found that sassafras reproduction following logging operations was primarily from root sprouts.

Red maple was present in the vegetation at all locations except Site 5. It was usually more important in the understory and seedling layers than in the canopy. This indicates successful germination under shaded conditions. Nevertheless, seed storage apparently was low. Sites 3 and 4 in Anderson County had the highest numbers of germinants, with 8 plants/m² in both cases. All seedlings emerged from the spring collection--mostly from the litter layer. These results suggest that the germinants arose from seeds dispersed during the current spring. However, Hutnik and Yawney (1961) and Marquis (1975) found that red maple seed may remain viable in the soil for several years in Pennsylvania. Further studies need to be done to verify such storage in the study area.

Sugar maple was present in the vegetation at all locations except Site 8. It was especially numerous in the understories at Sites 2, 3, and 5. However, only 1 seedling/m² germinated from the litter layer at Site 7. These results agree with those of Marquis (1975) who concluded that sugar maple seeds germinate the year after

they are dispersed and do not remain viable in the forest floor.

There seemed to be some storage of viable seed of ash (Fraxinus americana and F. pennsylvanica) in the soil. However, the numbers of germinants were very low and most seedlings emerged from the litter layer.

Tulip poplar was present in the canopy at all eight sites. Its numbers in the sapling and seedling stages were generally proportionately lower, suggesting that conditions under the forest canopy were not optimal for seedling emergence. The species, however, was one of the most numerous germinants from the buried seed populations. More germinants emerged from the low elevation site collections than from those in the mountains. In addition, seedlings arose from the litter layer and the two soil depths in relatively equal numbers. This suggests that tulip poplar seeds remain viable in the soil for longer than one year. Clark and Boyce (1964) and Marquis (1975) found that storage in the forest floor for two to five years is common. In addition, the latter worker showed that the seedlings will not survive unless they have access to moist mineral soil.

Sourwood was present in the canopy at Sites 1, 3, and 6. However, only a few saplings and no seedlings were recorded at any site. This indicates that extant conditions in the forest were not conducive to the germination and establishment of sourwood seedlings. Germination from the soil samples occurred only at those sites where sourwood was present in the canopy. Seedlings emerged in comparable numbers from all three sampling depths, thus indicating some accumulation of viable seed populations.

Several tree species germinated frequently from soil samples even though they were present in very low numbers or entirely absent from the vegetation. Such species included sweet birch (Betula lenta), red mulberry (Morus rubra), princess tree (Paulownia tomentosa), smooth sumac (Rhus glabra), and shining sumac (R. copallina).

Sweet birch germinated from soils collected from five sites, but most of the germinants came from the spring sample of Site 5. No individuals of the species were recorded in the canopy at that site, although seedlings emerged from all three sampling depths. The seeds, usually wind-dispersed, must have arrived from nearby sources. Frank and Safford (1970) and Marquis (1975) found that seeds of sweet birch may remain viable in the soil for two to five years. The large numbers emerging from Site 5 may represent several years' accumulation.

Red mulberry was not recorded in the vegetation at any site. However, it germinated in large numbers from soil from Sites 2 and 3. The seed probably arrived at the site transported by animals. The fact that the majority of the seeds emerged from the two lower sampling depths may indicate accumulation over several years.

The princess tree germinated in variable numbers from the soils from all eight sites but in greater quantities from the low elevations. The species were not recorded in the vegetation at any site and most of the germinants emerged from the lower soil depths. Site 5 was located near abandoned surface mine sites where the species was an invader. The tiny, winged seeds were probably well-dispersed into the surrounding areas.

Neither smooth nor shining sumac were recorded in the vegetation at any of the sites, but they were important germinants from the four low elevation locations. Most of the seedlings emerged from the 5-10 cm depth. Since seed of these species is dispersed almost entirely by birds or other animals (Brinkman 1974a), it is possible that some of the seed arrived in that way in the years preceding the sampling. However, the fact that most of it was stored at 5-10 cm may imply long-term storage since the last disturbance. The species are known to be colonizers of recently cleared sites.

Several other species of trees germinated in small numbers from the soil from various sites. Most of the seedlings emerged from the litter layer and often the species were not present in the site canopy. The implication is that the seeds were dispersed from nearby areas. The fact that most of them accumulated in the litter indicates low rates of dispersal and/or short-term viability. These species included tree-of-heaven (Ailanthus altissima), sycamore (Platanus occidentalis), black locust (Robinia pseudo-acacia), willow (Salix alba and S. nigra), winged elm (Ulmus alata), and American elm (U. americana).

The species which germinated in the greatest numbers from the soil samples were either absent from or poorly represented in the vegetation. For example, the shrub, Hydrangea arborescens, germinated in enormous numbers from the high elevation soils but was never recorded in the vegetation. Most of the germinants emerged from the two lower sampling depths, indicating that the seeds had been stored there for some time. Seed production of the species is prolific, with many seeds per capsule. The origin of the stored seed is unknown but several possibilities exist. Since all of the sites were located near

areas recently disturbed by surface mining and road-building, a variety of sources, including secondary forest expressions, abound. Perhaps incoming seed, over a period of years, had sifted down through the soil. However, the accumulated seed may have been the result of seed storage of material dispersed at a time when Hydrangea was abundant on-site. Unless dispersal into the site is monitored, conclusive interpretations cannot be made as to the origin and long-term viability of the seed.

Two other species which germinated in abundance were Rubus argutus and R. allegheniensis. Since these species generally were not found at the sites and most of the germinants emerged from the lower soil depths, it is likely that the seeds in the soil represent long-term accumulation. This suggestion is supported by the work of other researchers (Livingston and Allesio 1966; Olmsted and Curtis 1947) who found viable Rubus spp. seed buried at similar depths under mature forest stands and concluded that the seed had been stored there since the last disturbance. In the present study, although the seeds are dispersed by birds, it seems unlikely that such large accumulations would have developed from animal sources alone.

The most important herbaceous species which germinated were, at best, only an unimportant component of the vegetation. The majority of these species were composites or graminoid and included Erechtites hieracifolia, Eupatorium purpureum, E. rugosum, E. serotinum, Aster divaricatus, Panicum commutatum, P. dichotomum, Poa pratensis, and Andropogon virginicus. Other important germinants were Phytolacca americana, Juncus interior, Houstonia purpurea, and Lobelia inflata. The germination characteristics and patterns of these species are

discussed in another section. A general statement concerning these species is that they were not the typical woodland species present in the stands examined. The germinants were species usually found in disturbed sites where the canopy is open. Their presence as viable propagules at depths as great as 10 cm is a strong indication of long-term storage.

Summary

Similarity indices between the species composition of the standing vegetation and the buried seed populations computed for the eight study sites were generally low. A more detailed examination of the common species between the standing and buried populations, and of the most numerous species germinating from both the spring and summer samples at each of the eight sites allows a few conclusions to be drawn.

First, the most numerous germinants which were, by species, common to both buried and standing populations were usually trees or woody vines. This was particularly true at the low elevation sites, where Liriodendron tulipifera was a predominant species in the understory layer of the vegetation. At the high elevation sites there were greater numbers of herbaceous plants growing in the understory layer. Similarly, the tree species growing there generally did not germinate from the seed bank.

Second, the predominant and most numerous germinants at all sites were not, with the exception of Liriodendron, important or abundant members of the standing vegetation of any stratum. Perhaps the most important species in this regard was Hydrangea arborescens, which was the most numerous germinant from several of the sites and very abundant

at every other location except Sites 3 and 4. Other species which germinated in great numbers but were not prevalent in the standing vegetation at most of the sites included Houstonia purpurea, Rubus allegheniensis, R. argutus, Erechtites hieracifolia, Phytolacca americana, Eupatorium spp., Lobelia inflata, Juncus interior, Panicum spp., and other grasses.

Finally, the predominant species in the standing vegetation were generally not common germinants from the soil samples from the same sites. Most of the typical woodland herbaceous species were either absent from the buried seed populations or were unable to germinate under the greenhouse conditions provided. The latter explanation may apply to the various fern species which were important components of the vegetation at some sites but only germinated from samples stored in the more humid areas of the greenhouse.

CHAPTER XI

DISCUSSION

The Biology of Buried Seed Populations

There were large quantities of buried viable seeds and other plant propagules in these forest topsoils. The overall densities of emerging germinants from the different site soil collections ranged from 326 plants/m² to 2131 plants/m² from the spring samples and from 340 plants/m² to 1232 plants/m² from the summer samples. These quantities were generally of the same order of magnitude as were those reported in several other studies of deciduous forests of North America (Oosting and Humphreys 1940; Raynal and Bazzaz 1973).

There were distinct seasonal differences in the densities of germinable seeds in the soil from each location. On the average, over twice as many seedlings per square meter emerged from the spring collections as from the summer samples. It would be desirable to conduct seed germination studies with soils collected during the fall and winter seasons. Large quantities of viable seeds should be present in soils in the autumn, subsequent to late summer seed release.

Site location was an important variable determining the species composition and size of the seed bank. However, seed populations of sites from one elevation were most similar to those of other sites from the same elevation. The high elevation soils from the Cumberland Mountains produced significantly greater numbers of germinants than the low elevation soils from Norris.

The densities of germinants from several of the low elevation soils (Sites 1 and 3) were conspicuously low. In addition, the germinants from these soils included greater proportions of early successional tree species, such as tulip poplar, sourwood, smooth and shining sumacs, mulberry, and the princess tree.

The differences in seed populations may be partly accounted for by local variations in soil environments. For instance, the temperature regimes at the high elevation sites may be more conducive to long-term seed survival than the conditions which prevail at the low elevation locations. Ultimately, however, the composition of the buried seed populations and the vegetation is determined by the seed dispersal patterns in a given area. The results of this study indicate that dispersal patterns were very local in their effects. Since most seed is restricted to the vicinity of the parent plant, the accumulation of seed in the soil ought to reflect the clumped distribution patterns. Consequently, the populations do not readily lend themselves to analyses employing parametric statistics although the problem may be minimized if numerous soil samples are collected at each locale. The species--area curves indicated that the minimal area of floral homogeneity was not achieved. However, the major species and their relative proportions in the seed banks were probably well-represented.

At most of the sites, greater numbers of germinants emerged from the 5-10 cm soil depth than from the 0-5 cm depth. These results contrast those from several other studies (Kellman 1970; Strickler and Edgerton 1976; Moore and Wein 1977), where decreases in the numbers of seeds with increasing soil depth were reported. However, the first

two studies were concerned with conifer forests of western North America and therefore may not constitute valid comparisons. Moore and Wein sampled soil to greater depths (12-16 cm) than was done in the present study. It is possible that a decrease in seed numbers occurred below the 10 cm sampled.

However, there is evidence that seed longevity of some weed species increases with depth of storage. Seeds buried at shallow depths exist in a more variable environment, in terms of temperature, moisture levels, and light, conditions more conducive to germination (Chepil 1946a; Rampton and Ching 1966).

The rates of vertical movement of seeds through the soil are unknown. However, it is likely that the amount of movement necessary to bring large numbers of seeds to the depths found in the study would have occurred over many years.

Evidence in support of the idea of long-term storage of buried seeds may be found in the species patterns of emergence from the different depths. The species which germinated in abundance tended to be those which were not present in the vegetation of the site but rather were species typical of early successional environments. Most of these species germinated in the largest numbers from the lower soil depths. There is considerable evidence that seed of some of these species, including Poa pratensis, Phytolacca americana, Ambrosia artemisiifolia, Robinia pseudo-acacia, Rhus glabra, Solanum nigrum, and Verbascum thapsus, may remain viable in the soil for many years (Toole and Brown 1946).

Many of the species germinating in greatest numbers from the litter layer were trees, known for their short-term seed viability, or

shrubs and forbs present in the vegetation. The seeds of these species had probably been dispersed in the preceding seasons.

There may be several reasons for the apparent absence of the dominant vegetation species from the seed banks. First, many tree species do not produce seeds until they are twenty or more years of age. Since all of the stands examined in this study were secondary communities originating within the last 60 years, there may not have been a long enough time for sizeable seed crops to accumulate in the soil. Second, as the forest canopy closes, many of the herbaceous species surviving may be perennials capable of vegetative reproduction. Seed germination and seedling establishment of these plants may be less successful in a mature forest than in more open habitats. Herbaceous species adapted to such sites might be expected to rely mostly on other modes of reproduction. Finally, the most probable reason is that seeds of mature forest species simply may not remain viable for long periods of time, because of the lack of innate dormancy or high rates of predation, or they may germinate shortly after they are dispersed. If they do not germinate and establish seedlings by then, the embryo decays (Marquis 1975).

Each of the study sites was located close to roads or other disturbed areas, providing an outside source of seed. However, those species which were among the most abundant germinants from the site generally were not predominant in the nearby areas. For instance, Hydrangea arborescens was the most numerous germinant from the soil samples, but only a few individuals of the species were found growing along the forest edges or otherwise near these sites. Since the

capsules of Hydrangea produce many seeds, perhaps few plants are necessary to accumulate large quantities of seed in the soil. However, it seems probable that the enormous numbers of seeds obviously present in the soil could only have accumulated over many years. The same conclusion may be reached for many of the other important species of the seed banks.

Several areas for future studies are readily suggested. First, the individual species should be studied to determine rates of seed immigration, germination, in situ decay, and dispersal. The most evident candidate for such an analysis, among those species which germinated from the soils, is Hydrangea arborescens. A population study of this species may help elucidate any role it may have in community succession patterns, an area of interest given the capacity of Hydrangea to accumulate huge quantities of viable seed.

Second, other research should examine the seed population dynamics of the entire stands. The scope of the present study was limited in that it did not include the determination of rates of seed accumulation in the soil. Future work should include monitoring natural germination on permanent plots, in addition to quantifying buried seed populations, and determining rates of seed immigration into the stand using seed traps. Further investigations should compare the seed dynamics of the disturbed sites examined with those of more isolated forest stands, which are not as accessible to outside sources of seed.

Applications in Surface Mine Reclamation and Forest Regeneration

The rigorous microclimatic and edaphic conditions prevalent on surface mine spoil banks tend to restrict the kinds of plant species

likely to initiate revegetation. Stable plant communities of native species may develop only very slowly, particularly so on the steep slopes of abandoned mines and on many reclaimed sites in the region of the southern Appalachian Mountains. In the past, the emphasis in revegetation schemes has been on the use of introduced species noted for hardiness and ability to establish quick cover.

However, recent Federal legislation encourages the use of native plant species in revegetation and the storage of the topsoil originally removed from the site, with the requirement that it be replaced after mining operations cease. The present study represents an attempt to predict the potential of the topsoil as a source of revegetation material in terms of the quantities and species of propagules which might be obtained by spreading topsoil over surface mine spoil.

The results of the study show that there was an abundance of plant propagules in the litter layer and top 10 cm of soil in forests typical of those areas surface mined. The density of buried propagules was many times greater than that of the plants covering the forest floor, amounting to several millions of propagules/hectare.

However, it is likely that on-site storage of topsoil during mining activities would have a deleterious effect on the viability of some buried propagules. The microenvironment of stored topsoil is certain to be different from that prevailing under the original forest. There is evidence that soil structure may deteriorate under storage conditions (Hunter and Currie 1956). Research results reviewed by Tacey and Gossop (1980) show that the soil microbiota may change such

that conditions in the topsoil become anaerobic. Further studies need to be done to assess the effects of these and other microenvironmental changes on propagule viability.

The quality of the vegetation which would result from the germination of species present in the topsoil would be considerably different from the original stable composition of the forest stands. The majority of the apparently viable seeds present in the topsoil were of species typical of early successional environments. The composition of the vegetation resulting from germination in topsoil may be similar to that which develops on a forest site after logging activities.

The development of such early successional communities might be fortuitous, because it is unlikely that species of mature plant communities would germinate readily or survive well under the environmental conditions of spoil banks. In addition, the composition of the early successional communities likely to establish on topsoil would be affected by placement on spoil banks and certainly differ somewhat from the species obtained with the greenhouse germination studies.

The rate of in situ germination of seeds increases with rising soil temperatures and moisture levels (Schafer and Chilcote 1970). The seed-soil water relationship appears to be most crucial to viable seed quantities. Fully imbibed seeds retain the greatest germination capacity. However, when moisture levels become too high, the resulting anaerobic conditions cause embryo death. In general, the responses of seeds to soil-moisture gradients are considerably more narrow than those of adult plants (Pickett and Bazzaz 1978; Raynal and Bazzaz 1973; Villiers 1975).

Conditions on surface mine spoils tend to be characterized by extremes of moisture and temperature levels. In addition, such sites offer little protection to germinating seedlings from the wind, rain, high solar insolation, and animal predation. Toxic residues in the spoil material below the topsoil may have a detrimental effect on seedling survival.

Therefore, it must be concluded that, although the topsoil has great potential as a revegetation medium for native species, the spreading of this material on mine spoil will probably have pronounced effects on the species which are able to survive and grow. This indicates the need for further studies in which topsoil is placed on spoil material in both laboratory and field experiments in order that the revegetation potential may be assessed under more realistic conditions.

The presence of buried plant propagules in forest soil will influence the patterns and rapidity of revegetation following logging activities. If viable seed is stored in large quantities in the soil, forest managers would not necessarily need to time logging operations to take advantage of current seed crops. However, the composition of the revegetating seedlings would vary with the seed viabilities of the different species. In addition, different logging techniques would alter the environment in different ways.

For example, after clear-cutting operations, it would be expected that there would be much germination and sprouting of early successional species adapted to the high-intensity light conditions and temperature extremes prevailing at a site. Many of the original forest species require the shaded conditions and more moderate

temperature fluctuations found under a closed canopy. Clear-cuts represent drastic modifications of the landscape, sometimes on a large scale. The relative isolation of large tracts from undisturbed forests may have serious implications for succession patterns. The return to mature forest may be significantly delayed if dispersed propagules from forest species are unavailable. On the other hand, the species then most likely to persist at the revegetating site would originate from buried, viable propagules or well-dispersed seed. Such species would tend to be of the early successional type.

The process of revegetation and succession may be hastened somewhat by the employment of more restricted logging techniques such as patch-cutting or single species removal. In the case of the former, logging is done in localized areas and undisturbed forest stands are left surrounding any individual cut. Revegetation in patch-cut areas would begin with the early successional species buried as dormant propagules. However, the accessibility of the sites to seed sources would allow for the invasion of more typical forest species.

With single species removal, the revegetation process should be most rapid, depending upon the degree of disturbance created by such operations. If destruction is slight, single species removal may result in the release of suppressed sapling and seedlings and rapid woody growth in the open areas. The early successional species stored in the seed bank may have little opportunity to become established under the fairly shaded conditions of such sites.

Considerations such as the above emphasize the importance of viewing the role of the seed bank as a significant part of ecologically-integrated logging operations. If succession to original forest species

is to be encouraged, then reliance on the seed bank for revegetation may hamper the return to mature forest stands. This is particularly important in the case of large tracts of clear-cut areas where isolation from suitable seed sources may prolong early successional stages. Artificial seeding may be a necessity in such situations. However, where logging is restricted to small areas in close proximity to forest seed sources, revegetation and the return to closed forest may proceed at a rapid pace.

CHAPTER XII

SUMMARY AND CONCLUSIONS

The densities and species composition of buried viable propagules (seed banks) of forest soils in East Tennessee were assessed. The purpose of the research was to estimate the potential of forest topsoil as a source of viable propagules for use in surface mine revegetation. In addition, the species composition of the seed bank was compared to that of the standing vegetation of the original forest.

Eight study sites were located, four of them at high elevations (800-1000 m) in the Cumberland Mountains and four at low elevations (300-400 m) in the Great Valley of Tennessee. The standing vegetation at each site was sampled using nested quadrats. The canopy and understory data were summarized by calculating absolute and relative densities, basal areas, and importance values of each species.

In order to determine buried propagule populations, soil samples, including the litter layer, were collected at each site. The samples were incubated in flats in greenhouses and viable propagules present in the soil were allowed to germinate. Emergent seedlings grew until they could be identified and then were removed from the flats.

The densities and species composition of the buried propagules in the soil from the different sites were determined. The analysis of variance was performed for the numbers of germinants, testing for the following effects: elevation, site, soil depth, and interactions among the above. Patterns of germination of the most abundant species

were noted. The composition of the vegetation at each site was compared with that of the buried seed population using simple descriptive statistics.

The results of the study are summarized in the following statements:

1. There were large numbers of buried viable seeds in the soils, with germinants ranging from 300 to over 2,000 seedlings/m² of litter and topsoil from the spring collection. The comparable range from the summer collection was 300 to over 1200 seedlings/m².

2. The densities of germinants from the seed populations varied with the seasons. On the average, over twice as many seedlings/m² emerged from the spring collection as from the summer samples.

3. The buried seed populations varied greatly depending upon site location. The high elevation soils from the Cumberland Mountains produced significantly greater numbers of germinants than the low elevation sites at Norris with the spring collection. The same pattern was repeated with the summer collections, although the results were not significant.

4. The buried seed populations from all of the locations were characterized by a great deal of spatial heterogeneity on the forest floor.

5. Significantly lower numbers of germinants emerged from the litter than from the 0-5 cm and 5-10 cm depths. At most of the sites, there was an increase in the number of germinants with soil depth to 10 cm.

6. A grand total of 199 species germinated from all soil collections, including 170 species from the spring samples and 113 species

from the summer samples. The numbers of germinating species varied with the site, ranging from 54 to 95 species in the spring sample and from 36 to 73 species in the summer sample. A total of 129 genera and 53 families were represented. The breakdown of types was: trees - 24; shrubs - 9; woody vines - 7; perennial herbs - 112; annuals - 37; and biennials - 2. These numbers included 41 species of monocots.

7. Sites differed greatly from one another in terms of the species composition of the germinants. However, the low elevation sites tended to be more similar to one another than to the high elevation sites, and vice versa.

8. The similarity of species composition between the spring and summer samples from a particular site tended to be no greater than the similarities between different sites.

9. When all eight sites were considered together, the species germinating in greatest abundance included Hydrangea arborescens, Houstonia purpurea, Rubus allegheniensis, R. argutus, Eupatorium rugosum, E. serotinum, Liriodendron tulipifera, Erechtites hieracifolia, Phytolacca americana, Lobelia inflata, and species of grasses.

10. The greatest numbers of germinants emerged during the second and third weeks after placement of the soils in the greenhouse. However, each species exhibited its own characteristic pattern of germination.

11. Germination of the most abundant species, which included those generally typical of early successional environments, was primarily from the 5-10 cm layer. On the other hand, seedlings of trees and other species typical of forest communities, tended to

emerge in greatest numbers from the litter and 0-5 cm layer.

12. The species compositions of the buried seed populations were generally very different from those of the site vegetation. The dissimilarity is strong evidence that seeds of some species are stored in the soil for long periods of time in dormant states. They germinate when a disturbance causes their environment to change.

13. The implications of the buried seed populations in terms of surface mine revegetation were discussed. Although there is great potential within the topsoil for initiation of revegetation, the environmental conditions generally found on spoil banks will differentially and perhaps detrimentally affect the germination ability of the seed populations. At any rate, the composition of a flora derived from the seed bank would be substantially different from that of the original plant community. There is a need for further laboratory and field studies on this subject.

LITERATURE CITED

LITERATURE CITED

- Angevine, M. W. and B. F. Chabot. 1979. Seed germination syndromes in higher plants. In: O. T. Solbrig, S. Jain, G. B. Johnson, and P. H. Raven (Eds.), pp. 188-206. Topics in plant population biology. Columbia Univ. Press, New York. 589 pp.
- Barnhisel, R. I. and H. F. Massey. 1969. Chemical, mineralogical, and physical properties of eastern Kentucky acid-forming coal spoil materials. Soil Sci. 108:367-372.
- Barr, A. J., J. H. Goodnight, J. S. Sall, and J. T. Helwig. 1979. A user's guide to SAS 79. SAS Institute, Inc., Raleigh, N.C. 494 pp.
- Barton, L. V. 1962. The germination of weed seeds. Weeds 10:174-182.
- Baskin, J. M. and C. C. Baskin. 1971. Germination ecology and adaptation to habitat in Leavenworthia spp. (Cruciferae). Amer. Midland Nat. 85:22-35.
- Baskin, J. M. and C. C. Baskin. 1972. A contribution to the ecological life cycle of Leavenworthia stylosa. J. Tenn. Acad. Sci. 47: 91-93.
- Baskin, J. M. and C. C. Baskin. 1978. The seed bank in a population of an endemic plant species and its ecological significance. Biol. Conserv. 14:125-130.
- Bazzaz, T. A. 1979. The physiological ecology of plant succession. Ann. Rev. Ecol. Syst. 10:351-371.
- Beal, W. J. 1884. The vitality of seeds. Proc. Soc. Promot. Agr. Sci. 5:44-46.
- Beal, W. J. 1904. Vitality of seeds. Bot. Gaz. 37:222.
- Beal, W. J. 1905. The vitality of seeds. Bot. Gaz. 40:140-143.
- Beal, W. J. 1911. The vitality of seeds buried in the soil. Proc. Soc. Promot. Agr. Sci. 31:21-23.
- Beauchamp, H., R. Lang, and M. May. 1975. Topsoil as a seed source for reseeding strip mine spoils. Univ. Wyoming Agr. Exp. Stat. Res. 90:1-8.
- Billings, W. D. 1938. The structure and development of old field short-leaf pine stands and certain associated physical properties of the soil. Ecol. Mongr. 8:437-499.

- Blake, A. K. 1935. Viability and germination of seeds and early life history of prairie plants. *Ecol. Mongr.* 4:405-460.
- Bonner, T. T. and L. C. Maisenhelder. 1974. Sassafras albidum L. (Sassafras). In: H. A. Fowells (Ed.), pp. 761-762. Seeds of woody plants in the United States. Agriculture Handbook No. 450. U.S. Government Printing Office, Washington, D. C. 883 pp.
- Braun, E. L. 1942. Forests of the Cumberland Mountains. *Ecol. Mongr.* 12:414-447.
- Braun, E. L. 1950. Deciduous forests of eastern North America. Hafner Publishing Co., New York. 596 pp.
- Brenchley, W. E. 1918. Buried weed seeds. *J. Agr. Sci.* 9:1-31.
- Brenchley, W. E. and K. Warington. 1930. The weed seed population of arable soil. I. Numerical estimate of viable seeds and observations on natural dormancy. *J. Ecol.* 18:235-272.
- Brenchley, W. E. and K. Warington. 1933. The weed population of arable soil. II. The influence of crop, soil, and methods of cultivation upon the relative abundance of viable seeds. *J. Ecol.* 21:103-127.
- Brenchley, W. E. and K. Warington. 1936. The weed seed population of arable soil. III. The re-establishment of weed species after reduction by fallowing. *J. Ecol.* 24:479-501.
- Brenchley, W. E. and K. Warington. 1945. The influence of periodic fallowing on the prevalence of viable weed seeds on arable soil. *Ann. Appl. Biol.* 32:285-296.
- Brinkman, K. A. 1974a. Rhus L. (Sumac). In: H. A. Fowells (Ed.), Seeds of woody plants in the United States, pp. 715-719. Agriculture Handbook No. 450. U.S. Government Printing Office, Washington, D. C. 883 pp.
- Brinkman, K. A. 1974b. Cornus L. (Dogwood). In: H. A. Fowells (Ed.), Seeds of woody plants in the United States, pp. 336-342. Agriculture Handbook No. 450. U.S. Government Printing Office, Washington, D. C. 883 pp.
- Champness, S. S. 1949. Notes on the technique of sampling soil to determine the content of viable seeds. *J. Brit. Grassl. Soc.* 4:115-118.
- Champness, S. S. and K. Morris. 1948. The population of buried viable seeds in relation to contrasting pasture and soil types. *J. Ecol.* 36:149-173.

- Chepil, W. S. 1946a. Germination of weed seeds. I. Longevity, periodicity of germination, and vitality of seeds in cultivated soil. *Sci. Agr.* 26:307-346.
- Chepil, W. S. 1946b. Germination of weed seeds. II. The influence of tillage treatments on germination. *Sci. Agr.* 26:347-357.
- Chippendale, H. G. and W.E.J. Milton. 1934. On the viable seeds present in the soil beneath pastures. *J. Ecol.* 22:508-531.
- Clark, T. B. and S. G. Boyce. 1964. Yellow-poplar seed remains viable in forest litter. *J. Forestry* 62:564-567.
- Cohen, D. 1966. Optimizing reproduction in a randomly varying environment. *J. Theoret. Biol.* 12:119-129.
- Crocker, W. 1938. Life-span of seeds. *Bot. Rev.* 4:235-275.
- Crum, H. A., W. C. Steere, and L. E. Anderson. 1973. A new list of mosses of North America north of Mexico. *The Bryologist* 76: 85-130.
- Darlington, H. T. 1922. Dr. W. J. Beal's seed-viability experiment. *Am. J. Bot.* 9:266-269.
- Darlington, H. T. 1931. The 50-year period for Dr. Beal's seed viability experiment. *Amer. J. Bot.* 18:262-265.
- Darlington, H. T. 1941. The 60-year period of Dr. Beal's seed viability experiment. *Amer. J. Bot.* 28:271-273.
- Darlington, H. T. 1951. The seventy-year period for Dr. Beal's seed viability experiment. *Amer. J. Bot.* 38:379-381.
- Darlington, H. T. and G. P. Steinbauer. 1961. The eighty-year period of Dr. Beal's seed viability experiment. *Amer. J. Bot.* 48: 321-325.
- Day, P. R. 1956. Report of the committee on physical analysis, 1954-1955, *Soil Sci. Soc. Amer. Proc.* 20:167-169.
- Dickson, R. R. 1960. *Climates of the states: Tennessee.* U.S. Department of Commerce, Weather Bureau. U.S. Government Printing Office, Washington, D. C. 16 pp.
- Dore, W. E. and L. C. Raymond. 1942. Pasture studies. XXIV. Viable seeds in pasture soil and manure. *Sci. Agr.* 23:69-79.
- Duvel, J.W.T. 1902. Seeds buried in soil. *Science* 17:872-873.
- Epling, C., H. Lewis, and F. M. Ball. 1960. The breeding group and seed storage: A study in population dynamics. *Evolution* 14: 238-255.

- Ewart, A. J. 1908. On the longevity of seeds. *Proc. Royal Soc. Victoria* 21:181-211.
- Exell, A. W. 1931. The longevity of seeds. *Gard. Chron.* p. 283.
- Fenneman, N. M. 1938. *Physiography of the eastern United States*. McGraw-Hill Publishing Co., New York. 714 pp.
- Foth, H. D., L. V. Withee, H. S. Jacobs, and S. J. Thien. 1976. *Laboratory manual for introductory soil science*. W.M.C. Brown Co., Dubuque, Iowa. 115 pp.
- Frank, R. M. and L. O. Safford. 1970. Lack of viable seeds in the forest floor after clear-cutting. *J. Forestry* 68:716-778.
- Fribourg, H. A., R. H. Strand, J. V. Vaiksnoras, and J. M. Safley, Jr. 1974. Precipitation probabilities for East Tennessee. *Univ. Tenn. Agr. Exp. Stat. Bull. No.* 512.
- Gleason, H. A. 1952. *The new Britton and Brown illustrated flora of the northeastern United States and adjacent Canada*. Lancaster Press, Inc., Pennsylvania. 589 pp.
- Goss, W. L. 1924. The vitality of buried seeds. *J. Agr. Res.* 29: 349-362.
- Haig, I. T. 1932. Premature germination of forest tree seed during natural storage in duff. *Ecology* 13:311-312.
- Hamrick, J. L. 1979. Genetic variation and longevity. In: O. T. Solbrig, S. Jain, G. B. Johnson, and R. H. Raven (Eds.), pp. 84-113. *Topics in plant population biology*. Columbia Univ. Press, New York. 589 pp.
- Harper, J. L. 1977. *Population biology of plants*. Academic Press, London. 892 pp.
- Harper, J. L., P. H. Lovell, and K. G. Moore. 1970. The shapes and sizes of seeds. *Ann. Rev. Ecol. Syst.* 1:327-356.
- Harper, J. L. and J. White. 1971. The dynamics of plant populations. *Proc. Adv. Study Inst. Dynamics Numbers Popul.* (Oosterbeek, 1970), pp. 41-63.
- Horng, L. C. and L. S. Leu. 1978. The effects of depth and duration of burial on the germination of ten annual weed seeds. *Weed Sci.* 26:4-10.
- Howard, G. S. and M. J. Samuel. 1979. The value of fresh-stripped topsoil as a source of useful plants for surface mine revegetation. *J. Range Manag.* 32:76-77.

- Hunter, F. and J. A. Currie. 1956. Structural changes during bulk soil storage. *J. Soil Sci.* 7:75-80.
- Hutnik, R. J. and H. W. Yawney. 1961. Silvical characteristics of red maple. U.S. Forest Service, N.E. Forest Exp. Stat., Upper Darby, Pa. pap. 142, 18 pp.
- Johnson, E. A. 1975. Buried seed populations in subarctic forest east of Great Slave Lake, Northwest Territories. *Can. J. Bot.* 53:2933-2941.
- Keeley, J. E. 1977. Seed production, seed populations in soil, and seedling production after fire for two congeneric pairs of sprouting and nonsprouting chaparral shrubs. *Ecology* 58: 820-829.
- Kellman, M. C. 1970. The viable seed content of some forest soil in coastal British Columbia. *Can. J. Bot.* 48:1383-1385.
- Kellman, M. C. 1974a. Preliminary seed budgets for two plant communities in coastal British Columbia. *J. Biogeogr.* 1:123-133.
- Kellman, M. C. 1974b. The viable weed seed content of some tropical agricultural soils. *J. Appl. Ecol.* 11:669-677.
- Kellman, M. C. 1978. Microdistribution of viable weed seed in two tropical soils. *J. Biogeogr.* 5:291-300.
- Kivilaan, A. and R. S. Bandurski. 1973. The ninety-year period for Dr. Beal's seed viability experiment. *Amer. J. Bot.* 60:140-145.
- Knight, W. R. 1979. Relationship of soils and vegetation to topography and elevation in the Cumberland Mountains of Campbell County, Tennessee. M.S. Thesis. The University of Tennessee, Knoxville.
- Knipe, O. D. and H. W. Springfield. 1972. Germinable alkali sacaton seed content of soils in the Rio Puerco Basin, West Central New Mexico. *Ecology* 53:965-968.
- Kropáč, Z. 1966. Estimation of weed seeds in arable soil. *Pedobiologia* 6:105-128.
- Leck, M. A. and K. J. Graveline. 1979. The seed bank of a freshwater tidal marsh. *Amer. J. Bot.* 66:1006-1015.
- Lippert, R. D. and H. H. Hopkins. 1950. Study of viable seeds in various habitats in mixed prairie. *Trans. Kansas Acad. Sci.* 53:355-364.
- Livingston, R. B. and M. L. Allesio. 1968. Buried viable seed in successional field and forest stands, Harvard Forest, Massachusetts. *Bull. Torrey Bot. Club* 95:58-69.

- Luther, E. T. 1967. Geological map and mineral resources summary of the Block quadrangle, Tennessee. GM. 128-SE, MRS. 128-SE. Tennessee Division of Geology. U.S. Government Printing Office, Washington, D.C.
- Major, J. and W. T. Pyott. 1966. Buried, viable seeds in two California bunchgrass sites and their bearing on the definition of flora. *Vegetatio Acta Geobotanica* 13:253-282.
- Malone, C. R. 1967. A rapid method for enumeration of viable seeds in soil. *Weeds* 15:381-382.
- Marks, P. L. and F. H. Bormann. 1972. Re-vegetation following forest cutting: Mechanisms for return to steady state nutrient cycling. *Science* 176:914-915.
- Marquis, D. A. 1975. Seed storage and germination under northern hardwood forests. *J. Forest Res.* 5:478-484.
- Meyer, F. H. 1973. Distribution of ectomycorrhizae in native and man-made forests. In: G. C. Marks and T. T. Kozlowski (Eds.), pp. 79-105. *Ectomycorrhizae: Their ecology and physiology*. Academic Press, New York. 444 pp.
- Milton, W.E.J. 1939. The occurrence of buried viable seeds in soils at different elevations and on a salt marsh. *J. Ecol.* 27: 147-159.
- Moore, J. M. and R. W. Wein. 1977. Viable seed populations by soil depth and potential site recolonization after disturbance. *Can. J. Bot.* 55:2408-2412.
- Mueller-Dombois, D. and H. Ellenberg. 1974. *Aims and methods of vegetation ecology*. John Wiley, New York. 547 pp.
- Naylor, R.E.L. 1972. Aspects of the population dynamics of the weed *Alopecurus myosuroides* Huds. in winter cereal crops. *J. Appl. Ecol.* 9:127-139.
- Nelson, J. F. and R. M. Chew. 1977. Factors affecting seed reserves in the soil of a Mojave desert ecosystem, Rode Valley, Nye County, Nevada. *Amer. Midland Nat.* 97:300-320.
- Numata, M., I. Hayashi, T. Komura, and K. Oki. 1964. Ecological studies on the buried seed population in the soil as related to plant succession. *Jap. J. Ecol.* 14:207-215.
- Odum, E. P. 1971. *Fundamentals of ecology*. W. B. Saunders Co., Philadelphia, Pennsylvania. 574 pp.
- Olmsted, N. W. and J. D. Curtis. 1947. Seeds of the forest floor. *Ecology* 28:49-52.

- Olson, D. F. 1974. *Quercus* L. (Oak). In: H. A. Fowells (Ed.), *Seeds of woody plants in the United States*, pp. 692-703. Agriculture Handbook No. 450. U.S. Government Printing Office, Washington, D. C. 883 pp.
- Olson, E. 1979. Personal communication during interview. Norris, Tennessee.
- Oosting, H. J. and M. E. Humphreys. 1940. Buried viable seeds in a successional series of old field and forest soils. *Bull. Torrey Bot. Club* 67:253-273.
- Peter, A. 1894. Culturversuche mit "Ruhenden" Samen. II. Mittheilung. *Nachr. K. Gesell. Wiss. Gottingen*. 1893:673-691.
- Pickett, S.T.A. and F. A. Bazzaz. 1978. Germination of co-occurring annual species on a soil moisture gradient. *Bull. Torrey Bot. Club* 105:312-316.
- Pielou, E. C. 1975. *Ecological diversity*. John Wiley and Sons, New York. 165 pp.
- Quick, C. R. 1956. Viable seeds from the duff and soil of sugar pine forests. *Forest Sci.* 2:36-42.
- Rabotnov, T. A. 1969. On coenopopulations of perennial herbaceous plants in natural coenoses. *Vegetatio* 19:87-95.
- Radford, A. E., H. E. Ahles, and C. R. Bell. 1976. *Manual of the vascular flora of the Carolinas*. Univ. of North Carolina Press, Chapel Hill. 1183 pp.
- Rampton, H. H. and T. M. Ching. 1966. Longevity and dormancy in seeds of several cool-season grasses and legumes buried in soil. *Agron. J.* 58:220-221.
- Rampton, H. H. and T. M. Ching. 1970. Persistence of crop seeds in soil. *Agron. J.* 62:272-277.
- Raynal, D. J. and F. A. Bazzaz. 1973. Establishment of early successional plant populations on forest and prairie soil. *Ecology* 54:1335-1341.
- Roberts, H. A. 1968. The changing population of viable weed seeds in an arable soil. *Weed Research* 8:253-256.
- Roberts, H. A. and P. M. Feast. 1972. Fate of seeds of some annual weeds in different depths of cultivated and undisturbed soil. *Weed Research* 12:316-324.
- Roberts, H. A. and M. E. Ricketts. 1979. Quantitative relationships between the weed flora after cultivation and the seed population in the soil. *Weed Research* 19:269-275.

- Roberts, H. A. and F. G. Stokes. 1965. Studies on the weeds of vegetable crops. V. Final observations on an experiment with different primary cultivations. *J. Appl. Ecol.* 2:307-315.
- Robinson, E. C. and L. A. Kust. 1962. Distribution of witchweed seeds in the soil. *Weeds* 10:335.
- Safley, J. M. and W. L. Parks. 1974. Agricultural drought probabilities in Tennessee. *Univ. of Tenn. Agr. Exp. Stat. Bull.* No. 533.
- Sander, I. L. and F. B. Clark. 1971. Reproduction of upland hardwood forests in the central states. U.S. Department of Agriculture Handbook 405, U.S. Government Printing Office, 22 pp.
- Schafer, D. E. and D. O. Chilcote. 1969. Factors influencing persistence and depletion in buried seed populations. I. A model for analysis of parameters of buried seed persistence and depletion. *Crop Sci.* 9:417-419.
- Schafer, D. E. and D. O. Chilcote. 1970. Factors influencing persistence and depletion in buried seed populations. II. The effects of soil temperature and moisture. *Crop Sci.* 10:342-345.
- Snedecor, G. W. and W. G. Cochran. 1978. *Statistical methods.* Iowa State Univ. Press, Ames. 593 pp.
- Soil Survey Staff. 1953. Soil Survey: Norris area, Tennessee. Series 1939. No. 19. U.S. Department of Agriculture Soil Conservation Service, in cooperation with the Tenn. Agr. Stat. and the Tenn. Valley Authority. U.S. Government Printing Office, Washington, D.C.
- Solbrig, O. T. 1979. A cost-benefit analysis of recombination in plants. In: O. T. Solbrig, S. Jain, G. B. Johnson, and P. H. Raven (Eds.), pp. 114-130. *Topics in plant population biology.* Columbia Univ. Press, New York. 589 pp.
- Stoller, E. W. and L. M. Wax. 1973. Periodicity of germination and emergence of some annual weeds. *Weed Science* 21:574-580.
- Stoller, E. W. and L. M. Wax. 1974. Dormancy changes and fate of some annual weed seed in the soil. *Weed Science* 22:151-155.
- Strickler, G. S. and P. J. Edgerton. 1976. Emergent seedlings from coniferous litter and soil in eastern Oregon. *Ecology* 57: 801-807.
- Tacey, W. H. and B. L. Glossop. 1980. Assessment of topsoil handling techniques for rehabilitation of sites mined for bauxite within the jarrah forest of western Australia. *J. Appl. Ecol.* 17: 195-201.

- Taylorson, R. B. 1970. Changes in dormancy and viability of weed seeds in soils. *Weed Science* 18:265-269.
- Templeton, A. R. and D. A. Levin. 1979. Evolutionary consequences of seed pools. *Amer. Naturalist* 114:232-249.
- Tennessee Valley Authority. 1964. Forest inventory statistics, Anderson-Knox-Union County unit. *Forestry Bull.* 117. Norris, Tennessee. 19 pp.
- Tennessee Valley Authority. 1976. Forest inventory statistics, Anderson-Knox-Union County unit. *Forestry Bull.* 175. Norris, Tennessee. 32 pp.
- Thompson, P. A. 1973. Seed germination in relation to ecological and geographical distribution. In: V. H. Heywood (Ed.), pp. 93-119. *Taxonomy and ecology. Systematics Assoc. Special vol. 5*, Academic Press, London. 370 pp.
- Thorntwaite, C. W. 1948. An approach toward a rational classification of climate. *Geogr. Rev.* 38:55-94.
- Tisdale, R. M. 1974. Field characteristics and recognition of upper delta plain sediments, Vowell Mountain and Cross Mountain Formations, Windrock quadrangle, Tennessee. Master's thesis. The University of Tennessee, Knoxville.
- Toole, E. H. and E. Brown. 1946. Final results of the Duvel buried seed experiment. *J. Agr. Res.* 72:201-210.
- U.S. Department of Commerce. 1969. Climatological Data - Tennessee Annual Summary. vol. 74, no. 13. U.S. Government Printing Office, Washington, D. C.
- U.S. Department of Commerce. Environmental Science Services Administration. 1966-1970. Climatological Data - Tennessee. Annual Summaries. vols. 71-75. U.S. Government Printing Office, Washington, D.C.
- U.S. Department of Commerce. National Oceanic and Atmospheric Administration. 1970-1978. Climatological Data - Tennessee. Annual Summaries. vols. 76-83. U.S. Government Printing Office, Washington, D.C.
- U.S. Department of Commerce. Weather Bureau. 1961-1965. Climatological Data - Tennessee. Annual Summaries. vols. 66-70. U.S. Government Printing Office, Washington, D.C.
- U.S. Department of Commerce. Weather Bureau. 1965. Climatic Summary of the United States. no. 86-35. U.S. Government Printing Office, Washington, D.C.

- USDA Weather Bureau. 1951-1960. Climatic Summary of the United States - Eastern Tennessee. U.S. Government Printing Office, Washington, D.C.
- Vaiksneras, J. V. and W. C. Palmer. 1973. Meteorological drought in Tennessee. J. Tenn. Acad. Sci. 48:23-30.
- van der Valk, A. G. and C. B. Davis. 1976. The seed banks of prairie glacial marshes. Can. J. Bot. 54:1832-1838.
- van der Valk, A. G. and C. B. Davis. 1978. The role of seed banks in the vegetation dynamics of prairie glacial marshes. Ecology 59:322-335.
- van der Valk, A. G. and C. B. Davis. 1979. A reconstruction of the recent vegetational history of a prairie marsh, Eagle Lake, Iowa, from its seed bank. Aquat. Bot. 6:29-52.
- Villiers, T. A. 1973. Ageing and the longevity of seeds in field conditions. In: W. Heydecker (Ed.), pp. 265-288. Seed ecology. Penn. State Press, University Park, Penn. 578 pp.
- Wagner, R. H. 1965. The annual seed rain of adventive herbs in a radiation damaged forest. Ecology 46:517-520.
- Wendell, G. W. 1972. Longevity of black cherry seed in the forest floor. USDA Forest Service Research Note NE-149, U.S. Government Printing Office, Washington, D.C.
- Werner, P. A. 1979. Competition and coexistence of similar species. In: O. T. Solbrig, S. Jain, G. B. Johnson, and P. H. Raven (Eds.), pp. 287-310. Topics in plant population biology. Columbia Univ. Press, New York. 589 pp.
- Wesson, G. and P. F. Wareing. 1967. Light requirements of buried seed. Nature 213:600-601.
- Whipple, S. A. 1978. The relationship of buried germinating seeds to vegetation in an old-growth Colorado sub-alpine forest. Can. J. Bot. 56:1509.
- Williams, E. D. 1978. Germination and longevity of seeds of Agropyron repens L. Beauv. and Agrostis gigantea Roth. in soil in relation to different cultivation regimes. Weed Research 18:129-138.
- Young, J. A. and R. A. Evans. 1975. Germination of seed reserves in a big sagebrush community. Weed Science 23:358-364.

APPENDICES

APPENDIX A

DESCRIPTION OF THE STUDY AREA

THE STUDY AREA

Location

The landforms of East Tennessee are included in several major physiographic regions. The Great Valley is included in the Ridge and Valley Physiographic Province and encompasses an area 216 km long and 72 km wide. Elevations range from 225 m to 420 m. The Great Valley is bordered on the east by the Blue Ridge Physiographic Province with an elevation range of 1200 to 1800 m and on the west by the Appalachian Plateau Physiographic Province where the elevation averages about 510 m (Fenneman 1938).

The Cumberland Plateau in Tennessee is part of the Appalachian Plateau Physiographic Province. It is an elevated tableland which extends across the entire width of the state in a northeast-southwest direction. It is separated from the Central Basin of Tennessee by the wide fringe of the Highland Rim on the west and is bordered by the Great Valley on the east (Fenneman 1938).

The Cumberland Mountains are located at the northern margin of the Plateau in Tennessee, extending into Kentucky and Virginia over an area about 270 km long and 45 km wide. Elevation is greater and the dissection more mature in the mountains than in the adjacent plateau region (Fenneman 1938).

In the present study, eight sites were located in two areas of East Tennessee. In the Great Valley, sites were located in Anderson County in an area between 36 07' 30" and 35 15' north latitude and between 84 00' and 84 07' 30" west longitude (Norris Quadrangle,

USGS). In the Cumberland Mountains, the study area was in Campbell County between 36 15' and 36 22' north latitude and between 84 15' and 84 22' 30" west longitude (Block Quadrangle).

Climate

The regional climate of East Tennessee is classified as humid and mesothermal with little or no water deficiency during any season (Thorntwaite 1948). Much of the weather which affects the region originates elsewhere and frontal systems move in an easterly direction across the state. The Gulf of Mexico is the source of most of the moisture reaching the area, such that a gradual decrease in moisture occurs from north to south across the state (Dickson 1960; Fribourg et al. 1974).

Moisture patterns are greatly influenced by the regional topography. Precipitation tends to be greater at high elevations, because ascending air cools and condenses to release part of its moisture. In both study areas, the maximum amount of precipitation falls during winter and early spring; a secondary peak occurs in mid-summer with July having the highest rainfall of any month (Dickson 1960; Vaiksnoras and Palmer 1978). At Norris, the 30-year precipitation average is 12.4 cm in January and 11.4 cm in July. The minimum and maximum amounts of precipitation during the same period are 4.3 and 29.6 cm in January and 3.2 cm and 35.6 cm in July. The weather station closest to the Campbell County sites, where 28 years of precipitation and temperature data have been collected, is located in Allardt, Tennessee, approximately 54 km to the northwest. At Allardt, the precipitation average is 12.2 cm in January and 12.9 cm in July.

The minimum and maximum amounts of precipitation during the same period are 3.8 cm and 34.4 cm in January and 3.9 cm and 32.5 cm in July.*

Temperatures are influenced locally by topographic variations. Generally, there is an average decrease of 16C for every 333 m increase in elevation (Dickson 1960). In Anderson County, the nearest station with temperature records is at Oak Ridge, where 30-year averages were available. The average temperatures in January and July are 3.4C and 25C, respectively. The normal daily minimum and maximum air temperatures in January are -1.6C and 8.4C, and the normal daily minimum and maximum air temperatures in July are 19.1C and 30.6C.* At Allardt, the average air temperatures are 3.8C in January and 23.1C in July. Daily minimum and maximum air temperatures are available for only 10 years. The normal daily minimum and maximum air temperatures in January are -2.6C and 8.5C, and the normal daily minimum and maximum air temperatures in July are 16.8C and 29.5C.* The mean length of the annual frost-free period, which varies depending upon local microtopography, is 150 days or less in the Cumberland Mountains and approximately 180 days in the Norris area (Safley and Parks 1974; Soil Survey Staff 1953).

Severe drought periods in the East Tennessee area are rare events and those which do occur tend to be brief. Precipitation is most reliable during July while September and October are usually the driest months (Vaiksnoras and Palmer 1973).

*USDA Weather Bureau 1951-1960; U.S. Department of Commerce 1969; U.S. Department of Commerce. Weather Bureau 1961-1965, 1965; U.S. Department of Commerce. Environmental Science Services Administration 1966-1970; U.S. Department of Commerce. National Oceanic and Atmospheric Administration 1970-1978.

Severe storms are uncommon, and tornadoes are rare events. Hail may occasionally fall with the localized thunderstorms common during the summer. In times of excessive rainfall, flooding may occur along streams or rivers (Dickson 1960).

Physiography and geology. The Great Valley of East Tennessee includes a complex system of parallel ridges trending in a northeast-southwest direction and separated by a series of wide to narrow valleys. Folding, faulting, and the differential erosion of the underlying sedimentary strata have resulted in the exposure of rocks of several geological ages. However, the dominant beds include Paleozoic rocks of Cambrian and Ordovician age, consisting primarily of limestone and shale beds that were less resistant than the rocks underlying the adjacent ridges. The smooth, sand-topped ridges tend to have dolomite or dolomitic limestone in their uppermost strata while the steep, narrow ridges are usually capped by sandstone and shale. The valleys are underlain by beds of limestone, interbedded limestone and shale (Soil Survey Staff 1953).

The rocks of the Cumberland Mountains are early Pennsylvanian in age and representative of the Pottsville series. They consist primarily of sandstone, conglomerate, siltstone, shale, coal, and ironstone. The lower beds are represented by massive sandstone conglomerates, and equal percentages of sandstone and shale. The upper sequence has thinner sandstones and a larger percentage of shale. Coal deposits occur in layers of varying thickness, primarily in the middle and lower beds (Luther 1967). [Refer to Tisdale (1974) for stratigraphic details of the geologic formations underlying the study site locations.]

Soils

A 1953 survey by the U.S. Department of Agriculture (USDA) Soil Conservation Service is available concerning the soils of the Norris area of Anderson County, including the study areas. Soil association maps have been completed recently but, as of this writing, are unpublished. According to these maps, the low elevation study areas are included in the following soil series: Fullerton, Bodine, Claiborne, and Collegedale (Anderson County Soil Survey Staff, personal communication).

Considerably less information is available concerning the soils of Campbell County and maps have not yet been published. At the time of this writing, the USDA Soil Conservation Service was conducting a soil survey of Campbell County as part of the National Cooperative Soil Survey (Clarence Conner, Campbell County Soil Conservation Service, personal communication).

Recently, Knight (1979) completed a study of the soils of the Cumberland Mountains, sampling at 141 sites along transects in Campbell, including several areas which were nearby the study locations. He found that the common soil series included Gilpin, Shelocta, Muskingum, Berks, and Petros.

Vegetation

Braun (1950) placed the Great Valley in the Oak-Chestnut Region of the Deciduous Forest. Chestnut-oak communities are believed to have been formerly dominant on mesic slopes of the rolling uplands of this area.

Recent TVA forest inventory statistics estimate that oak-hickory communities comprise 33% to 38% of the forested sites in the Great Valley. However, the importance of pine communities, particularly on ridge tops and southern slopes, is emphasized by the fact that they comprise 22% to 44% of the trees in the study area (Tennessee Valley Authority 1964, 1976).

The TVA Forest Inventory Statistics for Anderson County show that the predominant forest types are oak-hickory (56%), tulip poplar (8%), Virginia pine (Pinus virginiana) (7%), red oak-basswood-ash (7%), and others (22%). Oak-hickory forests and some short-leaf pine (Pinus echinata) were predominant on dry uplands. Moist uplands had a greater diversity of stands, including oak-hickory, Virginia pine, tulip poplar, and red oak-basswood-ash. On the bottomlands, predominant forest types included elm-ash-maple, tulip poplar, and hemlock (Tsuga canadensis)-hardwood stands (Tennessee Valley Authority 1976).

The Cumberland Mountains of Kentucky, Virginia, and Tennessee were considered by Braun (1942) to have the best representation of the mixed mesophytic forest association. The dominant forest type is mixed deciduous, and the most important canopy trees include sugar maple, basswood, red oak, tulip poplar, white ash, cucumber magnolia, blackgum, and beech.

Human History

The first white settlers came to the Norris area of Anderson County about 1796. Prior to their arrival, Cherokee Indians had used the area irregularly as hunting grounds, but there is no evidence that they lived in permanent villages there (Soil Survey Staff 1953; E. Olson, personal communication).

Much of the area was in farmland when the TVA acquired it in 1933. The timber of the remaining forests was used locally by farmers, or sometimes portable sawmill operators were active in the area (E. Olson, personal communication).

Farming was abandoned on the land which TVA acquired. Aerial photographs taken in 1935 show the early stages of secondary succession in the old fields. Nearly all of the forest remnants were located close to cleared areas at that time. The more extensive wooded areas typically were to be found on steep valley slopes or on river bluffs (E. Olson, personal communication).

The Campbell County area of the Cumberland Mountains was much less intensely farmed and settled, due to inaccessibility, steep slopes, and poor soils. However, the mountains are underlain by extensive coal seams, and mining operations which began in 1900 are active to the present time. With the coming of the railroads, several large-scale commercial logging operations were begun with such intensity that essentially all of the forests of the area have usually been cut more than once (Luther 1967).

APPENDIX B

COMPOSITION OF THE VEGETATION
AT THE STUDY SITES

Table 18. Composition of the canopy and understory at Site 1 (Clear Creek).

Species	Canopy ^a			Understory ^a
	RD	RBA	IV	RD
<i>Acer rubrum</i>	6.7	1.7	8.3	23.5
<i>A. saccharum</i>	13.3	3.3	16.7	9.2
<i>Aesculus octandra</i>				1.0
<i>Carya glabra</i>				3.1
<i>C. ovalis</i>				1.0
<i>C. tomentosa</i>	20.0	27.2	47.2	2.0
<i>Cornus florida</i>				22.4
<i>Fagus grandifolia</i>				2.0
<i>Fraxinus americana</i>				1.0
<i>F. tomentosa</i>				1.0
<i>Juniperus virginiana</i>				1.0
<i>Nyssa sylvatica</i>				10.2
<i>Oxydendrum arboreum</i>	13.3	3.3	16.7	11.2
<i>Parthenocissus quinquefolia</i>				9.2
<i>Pinus echinata</i>	6.7	4.6	11.3	
<i>Quercus alba</i>	33.3	50.8	84.1	
<i>Q. falcata</i>	6.7	9.1	15.7	1.0
<i>Q. rubra</i>				1.0
	<u>100.0</u>	<u>99.8</u>		<u>99.8</u>
Stems/ha. ₂	250.0			1633.3
BA/ha. (m ²)	18.3			

^aRD = Relative Density
RBA = Relative Basal Area
IV = Importance Value.

Table 19. Composition of the groundcover at Site 1 (Clear Creek).^a

Species	Average Cover (%)	Frequency (%)
A. Species occurring with an average density of less than one plant/ m ² .		
<i>Ailanthus altissima</i>	r ^b	6
<i>Ambrosia artemisiifolia</i>	0.5	11
<i>Anisostichus capreolata</i>	0.1	6
<i>Botrychium virginianum</i>	r	6
<i>Carex</i> spp.	r	6
<i>Carya glabra</i>	0.5	11
<i>C. ovalis</i>	r	6
<i>C. tomentosa</i>	1.0	22
<i>Carya</i> spp.	0.2	6
<i>Cercis canadensis</i>	2.2	22
<i>Chimaphila maculata</i>	0.8	11
<i>Coreopsis major</i>	0.8	11
<i>Epigaea repens</i>	r	11
<i>Erechtites hieracifolia</i>	r	6
<i>Euonymus</i> sp.	0.7	33
<i>Eupatorium purpureum</i>	r	6
<i>Fagus grandifolia</i>	r	6
<i>Fragaria</i> sp.	r	11
<i>Gentiana saponaria</i>	0.2	11
<i>Goodyera pubescens</i>	1.1	11
<i>Liriodendron tulipifera</i>	0.2	39
<i>Magnolia acuminata</i>	r	11
<i>Nyssa sylvatica</i>	0.8	6
<i>Oxydendrum arboreum</i>	0.1	6
<i>Parthenocissus quinquefolia</i>	1.0	11
<i>Polygonatum biflorum</i>	r	6
<i>Quercus alba</i>	0.2	11
<i>Q. rubra</i>	r	6
<i>Q. velutina</i>	0.2	17
<i>Rhus radicans</i>	r	6
<i>Sanicula</i> sp. ^c	r	6
<i>Smilacina racemosa</i>	r	6
<i>Smilax glauca</i>	0.3	33
<i>S. hispida</i>	0.1	6
<i>S. rotundifolia</i>	0.8	17
<i>Solidago arguta</i>	r	11
<i>Ulmus americana</i>	0.8	6
<i>Vaccinium stamineum</i>	0.1	11
<i>V. vacillans</i>	1.0	11
<i>Viola</i> spp.	0.1	17

Table 19 (Continued)

Species	Average Cover (%)	Frequency (%)
B. Species occurring with an average density of one to five plants/m ² .		
<i>Acer rubrum</i>	1.4	61
<i>Cornus florida</i>	3.6	56
<i>Galium circaezans</i>	1.1	33
<i>Panicum boscii</i>	0.4	22
<i>Sassafras albidum</i>	3.5	50
<i>Uvularia perfoliata</i>	0.2	18
C. Species occurring with an average density of greater than five plants/m ² .		
<i>Desmodium</i> spp.	13.0	78
D. Summary:		
Total number of species - 47		
Average number of plants/m ² - all species - 35 ± 4 (SE)		
Average total cover - 37.0%		

^aBased on the results from 18 1 m² plots.

^br = < 0.1% average cover.

^cSanicula sp. may actually have been Ranunculus carolinianus.

Table 20. Composition of the canopy and understory at Site 2 (Greenbelt Cove).

Species	Canopy ^a			Understory ^a
	RD	RBA	IV	RD
<i>Acer rubrum</i>				3.5
<i>A. saccharum</i>	20.0	16.1	36.1	45.6
<i>Carya glabra</i>				5.3
<i>C. ovata</i>	5.0	5.4	10.4	1.8
<i>Cornus florida</i>	9.9	11.0	20.9	5.3
<i>Fagus grandifolia</i>	50.0	62.3	112.3	19.3
<i>Magnolia acuminata</i>				3.5
<i>Nyssa sylvatica</i>	5.0	2.4	7.4	
<i>Ostrya virginiana</i>				7.0
<i>Quercus alba</i>				5.3
<i>Q. rubra</i>	9.9	2.7	12.6	1.8
<i>Ulmus alata</i>				1.8
	99.8	99.9		100.2
Stems/ha.	333.3			950.0
BA/ha. (m ²)	22.4			

^aRD = Relative Density
 RBA = Relative Basal Area
 IV = Importance Value.

Table 21. Composition of the groundcover at Site 2 (Greenbelt Cove).^a

Species	Average Cover (%)	Frequency (%)
A. Species occurring with an average density of less than one plant /m ² .		
<i>Acer rubrum</i>	r ^b	17
<i>Aster cordifolius</i>	r	6
<i>A. divaricatus</i>	0.2	11
<i>Carex</i> spp.	r	6
<i>Carya cordiformis</i>	r	6
<i>C. glabra</i>	r	6
<i>Carya</i> spp.	r	6
<i>Cercis canadensis</i>	0.9	22
<i>Chamaelirium luteum</i>	0.8	17
<i>Cornus florida</i>	0.8	6
<i>Desmodium</i> spp.	0.1	17
<i>Dioscorea villosa</i>	0.1	6
<i>Erechtites hieracifolia</i>	r	6
<i>Euonymus americanus</i>	r	6
<i>Eupatorium purpureum</i>	r	6
<i>Euphorbia mericaulon</i> ^c	r	11
<i>Fagus grandifolia</i>	0.8	6
<i>Fraxinus americana</i>	0.9	17
<i>Galium circaezans</i>	r	11
<i>Geranium maculatum</i>	r	6
<i>Hepatica acutiloba</i>	r	6
<i>Houstonia caerulea</i>	r	6
<i>Ipomea purpurea</i>	r	6
<i>Liriodendron tulipifera</i>	0.1	22
<i>Magnolia acuminata</i>	r	6
<i>Microstegium virmineum</i>	r	6
<i>Nyssa sylvatica</i>	0.1	6
<i>Ostrya virginiana</i>	0.8	17
<i>Panicum boscii</i>	r	6
<i>Parthenocissus quinquefolia</i>	1.1	22
<i>Polygonatum biflorum</i>	1.0	11
<i>Quercus alba</i>	r	6
<i>Q. rubra</i>	r	6
<i>Q. velutina</i>	r	6
<i>Rhododendron</i> sp.	1.0	17
<i>Rhus radicans</i>	0.2	17
<i>Smilax glauca</i>	0.2	22
<i>Stellaria media</i>	r	6
<i>S. pubera</i>	r	6
<i>Taenidia integerrima</i>	0.8	11
<i>Thalictrum thalictroides</i>	0.3	22
<i>Uvularia perfoliata</i>	r	6
<i>Vaccinium vacillans</i>	0.3	17
<i>Viola</i> spp.	r	11

Table 21 (Continued)

Species	Average Cover (%)	Frequency (%)
<i>Vitis aestivalis</i>	0.1	17
<i>Waldsteinia fragarioides</i>	0.1	22

B. Species occurring with an average density of one to five plants/m².

<i>Acer saccharum</i>	12.0	83
Gramineae spp.	0.3	28
<i>Hexastylis arifolia</i>	0.4	66
<i>Polystichum acrostichoides</i>	1.0	11

C. Summary:

Total number of species - 50

Average number of plants/m² - all species - 15 ± 3 (SE)

Average total cover - 23.3%

^aBased on the results from 18 1 m² plots.

^br = < 0.1% average cover.

^cNomenclature follows Gleason (1952).

Table 22. Composition of the Canopy and Understory at Site 3 (River Bluff).

Species	Canopy ^a			Understory ^a
	RD	RBA	IV	RD
<i>Acer rubrum</i>				18.8
<i>A. saccharum</i>	9.9	1.8	11.7	51.8
<i>Carya glabra</i>				1.2
<i>C. ovalis</i>	9.9	1.3	11.2	2.4
<i>C. tomentosa</i>	9.9	19.4	29.3	1.2
<i>Cornus florida</i>				7.1
<i>Euonymus americanus</i>				3.5
<i>Fagus grandifolia</i>	5.0	1.2	6.2	
<i>Fraxinus americana</i>	5.0	0.6	5.6	2.4
<i>Liriodendron tulipifera</i>	5.0	0.6	5.6	
<i>Magnolia acuminata</i>				3.5
<i>Ostrya virginiana</i>				1.2
<i>Oxydendrum arboreum</i>	5.0	0.6	5.6	
<i>Quercus alba</i>	9.9	10.0	19.9	2.4
<i>Q. muhlenbergii</i>				1.2
<i>Q. prinus</i>	25.0	34.4	59.4	1.2
<i>Q. rubra</i>				1.2
<i>Q. velutina</i>	15.0	29.9	44.9	
<i>Tilia heterophylla</i>				1.2
	99.6	99.8		100.3
Stems/ha. ₂	333.3			1416.667
BA/ha. (m ²)	46.2			

^aRD = Relative Density
RBA = Relative Basal Area
IV = Importance Value.

Table 23. Composition of the groundcover at Site 3 (River Bluff).^a

Species	Average Cover (%)	Frequency (%)
A. Species occurring with an average density of less than one plant/m ² .		
Anisostichus capreolata	0.2	28
Campsis radicans	r ^b	6
Carpinus caroliniana	r	6
Carya ovalis	r	6
C. tomentosa	r	11
Cornus florida	0.2	22
Desmodium spp.	r	11
Euonymus americanus	0.1	22
E. atropurpureus	r	6
Euonymus spp.	r	6
Fraxinus americana	r	11
Galium circaezans	r	6
Liriodendron tulipifera	r	6
Magnolia acuminata	2.3	22
Ostrya virginiana	0.1	17
Prunus serotina	r	6
Quercus muhlenbergii	r	11
Q. rubra	0.8	6
Q. velutina	r	6
Rhus radicans	1.7	17
Sassafras albidum	0.8	15
Smilax glauca	0.1	17
Tipularia discolor	r	6
Viola spp.	r	6
Vitis aestivalis	0.2	11
V. rotundifolia	0.8	11
V. vulpina	0.8	6
Vitis spp.	0.1	22
B. Species occurring with an average density of one to five plants/m ² .		
Acer rubrum	1.8	83
A. saccharum	2.9	28
Chimaphila maculata	1.0	33
C. Species occurring with an average density of greater than five plants/m ² .		
Parthenocissus quinquefolia	7.1	83

Table 23 (Continued)

Species	Average Cover (%)	Frequency (%)
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D. Summary:

Total number of species - 32

Average number of plants/m² - all species - 19 ± 3 (SE)

Average total cover - 21.0

^aBased on the results from 18 1 m² plots.^br = < 0.1% average cover.

Table 24. Composition of the canopy and understory at Site 4 (State Park).

Species	Canopy ^a			Understory ^a
	RD	RBA	IV	RD
<i>Acer rubrum</i>	19.2	7.7	26.9	4.8
<i>A. saccharum</i>				2.4
<i>Carpinus caroliniana</i>				17.9
<i>Carya glabra</i>	3.8	2.0	5.8	6.0
<i>C. ovalis</i>	15.4	9.7	25.1	8.3
<i>C. tomentosa</i>				3.6
<i>Cornus florida</i>				15.5
<i>Fraxinus americana</i>	3.8	2.0	5.8	
<i>Liriodendron tulipifera</i>	26.9	56.9	83.8	
<i>Nyssa sylvatica</i>	7.7	3.1	10.8	25.0
<i>Pinus echinata</i>	3.8	3.1	6.8	
<i>Prunus serotina</i>				2.4
<i>Quercus alba</i>	3.8	2.0	5.8	2.4
<i>Q. velutina</i>	15.4	12.8	28.2	2.4
<i>Rhamnus caroliniana</i>				1.2
<i>Rhus radicans</i>				2.4
<i>Sassafras albidum</i>				2.4
<i>Tilia heterophylla</i>				1.2
	99.8	99.3		97.9
Stems/ha.	433.3			1400.0
BA/ha. (m ²)	26.7			

^aRD = Relative Density
RBA = Relative Basal Area
IV = Importance Value.

Table 25. Composition of the groundcover at Site 4 (State Park).^a

Species	Average Cover (%)	Frequency (%)
A. Species occurring with an average density of less than one plant/m ² .		
<i>Acer saccharum</i>	0.8	17
<i>Amphicarpa bracteata</i>	r ^b	6
<i>Anisostichus acrostichoides</i>	r	6
<i>Botrychium virginianum</i>	0.3	22
<i>Carpinus caroliniana</i>	r	11
<i>Carya glabra</i>	0.8	11
<i>C. tomentosa</i>	r	6
<i>Carya</i> spp.	r	6
<i>Carex</i> spp.	0.1	6
<i>Desmodium</i> spp.	r	6
<i>Eupatorium purpureum</i>	r	6
<i>Juniperus virginiana</i>	0.8	6
<i>Liriodendron tulipifera</i>	1.1	39
<i>Lonicera japonica</i>	0.1	6
<i>Nyssa sylvatica</i>	1.7	22
<i>Prunus serotina</i>	0.8	11
<i>Quercus alba</i>	0.8	6
<i>Q. velutina</i>	0.9	28
<i>Scutellaria elliptica</i>	r	11
<i>Viola</i> spp.	r	6
<i>Vitis aestivalis</i>	0.8	6
<i>Vitis</i> spp.	r	6
<i>Waldsteinia fragaroides</i>	0.2	22
Unknown spp.	r	6
B. Species occurring with an average density of one to five plants/m ² .		
<i>Acer rubrum</i>	2.2	67
<i>Chimaphila maculata</i>	0.3	28
<i>Cornus florida</i>	3.9	33
<i>Galium circaeans</i>	0.2	22
<i>Parthenocissus quinquefolia</i>	1.4	50
<i>Rhus radicans</i>	3.0	28
<i>Sassafras albidum</i>	2.6	33
<i>Smilax glauca</i>	0.3	50
<i>Uvularia perfoliata</i>	2.2	11

Table 25 (Continued)

Species	Average Cover (%)	Frequency (%)
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C. Summary:

Total number of species - 32

Average number of plants/m² - all species - 21 ± 4 (SE)

Average total cover - 25.4%

^aBased on the results from 18 1 m² plots.

br = < 0.1% average cover.

Table 26. Composition of the canopy and understory at Site 5
(Cross Mountain).

Species	Canopy*			Understory*
	RD	RBA	IV	RD
<i>Acer saccharum</i>	14.3	4.8	19.1	57.9
<i>Betula lenta</i>				1.9
<i>Carya ovalis</i>	7.1	4.3	11.4	
<i>C. ovata</i>	21.4	26.9	48.3	
<i>Cornus florida</i>				8.4
<i>Fraxinus americana</i>				3.7
<i>Liriodendron tulipifera</i>	35.7	33.5	69.2	11.2
<i>Magnolia acuminata</i>	7.1	6.7	13.8	2.8
<i>Nyssa sylvatica</i>				0.9
<i>Ostrya virginiana</i>	7.1	2.4	9.5	1.9
<i>Prunus serotina</i>				0.9
<i>Quercus rubra</i>	7.1	21.5	28.6	
<i>Robinia pseudo-acacia</i>				3.7
<i>Tilia heterophylla</i>				5.6
<i>Vitis vulpina</i>				0.9
	99.8	100.1		99.8
Stems/ha.	233.3			1783.3
BA/ha. (m ²)	12.7			

*RD = Relative Density
 RBA = Relative Basal Area
 IV = Importance Value.

Table 27. Composition of the groundcover at Site 5 (Cross Mountain).^a

Species	Average Cover (%)	Frequency (%)
A. Species occurring with an average density of less than one plant/m ² .		
<i>Acer saccharum</i>	11.2	22
<i>Actaea pachypoda</i>	0.1	6
<i>Anemone quinquefolia</i>	r ^b	6
<i>Arisaema triflorum</i>	1.1	33
<i>Botrychium virginianum</i>	r	11
<i>Carex</i> spp.	r	6
<i>Cimicifuga racemosa</i>	5.4	33
<i>Dryopteris marginalis</i>	0.1	6
<i>Eupatorium purpureum</i>	r	6
<i>Fraxinus americana</i>	0.1	28
<i>Galium circaezans</i>	0.2	22
<i>G. triflorum</i>	0.3	28
<i>Galium</i> spp.	r	11
<i>Liriodendron tulipifera</i>	r	6
<i>Parthenocissus quinquefolia</i>	r	6
<i>Polygonatum pubescens</i>	r	11
<i>Polystichum acrostichoides</i>	1.0	17
<i>Rhus radicans</i>	r	6
<i>Rubus</i> spp.	r	6
<i>Sambucus canadensis</i>	0.8	11
<i>Sanicula</i> sp. ^c	r	6
<i>Streptopus roseus</i>	0.8	11
<i>Thalictrum thalictroides</i>	r	11
<i>Tilia heterophylla</i>	0.8	6
<i>Vitis</i> spp.	r	11
<i>Waldsteinia fragarioides</i>	0.3	33
Unknown spp.	2.1	17
B. Species occurring with an average density of one to five plants/m ² .		
<i>Amphicarpa bracteata</i>	0.3	33
<i>Asarum canadense</i>	3.6	28
<i>Hepatica acutiloba</i>	1.7	39
<i>Impatiens</i> spp.	4.6	50
<i>Laportea canadensis</i>	13.3	67
<i>Osmorhiza claytonii</i>	2.1	11
<i>Sedum ternatum</i>	0.4	28
<i>Stellaria pubescens</i>	0.4	17
<i>Tiarella cordifolia</i>	1.9	39
<i>Viola canadensis</i>	2.5	56

Table 27 (Continued)

Species	Average Cover (%)	Frequency (%)
C. Species occurring with an average density of greater than five plants/m ² .		
Aster divaricatus	5.9	89
D. Summary:		
Total number of species - 38		
Average number of plants/m ² - all species - 38 ± 4 (SE)		
Average total cover - 62.3%		

^aBased on the results from 18 1 m² plots.

^br = < 0.1% average cover.

^cSanicula sp. may actually have been Ranunculus carolinianus.

Table 28. Composition of the canopy and understory at Site 6 (Hatmaker Knob).

Species	Canopy ^a			Understory ^a
	RD	RBA	IV	RD
<i>Acer rubrum</i>				9.5
<i>A. saccharum</i>	26.1	16.7	42.8	10.3
<i>Carya cordiformis</i>	4.3	0.9	5.2	4.8
<i>C. glabra</i>	4.3	8.0	12.3	5.6
<i>Clematis virginiana</i>				2.4
<i>Cornus florida</i>				3.2
<i>Fraxinus americana</i>				4.8
<i>Juglans nigra</i>	4.3	16.7	21.0	
<i>Liriodendron tulipifera</i>	8.7	12.7	21.4	1.6
<i>Magnolia acuminata</i>				0.8
<i>Oxydendrum arboreum</i>	4.3	3.6	21.0	0.8
<i>Prunus serotina</i>				5.6
<i>Quercus alba</i>	4.3	2.5	6.8	1.6
<i>Q. rubra</i>	39.1	35.3	74.4	3.9
<i>Robinia pseudo-acacia</i>	4.3	3.6	7.9	
<i>Rubus</i> spp.				2.4
<i>Sambucus canadensis</i>				2.4
<i>Sassafras albidum</i>				20.6
<i>Smilax glauca</i>				11.1
<i>Tilia heterophylla</i>				4.8
<i>Vitis aestivalis</i>				3.9
	99.7	100.0		100.1
Stems/ha. ₂	287.5			1575.0
BA/ha. (m ²)	25.6			

^aRD = Relative Density
 RBA = Relative Basal Area
 IV = Importance Value.

Table 29. Composition of the groundcover at Site 6 (Hatmaker Knob).^a

Species	Average Cover (%)	Frequency (%)
A. Species occurring with an average density of less than one plant/m ² .		
<i>Acer rubrum</i>	rb	29
<i>A. saccharum</i>	r	4
<i>Agrimonia rostellata</i>	0.1	4
<i>Arisaema triphyllum</i>	r	4
<i>Asarum canadense</i>	r	4
<i>Aster lateriflorus</i>	0.7	8
<i>A. novae-angliae</i>	0.1	4
<i>Cacalia atriplicifolia</i>	0.1	13
<i>Carex</i> spp.	r	4
<i>Carya cordiformis</i>	r	4
<i>C. glabra</i>	r	8
<i>Carya</i> spp.	r	4
<i>Chimaphila maculata</i>	0.1	4
<i>Coreopsis major</i>	0.6	4
<i>Dioscorea villosa</i>	1.3	21
<i>Euonymus americanus</i>	r	4
<i>Eupatorium purpureum</i>	0.7	29
<i>E. rugosum</i>	1.3	46
<i>Fragaria virginiana</i>	1.4	46
<i>Fraxinus americana</i>	r	8
<i>Galium latifolium</i>	r	4
<i>Galium</i> spp.	r	4
<i>Gentiana saponaria</i>	r	4
<i>Geum canadense</i>	r	13
<i>Gillenia trifoliata</i>	0.6	8
Gramineae spp.	0.8	17
<i>Helianthus microcephalus</i>	0.1	8
<i>Helianthus</i> spp.	r	4
<i>Houstonia purpurea</i>	r	4
<i>Lobelia inflata</i>	r	4
<i>Lysimachia quadrifolia</i>	0.1	4
<i>Monarda clinopodia</i>	1.8	38
<i>Monotropa uniflora</i>	r	4
<i>Osmorhiza claytonii</i>	r	4
<i>Polygonum convolvulus</i>	r	8
<i>Prenanthes altissima</i>	r	4
<i>Prunus serotina</i>	0.7	21
<i>Pueraria lobata</i>	r	4
<i>Quercus rubra</i>	r	8
<i>Q. velutina</i>	r	13
<i>Robinia pseudo-acacia</i>	r	4
<i>Rubus allegheniensis</i>	0.7	8

Table 29 (Continued)

Species	Average Cover (%)	Frequency (%)
<i>Sambucus canadensis</i>	0.6	13
<i>Sassafras albidum</i>	1.3	21
<i>Silene stellata</i>	r	4
<i>Smilacina racemosa</i>	0.6	4
<i>Solidago arguta</i>	1.3	8
<i>Solidago</i> spp.	0.7	17
<i>Stellaria pubera</i>	r	4
<i>Thalictrum thalictroides</i>	0.1	4
<i>Viola</i> sp.	0.2	29
<i>Waldsteinia fragarioides</i>	0.2	25
Unknown spp.	r	8

B. Species occurring with an average density of one to five plants/m².

<i>Amphicarpa bracteata</i>	0.4	42
<i>Aster cordifolius</i>	2.4	38
<i>Clematis virginiana</i>	2.6	38
<i>Fragaria virginiana</i>	1.4	46
<i>Impatiens</i> spp.	2.5	29
<i>Potentilla canadensis</i>	0.7	38
<i>Smilax glauca</i>	1.8	50
<i>Spigelia marilandica</i>	3.5	54
<i>Verbesina urticifolia</i>	3.1	17
<i>Vitis aestivalis</i>	3.6	4

C. Species occurring with an average density of greater than five plants/m².

<i>Panicum Boscii</i>	3.3	33
<i>Sedum ternatum</i>	15.6	25
<i>Solidago curtsii</i>	1.8	17

D. Summary:

Total number of species - 66

Average number of plants/m² - all species - 56 ± 5 (SE)

Average total cover - 57.9%

^aBased on the results from 24 1 m² plots.

^br = < 0.1% average cover.

Table 30. Composition of the canopy and understory at Site 7 (Big Bruce Ridge).

Species	Canopy ^a			Understory ^a
	RD	RBA	IV	RD
<i>Acer rubrum</i>	15.0	14.6	29.6	16.4
<i>A. saccharum</i>				24.1
<i>Amelanchier arborea</i>				0.9
<i>Carya glabra</i>	15.0	15.5	30.5	1.7
<i>C. ovata</i>	5.0	1.5	6.5	
<i>Cornus Florida</i>	9.9	3.0	12.9	23.3
<i>Hamemalis virginiana</i>				0.9
<i>Liriodendron tulipifera</i>				2.6
<i>Magnolia acuminata</i>				0.9
<i>Nyssa sylvatica</i>	5.0	2.6	7.6	9.5
<i>Quercus alba</i>	20.0	31.2	51.2	5.2
<i>Q. prinus</i>	30.0	31.6	61.6	5.2
<i>Q. rubra</i>				5.2
<i>Smilax rotundifolia</i>				4.3
	99.9	100.0		100.2
Stems/ha. ²	333.3			1933.3
BA/ha. (m ²)	20.5			

^aRD = Relative Density
RBA = Relative Basal Area
IV = Importance Value.

Table 31. Composition of the groundcover at Site 7 (Big Bruce Ridge).^a

Species	Average Cover (%)	Frequency (%)
A. Species occurring with an average density of less than one plant/m ² .		
<i>Agrimonia rostellata</i>	0.1	11
<i>Amphicarpa bracteata</i>	1.7	28
<i>Anisostichus capreolata</i>	r ^b	6
<i>Antennaria plantaginoides</i>	r	6
<i>Arisaema triphyllum</i>	0.1	11
<i>Aruncus dioicus</i>	r	6
<i>Aster cordifolius</i>	r	6
<i>Aster</i> spp.	0.2	11
<i>Botrychium virginianum</i>	r	17
<i>Campanula divaricata</i>	r	11
<i>Carya glabra</i>	1.7	11
<i>Cercis canadensis</i>	r	6
<i>Cimicifuga racemosa</i>	0.1	11
<i>Cornus florida</i>	r	11
<i>Dioscorea villosa</i>	0.8	22
<i>Euphorbia mericaulon</i> ^c	1.1	33
<i>Fragaria</i> sp.	0.1	6
<i>Fraxinus americana</i>	1.7	17
<i>Galium latifolium</i>	0.2	22
Graminae spp.	0.2	22
<i>Houstonia purpurea</i>	0.3	22
<i>Hydrangea arborescens</i>	r	6
<i>Impatiens</i> spp.	0.1	6
<i>Iris cristata</i>	0.3	22
<i>Liriodendron tulipifera</i>	r	17
<i>Magnolia acuminata</i>	0.8	28
<i>Nyssa sylvatica</i>	2.1	17
<i>Panicum boscii</i>	0.1	11
<i>Parthenocissus quinquefolia</i>	r	17
<i>Pedicularis canadensis</i>	0.9	11
<i>Phlox ovata</i>	r	11
<i>Polystichum acrostichoides</i>	0.1	11
<i>Potentilla canadensis</i>	0.3	22
<i>P. simplex</i>	r	11
<i>Potentilla</i> spp.	0.3	22
<i>Quercus prinus</i>	0.3	33
<i>Rubus allegheniensis</i>	r	6
<i>Rubus</i> spp.	r	6
<i>Scutellaria elliptica</i>	r	6
<i>Sedum ternatum</i>	r	6
<i>Smilax glauca</i>	0.3	39
<i>S. rotundifolia</i>	0.3	28

Table 31 (Continued)

Species	Average Cover (%)	Frequency (%)
Smilax spp.	r	6
Solidago caesia	0.1	28
Solidago spp.	r	6
Stellaria pubera	1.0	28
Taenidia integerrima	0.2	11
Viola palmata	r	6
Vitis aestivalis	0.8	6
Vitis spp.	r	17
Waldsteinia fragarioides	0.4	28
Unknown spp.	r	6

B. Species occurring with an average density of one to five plants/m².

Acer rubrum	2.6	39
A. saccharum	10.4	61
Aster divaricatus	0.5	39
Carex spp.	0.2	35
Dryopteris marginalis	2.1	6
Eupatorium purpureum	2.4	61
E. rugosum	0.3	28
Muhlenbergia tenuiflora	1.4	44
Rhus radicans	0.5	39
Solidago arguta	3.9	56
Thalictrum thalictroides	3.5	44
Viola papilionacea	0.2	4
Viola spp.	0.7	50

C. Summary:

Total number of species - 65

Average number of plants/m² - all species - 37 ± 5 (SE)

Average total cover - 45.9%

^aBased on the results from 18 1-m² plots.

^br = < 0.1% average cover.

^cNomenclature follows Gleason (1952).

Table 32. Composition of the canopy and understory at Site 8 (Wheeler Creek Cove).

Species	Canopy ^a			Understory ^a
	RD	RBA	IV	RD
<i>Acer rubrum</i>				31.7
<i>Carya glabra</i>	3.7	1.1	4.8	2.4
<i>Cornus florida</i>				1.6
<i>Nyssa sylvatica</i>	3.7	2.0	5.7	41.3
<i>Oxydendrum arboreum</i>				7.9
<i>Quercus alba</i>	3.7	3.2	6.9	
<i>Q. prinus</i>	25.9	24.7	50.6	0.8
<i>Q. rubra</i>	11.1	8.3	19.4	2.4
<i>Q. velutina</i>	51.9	60.7	12.6	0.8
<i>Sassafras albidum</i>				8.7
<i>Vaccinium vacillans</i>				2.4
	100.0	100.0		100.0
Stems/ha. ²	450.0			2100.0
BA/ha. (m ²)	26.8			

^aRD = Relative Density
 RBA = Relative Basal Area
 IV = Importance Value.

Table 33. Composition of the groundcover at Site 8 (Wheeler Creek Cove).^a

Species	Average Cover (%)	Frequency (%)
A. Species occurring with an average density of less than one plant/m ² .		
Aster infirmus	r	6
A. lateriflorus	0.1	6
A. patens	r	6
Aster spp.	r	6
Campanula divaricata	r	6
Carex spp.	r	11
Coreopsis major	r	11
Eupatorium purpureum	1.1	39
E. rugosum	r	6
Fagus grandifolia	r	6
Gentiana saponaria	r	11
Gramineae spp.	r	6
Helianthus microcephalus	0.1	6
Helianthus spp.	r	6
Hieracium paniculatum	0.1	17
Nyssa sylvatica	4.2	33
Quercus rubra	r	6
Rhododendron sp.	2.5	17
Rhus radicans	r	6
Smilax glauca	0.4	44
Solidago bicolor	r	6
S. caesia	r	17
S. curtsii	r	6
Solidago spp.	0.1	11
Triosteum angustifolium	r	6
Vaccinium vacillans	0.3	17
Viola spp.	r	6
Vitis spp.	r	6
B. Species occurring with an average density of one to five plants/m ² .		
Acer rubrum	1.0	72
Aster divaricatus	4.9	6
Chimaphila maculata	0.4	28
Mitchella repens	0.8	6
Quercus prinus	2.7	50
Rhododendron spp.	2.4	22
Sassafras albidum	3.4	56
Smilax rotundifolia	2.5	39
Solidago arguta	3.1	39

Table 33 (Continued)

Species	Average Cover (%)	Frequency (%)
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C. Summary:

Total number of species - 37

Average number of plants/m² - all species - 26 ± 6 (SE)

Average total cover - 30.1

^aBased on the results from 18 1 m² plots.^b_r = < 0.1% average cover.

APPENDIX C

FLORISTIC COMPOSITION OF THE BURIED VIABLE
SEED POPULATIONS

Table 34. Floristic composition of the buried viable seed population at Site 1.

Species	Spring Collection			Summer Collection		
	Frequency (Percent)	Number Plants:		Frequency (Percent)	Number Plants:	
		Average/m ² (± SE)	Percent of Total		Average/m ² (± SE)	Percent of Total
<i>Acalypha virginica</i>	0	0	0	17	2±2	0.5
<i>Acer rubrum</i>	20	2±1	0.6	0	0	0
<i>Andropogon virginicus</i>	40	5±2	1.5	50	7±3	1.9
<i>Anisostichus capreolata</i>	0	0	0	17	5±5	1.3
<i>Aster</i> spp.	10	1±1	0.3	17	3±3	0.8
<i>Carex nigromarginata</i> ^a	10	2±2	0.6	100	33±10	8.9
<i>C. platyphylla</i>	40	8±4	2.5	0	0	0
<i>C. virescens</i>	20	7±5	2.1	0	0	0
<i>Carex</i> spp.	50	6±2	1.8	33	7±5	1.9
<i>Ceanothus americanus</i>	10	1±1	0.3	0	0	0
<i>Cercis canadensis</i>	60	19±10	5.8	17	2±2	0.5
<i>Desmodium</i> spp.	10	1±1	0.3	0	0	0
<i>Digitaria sanguinalis</i>	10	1±1	0.3	0	0	0
<i>Eleocharis obtusa</i>	0	0	0	17	2±2	0.5
<i>Epigaea repens</i>	0	0	0	17	2±2	0.5
<i>Erechtites hieracifolia</i>	60	11±3	3.4	50	10±5	2.7
<i>Erigeron annuus</i>	0	0	0	33	3±2	0.8
<i>Erigeron</i> spp.	30	5±3	1.5	0	0	0
<i>Eupatorium rugosum</i>	10	1±1	0.3	17	2±2	0.5
<i>E. serotinum</i>	10	2±2	0.6	33	3±2	0.8
<i>Fragaria</i> sp.	20	2±1	0.6	0	0	0
<i>Galium circaezans</i>	0	0	0	17	2±2	0.5
<i>Galium obtusum</i>	10	2±2	0.6	0	0	0
<i>G. pilosum</i>	20	1±1	0.3	0	0	0
<i>G. triflorum</i>	10	1±1	0.3	0	0	0
<i>Galium</i> spp.	10	1±1	0.3	0	0	0

Table 34 (Continued)

Species	Spring Collection			Summer Collection		
	Frequency (Percent)	Average/m ² ($\pm$ SE)	Percent of Total	Frequency (Percent)	Average/m ² ($\pm$ SE)	Percent of Total
<i>Gnaphalium obtusifolium</i>	40	4 $\pm$ 2	1.2	0	0	0
<i>G. purpureum</i>	30	6 $\pm$ 4	1.8	17	2 $\pm$ 2	0.5
<i>Gnaphalium</i> spp.	40	4 $\pm$ 2	1.2	50	5 $\pm$ 2	1.3
Gramineae spp.	20	4 $\pm$ 3	1.2	17	2 $\pm$ 2	0.5
<i>Houstonia purpurea</i>	0	0	0	67	12 $\pm$ 6	3.2
<i>Hydrangea arborescens</i> *	30	4 $\pm$ 2	1.2	67	23 $\pm$ 11	6.2
<i>Hypericum punctatum</i>	0	0	0	17	2 $\pm$ 2	0.5
<i>Hypericum</i> sp.	0	0	0	17	2 $\pm$ 2	0.5
<i>Juncus interior</i>	20	3 $\pm$ 2	0.9	0	0	0
<i>Juncus</i> sp.	10	1 $\pm$ 1	0.3	0	0	0
<i>Lactuca</i> sp.	40	5 $\pm$ 2	1.5	17	2 $\pm$ 2	0.5
<i>Liriodendron tulipifera</i>	90	53 $\pm$ 11	16.3	100	27 $\pm$ 8	7.5
<i>Lobelia inflata</i>	10	1 $\pm$ 1	0.3	17	13 $\pm$ 13	3.5
<i>Mimulus alatus</i>	10	1 $\pm$ 1	0.3	0	0	0
<i>Muhlenbergia schreberi</i>	10	1 $\pm$ 1	0.3	0	0	0
<i>Oenothera biennis</i>	10	3 $\pm$ 3	0.9	17	2 $\pm$ 2	0.5
<i>Oxydendrum arboreum</i>	80	18 $\pm$ 4	5.5	17	10 $\pm$ 10	2.7
<i>Panicum Boscii</i>	0	0	0	33	3 $\pm$ 2	0.8
<i>P. commutatum</i>	40	18 $\pm$ 12	5.5	67	117 $\pm$ 86	31.5
<i>P. dichotomum</i>	40	24 $\pm$ 18	7.4	17	8 $\pm$ 8	2.2
<i>Panicum</i> spp.	20	2 $\pm$ 1	0.6	0	0	0
<i>Paulownia tomentosa</i>	50	8 $\pm$ 4	2.5	67	12 $\pm$ 5	3.2
<i>Physalis virginiana</i>	10	2 $\pm$ 2	0.6	0	0	0
<i>Phytolacca americana</i>	40	6 $\pm$ 2	1.8	33	3 $\pm$ 2	0.8
<i>Platanus occidentalis</i>	10	1 $\pm$ 1	0.3	0	0	0
<i>Potentilla canadensis</i>	0	0	0	33	3 $\pm$ 2	0.8

Table 34 (Continued)

Species	Spring Collection			Summer Collection		
	Frequency (Percent)	Average/m ² ($\pm$ SE)	Percent of Total	Frequency (Percent)	Average/m ² ($\pm$ SE)	Percent of Total
Potentilla sp.	10	1 $\pm$ 1	0.3	0	0	0
Rhus coppalina	30	18 $\pm$ 14	5.5	0	0	0
R. glabra	10	1 $\pm$ 1	0.3	17	2 $\pm$ 2	0.5
Rubus allegheniensis	20	2 $\pm$ 1	0.6	0	0	0
R. argutus	40	12 $\pm$ 7	3.7	50	10 $\pm$ 5	2.7
R. hispidus	10	1 $\pm$ 1	0.3	0	0	0
R. occidentalis	10	3 $\pm$ 3	0.9	0	0	0
Rhynchospora globularis	10	1 $\pm$ 1	0.3	0	0	0
Salix alba	10	2 $\pm$ 2	0.6	0	0	0
Sassafras albidum	10	1 $\pm$ 1	0.3	0	0	0
Scirpus sp.	0	0	0	17	2 $\pm$ 2	0.5
Setaria viridis	10	1 $\pm$ 1	0.3	0	0	0
Solanum carolinense	0	0	0	17	5 $\pm$ 5	1.3
Solidago altissima	10	3 $\pm$ 2	0.9	0	0	0
S. caesia	10	1 $\pm$ 1	0.3	17	2 $\pm$ 2	0.5
Solidago sp.	20	2 $\pm$ 1	0.6	0	0	0
Taraxacum officinale	20	2 $\pm$ 1	0.6	0	0	0
Taraxacum sp.	0	0	0	17	2 $\pm$ 2	0.5
Thalictrum thalictroides	0	0	0	17	2 $\pm$ 2	0.5
Tiarella cordifolia	0	0	0	17	10 $\pm$ 10	2.7
Typha latifolia	40	5 $\pm$ 2	1.5	0	0	0
Ulmus alata	10	1 $\pm$ 1	0.3	0	0	0
U. americana	0	0	0	17	2 $\pm$ 2	0.5

Table 34 (Continued)

Species	Spring Collection			Summer Collection		
	Frequency (Percent)	Average/m ² ($\pm$ SE)	Percent of Total	Frequency (Percent)	Average/m ² ($\pm$ SE)	Percent of Total
<i>Verbascum thapsus</i>	20	5 $\pm$ 4	1.5	50	7 $\pm$ 3	1.9
<i>Viola</i> spp.	30	3 $\pm$ 2	0.9	17	2 $\pm$ 3	0.5
<i>Vitis aestivalis</i>	30	3 $\pm$ 2	0.9	0	0	0
<i>V. vulpina</i>	10	1 $\pm$ 1	0.3	2	2 $\pm$ 2	0.3
Unknown spp.	30	8	2.5	0	0	0

*Mean number of plants/m² for the spring and summer samples were significantly different at the .05 level of probability.

Table 35. Floristic composition of the buried viable seed population at Site 2.

Species	Spring Collection			Summer Collection		
	Frequency (Percent)	Number Plants: Average/m ² ($\pm$ SE)	Percent of Total	Frequency (Percent)	Number Plants: Average/m ² ($\pm$ SE)	Percent of Total
<i>Acalypha rhomboidea</i>	20	4 $\pm$ 3	0.8	17	7 $\pm$ 7	0.9
<i>A. virginica</i>	40	15 $\pm$ 11	3.0	83	23 $\pm$ 11	2.8
<i>Ailanthus altissima</i>	0	0	0	17	2 $\pm$ 2	0.2
<i>Andropogon virginicus</i>	70	13 $\pm$ 4	2.6	83	13 $\pm$ 4	1.6
<i>Antennaria plantaginifolia</i>	0	0	0	33	3 $\pm$ 2	0.4
<i>Aralia racemosa</i>	10	1 $\pm$ 1	0.2	0	0	0
<i>Aster cordifolius</i>	20	16 $\pm$ 12	3.2	0	0	0
<i>A. laterflorus</i>	10	1 $\pm$ 1	0.2	0	0	0
<i>Aster</i> spp.	50	6 $\pm$ 2	1.2	0	0	0
<i>Asteraceae</i> sp.	10	1 $\pm$ 1	0.2	0	0	0
<i>Carex nigromarginata</i>	20	24 $\pm$ 22	4.8	0	0	0
<i>C. virescens</i>	10	29 $\pm$ 29	5.8	17	2 $\pm$ 2	0.2
<i>Carex</i> spp.	30	23 $\pm$ 16	4.6	0	0	0
<i>Cercis canadensis</i>	80	20 $\pm$ 10	4.0	67	17 $\pm$ 6	2.1
<i>Claytonia virginica</i>	10	2 $\pm$ 2	0.4	33	10 $\pm$ 7	1.2
<i>Cyperus lancastricensis</i>	10	1 $\pm$ 1	0.2	0	0	0
<i>Digitaria ischaemum</i>	10	2 $\pm$ 2	0.4	0	0	0
<i>Erechtites hieracifolia</i>	60	10 $\pm$ 4	2.0	67	8 $\pm$ 3	1.0
<i>Erigeron annuus</i>	20	2 $\pm$ 1	0.4	33	3 $\pm$ 2	0.4
<i>E. canadensis</i>	10	1 $\pm$ 1	0.2	0	0	0
<i>Erigeron</i> spp.	30	5 $\pm$ 3	1.0	0	0	0
<i>Eupatorium rugosum</i>	10	1 $\pm$ 1	0.2	0	0	0
<i>E. serotinum</i>	10	1 $\pm$ 1	0.2	0	0	0
<i>Fimbristylis autumnalis</i>	10	1 $\pm$ 1	0.2	0	0	0
<i>Gnaphalium obtusifolium</i>	10	1 $\pm$ 1	0.2	0	0	0
<i>G. purpureum</i>	10	1 $\pm$ 1	0.2	0	0	0

Table 35 (Continued)

Species	Spring Collection			Summer Collection		
	Frequency (Percent)	Number Plants: Average/m ² (± SE)	Percent of Total	Frequency (Percent)	Number Plants: Average/m ² (± SE)	Percent of Total
Gnaphalium spp.	50	11±6	2.2	17	3±3	0.4
Gramineae spp.	10	6±6	1.2	0	0	0
Hedeoma pulegioides	10	2±2	0.4	0	0	0
Heuchera americana	10	2±2	0.4	17	3±3	0.4
Houstonia purpurea	20	5±4	1.0	17	10±10	1.2
Hydrangea arborescens*	60	56±20	11.2	100	393±143	48.6
Hypericum punctatum	0	0	0	17	2±2	0.2
Hypericum sp.	10	1±1	0.2	0	0	0
Juncus interior	30	10±6	2.0	0	0	0
Lactuca sp.	30	3±2	0.6	0	0	0
Liriodendron tulipifera	80	23±2	4.6	83	37±17	4.6
Lobelia inflata	20	6±5	1.2	33	13±10	1.6
Morus rubra	100	32±9	6.4	67	18±9	2.2
Oenothera biennis	10	1±1	0.2	17	2±2	0.2
Oxalis stricta	10	13±12	2.6	17	2±2	0.2
Oxydendrum arboreum	10	1±1	0.2	0	0	0
Panicum commutatum	10	3±3	0.6	17	25±25	3.1
P. lanuginosum	10	8±8	1.6	0	0	0
Paulownia tomentosa*	70	11±3	2.2	17	2±2	0.2
Phytolacca americana	50	6±2	1.2	50	35±31	4.3
Pilea pumila	10	1±1	0.2	17	2±2	0.2
Platanus occidentalis	50	14±7	2.8	0	0	0
Poa pratensis	20	3±2	0.6	17	10±10	1.2
Potentilla canadensis	10	12±12	2.4	0	0	0
Rhus coppalina	10	1±1	0.2	0	0	0
R. glabra	20	2±1	0.4	0	0	0

Table 35 (Continued)

Species	Spring Collection			Summer Collection		
	Frequency (Percent)	Number Plants: Average/m ² ($\pm$ SE)	Percent of Total	Frequency (Percent)	Number Plants: Average/m ² ($\pm$ SE)	Percent of Total
Rosaceae sp.	0	0	0	17	3 $\pm$ 3	0.4
Rubus allegheniensis	20	4 $\pm$ 3	0.8	0	0	0
R. argutus	50	6 $\pm$ 3	1.2	33	95 $\pm$ 91	11.8
R. hispidus	10	1 $\pm$ 1	0.2	0	0	0
R. idaeus	0	0	0.2	33	8 $\pm$ 7	1.0
R. occidentalis	20	2 $\pm$ 1	0.4	0	0	0
Rubus spp.	10	1 $\pm$ 1	0.2	0	0	0
Sambucus canadensis	10	2 $\pm$ 2	0.4	0	0	0
Sassafras albidum	20	2 $\pm$ 1	0.4	33	5 $\pm$ 3	0.6
Scutellaria elliptica	10	5 $\pm$ 5	1.0	0	0	0
Solidago sp.	30	5 $\pm$ 3	1.0	17	2 $\pm$ 2	0.2
Stellaria media	0	0	0	17	13 $\pm$ 13	1.6
Taraxacum officinale	30	6 $\pm$ 3	1.2	0	0	0
Tiarella cordifolia	0	0	0	33	13 $\pm$ 9	1.6
Trifolium repens	10	2 $\pm$ 2	0.4	0	0	0
Typha latifolia	10	14 $\pm$ 14	2.8	0	0	0
Ulmus alata	20	6 $\pm$ 5	1.2	17	5 $\pm$ 5	0.6
U. americana	10	1 $\pm$ 1	0.2	0	0	0
U. rubra	10	2 $\pm$ 2	0.4	0	0	0
Verbascum thapsus	50	10 $\pm$ 4	2.0	17	2 $\pm$ 2	0.2
Viola palmata	0	0	0	17	2 $\pm$ 2	0.2
V. papilionacea	10	3 $\pm$ 3	0.6	17	2 $\pm$ 2	0.2
Viola spp.	40	5 $\pm$ 2	1.0	0	0	0
Vitis baileyana	10	1 $\pm$ 1	0.2	0	0	0
V. rotundifolia	0	0	0	33	3 $\pm$ 2	0.4

Table 35 (Continued)

Species	Spring Collection			Summer Collection		
	Frequency (Percent)	Average/m ² ($\pm$ SE)	Percent of Total	Frequency (Percent)	Average/m ² ($\pm$ SE)	Percent of Total
<i>V. vulpina</i>	20	2 $\pm$ 1	0.4	50	10 $\pm$ 6	1.2
Unknown spp.	20	6	1.2	0	0	0

*Mean number of plants/m² for the spring and summer samples were significantly different at the .05 level of probability.

Table 36. Floristic composition of the buried viable seed population at Site 3.

Species	Spring Collection			Summer Collection		
	Frequency (Percent)	Average/m ² ($\pm$ SE)	Percent of Total	Frequency (Percent)	Average/m ² ($\pm$ SE)	Percent of Total
<i>Acalypha rhomboidea</i>	0	0	0	17	3 $\pm$ 3	0.9
<i>Acer rubrum</i>	20	8 $\pm$ 4	2.3	0	0	0
<i>Ailanthus altissima</i>	30	4 $\pm$ 4	1.1	17	2 $\pm$ 2	0.6
<i>Amphicarpa bracteata</i>	10	3 $\pm$ 3	0.9	0	0	0
<i>Andropogon virginicus</i>	60	9 $\pm$ 3	2.6	17	2 $\pm$ 2	0.6
<i>Aster pilosus</i>	10	2 $\pm$ 2	0.6	0	0	0
<i>Aster spp.</i>	10	1 $\pm$ 1	0.3	0	0	0
<i>Asteraceae sp.</i>	10	1 $\pm$ 1	0.3	0	0	0
<i>Carex nigromarginata</i>	0	0	0	17	3 $\pm$ 3	0.9
<i>C. platyphylla</i>	10	1 $\pm$ 1	0.3	0	0	0
<i>Carex spp.</i>	10	4 $\pm$ 4	1.1	0	0	0
<i>Cercis canadensis</i>	30	7 $\pm$ 4	2.0	17	2 $\pm$ 2	0.6
<i>Cyperus lancastricensis</i>	10	1 $\pm$ 1	0.3	0	0	0
<i>Danthonia spicata</i>	0	0	0	17	5 $\pm$ 2	1.5
<i>Digitaria ischaemum</i>	10	1 $\pm$ 1	0.3	0	0	0
<i>Epigaea repens</i>	0	0	0	17	2 $\pm$ 3	0.6
<i>Erechtites hieracifolia</i>	50	6 $\pm$ 2	1.7	33	5 $\pm$ 2	1.5
<i>Erigeron annuus</i>	10	1 $\pm$ 1	0.3	17	2 $\pm$ 2	0.6
<i>E. canadensis</i>	20	2 $\pm$ 1	0.6	0	0	0
<i>Eupatorium purpureum</i>	10	1 $\pm$ 1	0.3	0	0	0
<i>E. serotinum</i>	20	4 $\pm$ 3	1.1	0	2 $\pm$ 2	0.6
<i>Fragaria sp.</i>	10	1 $\pm$ 1	0.3	0	0	0
<i>Gnaphalium obtusifolium</i>	10	1 $\pm$ 1	0.3	0	0	0
<i>G. purpureum</i>	20	2 $\pm$ 1	0.6	33	10 $\pm$ 8	2.9
<i>Gnaphalium spp.</i>	0	0	0	33	3 $\pm$ 2	0.9
<i>Gramineae sp.</i>	10	1 $\pm$ 1	0.3	0	0	0

Table 36 (Continued)

Species	Spring Collection			Summer Collection		
	Frequency (Percent)	Number Plants: Average/m ² (± SE)	Percent of Total	Frequency (Percent)	Number Plants: Average/m ² (± SE)	Percent of Total
<i>Houstonia purpurea</i>	0	0	0	17	25±25	7.4
<i>Hypericum punctatum</i>	10	1±1	0.3	17	2±2	0.6
<i>Hypericum</i> spp.	10	1±1	0.3	0	0	0
<i>Juncus interior</i>	10	3±3	0.9	0	0	0
<i>Juncus</i> sp.	10	1±1	0.3	0	0	0
<i>Lactuca</i> sp.	20	5±4	1.4	17	2±2	0.6
<i>Leguminosae</i> sp.	0	0	0	17	2±2	0.6
<i>Liriodendron tulipifera</i>	100	49±9	13.9	100	50±17	14.7
<i>Lobelia inflata</i>	0	0	0	17	8±8	2.4
<i>Morus rubra</i>	90	33±7	9.4	100	32±9	9.4
<i>Oenothera biennis</i>	10	1±1	0.3	0	0	0
<i>Oxydendrum arboreum</i>	80	22±6	6.3	67	33±24	9.7
<i>Panicum commutatum</i> *	30	11±8	3.2	67	30±16	8.8
<i>P. dichotomum</i>	40	29±23	8.2	33	3±2	0.9
<i>Parthenocissus quinquefolia</i>	10	1±1	0.3	0	0	0
<i>Paulownia tomentosa</i>	50	9±4	2.6	50	7±3	2.1
<i>Phytolacca americana</i>	70	61±27	17.3	83	20±7	5.9
<i>Potentilla canadensis</i>	10	2±2	0.6	17	2±2	0.6
<i>Rhus copallina</i>	20	8±5	2.3	0	0	0
<i>R. glabra</i>	50	7±3	2.0	0	0	0
<i>Rhus</i> spp.	20	2±1	0.6	0	0	0
<i>Robinia pseudo-acacia</i>	20	10±8	2.8	0	0	0
<i>Rubus allegheniensis</i>	10	1±1	0.3	17	2±2	0.6
<i>R. argutus</i>	40	15±9	4.3	50	10±6	2.9
<i>R. idaeus</i>	0	0	0	17	2±2	0.6
<i>Sassafras albidum</i>	10	1±1	0.3	50	5±2	1.5

Table 36 (Continued)

Species	Spring Collection			Summer Collection		
	Frequency (Percent)	Number Plants:		Frequency (Percent)	Number Plants:	
		Average/m ² (± SE)	Percent of Total		Average/m ² (± SE)	Percent of Total
<i>Solanum americanum</i>	10	5±5	1.4	17	37±37	10.9
<i>S. carolinense</i>	0	0	0	17	18±18	5.3
<i>Solidago</i> sp.	0	0	0	17	2±2	0.6
<i>Taraxacum officinale</i>	0	0	0	17	2±2	0.6
<i>Trifolium repens</i>	10	1±1	0.3	0	0	0
<i>Typha latifolia</i>	10	1±1	0.3	0	0	0
<i>Ulmus americana</i>	10	1±1	0.3	0	0	0
<i>Verbascum thapsus</i>	10	2±1	0.6	0	0	0
<i>Veronica peregrina</i>	10	2±2	0.6	0	0	0
<i>Viola</i> sp.	0	0	0	17	2±2	0.6
<i>Vitis aestivalis</i>	10	3±3	0.9	0	0	0
<i>V. baileyana</i>	0	0	0	33	3±3	0.9
<i>V. rotundifolia</i>	10	1±1	0.3	0	0	0
<i>V. vulpina</i>	10	1±1	0.3	33	3±2	0.9
<i>Vitis</i> sp.	10	1±1	0.3	0	0	0

*Mean number of plants/m² for the spring and summer samples were significantly different at the .05 level of probability.

Table 37. Floristic composition of the buried viable seed population at Site 4.

Species	Spring Collection			Summer Collection		
	Frequency (Percent)	Average/m ² ($\pm$ SE)	Percent of Total	Frequency (Percent)	Average/m ² ($\pm$ SE)	Percent of Total
<i>Acalypha rhomboidea</i>	10	4 $\pm$ 4	0.6	0	0	0
<i>Acer rubrum</i>	40	8 $\pm$ 4	1.1	0	0	0
<i>Ambrosia artemisiifolia</i>	20	7 $\pm$ 6	1.0	33	7 $\pm$ 5	1.3
<i>Amphicarpa bracteata</i>	10	2 $\pm$ 2	0.3	0	0	0
<i>Andropogon virginicus</i>	60	15 $\pm$ 5	2.1	33	3 $\pm$ 2	0.5
<i>Antennaria plantaginifolia</i>	0	0	0	17	8 $\pm$ 3	1.5
<i>Aster patens</i>	10	1 $\pm$ 1	0.1	0	0	0
<i>Aster spp.</i>	60	7 $\pm$ 2	1.0	17	2 $\pm$ 2	0.4
<i>Betula lenta</i>	10	1 $\pm$ 1	0.1	0	0	0
<i>Carex debilis</i>	0	0	0	17	3 $\pm$ 3	0.5
<i>C. nigromarginata</i>	0	0	0	17	7 $\pm$ 7	1.3
<i>C. pennsylvanica</i>	10	1 $\pm$ 1	0.1	0	0	0
<i>C. platyphylla</i>	10	2 $\pm$ 2	0.3	0	0	0
<i>C. virescens</i>	10	10 $\pm$ 10	1.4	0	0	0
<i>Carex spp.</i>	30	39 $\pm$ 35	5.4	0	0	0
<i>Cercis canadensis</i>	0	0	0	17	2 $\pm$ 2	0.4
<i>Chrysanthemum leucanthemum</i>	10	1 $\pm$ 1	0.1	0	0	0
<i>Collinsonia canadensis</i>	0	0	0	17	13 $\pm$ 13	2.4
<i>Cyperus lancastricensis</i>	10	2 $\pm$ 2	0.3	0	0	0
<i>C. pseudovegetus</i>	10	15 $\pm$ 15	2.1	0	0	0
<i>Danthonia spicata</i>	10	10 $\pm$ 10	1.4	0	0	0
<i>Desmodium sp.</i>	17	2 $\pm$ 2	0.3	0	0	0
<i>Digitaria ischaemum</i>	10	1 $\pm$ 1	0.1	0	0	0
<i>D. sanguinalis</i>	0	0	0	17	3 $\pm$ 3	0.6
<i>Eleusine indica</i>	10	1 $\pm$ 1	0.1	0	0	0
<i>Eragrostis sp.</i>	20	3 $\pm$ 2	0.4	0	0	0

Table 37 (Continued)

Species	Spring Collection			Summer Collection		
	Frequency (Percent)	Number Plants: Average/m ² ($\pm$ SE)	Percent of Total	Frequency (Percent)	Number Plants: Average/m ² ($\pm$ SE)	Percent of Total
<i>Erechtites hieracifolia</i>	100	55 $\pm$ 11	7.6	100	53 $\pm$ 22	9.7
<i>Erianthus alpecuroides</i>	10	1 $\pm$ 1	0.1	0	0	0
<i>Erianthus</i> sp.	10	1 $\pm$ 1	0.1	0	0	0
<i>Erigeron annuus</i>	0	0	0	33	3 $\pm$ 2	0.6
<i>E. strigosus</i>	10	1 $\pm$ 1	0.1	0	0	0
<i>Erigeron</i> spp.	30	6 $\pm$ 4	0.8	0	0	0
<i>Eupatorium purpureum</i>	10	8 $\pm$ 8	1.1	33	3 $\pm$ 2	0.6
<i>E. rugosum</i>	10	5 $\pm$ 5	0.7	33	5 $\pm$ 3	0.9
<i>E. serotinum</i>	80	37 $\pm$ 23	5.1	83	35 $\pm$ 21	6.4
<i>Festuca obtusa</i>	10	1 $\pm$ 1	0.1	0	0	0
<i>Fragaria virginiana</i>	20	4 $\pm$ 3	0.6	17	2 $\pm$ 2	0.4
<i>Galinsoga ciliata</i>	10	2 $\pm$ 2	0.3	0	0	0
<i>Galium circaezans</i>	0	0	0	17	2 $\pm$ 2	0.4
<i>Gnaphalium obtusifolium</i>	30	5 $\pm$ 3	0.7	0	0	0
<i>G. purpureum</i>	20	5 $\pm$ 3	0.7	17	3 $\pm$ 3	0.6
<i>Gnaphalium</i> spp.	50	14 $\pm$ 5	1.9	0	0	0
Gramineae spp.	10	8 $\pm$ 8	1.1	33	3 $\pm$ 2	0.6
<i>Hedeoma pulegioides</i>	20	17 $\pm$ 15	2.4	50	5 $\pm$ 2	0.9
<i>Helianthus microcephalus</i>	10	1 $\pm$ 1	0.1	0	0	0
<i>Hexastylis virginicus</i>	0	0	0	17	2 $\pm$ 2	0.4
<i>Houstonia purpurea</i>	10	6 $\pm$ 6	0.8	0	0	0
<i>Hydrangea arborescens</i>	0	0	0	17	2 $\pm$ 2	0.4
<i>Hypericum mutilum</i>	0	0	0	33	3 $\pm$ 2	0.6
<i>Juncus interior</i>	10	2 $\pm$ 2	0.3	0	0	0
<i>Juncus</i> sp.	10	12 $\pm$ 12	1.7	0	0	0
<i>Lactuca</i> sp.	40	10 $\pm$ 5	1.4	0	0	0

Table 37 (Continued)

Species	Spring Collection			Summer Collection		
	Frequency (Percent)	Average/m ² ($\pm$ SE)	Percent of Total	Frequency (Percent)	Average/m ² ($\pm$ SE)	Percent of Total
<i>Lespedeza hirta</i>	10	2 $\pm$ 2	0.3	0	0	0
<i>L. intermedia</i>	10	1 $\pm$ 1	0.1	0	0	0
<i>Liriodendron tulipifera</i>	80	31 $\pm$ 8	4.3	83	43 $\pm$ 24	7.9
<i>Lobelia inflata</i>	10	1 $\pm$ 1	0.1	50	45 $\pm$ 41	8.2
<i>Mollugo verticillata</i>	10	1 $\pm$ 1	0.1	0	0	0
<i>Monarda clinopodia</i>	10	1 $\pm$ 1	0.1	0	0	0
<i>Morus rubra</i>	10	4 $\pm$ 4	0.6	0	0	0
<i>Oenothera biennis</i>	30	7 $\pm$ 4	1.0	0	0	0
<i>Oxalis</i> spp.	10	2 $\pm$ 2	0.3	0	0	0
<i>Oxydendrum arboreum</i>	30	6 $\pm$ 3	0.8	0	0	0
<i>Panicum commutatum</i>	30	25 $\pm$ 16	3.4	17	32 $\pm$ 32	5.9
<i>P. dichotomum</i>	10	2 $\pm$ 2	0.3	50	25 $\pm$ 19	4.6
<i>P. gattingeri</i>	10	1 $\pm$ 1	0.1	0	0	0
<i>P. lanuginosum</i>	20	2 $\pm$ 1	0.3	0	0	0
<i>Panicum</i> spp.	30	48 $\pm$ 41	6.7	17	2 $\pm$ 2	0.4
<i>Paulownia tomentosa</i>	50	10 $\pm$ 4	1.4	69	7 $\pm$ 2	1.3
<i>Phytolacca americana</i>	60	15 $\pm$ 6	2.1	83	22 $\pm$ 10	4.0
<i>Potentilla simplex</i>	0	0	0	33	3 $\pm$ 2	0.6
<i>Rhus copallina</i>	50	12 $\pm$ 7	1.7	17	2 $\pm$ 2	0.4
<i>R. glabra</i>	80	33 $\pm$ 12	4.6	83	28 $\pm$ 10	5.1
<i>Rubus allegheniensis</i>	40	65 $\pm$ 55	9.0	17	10 $\pm$ 10	1.8
<i>R. argutus</i>	50	24 $\pm$ 11	3.3	50	20 $\pm$ 11	3.7
<i>R. hispidus</i>	10	1 $\pm$ 1	0.1	0	0	0
<i>R. idaeus</i>	0	0	0	33	7 $\pm$ 5	1.3
<i>R. occidentalis</i>	20	9 $\pm$ 8	1.3	0	0	0
<i>Rubus</i> spp.	0	0	0	17	2 $\pm$ 2	0.4

Table 37 (Continued)

Species	Spring Collection			Summer Collection		
	Frequency (Percent)	Number Plants:		Frequency (Percent)	Number Plants:	
		Average/m ² ($\pm$ SE)	Percent of Total		Average/m ² ($\pm$ SE)	Percent of Total
<i>Sassafras albidum</i>	50	7 $\pm$ 3	1.0	33	3 $\pm$ 2	0.6
<i>Scutellaria elliptica</i>	10	1 $\pm$ 1	0.1	17	3 $\pm$ 3	0.6
<i>Smilax glauca</i>	10	1 $\pm$ 1	0.1	17	3 $\pm$ 3	0.6
<i>Solanum americanum</i>	10	1 $\pm$ 1	0.1	0	0	0
<i>S. nigrum</i>	10	1 $\pm$ 1	0.1	0	0	0
<i>Solidago</i> spp.	20	2 $\pm$ 1	0.3	0	0	0
<i>Sonchus asper</i>	10	1 $\pm$ 1	0.1	0	0	0
<i>Taraxacum officinale</i>	10	1 $\pm$ 1	0.1	0	0	0
<i>Typha latifolia</i>	10	1 $\pm$ 1	0.1	0	0	0
<i>Ulmus alata</i>	0	0	0	17	2 $\pm$ 2	0.4
<i>U. americana</i>	10	1 $\pm$ 1	0.1	17	2 $\pm$ 2	0.4
<i>U. rubra</i>	10	1 $\pm$ 1	0.1	0	0	0
<i>Verbascum thapsus</i>	70	53 $\pm$ 38	7.4	67	93 $\pm$ 63	17.0
<i>Verbena urticifolia</i>	10	2 $\pm$ 1	0.3	17	20 $\pm$ 20	3.7
<i>Viola</i> spp.	10	1 $\pm$ 1	0.1	17	2 $\pm$ 2	0.4
<i>Vitis aestivalis</i>	10	2 $\pm$ 2	0.3	0	0	0
<i>V. baileyana</i>	10	1 $\pm$ 1	0.1	17	2 $\pm$ 2	0.4
<i>V. vulpina</i>	20	3 $\pm$ 2	0.3	0	0	0
Unknown spp.	30	3	0.3	0	0	0

Table 38. Floristic composition of the buried viable seed population at Site 5.

Species	Spring Collection			Summer Collection		
	Frequency (Percent)	Number Plants: Average/m ² ($\pm$ SE)	Percent of Total	Frequency (Percent)	Number Plants: Average/m ² ($\pm$ SE)	Percent of Total
<i>Acalypha virginica</i>	0	0	0	17	2 $\pm$ 2	0.4
<i>Acer rubrum</i>	10	1 $\pm$ 1	0.05	0	0	0
<i>Agrostis perennans</i>	0	0	0	17	12 $\pm$ 2	2.5
<i>Andropogon virginicus</i>	20	2 $\pm$ 1	0.1	0	0	0
<i>Antennaria plantaginifolia</i>	0	0	0	17	2 $\pm$ 2	0.4
<i>Aralia racemosa</i>	10	1 $\pm$ 1	0.05	0	0	0
<i>Aster cordifolius</i>	10	1 $\pm$ 1	0.05	0	0	0
<i>A. divaricatus</i>	10	15 $\pm$ 9	0.8	0	0	0
<i>A. lateriflorus</i>	10	1 $\pm$ 1	0.05	17	3 $\pm$ 3	0.6
<i>A. pilosus</i>	50	13 $\pm$ 5	0.7	0	0	0
<i>Aster spp.*</i>	100	56 $\pm$ 10	2.9	33	5 $\pm$ 3	1.0
<i>Betula lenta</i>	90	65 $\pm$ 14	3.3	0	0	0
<i>B. lutea</i>	20	23 $\pm$ 18	1.2	0	0	0
<i>Campanula divaricata</i>	0	0	0	33	8 $\pm$ 8	1.7
<i>Carex platyphylla</i>	10	6 $\pm$ 6	0.3	0	0	0
<i>C. virescens</i>	10	30 $\pm$ 30	1.5	0	0	0
<i>Carex sp.</i>	10	3 $\pm$ 3	0.2	0	0	0
<i>Clematis virginiana</i>	10	1 $\pm$ 1	0.05	0	0	0
<i>Danthonia spicata</i>	0	0	0	17	3 $\pm$ 3	0.6
<i>Digitaria ischaemum</i>	10	1 $\pm$ 1	0.05	0	0	0
<i>Duchesnea indica</i>	10	95 $\pm$ 95	4.9	0	0	0
<i>Eleusine indica</i>	10	1 $\pm$ 1	0.05	0	0	0
<i>Epigaea repens</i>	0	0	0	17	7 $\pm$ 7	1.4
<i>Epilobium coloratum</i>	40	6 $\pm$ 3	0.3	0	0	0
<i>Erechtites hieracifolia</i>	90	41 $\pm$ 10	2.1	83	28 $\pm$ 9	5.8
<i>Erigeron annuus</i>	10	1 $\pm$ 1	0.05	0	0	0

Table 38 (Continued)

Species	Spring Collection			Summer Collection		
	Frequency (Percent)	Number Plants:		Frequency (Percent)	Number Plants:	
		Average/m ² ($\pm$ SE)	Percent of Total		Average/m ² ($\pm$ SE)	Percent of Total
<i>E. canadensis</i>	20	5 $\pm$ 3	0.3	0	0	0
<i>Erigeron</i> spp.	40	26 $\pm$ 16	1.3	33	2 $\pm$ 2	0.4
<i>Eupatorium purpureum</i>	0	0	0	50	20 $\pm$ 10	4.1
<i>E. rugosum</i> *	100	108 $\pm$ 25	5.6	17	3 $\pm$ 3	0.6
<i>E. serotinum</i> *	100	104 $\pm$ 16	5.4	17	5 $\pm$ 5	1.0
<i>Festuca obtusa</i>	10	1 $\pm$ 1	0.05	0	0	0
<i>Fragaria</i> sp.	0	0	0	33	3 $\pm$ 2	0.6
<i>Fraxinus americana</i>	10	2 $\pm$ 2	0.1	0	0	0
<i>F. pennsylvanica</i>	10	4 $\pm$ 4	0.2	0	0	0
<i>Galium triflorum</i>	20	2 $\pm$ 1	0.1	0	0	0
<i>Gnaphalium obtusifolium</i>	10	1 $\pm$ 1	0.05	0	0	0
<i>G. purpureum</i>	0	0	0	17	2 $\pm$ 2	0.4
<i>Gnaphalium</i> spp.	20	2 $\pm$ 1	0.1	17	2 $\pm$ 2	0.4
Gramineae spp.	90	298 $\pm$ 79	15.3	50	8 $\pm$ 5	1.7
<i>Helianthus strumosus</i>	10	1 $\pm$ 1	0.05	0	0	0
<i>Hieracium paniculatum</i>	0	0	0	17	8 $\pm$ 8	1.7
<i>Houstonia purpurea</i>	0	0	0	50	130 $\pm$ 99	26.9
<i>Hydrangea arborescens</i>	100	434 $\pm$ 170	22.3	33	38 $\pm$ 35	7.9
<i>Hydrophyllum virginianum</i>	30	18 $\pm$ 11	0.9	0	0	0
<i>Hypericum punctatum</i>	0	0	0	17	12 $\pm$ 12	2.5
<i>Juncus interior</i>	0	0	0	33	7 $\pm$ 5	1.4
<i>Lactuca</i> sp.	40	4 $\pm$ 2	0.2	0	0	0
<i>Liriodendron tulipifera</i> *	100	53 $\pm$ 8	2.7	17	2 $\pm$ 2	0.4
<i>Lobelia inflata</i>	10	33 $\pm$ 3	1.7	0	0	0
<i>Lysimachia ciliata</i>	0	11 $\pm$ 7	0.6	0	0	0
<i>L. quadrifolia</i>	0	0	0	17	2 $\pm$ 2	0.4

Table 38 (Continued)

Species	Spring Collection			Summer Collection		
	Frequency (Percent)	Average/m ² ($\pm$ SE)	Percent of Total	Frequency (Percent)	Average/m ² ($\pm$ SE)	Percent of Total
Mollugo verticillata	10	1 $\pm$ 1	0.05	0	0	0
Monarda clinopodia	30	18 $\pm$ 14	0.9	0	0	0
Oenothera biennis	40	7 $\pm$ 4	0.4	17	2 $\pm$ 2	0.4
Oxydendrum arboreum	10	1 $\pm$ 1	0.05	33	3 $\pm$ 2	0.6
Panicum commutatum	0	0	0	33	13 $\pm$ 12	2.7
P. dichotomum	0	0	0	17	22 $\pm$ 22	4.6
Panicum spp.	20	19 $\pm$ 17	1.0	0	0	0
Parthenocissus quinquefolia	30	8 $\pm$ 4	0.4	0	0	0
Paulownia tomentosa	30	63 $\pm$ 53	3.2	0	0	0
Phytolacca americana	70	24 $\pm$ 11	1.2	67	17 $\pm$ 6	3.5
Pilea pumila	20	8 $\pm$ 6	0.4	0	0	0
Plantago major	10	2 $\pm$ 2	0.1	0	0	0
Potentilla canadensis	10	5 $\pm$ 5	0.3	17	2 $\pm$ 2	0.4
Robinia pseudo-acacia	20	2 $\pm$ 1	0.1	0	0	0
Rhododendron sp.	0	0	0	17	2 $\pm$ 2	0.4
Rubus allegheniensis	70	91 $\pm$ 40	4.7	83	33 $\pm$ 12	6.8
R. argutus	10	5 $\pm$ 5	0.3	50	10 $\pm$ 6	2.1
R. idaeus	0	0	0	33	43 $\pm$ 34	15.2
R. occidentalis	20	10 $\pm$ 8	0.5	0	0	0
Rubus sp.	10	2 $\pm$ 2	0.1	0	0	0
Sambucus canadensis	10	1 $\pm$ 1	0.05	0	0	0
Sassafras albidum	0	0	0	17	2 $\pm$ 2	0.4
Sedum ternatum	30	77 $\pm$ 71	4.0	0	0	0
Smilax glauca	10	1 $\pm$ 1	0.05	33	5 $\pm$ 3	1.0

Table 38 (Continued)

Species	Spring Collection			Summer Collection		
	Frequency (Percent)	Average/m ² ($\pm$ SE)	Percent of Total	Frequency (Percent)	Average/m ² ($\pm$ SE)	Percent of Total
<i>Solidago altissima</i>	40	9 $\pm$ 5	0.5	0	0	0
<i>S. caesia</i>	10	6 $\pm$ 6	0.3	0	0	0
<i>Solidago</i> spp.	20	5 $\pm$ 3	0.3	17	2 $\pm$ 2	0.4
<i>Sonchus asper</i>	10	2 $\pm$ 2	0.1	0	0	0
<i>Sphenopholis nitida</i>	0	0	0	17	2 $\pm$ 2	0.4
<i>Stellaria media</i>	20	3 $\pm$ 2	0.15	0	0	0
<i>S. pubera</i>	10	2 $\pm$ 1	0.1	0	0	0
<i>Taraxacum officinale</i>	10	1 $\pm$ 1	0.05	0	0	0
<i>Taraxacum</i> sp.	10	1 $\pm$ 1	0.05	0	0	0
<i>Thalictrum thalictroides</i>	10	2 $\pm$ 2	0.1	0	0	0
<i>Triosteum angustifolium</i>	0	0	0	33	3 $\pm$ 2	0.6
<i>Typha latifolia</i>	70	27 $\pm$ 10	1.4	0	0	0
<i>Ulmus americana</i>	10	27 $\pm$ 27	1.4	0	0	0
<i>Vaccinium</i> spp.	0	0	0	17	5 $\pm$ 5	1.0
<i>Viola papilionacea</i>	70	22 $\pm$ 9	1.1	0	0	0
<i>Viola</i> spp.	40	6 $\pm$ 3	0.3	0	0	0
<i>Vitis baileyana</i>	10	2 $\pm$ 2	0.1	0	0	0
<i>V. vulpina</i>	10	7 $\pm$ 7	0.4	17	2 $\pm$ 2	0.4
<i>Vitis</i> sp.	10	1 $\pm$ 1	0.05	0	0	0
Unknown spp.	20	4 $\pm$ 3	0.2	17	3 $\pm$ 2	0.6

*Mean number of plants/m² for the spring and summer samples were significantly different at the .05 level of probability.

Table 39. Floristic composition of the buried viable seed population at Site 6.

Species	Spring Collection			Summer Collection		
	Frequency (Percent)	Number Plants: Average/m ² (± SE)	Percent of Total	Frequency (Percent)	Number Plants: Average/m ² (± SE)	Percent of Total
<i>Acalypha rhomboidea</i>	0	0	0	17	2±2	0.2
<i>Agrostis perennans</i>	0	0	0	17	2±2	0.2
<i>A. stolonifera</i>	20	11±9	0.5	0	3±3	0.3
<i>Ambrosia artemisiifolia</i>	20	6±4	0.3	0	0	0
<i>Amphicarpa bracteata</i>	20	2±2	0.09	0	0	0
<i>Andropogon virginicus</i>	10	1±1	0.04	50	5±2	0.5
<i>Aster cordifolius</i>	0	0	0	17	2±2	0.2
<i>A. divaricatus</i>	0	0	0	17	2±2	0.2
<i>A. lateriflorus</i>	0	0	0	17	2±2	0.2
<i>A. pilosus</i>	0	0	0	17	2±2	0.2
<i>A. puniceus</i>	0	0	0	17	2±2	0.2
<i>Aster</i> spp.	40	5±2	0.2	50	15±8	1.4
<i>Betula lenta</i>	0	0	0	33	3±2	0.3
<i>Campanula divaricata</i>	20	97±95	4.6	17	2±2	0.2
<i>Carex virescens</i>	10	1±1	0.04	0	0	0
<i>Carex</i> spp.	20	2±1	0.09	0	0	0
<i>Caryophyllaceae</i> spp.	10	2±2	0.09	0	0	0
<i>Clematis dioscoreifolia</i>	10	2±2	0.09	0	0	0
<i>C. virginiana</i>	0	0	0	17	3±3	0.3
<i>Collinsonia canadensis</i>	0	0	0	50	37±31	3.4
<i>Convolvulus sepium</i>	10	1±1	0.04	0	0	0
<i>Danthonia spicata</i>	10	3±3	0.1	17	2±2	0.2
<i>Digitaria</i> spp.	10	18±18	0.8	0	0	0
<i>Dioscorea villosa</i>	0	0	0	17	2±2	0.2
<i>Erechtites hieracifolia</i>	80	28±9	1.3	67	13±6	1.2
<i>Erigeron annuus</i>	0	0	0	50	37±25	3.4

Table 39 (Continued)

Species	Spring Collection			Summer Collection		
	Frequency (Percent)	Average/m ² ($\pm$ SE)	Percent of Total	Frequency (Percent)	Average/m ² ($\pm$ SE)	Percent of Total
<i>E. canadensis</i>	20	4 $\pm$ 3	0.2	0	0	0
<i>Erigeron</i> spp.	60	9 $\pm$ 3	0.4	33	5 $\pm$ 3	0.5
<i>Eupatorium purpureum</i>	70	100 $\pm$ 34	4.7	67	27 $\pm$ 11	2.5
<i>E. rugosum</i>	60	137 $\pm$ 86	6.4	83	57 $\pm$ 26	5.3
<i>E. serotinum</i>	20	4 $\pm$ 3	0.2	0	0	0
<i>E. sessilifolium</i>	20	13 $\pm$ 11	0.6	0	0	0
<i>Fragaria virginiana</i>	40	8 $\pm$ 5	0.4	17	3 $\pm$ 3	0.3
<i>Fragaria</i> sp.	20	4 $\pm$ 3	0.2	17	8 $\pm$ 8	0.8
<i>Galium triflorum</i>	10	101 $\pm$ 101	4.7	33	13 $\pm$ 9	1.2
<i>Gnaphalium obtusifolium</i>	10	2 $\pm$ 2	0.09	0	0	0
<i>Gnaphalium</i> spp.	40	5 $\pm$ 2	0.2	33	3 $\pm$ 2	0.3
Gramineae spp.*	50	56 $\pm$ 47	2.6	50	10 $\pm$ 5	0.9
<i>Hedeoma pulegioides</i> *	40	34 $\pm$ 24	1.6	17	2 $\pm$ 2	0.2
<i>Helianthus microcephalus</i>	30	3 $\pm$ 2	0.1	0	0	0
<i>Helianthus</i> spp.	30	5 $\pm$ 3	0.2	17	2 $\pm$ 2	0.2
<i>Hieracium paniculatum</i>	20	16 $\pm$ 14	0.8	33	5 $\pm$ 3	0.5
<i>Houstonia purpurea</i>	70	175 $\pm$ 93	8.2	83	112 $\pm$ 41	10.4
<i>Hydrangea arborescens</i>	80	519 $\pm$ 420	24.4	83	160 $\pm$ 81	14.9
<i>Hypericum mutilum</i>	0	0	0	17	2 $\pm$ 2	0.2
<i>Impatiens capensis</i>	10	1 $\pm$ 1	0.04	0	0	0
<i>Juncus interior</i>	20	6 $\pm$ 4	0.3	17	2 $\pm$ 2	0.2
<i>Juncus</i> spp.	20	7 $\pm$ 6	0.3	0	0	0
<i>Lactuca</i> sp.	20	10 $\pm$ 7	0.5	17	7 $\pm$ 7	0.7
<i>Liriodendron tulipifera</i>	60	21 $\pm$ 8	1.0	100	25 $\pm$ 9	2.3
<i>Lobelia inflata</i>	10	6 $\pm$ 6	0.3	50	33 $\pm$ 28	3.1
<i>Ludwigia microcarpa</i>	10	1 $\pm$ 1	0.04	0	0	0

Table 39 (Continued)

Species	Spring Collection			Summer Collection		
	Frequency (Percent)	Number Plants:		Frequency (Percent)	Number Plants:	
		Average/m ² ($\pm$ SE)	Percent of Total		Average/m ² ($\pm$ SE)	Percent of Total
<i>Lysimachia ciliata</i>	10	1 $\pm$ 1	0.04	0	0	0
<i>Mikania scandens</i>	10	1 $\pm$ 1	0.04	0	0	0
<i>Monarda clinopodia</i>	10	1 $\pm$ 1	0.04	33	42 $\pm$ 40	3.9
<i>Oenothera biennis</i>	10	1 $\pm$ 1	0.04	0	0	0
<i>Oxalis stricta</i>	30	9 $\pm$ 6	0.4	50	8 $\pm$ 4	0.8
<i>Oxalis</i> sp.	10	1 $\pm$ 1	0.04	0	0	0
<i>Oxydendrum arboreum</i>	80	50 $\pm$ 30	2.3	17	2 $\pm$ 2	0.2
<i>Panicum commutatum</i>	30	13 $\pm$ 8	0.6	50	33 $\pm$ 29	3.1
<i>P. dichotomum</i>	20	18 $\pm$ 16	0.8	33	5 $\pm$ 3	0.5
<i>P. lanuginosum</i>	30	8 $\pm$ 6	0.4	0	0	0
<i>Panicum</i> sp.	10	1 $\pm$ 1	0.04	0	0	0
<i>Paronychia canadensis</i>	30	4 $\pm$ 2	0.2	0	0	0
<i>Paulownia tomentosa</i>	10	1 $\pm$ 1	0.04	0	0	0
<i>Phytolacca americana</i>	60	33 $\pm$ 19	1.5	67	30 $\pm$ 15	2.8
<i>Pilea pumila</i>	0	0	0	17	12 $\pm$ 12	1.1
<i>Poa cuspidata</i>	10	3 $\pm$ 2	0.1	0	0	0
<i>P. pratensis</i> *	20	5 $\pm$ 3	0.2	83	60 $\pm$ 32	5.6
<i>Polygonum scandens</i>	10	16 $\pm$ 16	0.8	0	0	0
<i>Potentilla canadensis</i>	30	4 $\pm$ 2	0.2	17	2 $\pm$ 2	0.2
<i>P. simplex</i>	10	2 $\pm$ 2	0.09	0	0	0
<i>Ranunculus carolinianus</i>	0	0	0	17	3 $\pm$ 3	0.3
<i>Robinia pseudo-acacia</i>	20	2 $\pm$ 1	0.09	0	0	0
<i>Rubus allegheniensis</i>	60	264 $\pm$ 127	12.4	83	88 $\pm$ 26	8.2
<i>R. argutus</i>	40	38 $\pm$ 19	1.8	33	15 $\pm$ 13	1.4
<i>R. idaeus</i>	0	0	0	17	3 $\pm$ 3	0.3
<i>R. occidentalis</i>	10	4 $\pm$ 4	0.2	0	0	0

Table 39 (Continued)

Species	Spring Collection			Summer Collection		
	Frequency (Percent)	Number Plants:		Frequency (Percent)	Number Plants:	
		Average/m ² ($\pm$ SE)	Percent of Total		Average/m ² ($\pm$ SE)	Percent of Total
Rubus spp.	10	1 $\pm$ 1	0.04	17	2 $\pm$ 2	0.2
Salix alba	10	1 $\pm$ 1	0.04	17	2 $\pm$ 2	0.2
Sambucus canadensis	10	1 $\pm$ 1	0.04	17	5 $\pm$ 5	0.5
Sanicula sp.*a	10	1 $\pm$ 1	0.04	33	8 $\pm$ 7	0.8
Sassafras albidum	20	2 $\pm$ 1	0.09	0	0	0
Scrophularia marilandica	10	1 $\pm$ 1	0.04	0	0	0
Scutellaria elliptica	10	2 $\pm$ 2	0.09	0	0	0
Silene stellata	10	2 $\pm$ 2	0.09	0	0	0
Smilax glauca	10	1 $\pm$ 1	0.04	17	5 $\pm$ 5	0.5
Solanum americanum	10	1 $\pm$ 1	0.04	0	0	0
S. nigrum	10	1 $\pm$ 1	0.04	17	2 $\pm$ 2	0.2
Solidago altissima	20	2 $\pm$ 1	0.09	0	0	0
S. caesia	50	18 $\pm$ 8	0.8	33	8 $\pm$ 5	0.8
Solidago spp.*	80	12 $\pm$ 3	0.6	17	2 $\pm$ 2	0.2
Stellaria media	10	44 $\pm$ 44	2.1	0	0	0
Streptopus roseus	0	0	0	17	2 $\pm$ 2	0.2
Taraxacum officinale	10	3 $\pm$ 3	0.1	17	12 $\pm$ 12	1.1
Taraxacum sp.	0	0	0	17	15 $\pm$ 15	1.4
Thalictrum thalictroides	20	2 $\pm$ 1	0.09	17	2 $\pm$ 2	0.2
Tradescantia ohiensis	10	19 $\pm$ 19	0.84	0	0	0
Triosteum angustifolium	0	0	0	17	2 $\pm$ 2	0.2
Vaccinium sp.	0	0	0	17	2 $\pm$ 2	0.2
Verbascum thapsus	10	4 $\pm$ 4	0.2	17	2 $\pm$ 2	0.2
Vicia spp.	10	2 $\pm$ 2	0.09	17	7 $\pm$ 7	0.7
Viola papilionacea	80	31 $\pm$ 14	1.5	33	17 $\pm$ 13	1.6
Viola spp.	70	18 $\pm$ 7	0.8	67	43 $\pm$ 34	4.0

Table 39 (Continued)

Species	Spring Collection			Summer Collection		
	Frequency (Percent)	Average/m ² ($\pm$ SE)	Percent of Total	Frequency (Percent)	Average/m ² ($\pm$ SE)	Percent of Total
<i>Vitis aestivalis</i>	0	0	0	17	3 $\pm$ 3	0.3
<i>V. baileyana</i>	30	7 $\pm$ 5	0.3	17	5 $\pm$ 5	0.5
<i>V. vulpina</i>	10	27 $\pm$ 27	1.3	33	10 $\pm$ 8	0.9
<i>Vitis</i> spp.	20	3 $\pm$ 2	0.1	0	0	0
Unknown spp.	50	19	0.9	17	8	0.8

*Mean number of plants/m² for the spring and summer samples were significantly different at the .05 level of probability.

^aSanicula sp. may have actually been Ranunculus carolinianus.

Table 40. Floristic composition of the buried viable seed population at Site 7.

Species	Spring Collection			Summer Collection		
	Frequency (Percent)	Number Plants: Average/m ² (± SE)	Percent of Total	Frequency (Percent)	Number Plants: Average/m ² (± SE)	Percent of Total
<i>Acalypha rhomboidea</i>	10	2±2	0.2	0	0	0
<i>Acer rubrum</i>	10	1±1	0.1	0	0	0
<i>A. saccharum</i>	10	1±1	0.1	0	0	0
<i>Agrostis hyemalis</i>	10	1±1	0.1	0	0	0
<i>A. perennans</i>	10	1±1	0.1	0	0	0
<i>A. stolonifera</i>	20	19±13	1.7	0	0	0
<i>Andropogon virginicus</i>	10	1±1	0.1	33	7±5	0.6
<i>Antennaria plantaginifolia</i>	0	0	0	17	2±2	0.2
<i>Aralia racemosa</i>	0	0	0	50	7±4	0.6
<i>Aster divaricatus</i>	0	0	0	83	105±54	8.5
<i>A. lateriflorus</i>	10	1±1	0.1	17	2±2	0.2
<i>A. pilosus</i>	10	1±1	0.1	50	15±10	1.2
<i>A. umbellatus</i>	10	1±1	0.1	0	0	0
<i>Aster spp.</i>	50	6±2	0.5	100	27±11	2.2
<i>Betula lenta</i>	0	0	0	83	23±7	1.9
<i>Campanula divaricata</i>	10	3±3	0.3	0	0	0
<i>Carex debilis</i>	0	0	0	17	2±2	0.2
<i>C. oxylepsis</i>	10	8±8	0.7	0	0	0
<i>Carex spp.</i>	40	8±4	0.7	17	5±5	0.4
<i>Chenopodium ambrosioides</i>	0	0	0	17	2±2	0.2
<i>Clematis virginiana</i>	0	0	0	33	2±2	0.2
<i>Cyperus odoratus</i>	10	1±1	0.1	0	0	0
<i>Danthonia spicata</i>	30	10±7	0.9	0	0	0
<i>Digitaria ischaemum</i>	10	1±1	0.1	0	0	0
<i>D. sanguinalis</i>	0	0	0	17	3±3	0.2
<i>Epilobium coloratum</i>	0	0	0	33	7±4	0.6

Table 40 (Continued)

Species	Spring Collection			Summer Collection		
	Frequency (Percent)	Number Plants:		Frequency (Percent)	Number Plants:	
		Average/m ² ($\pm$ SE)	Percent of Total		Average/m ² ($\pm$ SE)	Percent of Total
<i>Eragrostis intermedia</i>	10	1 $\pm$ 1	0.1	0	0	0
<i>Eragrostis</i> sp.	30	3 $\pm$ 2	0.3	0	0	0
<i>Erechtites hieracifolia</i>	70	57 $\pm$ 41	5.1	100	63 $\pm$ 17	5.1
<i>Erigeron annuus</i>	10	1 $\pm$ 1	0.1	17	2 $\pm$ 2	0.2
<i>E. canadensis</i>	30	4 $\pm$ 2	0.4	0	0	0
<i>Erigeron</i> spp.	30	7 $\pm$ 5	0.7	17	2 $\pm$ 2	0.2
<i>Eupatorium purpureum</i> *	80	33 $\pm$ 11	2.9	33	2 $\pm$ 2	0.2
<i>E. rugosum</i> *	50	8 $\pm$ 2	0.7	100	47 $\pm$ 12	3.8
<i>E. serotinum</i>	70	45 $\pm$ 30	4.0	100	100 $\pm$ 22	8.1
<i>E. sessifolium</i>	20	8 $\pm$ 7	0.7	0	0	0
<i>Festuca obtusa</i>	10	2 $\pm$ 2	0.2	0	0	0
<i>Fragaria virginiana</i>	30	5 $\pm$ 3	0.4	0	0	0
<i>Galium triflorum</i>	0	0	0	33	30 $\pm$ 26	2.4
<i>Gnaphalium obtusifolium</i>	20	2 $\pm$ 1	0.2	0	0	0
<i>G. purpureum</i>	10	2 $\pm$ 2	0.2	0	0	0
<i>Gnaphalium</i> spp.	10	1 $\pm$ 1	0.1	17	2 $\pm$ 2	0.2
<i>Goodyera repens</i>	10	6 $\pm$ 6	0.5	0	0	0
Gramineae spp.	80	42 $\pm$ 15	3.7	100	30 $\pm$ 14	2.4
<i>Helianthus microcephalus</i>	80	12 $\pm$ 3	1.1	0	0	0
<i>Helianthus</i> spp.	60	10 $\pm$ 4	0.9	0	0	0
<i>Hieracium paniculatum</i>	30	10 $\pm$ 7	0.9	0	0	0
<i>Houstonia purpurea</i>	70	106 $\pm$ 56	9.4	0	0	0
<i>Hydrangea arborescens</i>	70	148 $\pm$ 71	13.1	100	222 $\pm$ 87	18.0
<i>Hydrophyllum virginianum</i>	0	0	0	33	23 $\pm$ 15	1.9
<i>Juncus interior</i>	40	104 $\pm$ 86	9.2	0	0	0
<i>Juncus</i> sp.	20	2 $\pm$ 1	0.2	0	0	0

Table 40 (Continued)

Species	Spring Collection			Summer Collection		
	Frequency (Percent)	Number Plants:		Frequency (Percent)	Number Plants:	
		Average/m ² ($\pm$ SE)	Percent of Total		Average/m ² ($\pm$ SE)	Percent of Total
<i>Lactuca</i> sp.	30	5 $\pm$ 3	0.4	50	7 $\pm$ 5	0.6
<i>Lindernia anagallidea</i>	10	16 $\pm$ 16	1.4	0	0	0
<i>Liriodendron tulipifera</i> *	50	16 $\pm$ 7	1.4	100	57 $\pm$ 18	4.6
<i>Lobelia inflata</i>	20	8 $\pm$ 6	0.7	33	117 $\pm$ 115	9.5
<i>Lysimachia ciliata</i>	0	0	0	17	128 $\pm$ 128	10.4
<i>Oenothera biennis</i>	20	4 $\pm$ 3	0.4	17	3 $\pm$ 3	0.2
<i>Oxalis stricta</i>	10	3 $\pm$ 3	0.3	33	7 $\pm$ 5	0.6
<i>Oxydendrum arboreum</i>	10	7 $\pm$ 7	0.6	0	0	0
<i>Panicum commutatum</i>	0	0	0	33	3 $\pm$ 3	0.2
<i>P. dichotomum</i>	60	66 $\pm$ 25	5.9	0	0	0
<i>P. lanuginosum</i>	20	3 $\pm$ 2	0.3	0	0	0
<i>Panicum</i> spp.	30	4 $\pm$ 2	0.4	0	0	0
<i>Paronychia canadensis</i>	10	1 $\pm$ 1	0.1	0	0	0
<i>Parthenocissus quinquefolia</i>	10	1 $\pm$ 1	0.1	33	3 $\pm$ 2	0.2
<i>Paulownia tomentosa</i>	10	1 $\pm$ 1	0.1	0	0	0
<i>Phleum pratense</i>	0	0	0	17	2 $\pm$ 2	0.2
<i>Physalis pubescens</i> var. <i>grisea</i>	10	2 $\pm$ 2	0.2	0	0	0
<i>Phytolacca americana</i>	50	13 $\pm$ 5	1.2	67	23 $\pm$ 16	1.9
<i>Poa pratensis</i>	10	1 $\pm$ 1	0.1	0	0	0
<i>Portulaca oleracea</i>	10	3 $\pm$ 3	0.3	0	0	0
<i>Potentilla canadensis</i>	10	5 $\pm$ 5	0.4	0	0	0
<i>Quercus alba</i>	10	1 $\pm$ 1	0.1	0	0	0
<i>Ranunculus carolinianus</i>	0	0	0	33	10 $\pm$ 2	0.8
<i>Robinia pseudo-acacia</i>	10	1 $\pm$ 1	0.1	0	0	0
<i>Rubus allegheniensis</i>	80	111 $\pm$ 50	9.9	67	13 $\pm$ 6	1.1
<i>R. argutus</i>	20	53 $\pm$ 50	4.7	0	0	0

Table 40 (Continued)

Species	Spring Collection			Summer Collection		
	Frequency (Percent)	Number Plants: Average/m ² ($\pm$ SE)	Percent of Total	Frequency (Percent)	Number Plants: Average/m ² ($\pm$ SE)	Percent of Total
<i>R. occidentalis</i>	30	23 $\pm$ 20	2.0	0	0	0
<i>Salix alba</i>	20	2 $\pm$ 1	0.2	0	0	0
<i>S. nigra</i>	10	1 $\pm$ 1	0.1	0	0	0
<i>Sambucus canadensis</i>	0	0	0	17	2 $\pm$ 2	0.2
<i>Sanicula</i> sp.*a	0	0	0	67	35 $\pm$ 12	2.8
<i>Sassafras albidum</i>	0	0	0	17	2 $\pm$ 2	0.2
<i>Scirpus</i> sp.	0	0	0	17	2 $\pm$ 2	0.2
<i>Smilax glauca</i>	20	2 $\pm$ 1	0.2	0	0	0
<i>Solanum americanum</i>	10	1 $\pm$ 1	0.1	0	0	0
<i>Solidago altissima</i>	10	1 $\pm$ 1	0.1	0	0	0
<i>S. arguta</i>	20	2 $\pm$ 1	0.2	0	0	0
<i>S. caesia</i>	30	6 $\pm$ 3	0.5	50	8 $\pm$ 5	0.6
<i>Solidago</i> spp.	50	7 $\pm$ 3	0.6	50	5 $\pm$ 2	0.4
<i>Sonchus asper</i>	10	1 $\pm$ 1	0.1	0	0	0
<i>Stellaria media</i>	0	0	0	33	5 $\pm$ 3	0.4
<i>Stellaria pubera</i>	10	1 $\pm$ 1	0.1	0	0	0
<i>Taraxacum officinale</i>	20	2 $\pm$ 1	0.2	33	7 $\pm$ 5	0.6
<i>Thalictrum thalictroides</i>	0	0	0	17	7 $\pm$ 7	0.6
<i>Tiarella cordifolia</i>	0	0	0	33	13 $\pm$ 9	1.1
<i>Trifolium repens</i>	10	1 $\pm$ 1	0.1	0	0	0
<i>Triosteum angustifolium</i>	10	4 $\pm$ 4	0.4	0	0	0
<i>Typha latifolia</i>	10	1 $\pm$ 1	0.1	33	3 $\pm$ 2	0.2
<i>Vaccinium</i> sp.	10	10 $\pm$ 10	0.9	0	0	0
<i>Veronica peregrina</i>	10	10 $\pm$ 10	0.9	0	0	0
<i>Viola papilionacea</i>	50	25 $\pm$ 18	2.2	17	3 $\pm$ 3	0.2

Table 40 (Continued)

Species	Spring Collection			Summer Collection		
	Frequency (Percent)	Average/m ² ($\pm$ SE)	Percent of Total	Frequency (Percent)	Average/m ² ($\pm$ SE)	Percent of Total
Viola spp.	30	9 $\pm$ 6	0.8	50	12 $\pm$ 7	1.0
Vitis aestivalis	10	2 $\pm$ 2	0.2	0	0	0
V. baileyana	30	8 $\pm$ 5	0.7	0	0	0
V. vulpina	10	2 $\pm$ 2	0.2	33	17 $\pm$ 13	1.4
Unknown spp.	40	5	0.4	33	10	0.8

*Mean number of plants/m² for the spring and summer samples were significantly different at the .05 level of probability.

^aSanicula sp. may have actually been Ranunculus carolinianus.

Table 41. Floristic composition of the buried viable seed population at Site 8.

Species	Spring Collection			Summer Collection		
	Frequency (Percent)	Number Plants:		Frequency (Percent)	Number Plants:	
		Average/m ² ($\pm$ SE)	Percent of Total		Average/m ² ($\pm$ SE)	Percent of Total
<i>Acalypha rhomboidea</i>	10	1 $\pm$ 1	0.08	0	0	0
<i>A. virginica</i>	10	2 $\pm$ 2	0.15	0	0	0
<i>Acalypha</i> sp.	10	2 $\pm$ 2	0.15	0	0	0
<i>Agrostis stolonifera</i>	10	2 $\pm$ 2	0.15	0	0	0
<i>Ambrosia artemisiifolia</i>	0	0	0	17	2 $\pm$ 2	0.3
<i>Andropogon virginicus</i>	40	4 $\pm$ 2	0.3	0	0	0
<i>Aralia racemosa</i>	0	0	0	0	3 $\pm$ 3	0.4
<i>Aster acuminata</i>	10	4 $\pm$ 4	0.3	0	0	0
<i>A. cordifolius</i>	40	13 $\pm$ 7	1.0	17	2 $\pm$ 2	0.3
<i>A. lateriflorus</i>	40	5 $\pm$ 2	0.4	0	0	0
<i>A. pilosus</i>	50	6 $\pm$ 2	0.5	33	8 $\pm$ 7	1.1
<i>Aster</i> spp.	80	21 $\pm$ 5	1.6	67	13 $\pm$ 8	1.8
<i>Asteraceae</i> sp.	10	1 $\pm$ 1	0.08	0	0	0
<i>Betula lenta</i>	20	3 $\pm$ 2	0.2	17	2 $\pm$ 2	0.3
<i>Carex virescens</i>	20	2 $\pm$ 1	0.15	0	0	0
<i>Carex</i> spp.	60	10 $\pm$ 4	0.8	17	2 $\pm$ 2	0.3
<i>Caryophyllaceae</i> sp.	10	1 $\pm$ 1	0.08	0	0	0
<i>Cercis canadensis</i>	10	1 $\pm$ 1	0.08	0	0	0
<i>Clematis virginiana</i>	0	0	0	33	5 $\pm$ 3	0.7
<i>Epilobium coloratum</i>	10	1 $\pm$ 1	0.08	0	0	0
<i>Eragrostis</i> sp.	10	1 $\pm$ 1	0.08	0	0	0
<i>Erechtites hieracifolia</i>	100	44 $\pm$ 9	3.5	100	58 $\pm$ 17	7.9
<i>Erigeron annuus</i>	0	0	0	17	2 $\pm$ 2	0.3
<i>E. canadensis</i>	10	3 $\pm$ 3	0.2	0	0	0
<i>Erigeron</i> spp.	30	6 $\pm$ 3	0.45	0	0	0
<i>Eupatorium purpureum</i>	20	13 $\pm$ 12	1.0	33	13 $\pm$ 10	1.8

Table 41 (Continued)

Species	Spring Collection			Summer Collection		
	Frequency (Percent)	Number Plants:		Frequency (Percent)	Number Plants:	
		Average/m ² (± SE)	Percent of Total		Average/m ² (± SE)	Percent of Total
<i>E. rugosum</i>	80	42±13	3.3	67	25±12	3.4
<i>E. serotinum</i>	90	17±3	1.3	67	17±6	2.3
<i>E. sessifolium</i>	20	3±2	0.2	0	0	0
<i>Festuca obtusa</i>	10	2±2	0.15	0	0	0
<i>Fragaria virginiana</i>	50	25±11	2.0	0	0	0
<i>Fragaria</i> sp.	30	18±14	2.0	0	0	0
<i>Galium triflorum</i>	20	9±8	0.7	0	0	0
<i>Gnaphalium obtusifolium</i>	10	1±1	0.08	0	0	0
<i>Gnaphalium</i> spp.	10	4±4	0.3	0	0	0
Gramineae spp.*	80	39±9	3.1	50	8±4	1.1
<i>Helianthus microcephalus</i>	10	1±1	0	0	0	0
<i>Houstonia purpurea</i> *	100	249±56	19.5	67	78±37	10.7
<i>Hydrangea arborescens</i>	100	128±53	10.0	67	60±24	8.2
<i>Hypericum</i> sp.	10	8±8	0.6	0	0	0
<i>Juncus interior</i>	10	1±1	0.08	0	0	0
<i>Lactuca</i> sp.	20	2±1	0.15	50	5±2	0.7
<i>Liriodendron tulipifera</i>	80	30±7	2.4	100	38±12	5.2
<i>Lobelia inflata</i>	40	97±55	7.6	17	2±10	2.7
<i>L. siphilitica</i>	10	5±5	0.4	0	0	0
<i>Lolium multiflorum</i>	10	3±3	0.2	0	0	0
<i>Monarda clinopodia</i>	10	18±18	1.4	17	10±10	1.4
<i>Muhlenbergia tenuiflora</i>	10	2±2	0.15	0	0	0
<i>Oenothera biennis</i>	30	16±10	1.3	0	0	0
<i>Oxalis grandis</i>	10	2±2	0.15	0	0	0
<i>O. stricta</i>	20	2±1	0.15	0	0	0
<i>Oxydendron arboreum</i>	30	4±2	0.3	0	0	0

Table 41 (Continued)

Species	Spring Collection			Summer Collection		
	Frequency (Percent)	Number Plants:		Frequency (Percent)	Number Plants:	
		Average/m ² (± SE)	Percent of Total		Average/m ² (± SE)	Percent of Total
<i>Panicum commutatum</i>	20	17±15	1.8	67	40±22	5.5
<i>P. dichotomum</i>	30	4±2	0.3	0	0	0
<i>P. lanuginosum</i>	40	8±4	0.6	0	0	0
<i>Panicum</i> spp.	30	4±2	0.3	0	0	0
<i>Paronychia</i> sp.	10	2±2	0.15	0	0	0
<i>Paulownia tomentosa</i>	10	1±1	0.08	0	0	0
<i>Phleum pratense</i>	10	1±1	0.08	17	2±2	2.7
<i>Phytolacca americana</i>	70	21±8	1.6	83	22±7	3.0
<i>Pilea pumila</i>	0	0	0	17	3±3	4.1
<i>Poa cuspidata</i>	10	1±1	0.08	0	0	0
<i>P. pratensis</i> *	20	2±2	0.15	83	115±46	15.7
<i>Portulaca oleracea</i>	10	2±2	0.15	0	0	0
<i>Potentilla canadensis</i>	50	14±6	1.1	17	5±5	0.7
<i>P. simplex</i>	10	1±1	0.08	33	5±3	0.7
<i>Potentilla</i> sp.	10	1±1	0.08	0	0	0
<i>Rhus glabra</i>	20	2±1	0.15	0	0	0
<i>Robinia pseudo-acacia</i>	10	2±2	0.15	0	0	0
<i>Rubus allegheniensis</i>	80	103±44	8.1	50	103±88	14.1
<i>R. argutus</i>	10	2±2	0.15	17	17±13	2.3
<i>R. idaeus</i>	0	0	0	33	5±3	0.7
<i>R. hispidus</i>	10	1±1	0.08	0	0	0
<i>R. occidentalis</i>	30	5±3	0.4	0	0	0
<i>Rubus</i> spp.	0	0	0	17	3±3	4.1
<i>Rudbeckia hirta</i>	10	3±3	0.2	0	0	0
<i>Salix alba</i>	10	1±1	0.08	0	0	0

Table 41 (Continued)

Species	Spring Collection			Summer Collection		
	Frequency (Percent)	Number Plants: Average/m ² ($\pm$ SE)	Percent of Total	Frequency (Percent)	Number Plants: Average/m ² ($\pm$ SE)	Percent of Total
<i>S. nigra</i>	20	3 $\pm$ 2	0.2	0	0	0
<i>Sanicula</i> sp.*a	10	2 $\pm$ 2	0.15	0	0	0
<i>Sassafras albidum</i>	10	1 $\pm$ 1	0.08	0	0	0
<i>Solidago altissima</i>	40	4 $\pm$ 2	0.3	0	0	0
<i>S. caesia</i>	20	6 $\pm$ 4	0.5	17	2 $\pm$ 2	2.7
<i>Solidago</i> spp.	20	4 $\pm$ 3	0.3	33	3 $\pm$ 2	4.1
<i>Sonchus asper</i>	10	2 $\pm$ 2	0.15	0	0	0
<i>Stellaria media</i>	0	0	0	17	2 $\pm$ 2	2.7
<i>Taraxacum officinale</i>	10	1 $\pm$ 1	0.08	50	7 $\pm$ 5	1.0
<i>Thalictrum thalictroides</i>	20	2 $\pm$ 1	0.15	0	0	0
<i>Typha latifolia</i>	20	14 $\pm$ 10	1.1	17	2 $\pm$ 2	2.7
<i>Verbascum thapsus</i>	40	15 $\pm$ 12	1.2	17	2 $\pm$ 2	2.7
<i>Verbena urticifolia</i>	10	1 $\pm$ 1	0.08	0	0	0
<i>Veronica peregrina</i>	10	3 $\pm$ 3	0.2	0	0	0
<i>Viola palmata</i>	10	3 $\pm$ 3	0.2	0	0	0
<i>V. papilionacea</i>	90	77 $\pm$ 71	6.0	0	0	0
<i>Viola</i> spp.	70	27 $\pm$ 14	2.1	0	0	0
<i>Vitis aestivalis</i>	20	2 $\pm$ 1	0.15	17	23 $\pm$ 23	3.1
<i>V. baileyana</i>	20	5 $\pm$ 3	0.4	0	0	0
<i>V. vulpina</i>	20	6 $\pm$ 4	0.5	50	18 $\pm$ 13	2.5
<i>Vitis</i> spp.	20	8 $\pm$ 6	0.6	0	0	0
Unknown spp.	50	16 $\pm$ 13	1.3	0	0	0

*Mean number of plants/m² for the spring and summer samples were significantly different at the .05 level of probability.

^a*Sanicula* sp. may have actually been *Ranunculus carolinianus*.

APPENDIX D

SEED GERMINATION FROM DIFFERENT SOIL DEPTHS

Table 42. Overall summary of species germination from different soil depths.^a

Species	Soil Layer		
	Litter	0-5 cm	5-10 cm
A. Spring Samples			
1. Species germinating in greatest numbers from the litter layer.			
<i>Acer rubrum</i>	80	15	5
<i>Fragaria</i> spp.	100	0	0
<i>Fraxinus americana</i>	100	0	0
<i>Ranunculus carolinianus</i>	67	0	33
<i>Sedum ternatum</i>	85	15	2
<i>Ulmus americana</i>	64	37	0
2. Species germinating in nearly equal numbers from the litter and 0-5 cm layers.			
<i>Andropogon virginicus</i>	44	44	12
<i>Aralia racemosa</i>	50	50	0
<i>Aster divaricatus</i>	53	30	17
<i>Platanus occidentalis</i>	53	47	0
<i>Salix alba</i>	50	50	0
3. Species germinating in greatest numbers from the 0-5 cm layer.			
<i>Agrostis perennans</i>	0	100	0
<i>Amphicarpa bracteata</i>	0	100	0
<i>Betula lutea</i>	13	70	17
<i>Cercis canadensis</i>	2	62	36
<i>Danthonia spicata</i>	9	61	30
<i>Gnaphalium obtusifolium</i>	6	59	35
<i>Hieracium paniculatum</i>	4	77	19
<i>Lysimachia ciliata</i>	8	75	17
<i>Potentilla simplex</i>	33	77	0
4. Species germinating in nearly equal numbers from the 0-5 cm and 5-10 cm layers.			
<i>Aster pilosus</i>	9	50	41
<i>Campanula divaricatus</i>	1	46	53
<i>Carex nigromarginata</i>	4	50	46
<i>C. virescens</i>	4	46	50
<i>Duchesnea indica</i>	0	44	66
<i>Erechtites hieracifolia</i>	10	49	41
<i>Erigeron canadensis</i>	0	42	48
<i>Eupatorium rugosum</i>	14	40	46
<i>E. serotinum</i>	11	44	45
Gramineae spp.	18	43	38
<i>Hedeoma pulegioides</i>	2	47	51
<i>Helianthus microcephalus</i>	6	41	53
<i>Hydrangea arborescens</i>	19	36	45
<i>Hydrophyllum virginianum</i>	10	45	45
<i>Morus rubra</i>	9	38	53
<i>Panicum commutatum</i>	4	44	52
<i>P. lanuginosum</i>	0	38	62
<i>Paulownia tomentosa</i>	6	47	47

Table 42. (continued)

Species	Litter	Soil Layer	
		0-5 cm	5-10 cm
<i>Phytolacca americana</i>	5	53	42
<i>Potentilla canadensis</i>	0	28	72
<i>Robinia pseudo-acacia</i>	0	53	47
<i>Rubus allegheniensis</i>	5	39	56
<i>R. argutus</i>	1	45	44
<i>R. occidentalis</i>	16	38	46
<i>Sassafras albidum</i>	7	57	36
<i>Solidago altissima</i>	0	42	58
<i>S. caesia</i>	6	34	60
<i>Taraxacum officinale</i>	12	44	44
<i>Viola papilionacea</i>	7	41	52
<i>Vitis Baileyana</i>	13	42	45
<i>V. vulpina</i>	4	49	47
5. Species germinating in greatest numbers from the 5-10 cm layer.			
<i>Acalypha rhomboidea</i>	0	9	91
<i>A. virginica</i>	0	24	76
<i>Ambrosia artemisiifolia</i>	0	23	77
<i>Cyperus pseudovegetus</i>	0	0	100
<i>Eupatorium sessifolium</i>	1	29	70
<i>Fragaria virginiana</i>	0	0	100
<i>Gnaphalium purpureum</i>	0	31	69
<i>Houstonia purpurea</i>	3	35	62
<i>Juncus interior</i>	1	20	79
<i>Lobelia inflata</i>	5	29	66
<i>Oenothera biennis</i>	5	35	60
<i>Panicum lanuginosum</i>	35	38	58
<i>Rhus copallina</i>	2	36	62
<i>R. glabra</i>	0	31	69
<i>Tradescantia ohimensis</i>	0	17	83
<i>Verbascum thapsus</i>	6	21	73
6. Species germinating in fairly equal numbers from all three layers.			
<i>Aster cordifolius</i>	37	40	23
<i>Betula lenta</i>	30	30	40
<i>Lactuca sp.</i>	34	36	30
<i>Oxydendrum arboreum</i>	28	39	33
<i>Panicum dichotomum</i>	35	38	58
B. Summer Samples			
1. Species germinating in greatest numbers from the 0-5 cm layers.			
<i>Paulownia tomentosa</i>	18	53	29
<i>Vitis vulpina</i>	3	75	22
2. Species germinating in nearly equal numbers from the 0-5 cm and 5-10 cm layers.			
<i>Andropogon virginicus</i>	14	50	36
<i>Betula lenta</i>	18	41	41
<i>Carex nigromarginata</i>	52	44	4
<i>Collinsonia canadensis</i>	0	43	57

Table 42. (continued)

Species	Soil Layer		
	Litter	0-5 cm	5-10 cm
<i>Erechtites hieracifolia</i>	5	53	42
<i>Erigeron annuus</i>	10	35	55
<i>Eupatorium purpureum</i>	5	51	44
<i>E. rugosum</i>	1	35	64
<i>E. serotinum</i>	5	39	56
<i>Houstonia purpurea</i>	0	44	66
<i>Lysimachia ciliata</i>	0	51	49
<i>Panicum dichotomum</i>	0	50	50
<i>Phytolacca americana</i>	4	52	44
<i>Poa pratensis</i>	3	44	53
<i>Rhus glabra</i>	6	50	44
<i>Rubus argutus</i>	0	43	57
<i>R. idaeus</i>	7	56	37
<i>Solanum americanum</i>	0	59	41
<i>Tiarella cordifolia</i>	4	48	48
<i>Verbascum thapsus</i>	1	34	65
3. Species germinating in greatest numbers from the 5-10 cm layer.			
<i>Acalypha virginica</i>	6	13	81
<i>Aster divaricatus</i>	14	25	61
<i>Galium triflorum</i>	0	31	69
<i>Lobelia inflata</i>	0	25	75
<i>Panicum commutatum</i>	2	38	60
<i>Rubus allegheniensis</i>	3	37	60
<i>Solanum carolinense</i>	0	0	100
<i>Verbena urticifolia</i>	0	0	100
<i>Vitis aestivalis</i>	0	0	100

VITA

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In September 1973 she entered the University of Wisconsin, Green Bay, Wisconsin from which she received a Bachelor of Science degree in Environmental Science in June 1977.

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