To the Graduate Council:

I am submitting herewith a dissertation written by Gary Leon Wade entitled "Nutrient Capital Sequestration in Pioneer Plant Communities on Surface-Mine Spoil." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology.

Frank W. Woods

Frank W. Woods, Major Professor

We have read this dissertation and recommend its acceptance:

Clifford C. Gordon

H. R. DeSelm

Gary M. Lessman

Ronald L. Hay

Accepted for the Council:

C. W. Minkel

Vice Provost and
Dean of the Graduate School

NUTRIENT CAPITAL SEQUESTRATION IN PIONEER PLANT COMMUNITIES ON SURFACE-MINE SPOIL

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Gary Leon Wade

December 1985

ACKNOWLEDGMENTS

The author wishes to express his heartfelt appreciation to Dr. Frank W. Woods, Department of Forestry, The University of Tennessee, Knoxville, for his advice, guidance and encouragement during the course of this project and the author's doctoral studies.

To Dr. H. R. DeSelm and Dr. C. C. Amundsen, Department of Botany, Dr. R. L. Hay, Department of Forestry, and Dr. G. M. Lessman, Department of Plant and Soil Science, great appreciation is extended for their advice and participation on the author's advisory committee and for critical reading of this manuscript.

The Division of Land and Forest Resources, Tennessee Valley Authority, at Norris, Tennessee, provided space and resources that greatly assisted in this study. Dr. R. E. Farmer and Maureen Cunningham gave much important advice and help for which the author is most grateful.

Fellow graduate students, especially James D. Berg, Al Lyon, David Hammer and Juan Saldariaga, contributed labor, discussion and suggestions that greatly helped this study.

Mr. Hobart Bartley, Sugar Ridge Coal Company, Caryville, assisted in supplying and transporting suitable spoil material.

The author also wishes to thank his colleagues in the U.S. Forest Service who encouraged and aided the completion of this manuscript.

The author is indebted to his parents, Mr. and Mrs. Farris G. Wade, for their continual support and encouragement throughout his educational pursuits.

To my wife Maria, I wish to extend my undying appreciation and gratitude for her support, faith and encouragement throughout my graduate studies and this project.

This study was partly supported by MacIntyer-Stennis funds to the Department of Forestry, Fisheries and Wildlife, The University of Tennessee.

ABSTRACT

Biomass production and nutrient capital sequestration of four pioneer plant communities on a surface-mine spoil were compared. A Chenopodium album-dominated community (Treatment 4) produced the greatest amount of biomass. Next were a community derived from a forest topsoil seed bank spread over mine spoil (Treatment 2), a seed bank community with common reclamation species seeded into it (Treatment 3), and a mix of grasses and Lespedeza commonly used in reclamation (Treatment 1).

Treatments 1, 2, and 3 sequestered N in aboveground biomass in an amount approximately equal to that added as fertilizer, but Treatment 4 sequestered 237 percent of the amount of N added. Phosphorus in all aboveground vegetation was 14 to 27 percent of the amount added as fertilizer. Amounts of nutrients sequestered in vegetation were not strictly proportional to biomass. Community nutrient contents were largely influenced by community biomass and the nutrient uptake characteristics of the species with most biomass.

Significant changes in soil chemistry were found after one growing season. Available K, Fe, Cu and K base saturation were greater in topsoils of all treatments. Topsoil pH, buffer pH and available Mn, were greater in Treatments 1, 2, and 4, while Mg and Mg base saturation increased in Treatments 2, 3, and 4. Topsoil H saturation declined. Vegetation significantly affected changes in topsoil available K, K and Mg base saturation, and buffer pH. The

top ten cm of spoil showed a significant decrease in available K during the five-month period of the study which was modified by vegetation treatment.

The forest soil seed bank produced 84 taxa, of which 65 were identifiable to species. These included five tree species, seven shrubs or woody vines, 14 grasses, and 59 forbs.

Addition of the reclamation mix of grasses and Lespedeza to the seed bank resulted in significantly fewer established native species. Native species lost their normal dominance and exhibited stunted growth and phenological delay in Treatment 3.

Concentrations of N, P, K, Ca, Mg, Mn, Fe, Cu and Zn varied significantly between species. Community membership and underlying spoil influenced concentrations of some elements within species.

"Nutrient content niche," "nutrient content niche share," and niche breadth (Levins' B) were calculated for important species in each community. Native species generally had reduced niche breadths and niche shares when reclamation species were added to the community. Niche share of the reclamation species generally decreased when they were added to the seed bank community, but their niche breadths generally increased.

"Community content niche," the sums of species content niches, varied between different types of pioneer communities.

TABLE OF CONTENTS

CHAPTER		PAGE
I.	INTRODUCTION AND OBJECTIVES	1
II.	METHODS	5
	Construction and Establishment of Microplots	5
	Treatments	6
	Preharvest Care	8
	Preharvest Observations	8
	Microplot Harvesting and Sampling	9
	Soils	10
	Chemical Analysis of Plant Materials	12
	Calculation of Nutrient Contents	13
	Comparison of Nutrient Concentrations in Species Common to Treatment 2 and Treatment 3	14
III.	DEVELOPMENT OF PLANT COMMUNITIES	15
	Plant Communities from Soil Seed Banks	15
	Results	17
	Development of Vegetation	17
	Microclimatic Effects of Vegetation Treatment	18
	Plant Populations in Treatments at Harvest	21
	Discussion	30
IV.	SOILS	37
	Initial Conditions	37
	Final Conditions	41
	Discussion	45
V.	BIOMASS PRODUCTION AND NUTRIENT CAPITAL SEQUESTRATION	48
	The Role of Vegetation in Conservation of Nutrients	48
	Treatment Differences in Biomass Production and Nutrient Sequestration	51
	Results	51
	Discussion	53
	Nutrient Concentrations in Individual Species and Their Effects on Community Nutrient Sequestration	55
	Results	55
	Discussion	64
	Summary	69

CHAPTER PAGE

VI. SPECIES, COMMUNITY AND SPOIL EFFECTS ON PLANT NUTRIENT CONCENTRATIONS 70

Variations in Nutrient Concentrations in Plant Tissues 70
Seed Bank Species Nutrient Concentrations 71
Results 71
Discussion 77
Reclamation Species Nutrient Concentrations 78
Results 78
Discussion 84
Summary 84

VII. NUTRIENT CONCENTRATION, CONTENT AND NICHE 86

The Niche Concept in Plant Ecology 86
Extension of the Niche Concept in Plant Nutritional Relationships 89
Results 92
Seed Bank Species Niche Shares 92
Seed Bank Species Niche Breadths 96
Reclamation Species Niche Shares 96
Reclamation Species Niche Breadths 99
Community Niche 99
Discussion 103
Summary 106

VIII. SUMMARY AND CONCLUSIONS 107

LITERATURE CITED 111

APPENDICES 121

Appendix A 122
Appendix B 130

VITA 135

LIST OF TABLES

TABLE		PAGE
1.	Mean Vegetation Ground Cover in the Four Community Types	19
2.	Surface Soil Temperature, Light Intensity, and Soil Moisture Under Four Plant Community Types	20
3.	Plant Population Means by Treatment Expressed as Population per Hectare and Percent of Total Plant Population at Harvest	22
4.	Comparison of Dominant Species Population Ranks in Treatment 2 and Treatment 3	34
5.	Initial Chemical Properties of Spoils Used in Replication 1 of Each Treatment vs. Spoil Properties in Replications 2-4	38
6.	Topsoil Chemical Properties by Treatment at Start and End of Study	40
7.	Spoil Chemical Properties by Treatment at Start and End of Study	43
8.	Aboveground Biomass and Nutrient Contents in Each Treatment (kg/ha)	52
9.	Mean Nutrient Concentrations in Selected Species by Treatment	56
10.	Biomass and Nutrient Content (kg/ha) of Species Containing 1 Percent or More of Biomass in Each Treatment	60
11.	Percent of Population, Biomass and Nutrient Content of Species Containing 1 Percent or More of Treatment Biomass	62
12.	Factors Affecting Element Concentrations in Nine Species Common to Treatment 2 and Treatment 3	72
13.	Mean Nutrient Concentrations in Important Species Occurring in Both Treatment 2 and Treatment 3, by Treatment and Spoil	74

TABLE PAGE

14. Factors Affecting Element Concentrations in Seven Species Common to Treatment 1 and Treatment 2 80

15. Mean Nutrient Concentrations in Important Species Occurring in Both Treatment 1 and Treatment 3, by Treatment and Spoil 81

16. Tabularization of the Niche Concept Related to Vegetation and Nutrition 90

17. Species Niche Breadth (Levins' B) Based on Standardized Concentration Data and Content Niche Share S_s 93

18. Content Niche Share and Concentration Niche Breadth Changes in 18 Native Species When Reclamation Species Were Added to the Native Seed Bank Community 97

19. Content Niche Share and Concentration Niche Breadth Changes in 11 Species of the Reclamation Mix and Its Invaders When Added to the Native Seed Bank Community . . . 100

20. Mean Biomass (kg) per Hectare and Percent of Total Biomass in Each Taxa by Treatment 131

LIST OF FIGURES

FIGURE		PAGE
1.	A Representative Plot in Treatment 1, the Reclamation Species Mix, as it Was on September 1, 1980	26
2.	A Representative Plot in Treatment 2, the Native Seed Bank Community, as it Was on September 1, 1980	27
3.	A Representative Plot in Treatment 3, the Native Seed Bank Plus Reclamation Mix, as it Was on September 1, 1980	28
4.	A Representative Plot in Treatment 4, the Chenopodium Community, as it Was on September 1, 1980	29
5.	Populations of Native Herbaceous Species Occurring in Both Treatment 2 and Treatment 3	33
6.	Seed Bank Species Niche Shares (S_s) in Treatment 2 and Treatment 3	95
7.	Seed Bank Species Niche Breadths (Levins' B) in Treatment 2 and Treatment 3	98
8.	Reclamation Species Niche Shares (S_s) in Treatment 1 and Treatment 3	101
9.	Reclamation Species Niche Breadths (Levins' B) in Treatment 1 and Treatment 3	102

CHAPTER I

INTRODUCTION AND OBJECTIVES

Surface mining in the United States east of the 100th meridian[1] disturbs 208,000 hectares of land per year (Interstate Mining Compact 1985) which must be reclaimed to a productive status comparable to its premining condition. Much of this land is reclaimed to forestry, wildlife or grazing, land uses which are expected to be essentially self-sustaining ecosystems, after reclamation and performance bond release.

After liming and fertilization of the newly constructed ecosystems on surface mine spoils, nutrients may be lost through erosion and leaching. One solution to this problem is to sequester and conserve nutrients in biomass until adequate nutrient cycling mechanisms and their reserves are established. Farmer et al. (1982) determined that a first-year native species community derived from forest soil seed banks had the capability to sequester nitrogen and phosphorus added to surface-mine spoils at normal rates of fertilization. However, Schafer et al. (1980) found that sequestration of nitrogen in undecomposed litter was responsible for vegetation failure on reclaimed surface-mined land in Montana. They suggested that

---

[1]Land disturbed by surface mining in Alabama, Arkansas, Illinois, Indiana, Kentucky, Louisiana, Maryland, North Carolina, Ohio, Pennsylvania, South Carolina, Tennessee, Texas, Virginia, and West Virginia. No data for Iowa, Kansas and Michigan.

management practices which preclude excess biomass and litter accumulation, such as grazing and burning, should eliminate this problem. Carrel et al. (1979) determined that initial C:N ratio of litter is a major determinant of its rate of decay in minelands and other habitats. They also found that over half of the original N contained in fescue litter was lost within six months, so more factors than simple N tie-up in litter may be active in the mechanism of vegetation failure on reclaimed lands. Stroo and Jencks (1982) determined that high rates of microbial respiration in limed and highly fertilized surface-mine soils depleted soil organic matter and nitrogen reserves, causing failure of vegetation on a mined site in West Virginia.

Soil organic matter is a tremendously important soil nutrient sink and buffers a terrestrial ecosystem against catastrophic nutrient losses after severe disturbances. Much soil organic matter has its origins in plant biomass which has passed through one or more groups of detritivores and decomposers. It contains nutrient elements of the original biomass, nutrients added in cycling through microbial populations, and some sequestered from the soil solution.

Different plant materials decompose at differing rates depending upon their contents of nitrogen, lignin, cellulose, and secondary compounds such as tannins and phenols which may inhibit detritivores and decomposers. A diverse plant community might be expected to produce biomass with diverse characteristics in terms of degradability and rates of nutrient release, and it is also likely to have one or more

populations actively withdrawing available nutrients from the soil at any given time during the entire growing season.

A combination of strategies, including rapid production of a diverse biomass and sequestration of nutrients, rapid conversion of plant biomass to a functional soil organic matter, and establishment of efficient recycling mechanisms may be the long term best solution for retention of nutrient capital in surface-mined and reclaimed ecosystems. Ultimately it may lead to more productive ecosystems.

Pioneer vegetation on surface mines (here defined as the first plant community to be established on a site) is usually chosen for its ability to control erosion, fix nitrogen and provide wildlife food and cover. That some or all of the pioneer species will be replaced in community succession is expected, but the influence of the pioneer community on later ecosystem qualities is seldom considered; indeed, little information is available upon which to base such considerations. The subject of this study is the influence of the pioneer community and its component species on short-term biomass accumulation and nutrient sequestration.

The objectives of this study are:

1. to compare four pioneer plant communities on a surface-mine spoil in terms of biomass production and nutrient capital sequestration;
2. to compare these communities in terms of their short-term effects on spoils;

3. to determine how species, community membership and soils influence plant nutrient use;
4. to define plant species functional niche in terms of nutrient concentration and content;
5. to compare pioneer species in terms of functional niches in these communities;
6. determine how community composition influences species niche in these communities; and
7. to define these pioneer communities themselves in terms of functional niche.

CHAPTER II

METHODS

Construction and Establishment of Microplots

Sixteen microplots measuring 1.22 m x 1.22 m by 0.61 m deep were constructed from 1.27 cm (1.2 in.) plywood, lined with 6 mil polyethylene sheeting, fitted with drains near the bottom of one side corner and placed aboveground on a concrete block and wooden pallet base. The microplots were level or inclined less than 3 degrees toward the drains. Because of the method of assembly, top surface area of the microplots was 1.334 m. All microplots were located near the Tennessee Valley Authority Division of Land and Forest Resources laboratory near Norris, Tennessee, at an elevation of about 250 m.

Two truckloads of mine spoil overburden from the Peewee coal seam on Walnut Mountain, altitude about 850 m, Campbell County, Tennessee, were brought to Norris. This spoil was placed in microplots and leveled to a depth of about 60 cm. Settling reduced spoil depth to about 50 cm. Characteristics of the spoil are discussed in the results section.

A uniform spoil was desired for this study, but subtle differences in spoil material were noticed during the filling operation. Close examination, later supported by laboratory data, indicated that two slightly different spoil materials were being used. Four of the 16 microplots contained a different spoil, so the treatment

randomization plan was altered to include one plot with the second spoil in each treatment.

Forest topsoil was collected near Wheeler Gap on Cross Mountain in Anderson County, Tennessee. The forest was a second growth stand of Carya spp., Acer rubrum L., Quercus alba L., and Liriodendron tulipifera L. The understory was dominated by A. rubrum and Cornus florida L. The area was at a midslope position on a WNW-facing slope just above the Red Ash coal seam at an approximate elevation of 730 m. Leaf litter was carefully raked aside and the top 10 cm of the A_1 soil horizon was collected, placed in 75 L aluminum garbage cans and also transported to Norris.

The collected topsoil was mixed and spread on two large polyethylene sheets near the microplots. One pile was sterilized with 98 percent methyl bromide:2 percent chloropicrin (Dowfume). Sterilized soil was uncovered after two days and exposed for one week.

Treatments

Vegetation seeding and fertilization were accomplished on April 17, 1980.

Treatment 1, designated "reclamation mix," consisted of spreading and leveling 66 liters of sterilized forest topsoil over the surface of each of four microplots to an approximate depth of 5 cm. Ammonium nitrate and concentrated super-phosphate, equivalent to 57 kg/ha N and 59 kg/ha P respectively, were then evenly distributed over each microplot. Seed of Lespedeza cuneata (Dumont) G. Don and

Festuca arundinacea Schreb. var Ky-31 were seeded at the rate of 13.34 kg/ha. Eragrostis curvula (Schrad.) Nees and Lolium multiflorum Lam. were seeded at respective rates of 2.25 kg/ha and 4.50 kg/ha. Wheat straw mulch was applied at a rate of 4 t/ha after fertilization and seeding. Aluminum wire screen was placed over the microplots for two weeks to prevent wind loss of mulch.

Treatment 2 consisted of 66 liters of unsterilized forest topsoil spread over four microplots as in Treatment 1. Fertilization, mulching and wire screening were applied as in Treatment 1. Treatment 2 was designated "native seed bank community."

Treatment 3 was a repetition of conditions and procedures of Treatment 2, but Lespedeza cuneata, Festuca arundinacea, Eragrostis curvula and Lolium multiflorum were added at one-half the seeding rates used for each species in Treatment 1. Treatment 3 was designated "seed bank plus reclamation mix."

Treatment 4 was 66 liters of sterilized forest topsoil spread over microplots and fertilized as in preceding treatments. Stratified seed of Rumex acetocella L. (1.95 kg/ha), Phytolacca americana L. (375,000 seeds/ha), Eupatorium purpureum L. (750,000 seeds/ha), Chenopodium album L. (2.30 kg/ha) and Andropogon virginicus L. (1,500,000 seeds/ha) were sown in each plot. Rhus coppalina L. (300,000 seeds/ha) and Robinia pseudo-acacia L. (60,000 seeds/ha) were sown after treatment of 10 minutes and 2 hours respectively in concentrated sulfuric acid to break dormancy. L. cuneata and E. curvula were also shown at the same rates as in Treatment 3. Because of the

development of this treatment's plant community, it was designated "Chenopodium community."

Preharvest Care

All microplots were watered uniformly as necessary between rainfall events whenever plants began to show signs of water stress. Rainfall data were taken for record purposes from the Norris Dam rain gauge which was located about 1.7 km north of the study site.

Preharvest Observations

Microenvironment measurements to determine early effects of the vegetation cover were made in each plot during the period of 1 to 2 pm on August 14. The weather was sunny; 1.27 cm of rain had fallen two days prior. Three random sample points were chosen for each plot using a random number table to define x,y coordinates. Light measurements were taken at the soil surface by inserting a Sekonic Studio Pro incident light meter under microplot vegetation from the north side. The meter reading was then compared with another incident light measurement above the vegetation and recorded as percent of incident light. One topsoil sample was removed from each plot at the point of the first light measurement. The soil samples were placed in snap cap film cans for return to the lab where they were weighed, dried at 105°C, and reweighed to determine surface soil moisture. Soil surface temperatures were determined with an infrared radiometer.

Light measurements were log transformed to eliminate skewness before their correlations with soil temperature were calculated.

One-way analysis of variance and regression procedures used in this section were run on a Hewlett-Packard Model 10 calculator using "9810A Stat Pac" programs. Chi-square and Tukey's-w were calculated (Steel and Torrie 1980).

Microplot Harvesting and Sampling

Harvest of the microplots was started on September 2 and completed on September 20 which gave a mean growing period of 147 days. Microplots were chosen for harvest at random with the constraint that the first four, second four, third four, and last four microplots harvested would include one of each treatment. Populations of each species in each microplot were counted by individuals or clones as they were clipped at ground level. Individuals or clones of populous species were randomly chosen for chemical analysis. Small species populations were pooled for chemical analysis. The remaining bulk of major species was placed in paper bags for biomass determination only. Samples chosen for chemical analysis were washed to remove surface dust and soil. The washing procedure consisted of dunking and swishing specimens in a surfactant (0.1 percent "Tween-20" solution) for ten seconds, then a rinse in a large pail of tap water (changed frequently), followed by a distilled water final rinse. Vegetation samples were placed in labelled brown paper bags and placed in the sun until they were returned to the lab for oven drying at 65°C at the end of the day.

Three composited topsoil samples, three composited minespoil samples from the top 10 cm of spoil, and three composited spoil samples

from 30-40 cm spoil depth were collected from each microplot, air dried and stored in plastic bags until analysis.

During the harvesting of the plots, stem stubs of some individual plants were tagged with species identification. These root systems were exposed by washing the soil and spoil away with a hose. Depths, lateral extent, and character of root systems for many species were recorded.

Black and white and color slide photographs were made at all stages of the study from initiation to harvest including root and soil/spoil profiles. Oven-dried vegetation samples were weighed, assigned a sample number, and all data from sample bags were recorded on data sheets with this number. Vegetation and litter samples were ground to 20 mesh size in a small Wiley mill. Larger samples were first coarsely ground in a large Wiley mill to speed processing.

Soils

Stone content was determined by sieving soils and spoils with a 2 mm screen and weighing the resulting fractions. Textural determinations were carried out using the hydrometer method (Black 1965). Color determinations were made with Munsell Soil Color Charts (Munsell Color Company 1954).

Total Kjeldahl nitrogen of soils and spoils was determined on 1.0 g samples sieved to include only the fraction less than 2 mm in size. A standard Kjeldahl digestion using K_2SO_4 and H_2SO_4 with a Se catalyst was carried out in 75 ml glass tubes in a Tecator Model 40

digestion block. Steam distillation was carried out using a Tecator Model 1004 distilling unit with ammonia capture in a 5 percent boric acid solution with methyl red-bromcresol green indicator mix. The resulting ammonium-borate solution was then back-titrated to neutrality with 0.1 N HCl (Tecator, Inc. 1976).

Other soil chemical analyses were carried out by a commercial agricultural soil and plant analysis laboratory (A & L Agricultural Laboratories, Inc., Memphis, Tennessee). They used the following procedures and extracts of soil samples:

P - Bray-1 (Black 1965)

P - Bray-2 (Bray and Kurtz 1945)

K - ammonium acetate (Black 1965)

Ca - ammonium acetate (Black 1965)

Mg - ammonium acetate (Black 1965)

Mn - 0.1 N HCl (Black 1965)

Fe - 0.1 N HCl (Black 1965)

Cu - 0.1 N HCl (Black 1965)

Zn - 0.1 N HCl (Black 1965)

pH - 1:1 H_2O (Black 1965)

buffer pH - SMP (Shoemaker et al. 1962)

Cation Exchange Capacity (CEC) - calculated from exchangeable cations + H^+

% base saturation - computed from exchangeable cations and H^+, and

% organic matter - wet combustion with dichromate and sulfuric acid (Black 1965)

One-way analysis of variance and t-test procedures used in this section were carried out using a Hewlett-Packard Model 10 calculator with "9810A Stat Pac" programs. Treatment effects on soils data were analyzed using data converted to "change over time" (end value minus start value).

Chemical Analysis of Plant Materials

Chemical analysis of the vegetation samples started with a sulfuric acid-hydrogen peroxide digestion method (Allen 1974) which allows one digest of each sample to be subdivided for separate analyses of N, P, K, Ca, Mg, Mn, Fe, Cu and Zn. To prepare the digestion reagent, 350 ml of concentrated H_2SO_4 was added to 0.42 g Se metal powder and 14 g $LiSO_4$ in a liter flask. The flask was placed in an ice bath and 420 ml of 30% H_2O_2 was slowly added. When this reagent cooled sufficiently, it was stored at 4°C in an acid-washed polyethylene bottle until used.

Vegetation samples of 0.500 g were placed in 75 ml digestion tubes and 10.0 ml of the digestion reagent was added. After foaming subsided, tubes were placed in a 40-place Tekator digestion block for gradual heating to 410°C. Samples were digested for 30 minutes beyond the time required for the last sample to turn to a clear solution. The rack containing the tubes was then removed from the digestion block and allowed to cool to the point that 25 ml distilled H_2O could be added without over vigorous boiling and loss of sample. Upon cooling to room temperature, the tube contents were transferred to 50 ml volumetric flasks, brought to volume, and thoroughly mixed.

A 15 ml aliquot of each sample was removed from the volumetric flask and returned to its original digestion tube for the standard Kjeldahl distillation of ammonia into boric acid on a Tekator Model 1004 steam distillation unit. The resulting ammonium-borate solution with bromcresol green-methyl red indicator was then titrated to a neutral endpoint using 0.1 N H_2SO_4 (Tecator, Inc. 1979). A 10 ml aliquot of each sample was removed from the digest in the volumetric flask and stored in an acid-washed linear polyethylene scintillation vial. These samples were analyzed for phosphorus using the molybdenum blue-ascorbic acid method (Rand et al. 1976).

Two 10 ml aliquots were kept for metals analyses by atomic absorption flame photometry. One aliquot was used for analysis of iron, manganese, copper and zinc concentrations. The second aliquot was diluted as necessary for determinations of calcium, magnesium and potassium. Dilutions were made using 0.1 percent lanthanum chloride solution to suppress calcium-magnesium interferences (Allen 1974).

Calculation of Nutrient Contents

Nutrient contents of each species in each plot were determined by calculating mean concentration of each nutrient for each species in that plot. This mean was then multiplied by the total biomass of that species in that plot.

Comparison of Nutrient Concentrations in Species Common to Treatment 2 and Treatment 3

The nutrient concentration data and the design of the study allowed some comparisons of the influence of species, community membership, and spoil on the plant nutrient concentrations. Sufficient samples were available to compare nine species present in both the native seed bank mix (Treatment 2) and the native seed bank plus grasses (Treatment 3). To this end, nutrient concentration data for Aster divaricatus L., Digitaria ischaemum (Schreb.) Muhl., D. sanguinalis L., Erechtites hieracifolia L., Eupatorium rugosum Houtt., E. purpureum, E. serotinum Michx., Helianthus microcephalus T&G, and Phytolacca americana were analyzed by ANOVA (analysis of variance) using the GLM procedure of the SAS statistical program package (SAS Institute Inc. 1982). Type IV sums of squares were used to determine the influence of species, community membership, and spoil on vegetation nutrient concentrations. All two-way and three-way interactions were also examined.

Similar comparisons of species, community, and spoils were performed on seeded species and invaders in the reclamation mix, but comparison is between the reclamation mix (Treatment 1) and the native species plus reclamation mix (Treatment 3). Species used in the ANOVA were Digitaria ischaemum, D. sanguinalis, Eragrostis curvula, Festuca arundinacea, Lespedeza cuneata, Lolium multiflorum, and Lolium perenne.

CHAPTER III

DEVELOPMENT OF PLANT COMMUNITIES

Plant Communities from Soil Seed Banks

Soil seed banks are present in diverse types of ecosystems including natural and plantation forests (Oosting and Humphreys 1940, Livingston and Allessio 1968, Hill and Stevens 1981, Brown and Oosterhuis 1981, Dobberpuhl 1981), natural grasslands (Lippert and Hopkins 1950, Archibald 1981), cultivated lands (Brenchley and Warington 1930), pastures (Chippindale and Milton 1934), arid lands (Beauchamp et al. 1975, Barbour and Lange 1967, Howard and Samuel 1979), and wetlands (van der Valk and Davis 1976).

These seedbanks are frequently significant in the vegetation dynamics of the ecosystem containing them. Buried, viable seed is at least partly responsible for succession in old fields (Egler 1954), and it is very important in recovery of forest stands after disturbance by supplying species which are important in the early stages of secondary succession (Livingston and Allessio 1968). Seed banks and seed bank management are important in maintaining the presence of species which are dependent upon periodic disturbance for reestablishment in the community (Brown and Oosterhuis 1981).

A number of researchers have investigated the potential for using seed banks in topsoil for surface mine reclamation, with emphasis on the western U.S. and Canada in arid or semi-arid

ecosystems. Howard and Samuel (1979) investigated use of topsoil containing seed and rhizomes of perennial plants. Insufficient numbers of seedlings survived to meet reclamation requirements, but they found that this method introduced native species.

Beauchamp et al. (1975) found that additional seed was required to meet reclamation requirements when topsoil was used in Wyoming. Application of topsoils on mined lands after their removal from other locations resulted in higher components of native species in the resulting plant communities than when standard seeding mixes were used. Iverson and Wali (1982) reported that species derived from seed banks are important in introducing some native species to reclaimed lands. They placed a higher importance on immigrant species, however. Farmer et al. (1982) investigated the potential of Appalachian forest topsoils to supply native species for reclamation in the east. Seed banks from three different forests produced a total of 134 different taxa when spread over two minespoils and a control nursery soil. Furthermore, they estimated that a large proportion of the nitrogen and phosphorus added as fertilizer in that trial was taken up by the plants growing from the seed banks. They speculated that such sequestration of nutrients in vegetation could be important in later development of plant communities on spoils that are frequently deficient in essential nutrients. Important microbial populations can also be introduced in this manner (Argonne National Laboratory 1981).

An important consideration in use of topsoil seed banks in reclamation is the handling of the material. Topsoil stored for

significant periods of time can have reduced numbers of viable seed (Tacey and Glossop 1980, Argonne National Laboratory 1981). Season of topsoil collection can influence the emergence of species from the seed bank. Thompson and Grime (1979) and Grime (1981) showed that a soil may contain several types of seed banks which may range from transient to persistent based on the dormancy characteristics of the component species seeds. Different types of seed banks may be able to exploit only certain types of disturbances at certain seasons of the year (Grime 1981).

Results

Development of Vegetation

Thirty days after establishment of the plots, broad-leaved native herbaceous species had appeared above the mulch in Treatments 2 and 3. Individual grasses were also visible in Treatments 1 and 3. Many Chenopdoium album seedlings were visible in Treatment 4 with lesser numbers of other seeded species. At this time little difference between treatments in total vegetation cover was evident.

At 37 days, cover in Treatments 1, 3, and 4 was obviously greater than that in the native species Treatment 2. C. album in Treatment 4 was also the most important species in the seeded mix. Eragrostis curvula and two invader species of Digitaria were noticeable under the C. album, but most other seedlings of dicots had failed to become established.

At 60 days, ground cover was complete in Treatment 1 and somewhat less in Treatment 3. The native species in Treatment 2 provided only 50 to 70 percent ground cover. A lush growth of C. album had established nearly complete canopy cover in Treatment 4 by this time.

At 90 days, native species plots had developed a cover about the same as other treatments. When ground cover estimates were made 112 days after the start of the study on August 7, Treatments 1-3 had no significant differences in the amount of cover. Mean cover for these three treatments was 90 percent. Treatment 4 had significantly less cover (ANOVA, $\alpha = .05$) with a mean of 79 percent (Table 1).

Microclimatic Effects of Vegetation Treatment

Microclimatic effects of the vegetation treatments were compared on August 14 when the weather was sunny, air temperature at the plots was 37°C and bare soil had a surface temperature of 45°C. Mean surface soil temperature (Table 2) was highest in Treatment 4 and lowest in Treatment 2. Light intensity expressed as percent of the incident light measured above the vegetation was significantly higher ($\alpha = .05$) in Treatment 4 than in the other treatments. Soil moisture did not vary significantly between Treatments 1, 2 and 4 two days after a 12.7 mm rainfall. Treatment 3 soil moisture measurements were lost when samples were dropped during the weighing procedure.

Table 1. Mean vegetation ground cover (percent) in the four community types.

Treatment	Percent Cover	
1. Reclamation Mix	91.9 (4.0)[1]	a[2]
2. Native Seed Bank Community	90.6 (3.7)	a
3. Seed Bank plus Reclamation Mix	87.0 (4.4)	a
4. *Chenopodium* Community	78.9 (3.2)	b

[1]Standard deviation.

[2]Treatment means followed by the same letter are not significantly different, $\alpha = .05$, Tukey's-*w* after ANOVA.

Table 2. Surface soil temperature, light intensity, and soil moisture under four plant community types.[1,2]

Treatment	Temperature (C)	Light Intensity[3]	Soil Moisture (%)
1. Reclamation Mix	38.6 (1.3) ab	2.3 (2.3) b	18.0 (2.0) a
2. Native Seed Bank Community	37.9 (2.1) b	6.8 (9.8) b	17.8 (2.8) a
3. Seed Bank + Reclamation Mix	38.4 (1.9) ab	5.8 (6.4) b	-
4. *Chenopodium* Community	40.0 (1.9) a	13.1 (5.8) a	15.5 (1.0) a

[1]Standard deviations are in parentheses.

[2]Treatment means followed by the same letter are not significantly different, $\alpha = .05$, Tukey's-*w* after ANOVA.

[3]Percent of intensity above vegetation.

Plant Populations in Treatments at Harvest

The mean plant populations for each treatment at the time of harvest is expressed as the equivalent population per hectare in Table 3. Representative plots in each treatment are shown in Figures 1-4.

Although only four species were knowingly seeded into the Treatment 1 plots, a total of 18 were recovered. The Lolium multiflorum seed was apparently contaminated with L. perenne. Digitaria aschaemum and D. sanguinalis were important invaders in this treatment as well as in others. Digitaria spp. and Dactylis glomerata may have been introduced in the mulch despite the attempt to sterilize it with methyl bromide. Other invader species may have survived soil fumigation or were carried in by birds, mammals, or wind. The total number of plants or clones in one plot of this treatment was 124 less than the mean of the other three. Only one individual of Lespedeza cuneata was found and the Lolium populations were also small. This was probably due to grazing by field mice whose burrow was found in the spoil during the harvest of the plot. Mean population of the plots in this treatment was equivalent to 317 plants per square meter.

The native species seed bank in Treatments 2 and 3 produced 84 taxa. Sixty-five of these were identifiable to species, 14 taxa were identifiable only to genus, and 4 could only be placed in family. Several forb seedlings in different taxa which were too poorly developed for identification were classified in one taxon as "miscellaneous." Of taxa identified at least to genera, there were

Table 3. Plant population means by treatment expressed as population per hectare and percent of total plant population at harvest

Species	Treatment 1		2		3		4	
	Pop.	%	Pop.	%	Pop.	%	Pop.	%
Acalypha gracilens Gray					1,874	0.04		
A. rhomboidea Raf.			1,874	0.09	5,622	0.13	1,874	0.08
A. virginica L.			1,874	0.09	1,874	0.04		
Agrostis gigantea Roth			9,370	1.25	13,188	0.30	7,496	0.33
Amaranthus hybridus L.					1,874	0.04		
Anemonella thalictroides L.			35,607	1.80	24,363	0.55		
Aristolochia serpentaria L.			1,874	0.09				
Aster divaricatus L.			13,118	0.66	16,867	0.38		
A. pilosus Willd.			7,496	0.38				
A. schreberi Nees					3,748	0.09		
Aster sp.			7,496	0.38	9,370	0.21		
Bidens frondosa L.					1,874	0.04		
Bromus commutatus Schrad.			3,748	0.19	11,244	0.26		
Carya cordiformis (Wang) K. Koch			1,874	0.09				
Chenopodium album L.							640,930	28.50
Cimicifuga racemosa (L.) Nutt.			9,370	0.47				
Crotonopsis elliptica Willd.			1,874	0.09				
Cyperus esculentus L.			29,985	1.51				
Dactylis glomerata L.	56,222	1.78	13,118	0.66	58,096	1.32	3,748	0.17
Datura stramonium L.	1,874	0.06						
Digitaria ischaemum (Schreb.) Muhl.	241,754	7.64	65,592	3.31	144,302	3.28	181,784	8.08
D. sanguinalis (L.) Scop.	48,726	1.54	18,741	0.95	52,474	1.19	39,355	1.75
Eleusine indica Gaertn.					1,874	0.04		
Eragrostis curvula (Schrad.) Nees	978,261	30.90			910,795	20.73	781,484	34.75
Erechtites hieracifolia (L.) Raf.			170,540	8.60	101,199	2.30		
Erigeron canadensis L.			3,748	0.19			14,993	0.67
Euonymus atropurpureus Jacq.					5,622	0.13		

Table 3 (continued)

Species	Treatment 1 Pop.	1 %	2 Pop.	2 %	3 Pop.	3 %	4 Pop.	4 %
Eupatorium purpureum L.			41,299	2.08	39,355	0.90		
E. rugosum Houtt.			461,019	23.25	226,762	5.16		
E. serotinum Michx.			110,570	5.58	127,436	2.90		
Eupatorium sp.			1,874	0.09	1,874	0.04		
Festuca arundinacea Schreb.	732,759	23.15			655,922	14.93		
Galium triflorum Michx.			44,978	2.27	5,622	0.13		
Galium sp.					3,748	0.09		
Geum sp.			7,496	0.38				
Hedeoma pulegioides (L.) Pers.			3,748	0.19	1,874	0.04		
Helianthus decapetalus L.			5,622	0.28	3,748	0.09		
H. laevigatus T. & G.			1,874	0.09				
H. microcephalus T. & G.			20,615	1.04	33,733	0.77		
Helianthus sp.			1,874	0.09				
Krigia sp.			1,874	0.09				
Lactuca biennis (Moench) Fern.			33,733	1.70	11,244	0.26		
L. pulchella (Pursh) DC.			1,874	0.09				
L. scariola L.					1,874	0.04	1,874	0.08
Lactuca sp.			1,874	0.09				
Lespedeza cuneata (Dumont) G. Don	372,939	11.78			1,062,594	24.19	491,005	21.83
Liriodendron tulipifera L.			129,310	6.52	54,348	1.24		
Lolium multiflorum Lam.	594,078	18.77			198,651	4.52		
L. perenne L.	63,718	2.01			138,681	3.16	5,622	0.25
Lolium sp.							1,872	0.08
Misc. Apiaceae			1,874	0.09	3,748	0.09		
Misc. Asteraceae			28,111	1.42	24,363	0.55		
Misc. Fabaceae			1,874	0.09				
Misc. Poaceae	18,741	0.59	13,118	0.66			7,496	0.33
Miscanthus sinensis Anderss.					1,874	0.04		

Table 3 (continued)

Species	Treatment 1 Pop.	1 %	2 Pop.	2 %	3 Pop.	3 %	4 Pop.	4 %
Miscellaneous sp.			69,340	3.50	37,481	0.85		
Monarda clinopodia L.			35,607	1.80	20,615	0.47		
Muhlenbergia schreberi J.F. Gmel	31,859	1.01	7,496	0.38	14,993	0.34	16,867	0.75
Oxalis stricta L.			1,874	0.09				
Oxalis sp.			1,874	0.09	1,874	0.04		
Panicum agrostoides Spreng					5,622	0.13		
P. dicotomiflorum Michx.	5,622	0.18	1,874	0.09	26,237	0.60	3,748	0.17
Paronychia canadensis (L.) Wood			1,874	0.09				
Parthenocissus quinquefolia (L.) Planch.			5,622	0.28	13,118	0.30		
Paspalum circulare Nash	1,874	0.06						
P. laeve LeConte					1,874	0.04	5,622	0.25
Physalis heterophylla Nees			5,622	0.28	7,496	0.17		
P. pruinosa L.			1,874	0.04				
Phytolacca americana L.	1,874	0.06	134,933	6.81	93,703	2.13	7,496	0.33
Plantago lanceolata L.	7,496	0.24	3,748	0.19	3,748	0.09		
Portulaca oleracea L.			1,874	0.09				
Pyrrhopappus carolinianus (Walt.) DC			3,748	0.19				
Ranunculus septentrionalis Poir.			3,748	0.19	1,874	0.04		
Rhus copallina L.							14,993	0.67
Robinia pseudo-acacia L.	3,748	0.12	13,118	0.66	11,244	0.26	5,622	0.25
Rubus allegheniensis Porter			11,244	0.57	3,748	0.09		
R. occidentalis Bailey			29,985	1.51	1,874	0.04		
Rubus sp.			58,096	2.93	52,474	1.19		
Rumex acetosella L.							7,496	0.33
Sassafras albidum (Nutt.) Nees			9,370	0.47				
Scutellaria incana var. punctata (Chapm.) Mohr			3,748	0.19	5,622	0.13		
S. ovata Hill			14,993	0.76	11,244	0.26		
S. serrata Andr.			5,622	0.28				

Table 3 (continued)

Species	Treatment 1 Pop.	1 %	2 Pop.	2 %	3 Pop.	3 %	4 Pop.	4 %
Scutellaria sp.			1,874	0.09				
Solanum carolinense L.					1,874	0.04		
Solidago flexicaulis L.			5,622	0.28	3,748	0.09		
Solidago sp.			9,370	0.47				
Stachys tenuifolia Willd.			3,748	0.19				
Strophostyles helvola (L.) Ell.					1,874	0.04		
Trifolium repens L.							1,874	0.08
Tridens flavus (L.) Hitchc.	1,874	0.06						
Triticum aestivum L.					3,748	0.09	1,874	0.08
Ulmus sp.			1,874	0.09				
Uniola latifolia Michx.							1,874	0.08
Uvularia perfoliata L.			3,748	0.19				
Viola sagittata Aitt.			1,874	0.09				
Viola sp.			193,028	9.74	132,434	3.01		
Vitis sp.			20,615	1.04	1,874	0.04		
Mean sum	3,165,667		1,982,759		4,392,804		2,248,876	
σ	419,040		87,706		743,628		428,036	

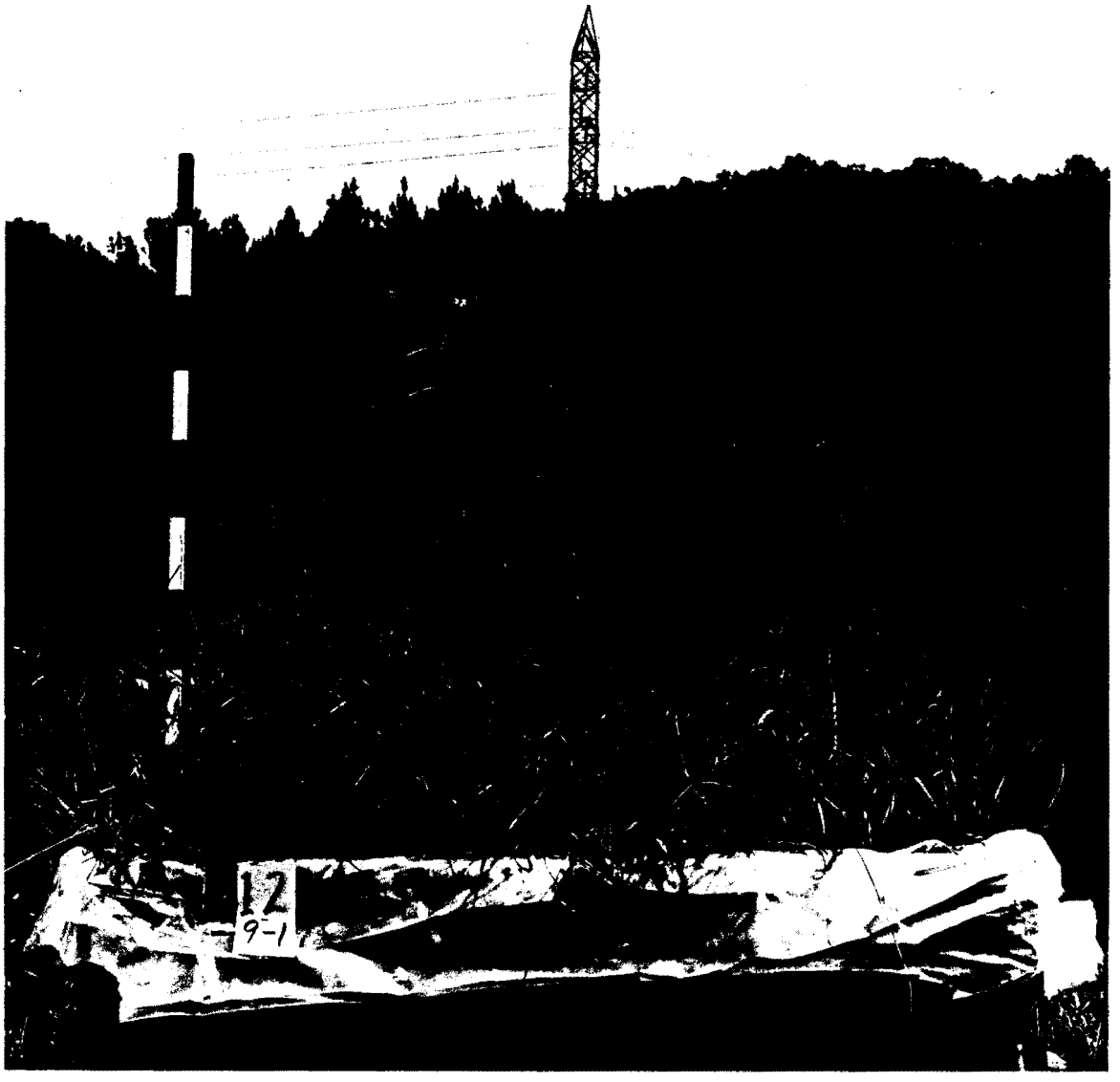


Figure 1. A representative plot in Treatment 1, the reclamation species mix, as it was on September 1, 1980.



Figure 2. A representative plot in Treatment 2, the native seed bank community, as it was on September 1, 1980.



Figure 3. A representative plot in Treatment 3, the native seed bank plus reclamation mix, as it was on September 1, 1980.

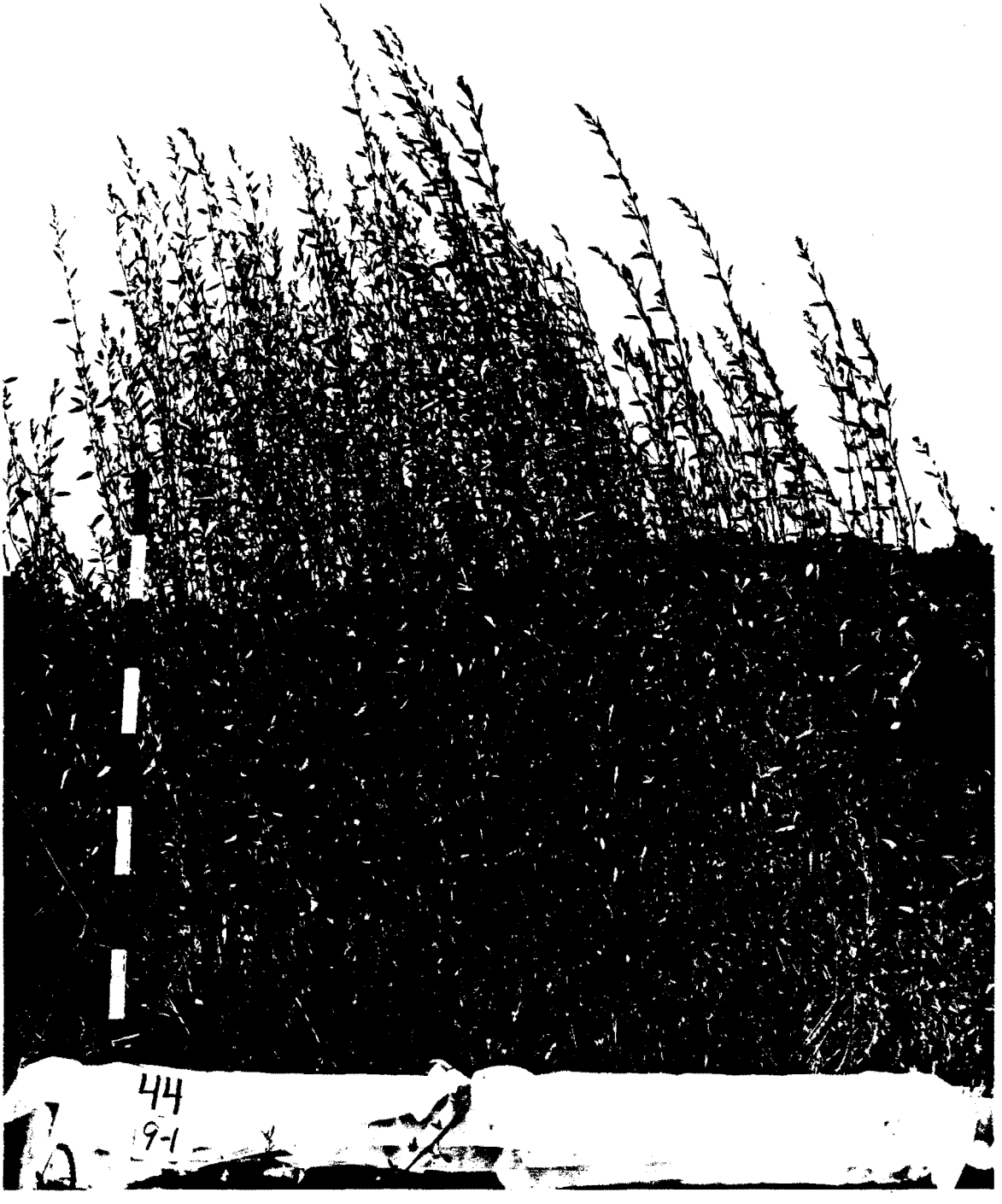


Figure 4. A representative plot in Treatment 4, the Chenopodium community, as it was on September 1, 1980.

five tree species, seven shrubs or woody vines, 14 grasses, one sedge, and 53 forbs. Three leguminous species including Robinia pseudo-acacia came out of the soil seed bank. Mean density was 198 and 439 plants per square meter for Treatments 2 and 3 respectively.

Of the ten species seeded into Treatment 4, only C. album, E. curvula, and L. cuneata became established in sufficient numbers to have any estimable impact on the community. No individuals of Eupatorium purpureum or Andropogon virginicus were in the plots at harvest time. The remaining intentionally seeded species each constituted less than 1 percent on the community plant populations. Of the 13 invader species, only the two Digitaria species attained over 1 percent each of the total plant population in this treatment. Mean plant density was 225 individuals per square meter.

Discussion

The addition of reclamation mix species to the native seed bank community allows some inferences to be made as to the influences which these exotics may have on native communities and their components.

The forest soil seed bank plus invaders produced 65 taxa identifiable to genus or species in Treatment 2. There were 52 species of similar origin not including the seeded grasses and L. cuneata in Treatment 3. Of the seed bank plus invader species, 39 occurred in both Treatments 2 and 3. Twenty-six were found only in Treatment 2, and 13 were found only in Treatment 3. This difference in number of species unique to treatment prompts the question as to whether the

grasses and L. cuneata sown in Treatment 3 eliminated some of the native species. A chi-square test performed on the treatment-unique species presence-absence data indicates that the reclamation mix added to the seed bank community did significantly ($\alpha = .05$) reduce the number of taxa. Among the five tree species, Carya cordiformis, Sassafrass albidum, Ulmus sp., Robinia pseudo-acacia, and Liriodendron tulipifera, only the latter two were found in Treatment 3. The populations of L. tulipifera and R. pseudo-acacia are significantly smaller in Treatment 3 than in Treatment 2 (t-test, $\alpha = .05$). The other three species were not numerous enough to make a statistical test meaningful, but their absence indicates that addition of reclamation mix species to the native community may have an inhibitory effect on forest development through inhibition of tree seed germination or seedling establishment through competition for light, water, nutrients or allelopathy.

Of the native forbs taxa of the forest soil seed bank which are present in both Treatments 2 and 3, there is a trend for populations to decrease in common with addition of the grasses and L. cuneata. The ratio of Treatment 2 to Treatment 3 native forb species is 2.1:1. Based on the number of species population increases vs. the number of decreases per se between Treatments 2 and 3, the number of population decreases is not significant (chi square test, $\alpha = .05$). A regression of each forb species population in Treatment 2 vs. its population in Treatment 3 gives the regression formula:

$$\log T_3 = 0.708 (\log T_2) + 1.134$$

$$r^2 = 0.596 \quad \text{significant at } \alpha = .001$$

where T_2 = Treatment 2 species population and T_3 = Treatment 3 species population. The intercept of the above equation indicates that there is a trend for less common species in Treatment 2 to increase in number when the reclamation mix is added to the native species community, but the more common species populations tend to decrease (Figure 5). The break point in the trend is a species population of about 7650 individuals per hectare in the native species only treatment. The trend is statistically significant when tested above but not below the break point (chi-square, $\alpha = .05$).

Another obvious consequence of adding the reclamation mix to the seed bank community is the shift in species importance as indicated by species populations. Strictly in terms of numbers, the seed bank community is dominated by Eupatorium rugosum, Viola sagittata, Erechtites hieracifolia, Phytolacca americana, Liriodendron tulipifera, and Eupatorium serotinum. These six species constitute 60 percent of the total population (Table 4). Lespedeza cuneata, Eragrostis curvula, and Festuca arundinacea fill the the same proportional place in Treatment 3. All of the dominant species of Treatment 2 have dropped in importance more than is accounted for by the increase in density when the reclamation mix is added.

The smaller populations observed when the reclamation mix is added to the seed bank community are statistically significant

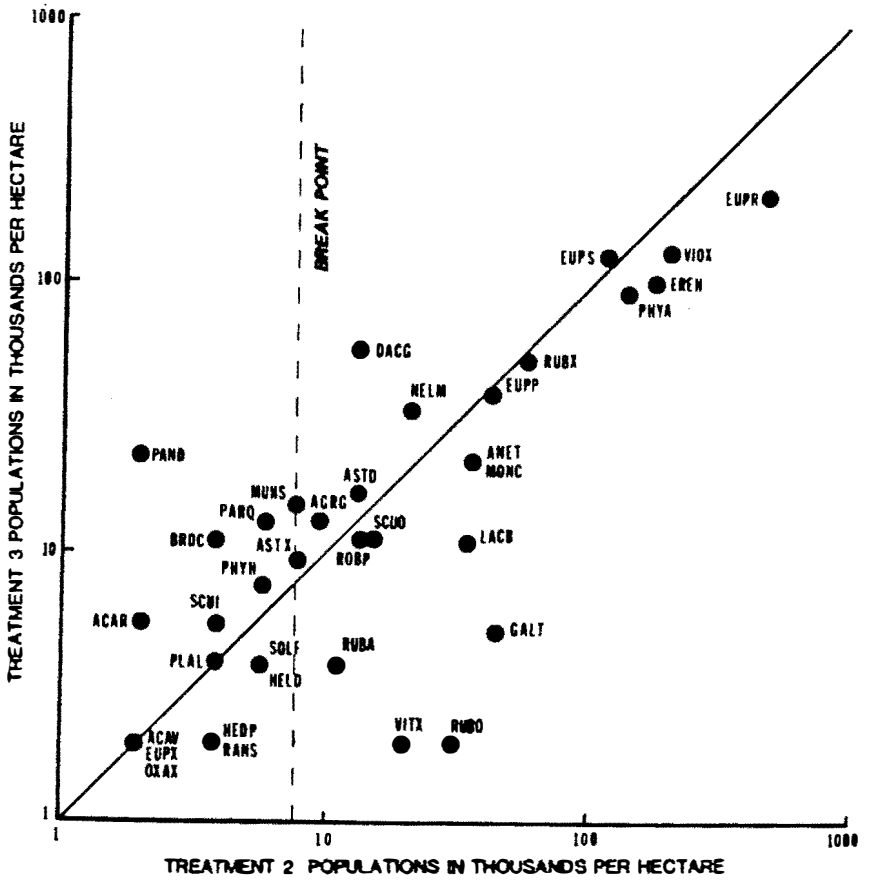


Figure 5. Populations of native herbaceous species occurring in both Treatment 2 and Treatment 3. ACAR = Acalypha rhomboidea, ACAV = A. virginica, AGRG = Agrostis gigantea, ANET = Anemonella thalictroides, ASTD = Aster divaricatus, ASTX = Aster sp., BROC = Bromus commutatus, DACG = Dactylis glomerata, EREH = Erechtites hieracifolia, EUPP = Eupatroium purpureum, EUPR = E. rugosum, EUPS = E. serotinum, EUPX = Eupatorium sp., GALT = Galium triflorum, HEDP = Hedeoma pulegioides, HELD = Helianthus decapetalus, HELM = Helianthus microcephalus, LACB = Lactuca biennis, LIRT = Liriodendron tulipifera, MONC = Monarda clinopodia, MUHS = Muhlenbergia schreberi, OXAX = Oxalis sp., PARQ = Parthenocissus quinquefolia, PHYH = Physalis heterophylla, PHYA = Phytolacca americana, PLAL = Plantago lanceolata, RANS = Ranunculus septentrionalis, ROBP = Robinia pseudo-acacia, RUBA = Rubus allegheniensis, RUBO = R. occidentalis, RUBX = Rubus sp., SCUI = Scutellaria incana var. punctata, SCUO = S. ovata, SOLF = Solidago flexicaulis, VIOX = Viola sp., VITX = Vitis sp. The diagonal line indicates the points of no difference between Treatment 2 and Treatment 3 populations. The break point is the point above which native species populations tend to decline when reclamation species are added to the community.

Table 4. Comparison of dominant species population ranks in Treatment 2 and Treatment 3.

Treatment 2			Treatment 3		
Species	Population % of Sum	Cumulative %	Treatment 3 % of Sum	Species	Population % of Sum	Cumulative %
Eupatorium rugosum	23.25	23.25	5.16	Lespedeza cuneata	24.19	24.19
Viola sagittata	9.74	32.00	0	Eragrostis curvula	20.73	44.92
Erechtites hieracifolia	8.60	41.59	2.30	Festuca arundinacea	14.93	59.85
Phytolacca americana	6.81	48.40	2.13			
Liriodendron tulipifera	6.52	54.92	1.24			
Eupatorium serotinum	5.58	60.50	2.90			

(t-test, α = .05) for E. rugosum, E. hieracifolia and L. tulipifera. The declines in P. americana and E. serotinum were not individually statistically significant but they follow the trend. Population decline for Viola sagittata was tested using all Viola species because less-developed Viola in Treatment 3 made species determination unreliable. The trend for decline in Viola was not statistically significant.

Also of interest is the effect of native populations on grasses and L. cuneata of the reclamation mix. Despite their being seeded into Treatment 3 at one-half of the rate of Treatment 1, E. curvula and E. arundinacea had approximately equal densities in both treatments. The summed Lolium populations dropped by approximately one-half. The Lolium sp. decrease was statistically significant (t-test, α = .05), but it cannot be determined whether this was a result of seeding rate or competitive effects of native species. The L. cuneata population density increased significantly (t-test, α = .05) by 285 percent when added to the native species community in spite of being seeded into Treatment at one-half of the Treatment 1 rate. Treatment 1 soil's microbial populations were initially eliminated or greatly reduced by fumigation; the microflora of Treatment 3 were not. This increased establishment of L. cuneata may be due to the advantages of symbiotic microflora or to reduced competition with grasses which had less biomass despite their numbers. In Treatment 4, which also had fumigated topsoil, L. cuneata populations were about the same as in Treatment 1, but again the seeding rate was only one-half of

that in Treatment 1. This suggests that reduction of soil microflora inhibited L. cuneata but competitive or allelopathic inhibition by C. album may also be partly responsible.

Results from this section reinforce the hypothesis that forest soil seed banks from the eastern U.S. can supply a diverse group of species capable of growing on surface-mine spoil (Farmer et al 1982). How well these native species might do on actual surface mines without the additional water supplied in this study is an open question that must be answered by further study. Topsoil seed bank material might be used on a surface mine as a supplement to standard seedings of ground cover species for the purpose of increasing diversity of the pioneer community and introducing native species. Results of this study show that such a mix will have a reduced number of native species and species populations due to competition of grasses. Larger native herbaceous and woody species introduced in this way might later shade out reclamation species and lead to a faster process of secondary succession.

CHAPTER IV

SOILS

Initial Conditions

Two similar but distinct spoils were used in this study. The principal spoil (Spoil 2) used in three of four plots in each treatment was a medium acid, light gray (Munsell color 2.5Y 7/2 dry, 2.5Y 5/2 wet), silt loam with a mean stone content of 39 percent. The other spoil (Spoil 1), used in one plot per treatment, was an extremely acid, light gray (Munsell color 5Y 7/1 dry, 5Y 4/1 wet) silt loam with a mean stone content of 37 percent. Texture and stoniness varied as much within treatments as between them. Color differences were slight, but consistent. Chemical properties of the two spoils were significantly different between spoils for many of the tested variables (Table 5). Percent organic matter was high in both spoils but this was due to coal fragments and carbonaceous materials in the dark shales. The spoil used in replicate 1 of each treatment (Spoil 1) had significantly lower pH, buffer pH, Bray-2 P, Ca, and Mg than Spoil 2. The cation exchange capacity (CEC) of Spoil 1 was higher, and K, Ca, and Mg base saturation percentages were lower than those of Spoil 2. Spoil 1 had significantly higher amounts of Fe, Cu, and Zn, and a higher H base saturation than Spoil 2.

In comparison to agricultural soils, readily soluble phosphorus (Bray-1) was low (6-13 ppm) in both spoils (Table 5), but reserve

Table 5. Initial chemical properties of spoils used in replication 1 of each treatment vs. spoil properties in replications 2-4.

Spoil Property	Spoil 1 Value	Spoil 1 Standard Deviation	Spoil 2 Value	Spoil 2 Standard Deviation	Significance
Organic Matter %	4.5	0.35	3.6	0.51	**
N %	0.18	0.030	0.16	0.034	ns
P1 ppm	10.8	1.48	8.4	15.92	ns
P2 ppm	45.8	4.42	56.4	7.88	**
K ppm	97	6.5	101	4.3	ns
Ca ppm	625	50	1029	32	**
Mg ppm	244	24	305	39	**
Mn ppm	65	5.5	67	13.6	ns
Fe ppm	223	5.7	186	12.8	**
Cu ppm	5.2	0.46	4.0	0.31	**
Zn ppm	11.2	0.90	7.3	0.60	**
pH	4.4	0.21	5.8	0.47	**
buffer pH	4.3	0.15	5.7	0.46	**
C.E.C.	15.7	3.93	9.9	0.80	*
K base sat. %	1.7	0.39	2.6	0.23	**
Ca base sat. %	20.7	4.77	52.1	7.98	**
Mg base sat. %	13.5	3.07	25.6	2.10	**
H sat. %	64.0	8.29	19.8	9.42	**

*Significantly different, t-test, $\alpha = .05$.

**Significantly different, t-test, $\alpha = .01$.

phosphorus (Bray-2) was high (40-58) in both spoils (Ankerman and Large 1974). Berg (1973) compared different phosphorus availability tests and concluded that Bray-1 phosphorus levels greater than 8 ppm were adequate for the establishment of an herbaceous groundcover on surface-mine spoils. Barnhisel (1975) recommended that phosphorus be added for reclamation if soil test P is below 30 ppm. Available potassium was low in both spoils. Barnhisel (1975) classified spoils with extractable potassium less than 125 ppm as "low" and recommended that up to 30 kg/ha potash be added for establishment of an herbaceous cover; double that for hay and pasture establishment. Calcium levels were not critically low in either spoil, but a low calcium base saturation in Spoil 1 was largely responsible for its high H^+ saturation and low pH. Magnesium levels of both spoils were within the ranges of extractable amounts and percentages of base saturation that produce reasonable growth on agricultural soils (Doll and Lucas 1973). Both spoils had levels of available manganese and iron which are rated very high (> 50 ppm) for agricultural soils (Ankerman and Large 1974). Available copper was also very high (> 3 ppm) (Ankerman and Large 1974). Available zinc was high (5.1-8.0 ppm) in Spoil 2 and very high (> 8.1 ppm) in Spoil 1 (Anderman and Large 1974).

The topsoil was a slightly acid, silty clay loam with a mean stone content of 19 percent. Readily available phosphorus (Bray-1) was very low (> 5 ppm) to high (20-28 ppm) (Ankerman and Large 1974) with a great deal of variation between treatments (Table 6). Bray-2 phosphorus was only slightly greater which indicates that the available

Table 6. Topsoil chemical properties by treatment at start and end of study.

	Treatment							
	1		2		3		4	
Value	Start	End	Start	End	Start	End	Start	End
Organic Matter %	6.5	7.2	6.0	6.7	5.9	5.9	6.4	6.9
N %	0.52	0.53	0.48	0.46	0.49	0.46	0.53	0.52
P1 ppm	21.0	55.8**	4.8	55.3**	6.8	56.0**	13.8	53.0**
P2 ppm	24.5	76.5**	6.8	85.0**	8.5	90.8**	19.0	76.5**
K ppm	172	261*b	155	188*b	160	243**b	171	404**a
Ca ppm	2050	2380	1837	1762	1850	1825	2000	1775
Mg ppm	216	240	174	228*	170	223**	183	209*
Mn ppm	164	198*	151	177*	144	173	173	200**
Fe ppm	12.3	18.0*	9.5	22.0**	8.8*	20.5**	10.8	18.3**
Cu ppm	1.3	1.7*c	1.4	3.2**a	1.3	2.1**bc	1.1	2.5**ab
Zn ppm	8.3	10.1	6.8	7.6	6.5	8.6	7.9	8.3
pH	6.1	6.7*	6.1	6.4*	6.1	6.3	6.4	6.9*
buffer pH	5.88	6.50**a	5.90	6.18*ab	6.00	6.10b	6.28	6.65*ab
C.E.C.	14.7	13.6	12.9	12.3	12.7	12.9	13.1	12.0
K base sat. %	3.0	4.9*b	3.1	3.9**b	3.2	4.9**b	3.4	8.7**a
Ca base sat. %	69.9	75.1	70.9	71.6	71.7	70.6	76.5	74.2
Mg base sat. %	12.3	14.7**b	11.2	15.4**a	11.1	14.4**c	11.7	14.6**bc
H sat. %	14.9	5.1*	14.9	9.3*	13.8	10.2	8.6	2.5*

*End value significantly different (ANOVA, α = .05) from the start value.

**End value significantly different (ANOVA, α = .01) from the start value.

a,b,c indicate that Treatment had a significant effect (Tukey's-w after ANOVA, α = .05) on the amount of change over time. Means followed by the same letter did not have significantly different change over time due to treatment effects.

phosphorus reserve was small. The initial fertilization after soil sampling effectively eliminated phosphorus fertility differences between the treatments. Available potassium, calcium and magnesium were greater in the topsoils than in the spoils. The amounts and relative base saturations of each were sufficient for acceptable plant growth (Doll and Lucas 1973). Available manganese was classified as very high (Mn > 50 ppm) for an agricultural soil (Ankerman and Large 1974). Available iron was low (4-11 ppm) compared to agricultural soils (Ankerman and Large 1974). Available copper was moderate (0.9-1.5 ppm) and available zinc was high (5.1-8.0 ppm) to very high (> 8.0 ppm) (Ankerman and Large 1974).

Levels of all nutrient elements except Cu were somewhat higher in the fumigated topsoils at the start of the study. Fumigation of the soils would have destroyed the soil microflora and released nutrients they contained (Warcup 1957). Another possible reason for the difference is that variation in forest floor characteristics may have been carried through topsoils pickup and spreading. In any case, N and P fertilization after the soil samples were taken would have masked the most important natural fertility differences.

Final Conditions

At the end of the study, the topsoil in all plots had settled to about 2/3 of the initial thicknesses.

A number of significant chemical changes took place in the topsoil over the five-month period (Table 6). Organic matter did not

increase significantly. Total N (Kjeldahl) did not increase despite the initial fertilization. This indicates that N applied as fertilizer was either lost by leaching or taken up by vegetation growing on the plots. The latter explanation is likely because the amount of N applied in fertilizer was approximately equal to the amount in the aboveground biomass of Treatments 1-3. Aboveground biomass in Treatment 4, however, contained about 2.5 times the nitrogen applied in fertilizer, so some nitrogen was also being derived from the topsoils and spoils. A nitrogen decrease was noted in the top 10 cm of spoils under Treatment 4, but the statistical test results do not indicate that this difference was real. Nitrogen content of excluded roots was not determined, but it also would have been important.

Bray-1 P and Bray-2 P increased significantly in the topsoils but not in the spoils. The topsoil differences are most likely a residual effect of fertilization, as much more P was added as fertilizer than was used in the aboveground vegetation. Changes over time were not significantly related to vegetation treatment.

Potassium levels in the topsoil increased significantly over the study period and there was a significant ($\alpha = .05$) difference between treatments in the amounts of K increase. This topsoil K increase was matched by a significant K decrease in the top 10 cm of the spoils (Table 7). Vegetation treatment significantly affected the amount of change in available K in the spoil also. The greatest spoil K decrease occurred under Treatment 4. Potassium base saturation followed the same trend in the topsoils and spoils. In spoils, the

Table 7. Spoil chemical properties by treatment at start and end of study.

	Treatment							
	1		2		3		4	
Value	Start	End	Start	End	Start	End	Start	End
Organic Matter %	3.8	4.8	3.7	3.9	3.9	3.6	4.0	4.4
N %	0.16	0.17	0.14	0.15	0.16	0.16	0.21	0.16
P1 ppm	10.5	12.5	7.8	10.5	8.3	9.3	9.5	15.5
P2 ppm	47.8	52.8	58.5	58.3	55.3	58.0	53.5	51.0
K ppm	97.0	85.3*ab	104.5	90.5*ab	101.5	93.0*b	96.3	72.3*a
Ca ppm	875	980	1025	1037	938	1113	875	1000
Mg ppm	276	278	300	269	301	301	283	276
Mn ppm	72	74	73	75	60	76	63	76
Fe ppm	189	187	201	174	202	174	191	187
Cu ppm	4.3	4.3	4.4	4.3	4.3	4.3	4.3	4.4
Zn ppm	8.4	9.7	8.3	7.5	8.2	8.8	8.1	9.0
pH	5.2	5.1	5.9	5.7	5.4	5.6	5.4	5.0
Buffer pH	5.05	4.93	5.65	5.53	5.33	5.48	5.23	4.83
C.E.C.	12.7	15.0	11.5	11.3	11.1	14.5	10.2	16.3
K base sat. %	2.2	1.7	2.6	2.2	2.4	2.0	2.4	1.4
Ca base sat. %	38.9	39.1	50.1	49.7	44.0	47.5	43.5	37.5
Mg base sat. %	20.1	18.0	23.6	21.0	23.2	21.0	23.3	17.2
H sat. %	38.8	41.3	23.3	27.0	30.5	29.4	30.8	33.8

*End value significantly different (t-test, α = .05) from the start value.

**End value significantly different (t-test, α = .01) from the start value.

a,b,c indicate that Treatment had a significant effect (Tukey's-w after ANOVA, α = .05) on the amount of change over time. Means followed by the same letter did not have significantly different change over time due to treatment effects.

trend was statistically significant only in Treatment 4. Potassium had the highest mean concentration in plants of any of the nutrients investigated in this study. As K is also one of the nutrients leached most easily from plant tissues by rainwater, this suggests that the vegetation on these plots performed as "pumps" in bringing K to the surface. Black (1968) indicates that this K pumping action is possible, and Klopatek (1978) showed its importance in soils of riverine marshes.

There was no uniform trend for Ca concentration changes in topsoil, but Treatment 4 showed a significant decline in the surface soil Ca levels. This might reflect the high amount of Ca uptake by C. album, but a similar decline was not noted under Treatment 2 vegetation which sequestered the same amount of Ca in aboveground biomass.

Magnesium increased in topsoil concentrations over time in all but Treatment 1, but the amount of change was not significantly related to treatment. Percent base saturation was more sensitive to treatment with significant differences related to both time and treatment. The greatest increase occurred in Treatment 2.

Topsoil Mn increased significantly in Treatments 1, 2 and 4, but there were no statistically significant effects due to treatment. The increase in Treatment 3 was as large as those in other treatments, but greater variability within Treatment 3 precluded statistical significance.

Iron was significantly greater in the topsoils at the end of the study, but there were no detectable treatment effects.

Topsoil Cu concentration increased over time and a significant treatment effect showed up as well. Treatment 2 had the greatest increase; the least increase occurred under Treatment 1.

Zinc concentration in topsoil and spoil did not change significantly.

Topsoil pH increased significantly in all but Treatment 3. This may be partly due to the increase in cation base saturation due to weathering of soil material, cations released from soil organic matter breakdown and the cation pumping action of vegetation.

Buffer pH was also sensitive to change over time and showed statistically significant treatment effects as well. The magnitude of change was approximately equal to the change in water pH of the topsoils.

Chemical changes in the mine spoils were small compared to topsoil changes (Table 7). Only changes already discussed in conjunction with topsoils were significant.

Discussion

Changes in soils and development of soils from mine spoils are very complex processes that are influenced by nature of the parent material, microclimate, microorganisms, vegetation, topography, management and time. The most marked chemical changes occurred in the topsoil which was most heavily exploited by plants and most affected by microclimate. Small, nonsignificant increases in organic matter observed here were probably due to new fine roots, microbial

biomass and organic excretions. Undoubtedly, "old" organic matter in the applied topsoil underwent degradation in this new regimen. Apart from increases due to the initial fertilization, some increased nutrients in the topsoils may have been released by breakdown of the old organic matter and release of its nutrient reserve. As apparently happened with K, cation pumping action by vegetation may also have occurred, but if so, it was more subtle and may have been obscured by nutrient release from weathering spoil. The data show that even in one growing season, significant soil changes occurred in these small ecosystems, some of which were vegetation-caused or vegetation-modified.

In four out of five cases where vegetation treatment effects showed a statistically significant influence on soil chemical characteristics, Treatment 4 soils showed changes as large as or larger than changes among other treatments (K, Cu, buffer pH, and K base saturation-magnesium base saturation was significantly greatest under Treatment 2). In these same cases, soils under Treatment 3 had changes which were smallest or not statistically different from the smallest changes. Treatment 4 had the greatest biomass and in most cases took up the most nutrients into the aboveground biomass (see Chapter V). Leaching of some of these elements from foliage back to the topsoil may have accounted for some of the soil changes.

Influences of nutrient input via precipitation and tapwater irrigation were not accounted for, but are probably trivial. Precipitation in temperate zones usually contains 1-5 kg/ha N,

0.2-0.6 kg/ha P, 1-10 kg/ha K, 3-19 kg/ha Ca, and 4-11 kg/ha Mg (Ovington 1968, cited by Duvineaud and Denaeger-DeSmet 1973). This is 1-2 orders of magnitude less than the amounts of N and P added as fertilizer. Tapwater contains basic salts but they are present in low concentrations when compared with the levels in soil solution.

Uniform amounts of water were applied to each plot, yet topsoil chemical changes were not uniform across treatments. It seems, therefore, that the role of irrigation was minimal as a nutrient source.

CHAPTER V

BIOMASS PRODUCTION AND NUTRIENT CAPITAL SEQUESTRATION

The Role of Vegetation in Conservation of Nutrients

Vegetation can slow nutrient loss from an ecosystem through a number of mechanisms. For example, nutrients may be retained in the ecosystem by rapid incorporation into biomass, enhancement of the nutrient-holding capacity of soil by adding organic matter to it, and protection of surface soil structure from breakdown by heavy rains (Harcombe 1977). Dead roots and root excretions may also provide organic matter substrates for microbial populations which bind nitrogen in microbial biomass (Huntjens 1971). Allelochemics may retard nitrification in soils (Rice and Pancholy 1972, Lodhi 1977) and prevent loss of nitrogen through leaching of nitrate and the accompanying cation losses.

After severe disturbance, rapid uptake of available nutrients by vegetation is one of the mechanisms for a system's return to a steady state (Marks and Bormann 1972). The importance of vegetation in nutrient capital sequestration and site stabilization was amply demonstrated by the clearcutting and herbiciding of the Hubbard Brook watershed (Likens et al. 1970). Sopper (1975) reviewed timber harvesting technique effects on water quality and concluded that rapid regrowth of vegetation was responsible for negligible nutrient losses after clearcutting. Tamm et al. (1974) concluded that nutrient losses

after forest cutting were significant only in areas of high site quality, probably because of better conditions for nitrification on better sites. Bartholomew et al. (1953) stressed the importance of prevention of nutrient losses in tropical systems through storage of nutrients in plant tissues. Species composition and growth form influenced the rate of plant nutrient uptake. They also stated that rapid uptake during the first years of succession may result in depletion rather than a buildup of soil fertility. The currently accepted idea is that little of the nutrient capital of tropical forests is in the mineral soil per se, rather it is bound in the biomass. Even in recycling, it may not be "available" in the soil solution.

In a relatively eutrophic tropical forest on volcanic soil, Harcombe (1977) found that vegetative regrowth retained 13 to 100 percent of available N, K, Ca and Mg that would have been lost after disturbance. Retention of nutrients in that system was significant but not important as soil weathering and atmospheric inputs could replace the amounts lost. Nutrient retention was not found to be significantly affected by differences in biomass, species composition, or nutrient concentration.

Importance of nutrient sequestration and conservation in biomass may vary from system to system and species to species. Khanna (1975) found that the nitrate concentration in water percolating from litter to the deepest part of the rooting zone in a spruce stand decreased 75 to 80 percent during the period of active nitrate uptake by the

vegetation. Marks (1974) stated that nutrient retention is determined by the rapidity of successional regeneration. The nutrient uptake characteristics of pin cherry (Prunus pennsylvanica L.f.) are very important in northern hardwood ecosystems in this regard. Muller and Bormann (1976) and Muller (1978) advanced the hypothesis that a spring herb, Erythronium americanum Ker. is important to northern hardwood ecosystems nutrient budgets through its ability to sequester nitrogen and potassium in its biomass from the period of the start of spring runoff to the close of the forest canopy when its tissues senesce and release accumulated nutrients to later-growing forest species. This is termed the "vernal dam hypothesis."

Blank et al. (1980) studied uptake of nutrients by a spring ephemeral community in south-central Indiana. They found nitrogen and potassium uptake to be about equal to the annual leaching losses from soils. Nitrogen flux of the system could have been significantly affected, but they could reach no conclusion on the validity of the vernal dam hypothesis as they could not prove that vegetation-sequestered nutrients would have otherwise been lost. Van Andel et al. (1979) studied nutrient cycling in forest clearings and stated that some plant populations can have significant impact on succession if they are capable of withdrawing relatively large amounts of nitrogen, phosphorus, and potassium from the short-term recycling process by dispersing them in wind-disseminated seed or accumulation of nutrients in long-term biomass storage and using these nutrients in later growth. Foster et al. (1980) studied the role of Ambrosia

artemisiifolia on nitrogen and phosphorus cycling in a first-year old-field. They concluded that A. artemisiifolia could reduce nitrogen losses very early in succession by taking up and storing nitrogen in shoots and seeds. Most of that nitrogen would have been available to plants in subsequent years, but the amount stored in ragweed seed in the soil might be lost to the system for a substantial period of time. Klopatek (1978) found that emergent macrophytes played a key role in the regulation of nitrogen, phosphorus, and potassium in soils of riverine marshes. Vegetation operated as nutrient pumps taking ions from the soils and immobilizing them in above- and below-ground biomass. By taking up phosphorus they facilitated greater movement of phosphorus from water to soil (a slow process). He hypothesized that uptake of cations from the soil freed exchange sites to hold new cations in interstitial water.

Treatment Differences in Biomass Production and Nutrient Sequestration

Results

The Chenopodium-dominated Treatment 4 produced significantly more biomass and sequestered more nutrients in aboveground biomass than any other treatment (Table 8). Biomass nutrient contents were significantly greatest in Treatment 4 except for Ca and Fe. Potassium, Mg and Mn contents were four-fold those of Treatment 1.

Treatment 2 (native seed bank species) produced more biomass and sequestered more nutrients in aboveground biomass than Treatments 1 and 3, but differences were not statistically significant for N, Mn,

Table 8. Aboveground biomass and nutrient contents in each treatment (kg/ha).*

Treatment	Biomass	N	P	K	Ca	Mg	Mn	Fe	Cu	Zn
1. Reclam. Mix	5,533c	53b	9.2c	86c	23b	6.9c	2.5b	0.60b	0.052b	0.41b
2. Seed Bank	8,231b	62b	12.5b	173b	66a	15.3b	6.7b	1.10a	0.065b	0.50b
3. Seed Bank + Reclam. Mix	6,262bc	51b	8.5c	87c	34b	8.2c	3.0b	0.57b	0.049b	0.41b
4. Chenopodium	15,377a	135a	16.2a	355a	66a	31.9a	10.7a	1.48a	0.095a	1.08a
r^2 with biomass**		.943	.841	.956	.534	.940	.673	.540	.879	.906

*Biomass and element means followed by the same letter are not significantly different (Tukey's-w following ANOVA, $\alpha = .05$).

**From correlations of plot contents.

Cu and Zn. Differences in vegetation contents of the major cationic nutrients are particularly striking. Treatment 2 vegetation contained two to three times more K, Ca, Mg, Mn and Fe than Treatment 1. The first three treatments did not vary significantly in the amount of nitrogen in aboveground biomass. There was significantly more P in biomass of Treatment 2 than in Treatments 1 and 3.

Community nutrient content in aboveground biomass was significantly correlated with community biomass (α = .05) in the case of all elements determined. This indicates that choosing communities with rapid biomass production is an important factor in sequestering nutrient capital in vegetation, but the r-square values of Ca, Fe and Mn reveal that something other than biomass production influenced nutrient accumulation.

Discussion

The amounts of biomass produced in Treatment 1 are comparable to amounts found on surface mines in Appalachia. Richards et al. (1984) found 10-year-old fescue-dominated grass areas on a surface mine contained 5061 kg/ha of live and dead biomass. Total N, Ca and Mg contents in biomass were also similar. Phosphorus and potassium were considerably lower, probably due to the large share of dead material in their plots. In a study of different forest soil seed banks spread over different surface mine spoils in microplots, Farmer et al. (1982) produced native species averaging 5.7 t/ha of oven-dry biomass. From limited chemical analyses, they determined that the native seed bank species contained 45.5 kg/ha N and 16.8 kg/ha P; amounts similar to

those found in this study. Vail and Wittwer (1982) studied biomass and nutrient accumulation in 10-year-old eastern cottonwood, Virginia pine and black locust plantations on an eastern Kentucky surface-mine spoil. These plantations were planted in plots with and without an herbaceous cover of Eragrostis curvula, Festuca arundinacea, Lespedeza cuneata and Lespedeza stipulacea. About one-third more N, P, Ca and Mg was contained in litter and biomass of the cottonwood plantation that was started with an herbaceous cover, but herbaceous cover had little effect on biomass and contents in the other two plantation types. Potassium held in biomass of Treatments 2 and 4 of the work reported here exceeded that held in several of their plantations after ten years.

Nitrogen was added to microplots at a rate equivalent to 57 kg/ha. The Treatment 2 native species community gathered somewhat more than this in shoot material alone. The reclamation mix (Treatment 1) and the native seed bank plus reclamation mix (Treatment 3) contained slightly less. The Chenopodium community shoot material contained 237 percent more than the amount of N applied as fertilizer to that treatment. This may be related to the 24 percent decrease of upper spoil N noted over the course of this study. Phosphorus was applied at a rate equivalent to 59 kg/ha. None of the four treatments in this study sequestered anything near this amount. Shoot P content was 14 to 27 percent of that applied. A reasonable estimate of the proportional amount tied up in roots, one-third (Farmer et al. 1982), does not account for this. Much of the phosphorus not tied up in

plants is available in the soils (Table 6, p. 40; Table 7, p. 43), but the complexities of phosphorus's soil chemistry/biodata dynamics thwart a detailed accounting. The topsoil spread over the soils and the spoils themselves contained some N and P which would have been available to the plants, especially as topsoil organic matter was broken down. This N release was obviously important for vegetation development. As nitrate in the soil is very mobile, and much soil ammonia is converted to nitrate, the plant communities' sequestration of nitrogen in the form of biomass may be very important in the development of a long-term nitrogen economy. The direct influence of the pioneer plant community on system P content is not great, apparently, but it may be important over the long term.

Nutrient Concentrations in Individual Species and Their Effects on Community Nutrient Sequestration

Results

Table 9 shows nutrient concentrations in many of the species of the four treatments. There are marked differences between species. Some differences are important, from an ecosystems point of view, because nutrient concentrations of a species multiplied by its biomass equals its total nutrient content. Thus the nutrient conservation characteristics of a plant community will depend upon the nutrient characteristics of its individuals. Table 10 details biomass and nutrient contents of important species in all treatments and Table 11 shows the same data in terms of shares of total in the aboveground community.

Table 9. Mean nutrient concentrations in selected species by treatment.

Name	%					ppm			
	N	P	K	Ca	Mg	Mn	Fe	Cu	Zn
Treatment 1									
Dactylis glomerata	1.27	0.25	2.82	0.37	0.17	526	104	9.8	42
Datura stramonium	0.91	0.16	2.10	0.64	0.07	169	72	6.0	54
Digitaria ischaemum	0.61	0.18	1.42	0.23	0.09	251	97	6.8	49
D. sanguinalis	0.38	0.13	1.70	0.35	0.19	715	101	10.8	75
Eragrostis curvula	0.99	0.09	0.74	0.22	0.04	222	112	8.5	38
Festuca arundinacea	0.78	0.19	2.34	0.39	0.17	401	53	8.7	53
Lespedeza cuneata	2.17	0.15	1.24	0.77	0.10	241	116	5.6	53
Lolium multiflorum	1.22	0.17	1.38	0.61	0.14	671	117	11.1	97
L. perenne	0.87	0.16	1.90	0.55	0.15	668	155	11.3	147
Misc. Poaceae	1.29	0.24	2.85	0.37	0.16	604	108	8.0	56
Muhlenbergia schreberi	1.00	0.17	1.06	0.36	0.09	431	92	7.4	72
Panicum dichotomiflorum	0.61	0.24	1.27	0.29	0.17	515	163	9.0	65
Paspalum circulare	0.61	0.19	2.18	0.21	0.08	365	85	7.0	41
Phytolacca americana	1.42	0.26	3.68	0.86	0.43	3438	273	15.0	106
Robinia pseudo-acacia	3.09	0.19	2.13	0.89	0.11	88	345	5.0	30
Treatment 2									
Acalypha rhomboidea	0.95	0.27	1.95	1.93	0.21	2079	93	10.0	96
A. virginica	0.75	0.37	-	-	-	504	119	8.0	71
Agrostis gigantea	1.46	0.19	2.91	1.01	0.15	1139	119	9.7	52
Aster divaricatus	0.84	0.15	2.19	0.92	0.08	624	93	7.1	70
Crotonopsis elliptica	0.82	0.13	1.68	0.78	0.22	635	145	7.0	65
Cyperus esculentus	0.70	0.07	3.37	0.55	0.12	3299	99	7.5	106
Dactylis glomerata	1.36	0.15	2.14	0.64	0.12	808	241	1.0	39
Digitaria ischaemum	0.56	0.10	1.39	0.23	0.09	291	132	9.0	46
D. sanguinalis	0.44	0.09	1.52	0.30	0.15	737	151	13.1	55
Echetites hieracifolia	0.77	0.20	2.19	0.91	0.12	449	142	10.1	76

Table 9 (continued)

Name	%					ppm			
	N	P	K	Ca	Mg	Mn	Fe	Cu	Zn
Treatment 2 (continued)									
Eupatorium purpureum	0.79	0.16	2.17	1.92	0.40	651	130	8.4	41
E. rugosum	0.75	0.17	1.73	1.32	0.26	368	98	7.6	35
E. serotinum	0.82	0.16	1.44	0.88	0.13	538	89	6.0	77
Eupatorium sp.	0.97	0.22	1.46	1.45	0.18	1320	128	8.0	105
Hedeoma pulegioides	0.85	0.31	1.85	1.65	0.24	362	118	1.0	52
Helianthus decapetalis	0.66	0.16	2.09	0.73	0.14	581	71	10.5	78
H. laevigatus	0.84	0.11	2.52	0.69	0.15	842	152	8.0	103
H. microcephalus	0.64	0.16	2.15	0.69	0.11	306	90	6.1	57
Helianthus sp.	0.72	0.12	1.54	1.07	0.20	1045	189	3.0	101
Lactuca biennis	1.34	0.17	3.66	1.54	0.19	589	103	9.4	71
L. pulchella	1.44	0.16	4.12	1.54	0.22	497	24	8.0	66
Liriodendron tulipifera	1.24	0.12	1.95	1.04	0.23	918	82	5.9	36
Misc. Asteraceae	0.92	0.14	2.50	2.22	0.54	2488	213	12.0	215
Monarda clinopodia	0.78	0.21	1.80	1.57	0.22	445	139	5.6	48
Panicum dichotomiflorum	0.26	0.04	0.82	0.22	0.11	467	37	8.0	52
Physalis pruinosa	1.21	0.24	3.09	0.52	0.13	216	130	7.0	71
Phytolacca americana	0.94	0.14	2.62	0.90	0.34	1664	125	7.1	62
Plantago lanceolata	1.25	0.17	2.29	1.24	0.22	894	176	12.0	261
Ranunculus septentrionalis	1.09	0.22	2.65	1.95	0.25	1088	314	5.0	74
Robinia pseudo-acacia	2.37	0.15	1.25	1.65	0.15	141	80	6.5	45
Rubus occidentalis	1.03	0.16	1.39	1.08	0.24	1412	124	5.8	44
Rubus sp.	1.06	0.15	1.73	1.21	0.23	4212	145	7.0	127
Scutellaria ovata	0.78	0.10	1.94	2.00	0.30	2992	159	5.9	45
Solidago flexicaulis	0.91	0.16	2.84	1.01	0.14	862	151	6.0	114
Viola sp.	1.08	0.18	3.27	1.52	0.33	877	259	7.5	112
Vitis sp.	1.10	0.16	1.61	1.66	0.19	1511	102	9.0	23

Table 9 (continued)

Name	%					ppm			
	N	P	K	Ca	Mg	Mn	Fe	Cu	Zn
Treatment 3									
Acalypha rhomboidea	1.14	0.41	2.06	2.04	0.24	692	78	9.0	80
A. virginica	0.72	0.44	1.65	1.69	0.14	257	110	9.0	70
Agrostis gigantea	1.02	0.16	2.05	0.43	0.10	380	34	11.0	48
Amaranthus hybridus	1.20	0.22	2.77	0.96	0.31	292	75	6.0	60
Aster divaricatus	1.00	0.24	2.45	1.02	0.11	613	77	6.9	70
Bidens frondosa	0.72	0.24	1.45	0.88	0.21	1158	44	8.0	156
Bromus commutatus	0.88	0.12	1.51	0.48	0.10	530	98	8.2	27
Dactylis glomerata	1.05	0.20	2.75	0.50	0.14	615	75	8.9	49
Digitaria ischaemum	0.42	0.11	1.14	0.24	0.10	259	84	7.6	45
D. sanguinalis	0.58	0.19	1.72	0.32	0.21	677	82	10.2	94
Eragrostis curvula	0.59	0.07	0.62	0.24	0.04	231	81	4.8	35
Erechtites hieracifolia	0.76	0.23	2.23	0.97	0.13	298	96	8.4	91
Eupatorium purpureum	0.81	0.12	2.99	1.94	0.51	1376	168	10.5	111
E. rugosum	0.89	0.23	2.62	1.51	0.27	297	118	7.5	51
E. serotinum	0.97	0.23	2.15	1.05	0.17	430	100	7.1	95
Festuca arundinacea	0.87	0.13	2.09	0.30	0.17	383	66	5.1	41
Helianthus decapetalus	0.76	0.20	2.07	1.12	0.12	388	127	6.2	65
H. microcephalus	0.82	0.24	2.61	1.02	0.14	312	87	7.1	88
Lactuca biennis	1.16	0.18	3.85	1.11	0.16	402	258	13.0	90
Lespedeza cuneata	2.23	0.16	1.03	0.91	0.13	243	116	6.7	46
Lolium multiflorum	1.11	0.13	1.01	0.65	0.13	245	127	11.3	93
L. perenne	0.90	0.11	1.14	0.61	0.13	579	110	7.5	94
Muhlenbergia schreberi	0.40	0.10	0.70	0.39	0.08	340	198	8.0	76
Panicum agrostoides	0.37	0.05	0.61	0.20	0.15	293	69	9.0	63
P. dichotomiflorum	0.40	0.05	-	-	-	-	-	-	-
Phytolacca americana	1.09	0.20	3.27	0.94	0.30	2132	145	7.4	79
Robinia pseudo-acacia	3.42	0.21	2.48	1.27	0.17	141	85	7.0	47

Table 9 (continued)

Name	%					ppm			
	N	P	K	Ca	Mg	Mn	Fe	Cu	Zn
Treatment 3 (continued)									
Scutellaria ovata	0.99	0.22	2.84	1.32	0.23	2556	134	5.8	76
Solanum carolinense	1.34	0.15	1.91	2.30	0.63	549	103	18.0	88
Solidago flexicaulis	0.81	0.18	1.80	0.95	0.11	371	104	4.8	69
Triticum aestivum	0.84	0.13	1.27	0.33	0.09	450	56	8.0	63
Viola sp.	1.11	0.18	3.89	1.46	0.32	717	453	7.0	77
---------- Treatment 4 ----------									
Acalypha rhomboidea	0.55	0.21	2.04	0.82	0.23	1709	214	29.0	364
Agrostis gigantea	1.71	0.12	2.18	0.64	0.15	1153	124	10.0	94
Chenopodium album	0.90	0.11	2.46	0.43	0.22	666	88	6.0	73
Dactylis glomerata	1.78	0.25	3.08	0.64	0.15	635	113	10.0	79
Digitaria ischaemum	0.56	0.07	1.22	0.20	0.09	253	91	6.1	47
D. sanguinalis	0.70	0.11	1.83	0.35	0.14	566	92	10.2	64
Eragrostis curvula	0.82	0.08	0.78	0.29	0.06	331	61	9.4	44
Lespedeza cuneata	1.80	0.11	1.29	0.90	0.10	400	121	6.2	41
Lolium perenne	1.38	0.14	1.57	0.59	0.16	839	220	17.0	246
Lolium sp.	1.26	0.15	0.50	1.05	0.17	913	184	11.0	144
Misc. Poaceae	1.10	0.23	1.10	0.33	0.09	384	138	12.0	105
Muhlenbergia schreberi	1.06	0.21	1.25	0.44	0.09	484	107	7.0	68
Panicum dicotomiflorum	0.65	0.05	1.68	0.26	0.13	740	88	6.0	59
Paspalum laeve	0.79	0.09	2.20	0.21	0.10	260	126	7.0	54

Table 10. Biomass and nutrient content (kg/ha) of species containing 1 percent or more of biomass in each treatment.

Name	Biomass	N	P	K	Ca	Mg	Mn	Fe	Cu	Zn
Treatment 1										
Lolium multiflorum	1859	22.98	3.08	29.62	11.37	2.72	1.26	0.216	0.0205	0.197
Digitaria ischaemum	1490	9.30	2.78	20.70	3.83	1.46	0.37	0.139	0.0104	0.086
Eragrostis curvula	745	7.16	0.68	5.73	1.86	0.37	0.20	0.092	0.0077	0.030
Festuca arundinacea	628	6.60	1.25	14.71	2.51	1.08	0.27	0.053	0.0058	0.035
Digitaria sanguinalis	358	1.85	0.55	6.38	1.41	0.66	0.22	0.037	0.0040	0.028
Lolium perenne	148	1.37	0.24	2.79	0.37	0.23	0.10	0.023	0.0017	0.022
Datura stramonium	108	0.99	0.17	2.28	0.69	0.08	0.02	0.008	0.0006	0.006
Dactylis glomerata	75	0.99	0.19	2.14	0.30	0.13	0.04	0.009	0.0007	0.003
Treatment Sum	5533	52.56	9.15	86.08	22.83	6.94	2.54	0.592	0.0524	0.413
Treatment 2										
Phytolacca americana	2053	19.46	2.99	55.71	18.94	6.89	3.57	0.293	0.0106	0.093
Erechtites hieracifolia	1965	15.25	4.01	43.26	18.00	2.45	0.92	0.319	0.0200	0.172
Digitaria ischaemum	1138	5.74	1.19	17.96	2.29	1.00	0.31	0.157	0.0092	0.050
Helianthus microcephalus	601	3.84	0.95	12.41	4.53	0.72	0.18	0.061	0.0040	0.035
Eupatorium rugosum	475	3.59	0.80	8.54	6.44	1.20	0.20	0.060	0.0037	0.023
Helianthus decapetalus	407	2.69	0.63	8.47	3.26	0.55	0.24	0.030	0.0042	0.034
Digitaria sanguinalis	352	1.53	0.35	5.36	1.11	0.56	0.28	0.053	0.0049	0.020
Eupatorium serotinum	270	2.24	0.48	4.10	2.63	0.41	0.17	0.027	0.0017	0.024
Panicum dicotomiflorum	174	0.45	0.07	1.42	0.38	0.19	0.08	0.006	0.0014	0.009
Agrostis gigantea	104	1.52	0.20	3.04	1.06	0.16	0.12	0.0120	0.0010	0.005
Treatment Sum	8231	62.23	12.48	172.59	66.40	15.31	6.66	1.097	0.0649	0.500

Table 10 (continued)

Name	Biomass	N	P	K	Ca	Mg	Mn	Fe	Cu	Zn
				Treatment 3						
Digitaria ischaemum	1350	5.35	1.35	14.04	3.52	1.60	0.43	0.067	0.0121	0.040
Eragrostis curvula	1148	6.85	0.81	7.28	2.82	0.45	0.26	0.095	0.0055	0.044
Festuca arundinacea	636	5.52	0.82	13.88	1.91	1.11	0.25	0.051	0.0041	0.045
Lolium perenne	483	4.41	0.62	7.07	3.58	0.81	0.27	0.052	0.0034	0.047
L. multiflorum	460	5.10	0.59	2.54	3.08	0.60	0.30	0.062	0.0057	0.043
Erechtites hieracifolia	438	3.36	1.04	9.63	4.33	0.55	0.16	0.047	0.0038	0.045
Lespedeza cuneata	398	8.96	0.62	4.17	3.72	0.50	0.10	0.048	0.0028	0.018
Phytolacca americana	247	2.77	0.50	5.90	2.33	0.77	0.60	0.039	0.0020	0.045
Helianthus microcephalus	244	1.91	0.52	6.16	2.24	0.30	0.10	0.022	0.0017	0.024
Digitaria sanguinalis	180	0.93	0.35	3.22	0.79	0.41	0.17	0.020	0.0030	0.017
Helianthus decapetalus	163	1.21	0.33	3.29	1.77	0.18	0.06	0.020	0.0010	0.011
Amaranthus hybridus	111	1.33	0.24	3.06	1.06	0.34	0.03	0.008	0.0007	0.007
Treatment Sum	6262	50.90	8.51	87.33	34.42	8.24	2.95	0.566	0.0485	0.412
				Treatment 4						
Chenopodium album	13,592	123.05	14.73	335.69	59.16	30.36	10.25	1.280	0.0823	0.999
Digitaria ischaemum	706	3.98	0.60	9.66	1.59	0.74	0.11	0.049	0.0019	0.033
Eragrostis curvula	613	4.94	0.46	4.87	1.82	0.34	0.20	0.049	0.0055	0.026
Treatment Sum	15,377	134.50	16.09	354.50	64.20	31.92	10.73	1.484	0.0950	1.080

Table 11. Percent of population, biomass, and nutrient content of species containing 1 percent or more of treatment biomass.

Name	Pop. %	Biomass %	N %	P %	K %	Ca %	Mg %	Mn %	Fe %	Cu %	Zn %
Treatment 1											
Lolium multiflorum	18.8	33.6	43.7	33.7	34.4	49.8	39.2	49.6	36.5	39.1	47.7
Digitaria ischaemum	7.6	26.9	17.7	30.4	24.0	16.8	21.0	14.6	23.5	19.8	20.8
Eragrostis curvula	30.9	13.5	13.6	7.4	6.7	8.1	5.3	7.9	15.5	14.7	7.3
Festuca arundinacea	23.2	11.4	12.6	13.7	17.1	11.0	15.6	10.6	9.0	11.1	8.5
Digitaria sanguinalis	1.5	6.5	3.5	6.0	7.4	6.2	9.5	8.7	6.3	7.6	6.8
Lolium perenne	11.8	2.7	2.6	2.6	3.2	1.6	3.3	3.9	3.9	3.2	5.3
Datura stramonium	0.1	2.0	1.9	1.9	2.6	3.0	1.2	0.8	1.4	1.1	1.5
Dactylis glomerata	1.8	1.4	1.9	2.1	2.5	1.3	1.9	1.6	1.5	1.3	0.7
Others	4.3	2.0	2.5	2.2	2.1	2.2	3.0	2.3	2.4	2.1	1.4
Treatment 2											
Phytolacca americana	6.8	24.9	31.2	24.0	32.3	28.5	45.0	53.6	26.7	16.3	18.6
Erechtites hieracifolia	8.6	23.9	24.5	32.1	25.1	27.1	16.0	13.8	29.1	30.8	34.4
Digitaria ischaemum	3.3	13.8	9.2	9.5	10.4	3.4	6.5	4.7	14.3	14.2	10.0
Helianthus microcephalus	1.0	7.3	6.2	7.6	7.2	6.8	4.7	2.7	5.6	6.2	7.0
Eupatorium rugosum	23.3	5.8	5.8	6.4	4.9	9.7	7.8	3.0	5.5	5.7	4.6
Helianthus decapetalus	0.3	4.9	4.3	5.0	4.9	4.9	3.6	3.6	2.7	6.5	6.8
Digitaria sanguinalis	1.0	4.3	2.5	2.8	3.1	1.7	3.7	4.2	4.8	7.6	4.0
Eupatorium serotinum	5.6	3.3	3.6	3.8	2.4	4.0	2.7	2.6	2.5	2.6	4.8
Panicum dicotomiflorum	0.1	2.1	0.7	0.6	0.8	0.6	1.2	1.2	0.5	2.2	1.8
Agrostis gigantea	1.3	1.3	2.4	1.6	1.8	1.6	1.0	1.8	1.1	1.5	1.0
Others	48.7	8.4	9.6	6.6	7.1	11.7	7.8	8.8	7.2	6.4	7.0

Table 11 (continued)

Name	Pop. %	Biomass %	N %	P %	K %	Ca %	Mg %	Mn %	Fe %	Cu %	Zn %
Treatment 3											
Digitaria ischaemum	3.3	21.6	10.5	15.9	16.1	10.2	19.4	14.6	11.8	24.9	9.7
Eragrostis curvula	20.7	18.3	13.5	9.5	8.3	8.2	5.5	8.8	16.8	11.3	10.7
Festuca arundinacea	14.9	10.2	10.8	9.6	15.9	5.5	13.5	8.5	9.0	8.5	10.9
Lolium perenne	3.2	7.7	8.7	7.3	8.1	10.4	9.8	9.2	9.2	7.0	11.4
L. multiflorum	4.5	7.3	10.0	6.9	2.9	8.9	7.3	10.2	11.0	11.8	10.4
Erechtites hieracifolia	2.3	7.0	6.6	12.2	11.0	12.6	6.7	5.4	8.3	7.8	10.9
Lespedeza cuneata	24.2	6.4	17.6	7.3	4.8	10.8	6.1	3.4	8.5	5.8	4.4
Phytolacca americana	2.1	3.9	5.4	5.9	6.8	6.8	9.3	20.3	6.9	4.1	10.9
Helianthus microcephalus	0.8	3.0	3.8	6.1	7.1	6.5	3.6	3.4	3.9	3.5	5.8
Digitaria sanguinalis	1.2	2.9	1.8	4.1	3.7	2.3	5.0	5.8	3.5	6.2	4.1
Helianthus decapetalus	0.1	2.6	2.4	3.9	3.8	5.1	2.2	2.0	3.5	2.1	2.7
Amaranthus hybridus	0.0	1.8	2.6	2.8	3.5	3.1	4.1	1.0	1.4	1.4	1.7
Others	22.7	6.3	6.3	8.5	8.0	9.6	7.5	7.4	6.2	5.6	6.4
Treatment 4											
Chenopodium album	28.5	88.4	91.5	91.0	94.2	92.1	95.1	95.5	86.3	86.6	92.5
Digitaria ischaemum	8.1	4.6	2.9	3.7	2.7	2.4	2.3	1.0	3.3	2.0	3.0
Eragrostis curvula	34.8	4.0	3.6	2.8	1.4	2.7	1.0	1.8	3.3	5.8	2.4
Others	28.6	3.0	2.0	2.5	1.7	3.8	1.6	1.7	7.1	5.6	2.1

Discussion

In Treatment 1, Lolium multiflorum contained 33 percent of the biomass and constituted 19 percent of the mean total treatment population. L. multiflorum contained 43 percent of the community's nitrogen, and also shares of the other nutrients greater than its share of biomass. It was particularly important in the community content of N, Ca, Mn and Zn which the second- and third-ranked species, Digitaria ischaemum and Eregrostis curvula, contained in low concentrations (except N in E. curvula).

Digitaria ischaemum ranked second in terms of biomass, produced 27 percent of the community sum and constituted 8 percent of the total population. D. ischaemum's share of all nutrients except phosphorus was less than its share of biomass and nitrogen was particularly low. Eragrostis curvula, with 13 percent of the biomass and 31 percent of the population, contained much less than its proportional share of all nutrients except nitrogen. Festuca arundincea had 11 percent of the total biomass and 23 percent of the population. Like L. multiflorum, it had a proportional share of each nutrient that was equal to or greater than its share of the total biomass. These four species contained 84 percent of the biomass and were 81 percent of the population. They contained 87 percent of the N, 84 percent of the P, 82 percent of the K, 86 percent of the Ca, 81 percent of the Mg, and 84 percent of the Mn. Altogether the dominants in this community controlled about their share of the nutrient capital.

Population-biomass inequalities in Treatment 2 were greater than those in Treatment 1. Phytolacca americana produced 25 percent of the total biomass and 7 percent of the population. Its share of all nutrients except copper and zinc was proportionally greater than its biomass. Magnesium and Mn were strongly concentrated in this species, and this was largely responsible for the large amount of Mg and Mn found in Treatment 2 biomass. P. americana's large contributions to Treatment 2's N and K content were due to higher than average but unspectacular concentrations multiplied by high biomass. Erechtites hieracifolia contained 24 percent of the biomass and 9 percent of the treatment populations. This species contained its share or more of all elements except magnesium and manganese. E. hieracifolia's high concentrations of P, Cu and Zn and high biomass contributed significantly to this community's content of these elements. Interestingly, P. americana had a disproportionally larger share of nitrogen and potassium, while E. hieracifolia had a larger share of phosphorus. For Mg, Mn, Fe, Cu and Zn, these two species had complimentary pairings of nutrient fair share and excess. Digitaria ischaemum contained 14 percent of the biomass and 3 percent of the population. It contained less than its proportional share of all elements except iron and copper. Helianthus microcephalus represented 7 percent of the biomass and 1 percent of the treatment population. Its nutrient shares were approximately equal to or less than its share of biomass. These four leading species contained 70 percent of the total biomass in 20 percent of the Treatment 2 population. They

controlled 71 percent of the N, 74 percent of the P. 78 percent of the K, 73 percent of the Mg, 75 percent of the Mn, and 70 percent of the Fe. Their shares of Ca, Cu and Zn were over 60 percent of the total but under their combined biomass shares. The miscellaneous Asteraceae and Viola spp. had high Mg concentrations similar to P. americana, and several other species had higher Mn concentrations, but their community biomass share made their community contributions minor. In general, the dominants in this community contained a similar, dominant share of the nutrients.

Addition of grasses to the forest soil seed bank resulted in a grass-dominated community in terms of biomass (68 percent). Digitaria ischaemum, with 22 percent of the biomass and 3 percent of the population, controlled less than its proportional share of each element except copper. Eragrostis curvula also contained less nutrients than its share of both biomass and population, 18 and 21 percent respectively. Festuca arundinacea had 10 percent of the biomass and 15 percent of the treatment population. Nitrogen, P and Zn shares were approximately proportional to biomass, K and Mg were higher, and the remainder were lower. High K and Mg shares were also noted in Treatment 1, but Festuca's Treatment 1 high share of calcium was not duplicated in Treatment 3. Lolium perenne and L. multiflorum had 8 and 7 percent of the biomass and 3 and 5 percent of the population respectively. Both Lolium species contained nutrient shares equivalent to their biomass or higher, except for L. multiflorum's rather low share of potassium which was not its characteristic in Treatment 1.

Altogether, five species in Treatment 3 controlled 71 percent of the biomass, about the same proportion as the top four species in Treatment 2. The five dominants constituted 47 percent of the Treatment 3 population. The dominant 71 percent of the biomass had only 53 percent of the N, 50 percent of the P, 51 percent of the K, 38 percent of the Ca, 56 percent of the Mg, 50 percent of the Mn, 58 percent of the Fe, 64 percent of the Cu, and 53 percent of the Zn. Biomass dominance was achieved in this community, with less than a proportional share of nutrients and the total nutrient content of the community reflects this. The low nutrient use characteristics of the two leading dominants, D. ischaemum and E. curvula, were responsible for the proportionally low nutrient content of this community. Species which were good accumulators of nutrients did not produce enough biomass to make an important difference in the Treatment 1 biomass nutrient contents.

One of the original hypotheses of this study was that species composition, not necessarily biomass, is an important determinant of total nutrient capital sequestration, at least among pioneering herbaceous communities. The Treatment 4 species composition was chosen with the goal of maximizing uptake and biomass concentration of each nutrient. Chenopodium album was chosen for its apparent role as a potassium and magnesium accumulator in a study the year prior to this study. It fulfilled this role admirably here and it dominated Treatment 4's nutrient content characteristics. The mean K and Mg concentrations in C. album were 2.46 and 0.22 percent

respectively. Several other species in this and other treatments contained similar and even greater concentrations. But, because of the large size of individual plants, C. album produced 88 percent of the community biomass, and the community biomass of Treatment 4 was two to three times greater than the biomass of any other treatment. Its large amounts of biomass and high concentrations of K and Mg resulted in C. album containing more K and Mg than in Treatments 1-3 combined. This illustrates the tremendous effect that nutrient uptake characteristics of a single dominant species can have on community nutrient cycling. Nitrogen, Mn and Zn were also accumulated in amounts proportional to biomass produced by the community. Treatment 4 accumulated no more of Ca than Treatment 2, despite its having twice the Treatment 2 biomass. C. album accumulated calcium in concentrations much less than Treatment 2's Phytolacca americana, Erechtites hieracifolia, Helianthus microcephalus, Eupatorium rugosum, H. decapetalus, Eupatorium serotinum and Agrostis gigantea which constitute 68 percent of the biomass and 83 percent of the Ca content of Treatment 2. Accumulation of P, Fe and Cu were also lower in Treatment 4 than biomass alone suggested that they might be. C. album and its accompanying grasses all had relatively low concentrations of these three elements compared to the dominants of the other three treatments. The lower than expected Treatment 4 community content of P, Ca, Fe and Cu thus reflected the nutrient acquisition characteristics of its component species.

Summary

The four pioneer communities in this study produced different amounts of aboveground biomass and sequestered different amounts of the initial nutrient capital. Nutrients contained in each community were not strictly proportional to biomass. Community sequestration of N, K, Mg and Zn was most strongly related to biomass; community Ca, Mn and Fe contents were least related to biomass. A community's nutrient contents were largely influenced by the biomass and nutrient uptake characteristics of its dominant species.

CHAPTER VI

SPECIES, COMMUNITY AND SPOIL EFFECTS ON PLANT NUTRIENT CONCENTRATIONS

Variations in Nutrient Concentrations in Plant Tissues

Plants vary widely between species and varieties with regard to the amounts of nutrients in their tissues (Gerloff et al. 1964, Jorgan 1977, Cotrufo 1977, Mugwira et al. 1980, Clark 1983). They differ in absolute amounts of specific elements and ratios of certain elements required for normal physiological functions (DeKock 1964), in the specificity of physiological mechanisms of ion uptake (Epstein 1972), and in their capacity to sequester toxic metals in roots while other species or varieties pass them on to the shoot (Jarvis and Whitehead 1981). Form of available nitrogen can lead to differences in nutrient concentrations (Cole 1981, McGrath and Robinson 1982). Ability to take up water and nutrients dissolved therein can vary between species during times of water stress (Nambiar 1976, 1977). Species also vary in their nutrient uptake and resulting concentrations from effects of excess soil moisture (van den Driessche 1974), temperature stress (Miller 1966, Nordin 1977), light intensity (van den Driessche 1974), and soil oxygen (Saif 1983). Nutrient concentrations can change due to dilution effects of rapid growth (Grigal and Ohmann 1980) and translocation before senescence (Fife and Nambiar 1982, Ostman and Weaver 1982). Plant nutrient

concentrations are also affected by nutrient concentrations and ratios in soil solutions (Bard 1945, Haynes and Ludecke 1981, Parrish and Bazzaz 1982). Some plant species have the ability to accelerate dissolution of minerals and make their nutrients available through excretion of chelators (Kramer 1983) or organic compounds (Nambiar 1976, 1977, Bowen and Theodorou 1973, Boerd and Thien 1979), and causing change in soil pH (Riley and Barber 1971). Inter- and intraspecific competition influences plant nutrient levels (Kennedy 1981). Allelochemics also may interfere with plant ion uptake and influence species nutrient concentrations (Rice 1974). Many species characteristically ultimately root at different depths, so soil horizon fertility differences may be important. The extent of a species exploitation of a soil mass may influence shoot nutrient concentration (Jarvis and Whitehead 1981).

Seed Bank Species Nutrient Concentrations

Results

Concentrations of all nine elements in vegetation of the nine important species common to Treatment 2 and Treatment 3 varied significantly between species (Table 12). Community membership significantly influenced the concentration of seven elements, N, P, K, Ca, Mn, Fe and Zn. Spoil significantly influenced concentrations of five elements, N, Ca, Mn, Fe and Zn.

Nitrogen concentration was significantly influenced by species, community membership, and spoil (Table 12). There was also a

Table 12. Factors affecting element concentrations in nine species common to Treatment 2 and Treatment 3.

Effect	N	P	K	Ca	Mg	Mn	Fe	Cu	Zn
Species	***[1]	***	***	***	***	***	***	***	***
Community	*	***	**	*		*	*		***
Spoil	*			**		***	*		***
Species x Community	*					**	*		
Species x Spoil						***	*	***	***
Community x Spoil							*		
Species x Community x Spoil						**			

[1]Significance of Type IV Sum of Squares: *α = .05
**α = .01
***α = .001

significant species x community interaction effect; six of the nine species had higher N concentration in the native seed bank plus reclamation species community (Table 13). This may be due to dilution with greater growth in the native seed bank community. There was also a trend for N concentrations to be higher in vegetation on Spoil 1. Topsoil and spoil total N values do not account for this. This might have been a dilution-with-growth phenomenon if poorer quality of Spoil 1 was retarding plant growth, but the sampling design of the study (random samples) did not allow a test of this hypothesis.

Phosphorus and potassium concentrations were significantly influenced by species and community, but spoil showed no significant effect and there were no significant interactions. Phosphorus and potassium concentrations were higher in the seed bank species plus reclamation mix than in the seed bank species alone. Differences in extractable P between spoils were not significantly different, so a lack of spoil effect on vegetation concentration is quite reasonable. Soil test K levels were very similar in the two spoils. A greater difference in spoils might have been reflected in significant plant K concentration differences.

Calcium concentration varied significantly due to species, community membership, and spoils. There were no interaction effects. Ca concentrations were higher in the seed bank species plus reclamation mix than in the seed bank species alone. Ca concentrations were higher in vegetation on Spoil 2 than on Spoil 1. Spoil 2 had greater available Ca (Table 5, p. 38). Relative vegetation differences in Ca

Table 13. Mean nutrient concentrations in important species occurring in both Treatment 2 and Treatment 3, by treatment and spoil.

Species	Treatment	Spoil	%					ppm			
			N	P	K	Ca	Mg	Mn	Fe	Cu	Zn
Aster	2	1	.83	.17	2.28	.74	0.08	936	128	7.0	97
divaricata		2	.83	.14	2.23	1.03	0.10	557	98	7.0	60
	3	1	.99	.24	2.67	1.07	0.16	882	61	8.5	136
		2	1.25	.26	2.41	1.07	0.11	611	89	7.0	64
Digitaria	2	1	.56	.12	1.47	.25	0.12	281	116	12.0	62
ischaemum		2	.48	.08	1.40	.22	0.08	301	142	8.0	41
	3	1	.42	.12	1.04	.23	0.12	215	-	11.0	-
		2	.39	.11	1.13	.26	0.11	357	84	7.3	48
D.	2	1	-	-	-	-	-	-	-	-	-
sanguinalis		2	.43	.11	1.54	.33	0.17	832	144	15.0	59
	3	1	.69	.18	2.40	.23	0.17	490	55	6.0	101
		2	.54	.20	1.59	.42	0.24	859	109	16.0	91
Erechtites	2	1	.90	.18	2.83	.90	0.17	744	290	12.0	178
hieracifolia		2	.74	.21	2.06	.92	0.11	402	133	9.8	64
	3	1	.65	.19	2.05	.90	0.16	654	64	8.0	175
		2	.81	.26	2.31	1.02	0.12	270	114	8.5	78
Eupatorium	2	1	-	-	-	-	-	-	-	-	-
purpureum		2	.81	.16	2.27	1.99	0.46	708	125	8.3	43

Table 13 (continued)

Species	Treat-ment	Spoil	%					ppm			
			N	P	K	Ca	Mg	Mn	Fe	Cu	Zn
Eupatorium	3	1	.94	.12	2.99	1.72	0.57	1618	176	10.0	156
purpureum (continued)		2	.93	.13	2.99	2.23	0.46	1197	163	11.0	87
E.	2	1	.84	.15	2.14	1.13	0.24	601	216	8.0	101
rugosum		2	.72	.17	1.67	1.43	0.26	333	91	7.9	28
	3	1	.86	.23	3.15	1.46	0.29	579	133	9.0	99
		2	.88	.23	2.43	1.50	0.26	257	126	7.5	43
E.	2	1	1.11	.16	1.66	.87	0.28	1054	96	6.0	147
serotinum		2	.84	.17	1.51	1.00	0.13	485	88	6.2	72
	3	1	.89	.17	1.83	.81	0.17	1128	82	6.0	154
		2	.98	.27	2.27	1.16	0.18	489	118	7.5	85
Helianthus	2	1	.72	.21	2.38	.70	0.14	567	74	5.0	94
microcephalus		2	.65	.15	2.04	.73	0.11	248	104	7.0	49
	3	1	.72	.17	2.41	.72	0.10	479	87	6.5	113
		2	.83	.27	2.60	1.16	0.15	338	87	7.0	79
Phytolacca	2	1	1.08	.16	3.02	.72	0.30	1719	229	-	-
americana		2	.91	.13	2.54	.99	0.35	1724	109	7.1	62
	3	1	1.48	.25	-	.80	0.34	3994	245	13.1	518
		2	1.00	.18	3.34	1.08	0.33	1782	119	7.0	63

concentrations due to spoils were not as great as the relative differences between the spoils themselves. This may have been due to amelioration of spoil differences by the common topsoil or plant species not requiring full exploitation of the differences.

Magnesium concentration differences were significantly linked only to species. Community membership had little influence. Magnesium did not show the generally higher vegetation concentrations in Treatment 3 that were common with other elements. It may be that these species do not absorb more Mg than necessary for physiological processes. Spoil 2 had 25 percent higher available magnesium and nearly double the Mg base saturation, but these differences had no significant effect on vegetation Mg concentration.

Manganese concentration in the tissues of these nine species varied significantly between species, community, and spoils. There were also significant species x community, species x spoil, and species x community x spoil interactions. The dicots generally had higher Mn concentrations on Spoil 1. Such a broad trend was less visible with community membership, however. Interaction effects made the community trend less readily visible. Both spoils had similar soil test Mn concentrations, but other factors such as pH and relative base saturation may have been influential in producing the soils effects. Godo and Reisenauer (1980) found that soil properties, such as pH and plant exudates which break down MnO_2 and complex the Mn cation, combine to make Mn availability and plant response a very complex phenomenon.

Iron concentration in vegetation varied significantly with species, community, and spoil and with all two-way interactions. There were no general trends across species for higher iron concentration associated with either spoil or community among the nine species from the seed bank as interaction effects obscured them.

Copper concentrations varied significantly between species. There was also a significant species x community interaction, even though community by itself was not statistically significant. Like Mg, Cu concentration was not greater in seed bank species of Treatment 3 than in Treatment 2. The spoil effect was not significant even though Spoil 1 had a 30 percent higher Cu content.

Zinc concentrations were significantly affected by species, community, and spoils. There was also a significant species x spoil interaction. Zinc concentrations were higher in the native species plus reclamation mix than in the native species alone in eight of nine species. It was markedly higher on Spoil 1 than on Spoil 2.

Discussion

Treatment 2 and Treatment 3 communities show differences in interspecific competition resulting from the addition of grasses to the seed bank community, and possibly changes in intraspecific competition as the importance of some of these species differed greatly between communities. Interspecific competition in Treatment 3 may very well have included allelopathic effects of the introduced grasses. *Festuca arundinacea* has been shown to be allelopathic (Peters 1968) as have *Lolium* (Fales and Wakefield 1981) and *Digitaria sanguinalis*

(Rice 1964, Parenti and Rice 1969). Eragrostis curvula also produces root exudates that have been implicated in allelopathy (Creek and Wade 1985). The physiological mechanism of allelopathy are numerous and include interference with ion uptake, photosynthesis, cell division, membrane permeability, respiration, protein synthesis, enzyme activity (Rice 1974) and water relations (Colton and Einhellig 1980). The inferior status of Treatment 3 species which were dominant in Treatment 2 does not generally seem to be due to competition for nutrients as there is a trend for nutrient concentrations in these species to be higher in Treatment 3 than in Treatment 2. This may have resulted from non-dilution with growth or relatively higher uptake of some elements in some species.

Competition for water may have been a reason for the displacement in dominance of some of the native species in Treatment 3. The grasses had shallow root systems concentrated in topsoil and upper zone of the spoils. Most of the native species had root systems extending to greater depths with less exploitation of the surface. The native species would have been at a disadvantage in competition for small amounts of rainfall or irrigation water that did not penetrate to greater depths in the microplots.

Reclamation Species Nutrient Concentrations

Results

Species was a significant factor determining the N, P, K, Ca, Mg, Mn, Cu and Zn contents of vegetation among the reclamation mix

species present in Treatment 1 and Treatment 3 (Table 14). Community and spoil effects were not as widespread as they were in the species and communities just discussed. Community membership significantly influenced only P, Cu and Zn concentrations in vegetation. Calcium and Zn only had significant responses to spoil differences.

Species was the only significant single factor related to nitrogen content in the seven reclamation mix species used in the analysis (Table 14). Significant interaction effects were found for species x community, community x spoil, and species x community spoil. These interactions make interpretation of a simple table of species nutrient concentrations by community and spoils very difficult (Table 15).

Phosphorus concentrations varied significantly between species and communities, but there were no significant influences due to spoils or interaction effects. However, there was a nonsignificant trend for soil, species x community, and community x soil influences. Phosphorus concentrations were generally highest in F. arundinacea and lowest in E. curvula. Phosphorus concentrations in the reclamation species were generally lower in Treatment 3 than in Treatment 1.

Potassium variation was significant only between species. Festuca arundinacea generally had the highest tissue K concentrations, and E. curvula had the lowest. Community, spoil and interaction effects were not significant. Parrish and Bazzaz (1982) also found a general plant insensitivity to soil K availability among assemblages of early and late successional plants; plant species identity was the

Table 14. Factors affecting element concentrations in seven species common to Treatment 1 and Treatment 2.

Effect	N	P	K	Ca	Mg	Mn	Fe	Cu	Zn
Species	***	***	***	***	***	***		***	***
Community		*						*	*
Spoil				**					*
Species x Community	*							*	
Species x Spoil									
Community x Spoil	*								
Species x Community x Spoil	*							***	

[1]Significance of Type IV Sum of Squares: $*\alpha = .05$, $**\alpha = .01$, $***\alpha = .001$

Table 15. Mean nutrient concentrations in important species occurring in both Treatment 1 and Treatment 3, by treatment and spoil.

Species	Treatment	Spoil	%					ppm			
			N	P	K	Ca	Mg	Mn	Fe	Cu	Zn
Digitaria	1	1	-	-	-	-	-	-	-	-	-
ischaemum		2	.63	.19	1.40	.26	0.10	250	95	7.0	58
	3	1	.42	.09	1.04	.23	0.12	215	-	11.0	-
		2	.39	.12	1.13	.26	0.11	357	84	7.3	48
D.	1	1	.20	.09	1.59	.23	0.17	673	95	13.0	93
sanguinalis		2	.70	.18	1.83	.48	0.20	747	107	10.0	68
	3	1	.69	.18	2.40	.23	0.17	490	55	6.0	101
		2	.54	.20	1.59	.42	0.24	859	109	16.0	91
Eragrostis	1	1	.88	.08	.78	.30	0.06	348	97	13.0	48
curvula		2	1.08	.09	.72	.21	0.05	194	116	7.8	37
	3	1	.52	.06	.75	.25	0.04	214	67	5.0	51
		2	.62	.06	.59	.25	0.04	236	84	4.6	33
Festuca	1	1	.37	.16	2.22	.36	0.20	431	96	10.0	41
arundinacea		2	1.24	.21	2.40	.42	0.17	384	74	8.5	60
	3	1	.93	.14	2.34	.27	0.18	314	45	3.0	-
		2	.85	.12	1.96	.34	0.17	414	93	7.0	59
Lespedeza	1	1	1.88	.12	1.31	.65	0.10	488	140	6.0	158
cuneata		2	2.35	.18	1.21	.84	0.11	203	108	5.5	40

Table 15 (continued)

Species	Treatment	Spoil	%					ppm			
			N	P	K	Ca	Mg	Mn	Fe	Cu	Zn
Lespedeza	3	1	2.08	.15	1.01	.76	0.14	383	98	6.0	66
cuneata (continued)		2	2.27	.16	1.02	.97	0.12	217	123	6.8	44
Lolium	1	1	1.22	.17	1.76	.49	0.17	705	103	10.0	140
multiflorum		2	1.40	.19	1.21	.76	0.16	763	130	12.8	103
	3	1	1.20	.14	-	.59	0.12	138	107	17.0	92
		2	1.04	.12	1.01	.74	0.14	1080	156	8.5	94
L.	1	1	1.24	.16	1.95	.55	0.19	654	152	10.0	154
perenne		2	.67	.16	1.85	-	0.13	683	159	13.0	140
	3	1	.90	.11	1.40	.47	0.10	595	113	10.0	114
		2	1.01	.12	1.33	.83	0.16	597	109	7.5	107

only significant component in a regression on K concentration in vegetation.

Calcium concentration levels in the reclamation species mix were significantly affected by species and spoil. Lespedeza cuneata and Lolium multiflorum had the highest Ca concentrations; Digitaria ischaemum and Eragrostis curvula had the lowest. Except for E. curvula, Ca concentrations were lower on Spoil 1. Community membership and interactions had no effects.

Magnesium and manganese concentrations were significantly affected only by species. Greatest Mg concentrations were in the tissues of Digitaria sanguinalis and F. arundinacea; lowest concentrations were in E. curvula. Lolium multiflorum and D. sangunalis had the highest Mn concentrations, and E. curvula and L. cuneata had the lowest Mn concentrations. Community, spoil, and interaction effects were not significant.

No significant variation in iron could be attributed to species, community, spoil, or their interactions.

Copper showed significant differences due to species and community, and the interactions containing them, species x community, and species x community x spoil. Lolium multiforum and D. sanguinalis had the highest Cu concentrations, and E. curvula and L. cuneata had the lowest Cu concentrations. Community effects varied strongly between species; D. ischaemum, D. sanguinalis, and L. cuneata had highest Cu concentrations in Treatment 3. The others had highest concentrations in Treatment 1.

Zinc concentrations varied significantly with species, community and soil, but there were no significant interaction effects. Lolium perenne and L. multiflorum had the highest tissue Zn concentrations, and E. curvula had the lowest Zn concentrations. Zinc concentrations were higher in Treatment 1, except in D. sanguinalis and F. arundinacea. Zinc concentrations were higher on Spoil 1 except in F. arundinacea.

Discussion

Spoil differences were not as influential on the reclamation species as on the seed bank species. These differences in the amount of response to spoils may lie in differences in the rooting zones. Heavy exploitation of topsoil by the shallow, fibrous-rooting grasses may have made underlying spoil differences less influential, especially as there was generally an adequate amount of water in the topsoil and upper spoil layers.

Lack of community differences among the reclamation species may be due to the character of the Treatment 1 and Treatment 3 communities—both were grass dominated. A change from Treatment 1 to Treatment 3 resulted in addition of species of relatively minor importance compared to the grasses.

Summary

Among the native species and important invaders of Treatment 2, tissue concentrations of the nine elements varied significantly between species. Community membership affected concentrations of N, P,

K, Ca, Mn, Fe and Zn. Spoil type affected levels of N, Ca, Mn, Fe, and Zn. Interaction effects were found in N, Mn, Fe, Cu, and Zn. Nitrogen, P, K, Ca, and Zn were generally higher in native species when they were growing with seeded-in grasses and Lespedeza. Such higher nutrient concentrations may in part be due to less dilution with growth caused by repression of the native species by the grasses of Treatment 3.

Among the reclamation species and two important volunteers, tissue concentrations of all elements except Fe varied significantly due to species. Community membership effects were significant for P, Cu, and Zn. Spoil significantly affected concentrations of Ca and Zn. Significant interaction effects for the above factors were found for N and Cu. Ca concentrations were lower and Zn concentrations were higher on Spoil 1. Most reclamation species had lower Zn concentrations when growing with native species.

The reclamation species were like the seed bank species in that they had significant differences in nutrient concentrations between species. The reclamation species showed far fewer responses to community membership than did the native seed bank species. The grasses were less affected by the presence of the dicots than the dicots were by the presence of the grasses. The reclamation species were also less affected by spoil differences, possibly due to greater exploitation of the topsoil and less exploitation of the spoil by the grasses.

CHAPTER VII

NUTRIENT CONCENTRATION, CONTENT AND NICHE

The Niche Concept in Plant Ecology

Grinnell (1917) first used the term "niche" in an ecological sense as being an organism's habitat. He also defined niches as structural units of the ecological community and stated that no two species regularly established in a community would have the same niche. In his 1928 paper he further defined niche as the ultimate unit of species distribution. Elton (1927) defined niche as the function of an organism in a community and its relationships to food and enemies. He also defined niche as a unit of community organization and as a common structural component in separate communities. Both concepts, "habitat niche" and "functional niche" have remained in use under the common term "niche" or "ecological niche" causing confusion and fueling semantic debate among ecologists. Clarke (1954) suggested that separate names would be eventually given to the two concepts.

Hutchinson (1958) proposed that niche be considered an n-dimensional hypervolume. Each dimension is a quantified environmental variable that affects a species. By defining the limits of a population in each dimension, that population's fundamental niche is then defined. Due to competition, however, a population seldom reaches the potentialities defined in the fundamental niche, and the

reduced volume of the population in the hyperspace is considered to be the realized niche. The n-dimensional niche concept has since been used in the context of both habitat and functional niches although Whittaker et al. (1973) suggest that Hutchinson was more concerned with intracommunity, functional niche at the time and that application of the concept to habitat niche was not intended. Either way, the concept has proved very useful. Whittaker et al. (1973) reviewed the problems in niche terminology and proposed that "habitat" be reserved for "place niche" or intercommunity variables formerly associated with niche. The complementary term "niche" would then be reserved for intracommunity, functional variables. Where both meanings are desired, the term "ecotope" (habitat + niche) is suggested. Whittaker et al. (1973) cite the term "ecotope" as variously used by Schmithüsen (1968) and Troll (1968).

McNaughton and Wolf (1970) extended the concept of the niche hypervolume to the community, saying that, "the community also has a niche hypervolume defined by the hypervolumes of its constituent species." Whittaker et al. (1973) hypothesized that addition of a new species with its own hypervolume will alter the niche hyperspace of the community.

The functional niche is emphasized in system structure. The niche of Elton (1927) and Whittaker (1973) becomes a general systems functional structure. Grinnell's (1917, 1928) niche (Whittaker et al.'s (1973) habitat) becomes a set of parameters that establishes viability of particular species in a particular ecosystem. Patten and

Auble (1980) took a systems approach to niche and formulated a "niche concept in the formalism of general system theory." "Holon" is coined for systems that are simultaneously part of a greater whole and a whole made of lesser parts. This may be a single population or all populations at a given trophic level. The holon has two subsystems: (1) a "creaon" which defines resources used by the holon, stimuli, or input function, and (2) a "genon," the holon's effect on the system, the responses, or the output function. The creaon is equivalent to Hutchinson's realized niche, the set of direct inputs to a holon. The holon concept goes beyond the niche concept in that nonliving components of systems may be defined as holons. Patten and Auble (1980) balk at giving nonliving holons niches, but state that such an extension might be useful in systems ecology. Input and output "environs" are also defined. These are the summed direct and indirect (as far as they can be traced through other holons) inputs and outputs respectively. Together they are equivalent to the "extended niche" of Levine (1977). Patten and Auble (1980) point out that there is also no precedent for extending the traditional niche concept (as diverse as it is) to include indirect influences.

The theory of niche in plant ecology has suffered somewhat in that most of the significant niche theory has been developed in the context of animal populations and systems ecology. This is particularly true when nutritional niches of plants are discussed. The nutritional definitions of niche so useful in animal ecology have had little utility for plants (Wuenscher 1969, cited by Whittaker et al.

1973). The difficulty lies in use of plant tissue nutrient concentrations data for niche studies. All species in a plant community exploit the same suite of essential elements, water, and light. Relative use of each resource varies from species to species in the same community and this relative difference has been equated to niche difference. Woodwell et al. (1975) showed, using principal components and a Bray-Curtis ordination, that woody species in the Brookhaven oak-pine forest are dispersed in a hyperspace defined by relative concentrations of different nutrient elements. They stated that nutrient concentration in plants "may be an important aspect or expression of niche differentiation." Garten (1978) used discriminant analysis based on foliage nutrient concentration to describe plant species' positions in an 11-dimensional space. Differences and similarities in position were equated to differences and similarities in nutrient cycling niche. Such complete separation of plant species in hypervolumes in mathematical multivariate space does not necessarily show niche separation in the ultimate sense. Only the relative dissimilarity of what I will call "nutrient concentration niche" can be shown.

Extension of the Niche Concept in Plant Nutritional Relationships

A meaningful discussion of plant nutrition and species niche requires extension of niche terminology. For this, I elect to use adjective modifiers for "niche" which will largely explain what is meant, rather than coin new words which would not, in themselves convey any information (Table 16).

Table 16. Tabularization of the niche concept related to vegetation and nutrition.

Niche Type	Characteristics	Measure
Species Population Nutrient Concentration Niche	Functional Realized Qualitative Species-centered Dynamic	Niche Breadth - proportional use or concentrations of all nutrients. Niche Width - mean or range of concentrations of one element.
Species Population Nutrient Content Niche	Functional Realized Quantitative Community-centered Dynamic	Niche Share - proportion of the total community nutrient capital sequestered by a population.
Species Community Nutrient Content Niche	Functional Realized Quantitative Ecosystem-centered Dynamic	Community Content Niche - total nutrients sequested in biomass by a plant community.

"Nutrient concentration niche" is a species-centered, realized, qualitative, functional niche in terms of a population's food value to herbivores, speed of decomposition and effects of relative element uptake on soil processes. Niche breadth and width have been used interchangeably in ecological literature, but here they will have precise definitions. Concentration "niche breadth" is a measure of a population's proportional content of the various nutrients using such formulas as those proposed by Levins (1968). Concentration "niche width" is reserved to refer to a mean or a range of concentration of one element, but it will not be used in this discussion.

"Content niche" is a community-centered or system-centered, realized, quantitative functional niche. Content "niche share" is a measure of community nutrient capital allocated to or sequestered by a given species. For example, one might define a "phosphorus niche share." The undifferentiated "niche share" is a mean share of all elements considered. Expressing functional niche in terms of "what an organism does as well as how much of what there is to do" moves the functional niche concept from the qualitative functional definition it has primarily had in the past to a very useful operative, quantitative definition.

To illustrate content niche, niche share "S_s" is calculated,

$$S_s = \overline{x}_{es}$$

where "x" is the species "s" mean fractional share of each nutrient "e" in the aboveground biomass of each treatment. This value gives a species mean importance across all included nutrient axes.

For comparison, a modified Levins' B (1968) is calculated

$$B = \frac{1}{r \Sigma p_{se}^2}$$

where "r" is the number of niche parameters (9 elements) used in the calculation, and "p" equals the mean concentration of element "e" in species "s." For this calculation, nutrient concentration means "$\bar{o}_e$" were determined for each element "e" using all observations. The treatment "t" element means "$\bar{o}_{ets}$" were then calculated for each species "s" and standardized as fractions of the overall element means "$\bar{o}_{ets}/\bar{o}_e$." These fractional values for each element were then expressed as a proportion of the sum of the values for all nine elements for each species per treatment

$$p = \frac{(\bar{o}_{ets}/\bar{o}_e)}{\Sigma(\bar{o}_{ets}/\bar{o}_e)}$$

in order to calculate Levins' B on proportional element use data. Levins' B has a value of 1.0 when all resources are used in the same proportional amount and a value of 1/r when only one of r resources is used.

Results

Seed Bank Species Niche Shares

The effects of community composition on component species niches can be observed by comparing niche breadths (B) and niche shares (S_s) in species common to Treatment 2 and Treatment 3 (Table 17 and Figure 6). When the reclamation mix species were added to the native

Table 17. Species niche breadth (Levin's B) based on standardized concentration data and content niche share S_s.

Species	Treatment 1		2		3		4	
	Levins' B	S_s	Levins' B	S_s	Levins' B	S_s	Levins' B	S_s
Acalypha rhomboidea			.765	.001	.688	.002	.681	.001
A. virginica					.593	.001		
Agrostis gigantea			.866	.016	.829	.001	.890	.000
Amaranthus hybridus					.803	.024		
Aster divaricatus			.878	.005	.825	.008		
Bidens frondosa					.797	.009		
Bromus commutatus					.915	.004		
Chenopodium album							.907	.886
Crotonopsis elliptica			.957	.000				
Cyperus esculentus			.549	.004				
Dactylis glomerata	.812	.017	.886	.008	.860	.008	.835	.000
Datura stramonium	.794	.017						
Digitaria ischaemum	.794	.210	.926	.091	.905	.148	.940	.027
D. sanguinalis	.928	.069	.930	.038	.883	.041	.950	.009
Eragrostis curvula	.818	.096			.919	.103	.874	.027
Erechtites hieracifolia			.902	.259	.814	.091		
Eupatorium purpureum			.728	.011	.817	.003		
E. rugosum			.804	.059	.793	.013		
E. serotinum			.889	.032	.841	.011		
Eupatorium sp.			.840	.001				
Festuca arundinacea	.848	.121			.888	.102		
Hedeoma pulegioides			.710	.002				
Helianthus decapetalus			.906	.047	.820	.031		
H. laevigatus			.935	.001				
H. microcephalus			.864	.060	.794	.048		
Helianthus sp.			.871	.002				

Table 17 (continued)

Species	Treatment 1		2		3		4	
	Levins' B	S_s	Levins' B	S_s	Levins' B	S_s	Levins' B	S_s
Lactuca biennis			.797	.008	.891	.001		
L. pulchella			.746	.002				
Lespedeza cuneata	.707	.046			.682	.076	.766	.002
Liriodendron tulipifera			.855	.002				
Lolium multiflorum	.920	.416			.922	.088		
L. perenne	.891	.033			.909	.090	.762	.001
Misc. Asteraceae			.792	.001				
Misc. Poaceae	.815	.003					.790	.000
Monarda clinopodia			.767	.002				
Muhlenbergia schreberi	.810	.004			.893	.002	.825	.000
Panicum agrostoides					.845	.000		
P. dicotomiflorum	.821	.004	.862	.011			.902	.001
Paspalum circulare	.754	.001						
P. laeve							.862	.001
Physalis pruinosa			.779	.001				
Phytolacca americana	.808	.004	.856	.307	.829	.085		
Plantago lanceolata			.786	.001				
Ranunculus septentrionalis			.826	.001				
Robinia pseudo-acacia	.604	.001	.601	.006	.591	.001		
Rubus occidentalis			.834	.002				
Rubus sp.			.579	.001				
Scutellaria ovata			.608	.012	.760	.003		
Solanum carolinense					.715	.001		
Solidago flexicaulis			.890	.000	.843	.003		
Triticum aestivum					.888	.002		
Viola sp.			.916	.008	.883	.001		
Vitis sp.			.743	.000				

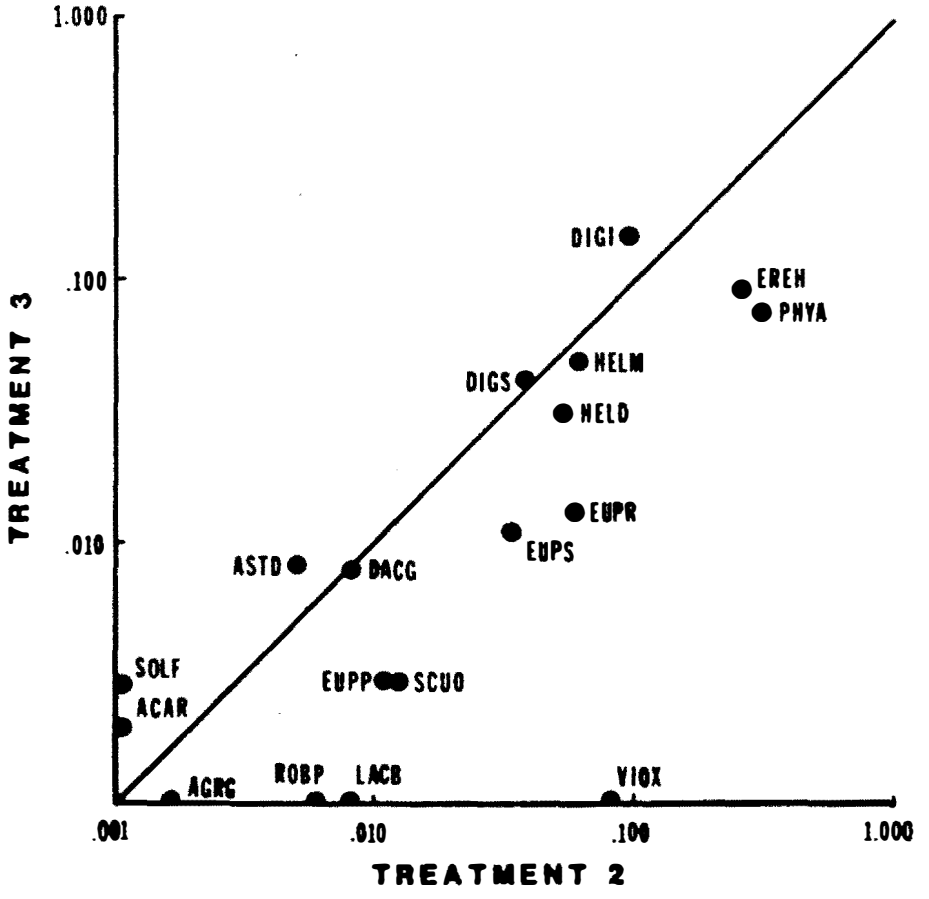


Figure 6. Seed bank species niche shares (S_s) in Treatment 2 and Treatment 3. The diagonal line shows points at which species niche shares are equal in Treatment 2 and Treatment 3 communities.

species community, the niche shares of most native species declined. Of 18 species common to Treatments 2 and 3, for which enough data were available to calculate niche shares, niche share of 12 decreased, five increased, and one remained the same (Table 18). Among 12 species with decreased niche shares, population decreased in nine, and biomass of all species decreased. Of the five native species with increased niche shares, populations increased in four and species biomass increased in only three. Niche share of Solidago flexicaulis increased despite decrease in both population and biomass; biomass change was offset by concentration increases that influenced niche share. The five species with niche share increases were of relatively minor importance in the native seed bank species community. Competition with the dominant grasses of Treatment 3 may not have been so severe as competition with species that normally dominate them. Additional competition from the introduced species apparently did not affect all native species equally.

Seed Bank Species Niche Breadths

Concentration niche breadths for 15 of the above 18 seed bank species decreased and 3 increased when reclamation mix species were added to the community (Table 18 and Figure 7). Of the three with increased niche breadth, all had smaller species populations and less biomass, and none were among the species with increased niche share.

Reclamation Species Niche Shares

For reclamation mix species and volunteers.in Treatment 1, seven had a smaller niche share when they occurred with the native

Table 18. Content niche share and concentration niche breadth changes in 18 native species when reclamation species were added to the native seed bank community.

	Niche Breadth (B) Decrease	Niche Breadth (B) Increase
Niche Share (S_s) Decrease	Agrostis gigantea pi, bd[1] Erechtites hieracifolia pd, bd Eupatorium rugosum pd, bd E. serotinum pi, bd Helianthus decapetalus pd, bd H. microcephalus pi, bd Phytolacca americana pd, bd Robinia pseudo-acacia pd, bd Viola sp. pd, bd	Eupatorium purpureum pd, bd Lactuca biennis pd, bd Scutellaria ovata pd, bd
Niche Share (S_s) Increase	Acalypha rhomboidea pi, bi Aster divaricatus pi, bd Digitaria ischaemum pi, bi D. sanguinalis pi, bi Solidago flexicaulis pd, bd	
No Change	Dactylis glomerata pi, bd	

[1] pi - population increased when reclamation species were added to the seed bank community.
pd - population decreased when reclamation species were added to the seed bank community.
bi - biomass increased when reclamation species were added to the seed bank community.
bd - biomass decreased when reclamation species were added to the seed bank community.

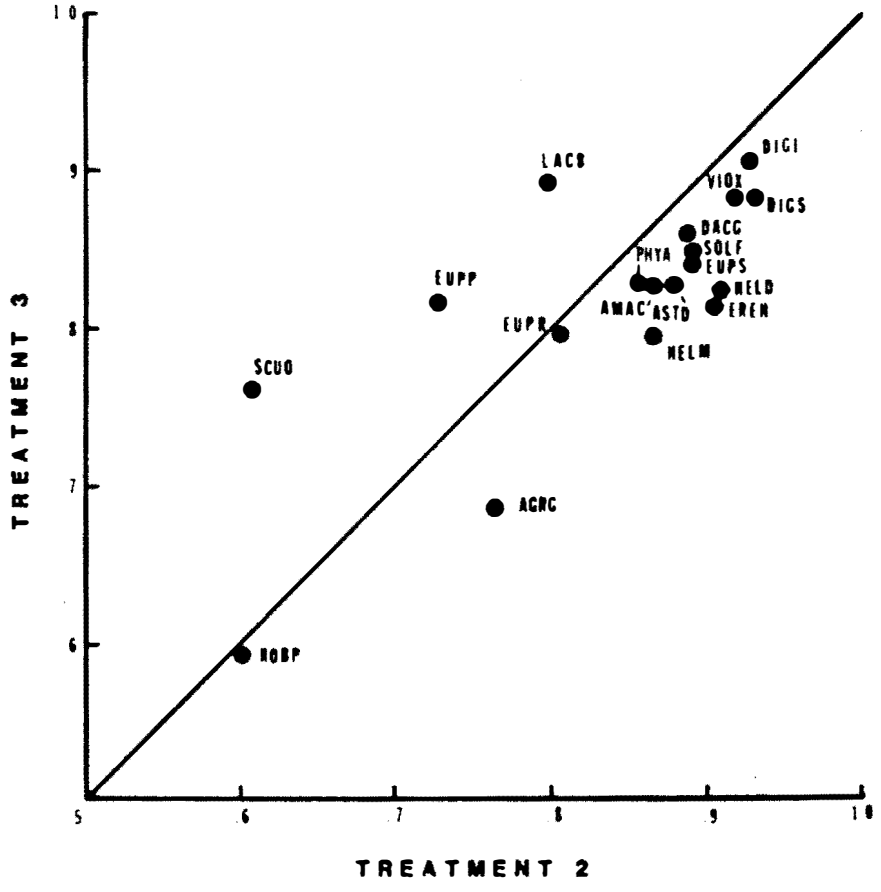


Figure 7. Seed bank species niche breadths (Levins' B) in Treatment 2 and Treatment 3. Diagonal line shows the points at which species niche breadths are equal in Treatment 2 and Treatment 3 communities.

species in Treatment 3 (Table 19 and Figure 8). This may have resulted from the addition of seeded species at one-half the Treatment 1 rate. Of the seven species with decreased niche share, two had larger numbers and two others had greater biomass. The three species with greater niche shares in Treatment 3 also had more biomass and higher species populations. One of these three, Phytolacca americana, was a rare volunteer in Treatment 1 but a component of the seed bank used in Treatment 3 so its greater status is easily understandable.

Reclamation Species Niche Breadths

Niche breadth as measured by Levins' B increased for nine of the 11 Treatment 1 species when mixed with the native species (Table 18 and Figure 9). Of the nine species in which Levins' B increased, biomass increased in four, and populations increased in four. There was no correlation between biomass and population change when niche breadth increased.

Community Niche

If nutrient niche share is summed for all species in a community, a community niche (McNaughton and Wolf 1970, Whittaker et al. 1973) in the nutrient cycle is then defined. Each of the four communities in this study then have quantitatively different nutrient cycling niches which are quantified as kg/ha of each element. Table 8 (p. 52) quantifies the nutrient content niche of each of the four plant communities in this study.

Table 19. Content niche share and concentration niche breadth changes in 11 species of the reclamation mix and its invaders when added to the native seed bank community.

	Niche Breadth (B) Decrease	Niche Breadth (B) Increase
Niche Share (S_s) Decrease	*Digitaria sanguinalis* pi, bi[1]	*Dactylis glomerata* pi, bd *Digitaria ischaemum* pd, bd *Eragrostis curvula* pd, bi *Festuca arundinacea* pd, bi *Lolium multiflorum* pd, bd *Muhlenbergia schreberi* pd, bd
Niche Share (S_s) Increase	*Lespedeza cuneata* pi, bi	*Lolium perenne* pi, bi *Phytolacca americana* pi, bi
No Change		*Robinia pseudo-acacia* pi, bd

[1] pi - population increased when reclamation species were added to the seed bank community.
pd - population decreased when reclamation species were added to the seed bank community.
bi - biomass increased when reclamation species were added to the seed bank community.
bd - biomass decreased when reclamation species were added to the seed bank community.

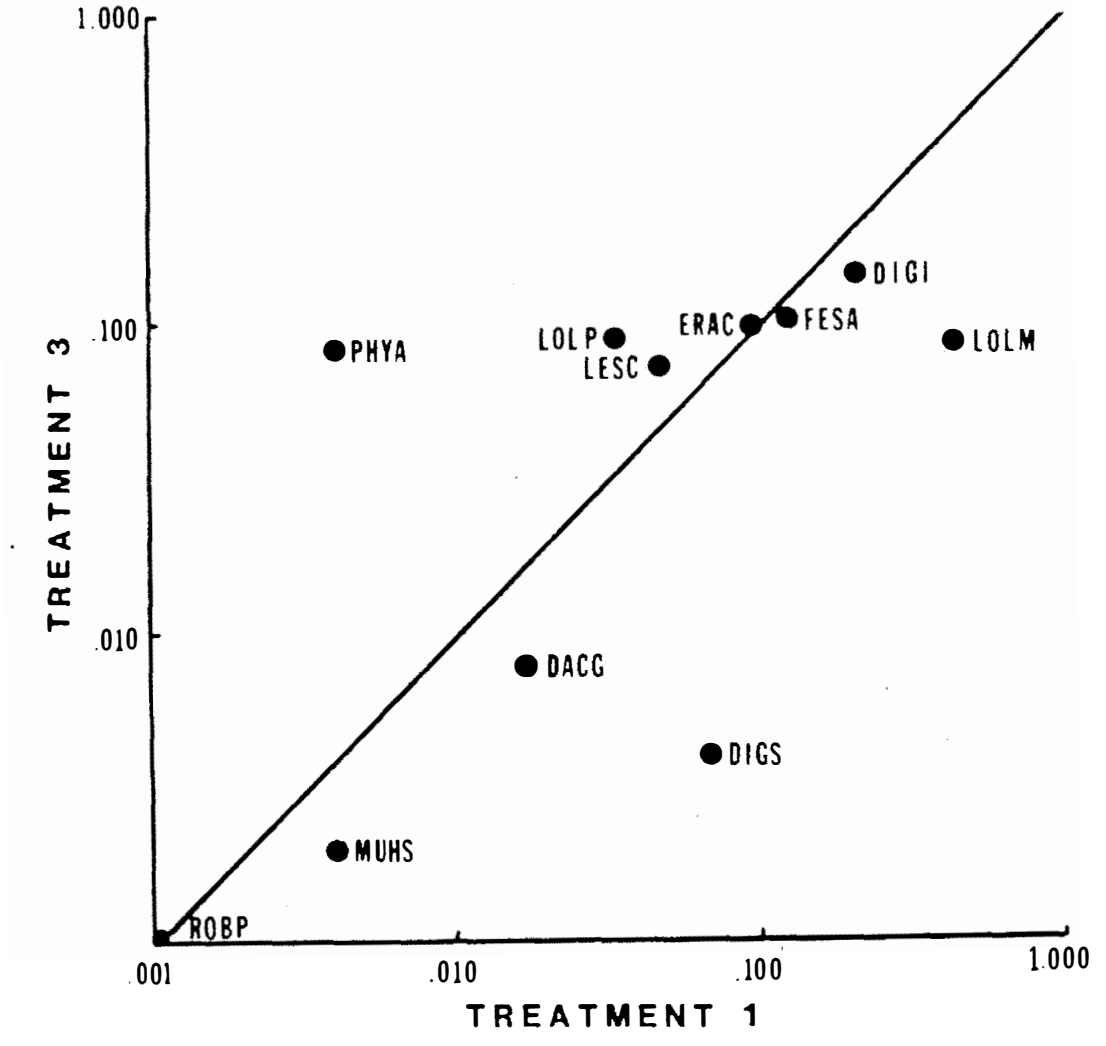


Figure 8. Reclamation species niche shares (S_s) in Treatment 1 and Treatment 3. The diagonal line shows points at which species niche shares are equal in Treatment 1 and Treatment 3 communities.

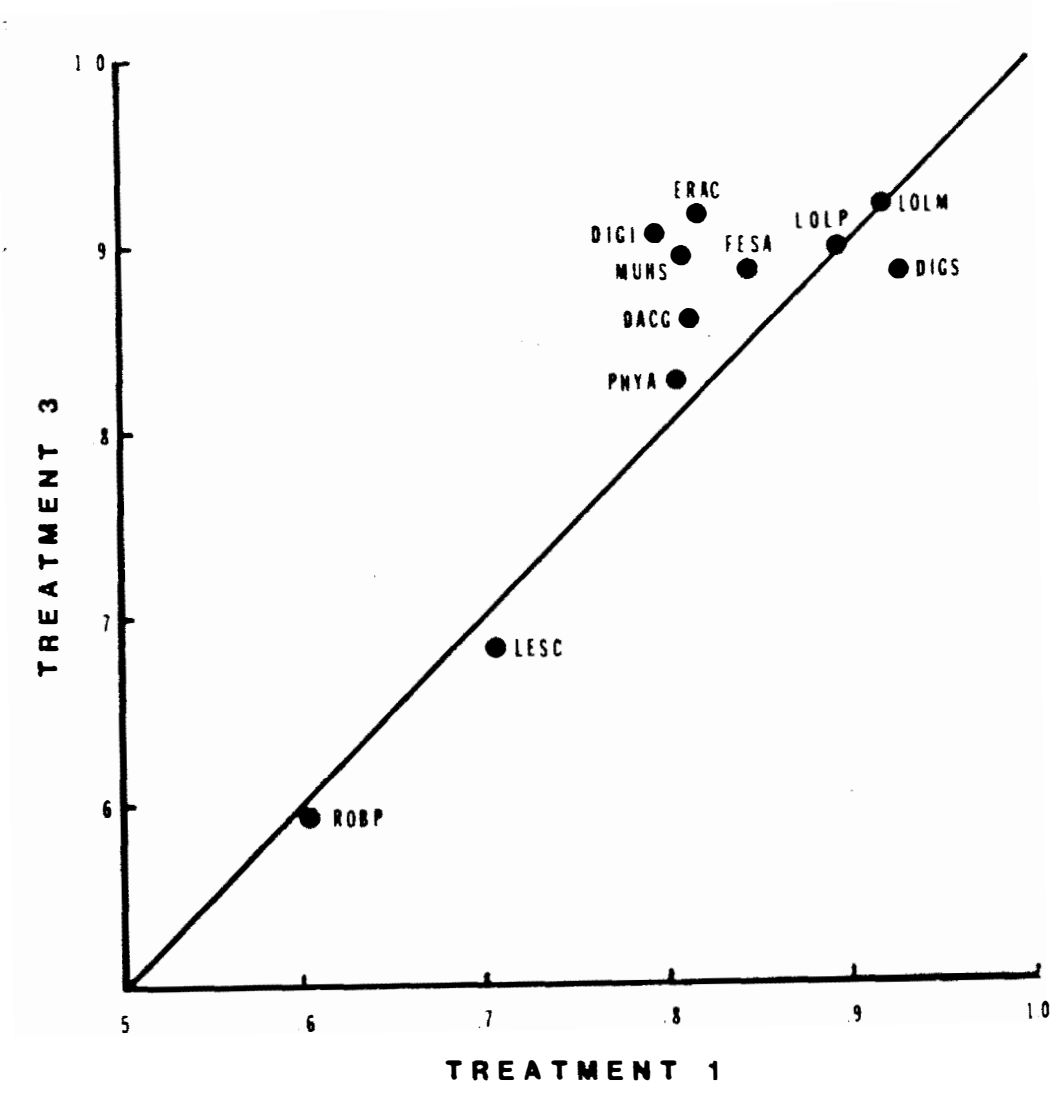


Figure 9. Reclamation species niche breadths (Levins' B) in Treatment 1 and Treatment 3. The diagonal line shows the points at which species niche breadths are equal in Treatment 1 and Treatment 3 communities.

Discussion

Niche breadth is defined as "evenness of resource use by a species," so decreased niche share indicates less even proportional use of nutrient resources. A general trend among the native dicots in the forest soil seed bank was for nutrient concentrations to increase when the reclamation species were seeded into the community. The concentration data (Table 9, p. 56) shows that these increases were not uniform, and substantial decreases also occurred for some species. Because many native species had smaller niche breadths in Treatment 3, many of them were stressed (stunted growth and phenological delay as compared with Treatment 2), and populations, community biomass and nutrient shares were decreased, I advance the hypothesis that a decrease in nutrient niche breadth is generally indicative of competitive stress in a species. However, Acalypha rhomboidea, Digitaria ischaemum and D. sanguinalis all had lower niche breadth but greater niche shares, populations, and biomass in Treatment 3 than Treatment 2.

Niche share for purposes of discussion here has been based on shares in aboveground biomass. Niche share might also be based on "total nutrients available" or "total nutrients in the ecosystem." Each community type in this study sequestered different quantities of the nutrient capital, thus the base for niche share is different in each community type. A niche share based on availability also presents some problems. Different plant species exploit soils unequally to different depths. The volume of soil exploited under a

given plant community can thus vary depending upon its component species, so that nutrients available to that community may vary. Likewise, two species exploiting the same volume of soil may not have the same nutrients "available" to each due to differences in ability to exploit smaller pore sizes, differences in exchange capacities of roots, mycorrhizal fungi relationships, ability of one species to dissolve nutrients from mineral forms, etc. The base for niche share, and niche share itself, may best be thought of as a dynamic property of a community in an ecosystem. This study determined niche share at only one point in time, but it illustrates the niche share concept.

Two competitive strategies involving use of nutrient resources may be used by species in herbaceous communities to achieve dominance: (1) rapid and highly efficient uptake of nutrients which may limit nutrients (or a limiting nutrient's) availability to competitors, or (2) efficient use of mineral nutrients to quickly produce large amounts of aboveground biomass to grab space and light resources, and to produce large belowground root systems to even further monopolize water and nutrients.

Mechanism 1, which I term a type "Q" strategy for its emphasis on quantity, would be advantageous in relatively eutrophic environments. Besides possible advantages of a type Q strategy to its user species, it would benefit the system by greater conservation of nutrient capital through its sequestration in vegetation. There might have been selection of this type of strategy among the species of the seed bank through periodic disturbance of relatively eutrophic forest

ecosystems. The second competition strategy, type "E" for efficiency, would be effective in oligotrophic environments where type Q strategy would be at a disadvantage without sufficient nutrient capital to support it. Type E might also be effective, from the species short-term point of view, in eutrophic environments. This might have been the case in Treatment 3, where nutrient-use-efficient grass species took dominance away from less efficient native dicots. Other factors such as allelopathy or greater efficiency at capturing water may also have contributed. But a type E strategy among component species would be less likely to result in as great of a system nutrient conservation after disturbance as was the case in Treatment 3. Experiments such as were carried out by Parrish and Bazzar (1982) would be necessary to test this hypothesis. The concept of community niche can be carried beyond nutrient cycling. As each population in a community has a functional niche—a space occupied, resources sequestered unto itself, and a set of functions which affect the environment—a community in an ecosystem has a niche which is the sum of its component species niches. Alternative communities considered for establishment in ecosystem construction may have alternative niches. A plant community may be established primarily for its function in erosion control, specific wildlife habitat, or soil building processes. All of the potential communities have common properties that differ only in degree such as potential for nutrient sequestration and erosion control. Large human-fabricated ecosystems, such as those embracing large watersheds with a diversity of environments, may have several plant (and resultant

animal) communities, each with different characteristics, sums of functions, and thus differing niches.

Summary

Niche share and niche breadth tended to decrease in native species when reclamation mix species were added to the seed bank community. Among the reclamation community species, niche share decreased but niche breadth, as determined by use of Levins' B, increased when native species were added. Comparisons of niche share gave useful information about how a species' community role changed with change in community. Niche breadth indicated that relative nutrient use changes in a species took place when that species' community membership changed.

The concept of niche can be used in a range from the space occupied by a species in a community (habitat or habitat niche), to the qualitative way it functions in terms of resource use (qualitative functional niche), to the species operative functional niche (function of a species as a cog in the community machine), to the community operative niche (the function of a community as a machine in an ecosystem). All of these niche concepts are potentially useful tools to anyone planning the construction of an ecosystem as part of land reclamation or analyzing niche in an ecosystem context.

CHAPTER VIII

SUMMARY AND CONCLUSIONS

Four pioneer plant communities on a surface-mine spoil were compared in terms of biomass production and nutrient capital sequestration. A Chenopodium album-dominated community (T4) produced the greatest amount of aboveground biomass, followed by a pioneer community derived from a forest topsoil seed bank (T2), a seed bank community with reclamation seeded into it (T3), and a common reclamation species mix (T1). Nutrients sequestered in aboveground biomass, ranked by treatment, were N, T4 > T2 = T3 = T1; P, T4 > T2 > T1 = T3; K, T4 > T2 > T3 = T1; Ca, T2 = T4 > T3 = T1; Mg, T4 > T2 > T3 = T1; Mn, T4 > T2 = T3 = T1; Fe, T4 = T2 > T1 = T3; Cu, T4 > T2 = T1 = T3; Zn, T4 > T2 = T1 = T3.

Treatments 1, 2, and 3 sequestered N in aboveground biomass in amounts approximately equal to the amount of N added as fertilizer (57 kg/ha). Treatment 4 sequestered 237 percent of this amount. Aboveground P sequestered in vegetation ranged from 14 to 27 percent of the amount applied (59 kg/ha). The amounts of nutrients sequestered in aboveground biomass were not strictly proportional to the amounts of biomass produced. Community N, K, Mg and Zn contents were most strongly correlated with biomass; Ca, Mn and Fe contents were least correlated with biomass. Community nutrient contents were largely influenced by the biomass and the nutrient uptake characteristics of the species with greater biomass more than by the community species

composition. Choice of pioneer community for land reclamation purposes can have important effects on nutrient cycling and short-term (at least) nutrient capital retention by a developing ecosystem.

There were no significant changes in total N (Kjeldahl) content of topsoil by the end of the study despite fertilization at the beginning. There was a marked increase in available P attributable to fertilization. Potassium, Mg, Mn, Fe, Cu, pH, buffer pH, K base saturation and Mg base saturation increased in the topsoils during the study period. Topsoil H base saturation declined. Vegetation effects were discernible in the amount of change in topsoil available K, K and Mg base saturation, and buffer pH. The top 10 cm of mine spoil showed a significant decrease in available K over time; this decrease was modified by vegetation treatment.

The forest soil seed bank produced 84 taxa of which sixty-five taxa were identifiable to species, 14 to genus, and 4 to family. A few remaining seedlings were lumped as "miscellaneous." Seed bank species included five tree species, seven shrubs or woody vines, 14 grasses, and 53 forbs. Three species were legumes.

Addition of the reclamation mix of grasses and Lespedeza to the seed bank resulted in significantly fewer established native species in the mixed community. The most common and dominant native seed bank species had lower populations in the reclamation mix-seed bank community. Native species lost their positions of community dominance when the reclamation mix species were seeded into the seed bank soil. Many of the most important native species showed stunted growth and

phenological delay when reclamation mix grasses were an important part of the community. Although forest topsoils in the eastern United States can serve as sources of native species for land reclamation purposes, direct addition of exotic reclamation species to the seed bank may result in a decreased number of native taxa with possible effects on the speed of natural succession.

Among species of the seed bank community, the concentrations of the nine elements varied significantly between species. Community membership affected concentrations of N, P, K, Ca, Mn, Fe and Zn. Spoil affected concentrations of N, Ca, Mn, Fe, and Zn. Interaction effects between species, community, and/or spoils were found for N, Mn, Fe, Cu, and Zn. Nitrogen, P, K, Ca, and Zn concentrations were generally higher in native species when they were growing with introduced grasses and Lespedeza.

Among the reclamation species and two important invaders, tissue concentrations of all elements except Fe varied significantly between species. Community membership effects were significant for P, Cu, and Zn. Spoil significantly affected concentrations of Ca and Zn. Significant interaction effects for the above factors were found for N and Cu. Ca concentrations were lower and Zn concentrations were higher on Spoil 1. Most of the reclamation species had lower Zn concentrations when they were grown with the native species.

Plant species niches were compared in three communities using niche breadth (Levins' B) based on tissue nutrient concentrations, and using "nutrient content niche" and "nutrient content niche share"

which were based on species' proportional content of the total amount of each element contained in aboveground biomass. The native species generally had reduced niche breadths and niche shares when the reclamation species were added to the community. Niche shares of the reclamation species generally decreased when they were added to the seed bank community; niche breadth, however, generally increased. "Community content niche" can be quantified by summing the content niches of the component species populations. Each of the four pioneer plant communities in this study had defined and different content niches.

LITERATURE CITED

LITERATURE CITED

Allen, S. E. (ed.). 1974. Chemical Analysis of Ecological Materials, Blackwell Scientific Publications, Oxford.

Ankerman, D., and R. Large. 1974. Soil and Plant Analysis. A & L Agricultural Laboratories, Inc., Memphis, Tennessee.

Archibald, O. W. 1981. Buried viable seed in native prairie and adjacent agricultural sites in central Saskatchewan. Canadian Journal of Botany 59:701-706.

Argonne National Laboratory. 1981. Land Reclamation Program. Annual Report.

Barbour, M. G., and R. T. Lange. 1967. Seed populations in some natural Australia topsoils. Ecology 48:153-155.

Bard, G. E. 1945. The mineral nutrient content of the foliage of forest trees on three soil types of varying limestone content. Soil Science Society of America Proceedings 10:419-422.

Barnhisel, R. I. 1975. Lime and fertilizer recommendations for reclamation of surface-mined spoils. University of Kentucky, College of Agriculture, Cooperative Extension Service. Lexington, Kentucky. AGR-40.

Bartholomew, W. V., J. Meyer, and H. Laudelot. 1953. Mineral Nutrient Immobilization under forest and grass fallow in the Yangambe (Belgian Congo) Region. I.N.E.A.C. Publ. No. 57 Serie, Scientifique.

Beauchamp, H., R. Lang, and M. May. 1975. Topsoil as a seed source for reseeding strip mine spoils. University of Wyoming, Laramie, Agriculture Experiment Station, Research Journal 90:1-8.

Berg, W. A. 1973. Evaluation of P and K soil fertility tests on coal-mine spoils. pp. 93-104 In: Hutnik, R. J. and G. Davis (eds.), Ecology and Reclamation of Devastated Land. Vol. 1. Gordon and Breach, New York.

Bishop, D. M., and M. E. Stevens. 1964. Landslides on logged areas in southeast Alaska. USDA Forest Service, Northern Forest Experiment Station, Juneau, Alaska. Res. Pap. NOR-1.

Black, C. A. 1968. Soil-Plant Relationships, 2nd ed. John Wiley and Sons, Inc., New York.

Black, C. A. (ed.). 1965. Methods of Soil Analysis. Part 2. American Society of Agronomy, Inc., Madison, Wisconsin.

Blank, J. L., R. K. Olson, and P. M. Vitousek. 1980. Nutrient uptake by a diverse spring ephemeral community. Oecologia 47:96-98.

Boerd, G., and S. Thien. 1979. Phosphatase activity and phosphorus availability in the rhizosphere of corn roots. pp. 231-242 In: Harley, J. L., and R. S. Russel (eds.), The Soil-Root Interface. Academic Press, London.

Bowen, G. D., and C. Theodorou. 1973. Growth of ectomycorrhizal fungi around seeds and roots. pp. 122-125 In: Marks, G. C., and T. T. Kozlowski (eds.). Ectomycorrhizae - Their Ecology and Physiology. Academic Press, New York.

Bray, R. H., and L. T. Kurtz. 1945. Determination of total, organic and available form of phosphorus in soil. Soil Science 59:39-45.

Brenchley, W. E., and K. Warington. 1930. The weed seed population of arable soil. Journal of Ecology 18:235-272.

Brown, A. H. F., and L. Oosterhuis. 1981. The role of buried seed in coppicewoods. Biological Conservation 21:19-38.

Carrel, J. E., K. Wieder, V. Leftwich, S. Weems, C. L. Kucera, L. Bouchard, and M. Game. 1978. Strip-mine reclamation: production and decomposition of plant litter. pp. 670-676 In: Wali, M. K. (ed.), Ecology and Coal Resource Development. Vol. 2. Pergamon Press, New York.

Chippindale, H. G., and W. E. J. Milton. 1934. On the viable seeds present in the soil beneath pastures. Journal of Ecology 22:508-531.

Clark, R. B. 1983. Plant genotype differences in the uptake, translocation, accumulation, and use of mineral elements required for plant growth. Plant and Soil 72:175-196.

Clarke, G. L. 1954. Elements of Ecology. Wiley, New York.

Cole, D. W. 1981. Nitrogen uptake and translocation by forest ecosystems. Ecology Bulletin 33:219-232.

Colton, C. E., and F. A. Einhellig. 1980. Allelopathic mechanisms of velvetleaf (Abutilon theophrasti Medic., Malvaceae) on soybean. American Journal of Botany 67:1407-1413.

Cotrufo, C. 1977. Nutrient content in litterfall of an Appalachian hardwood stand. The Journal of the Elisha Mitchell Scientific Society 93:27-33.

Creek, R., and G. L. Wade. 1985. Excretion of phenolic compounds from the roots of Festuca arundinacea, Eragrostis curvula, and Lespedeza striata. Transactions of the Kentucky Academy of Science 46:51-55.

DeKock, P. C. 1964. The physiological significance of the potassium-calcium relationship in plant growth. Outlook on Agriculture 4: 93-98.

Dobberpuhl, J. M. 1981. Seed banks of forest soils in east Tennessee. M.S. Thesis, The University of Tennessee, Knoxville.

Doll, E. C., and R. E. Lucas. 1973. Testing soils for potassium, calcium, and magnesium. pp. 133-151 In: Walsh, L. M., and J. D. Beaton (eds.), Soil Testing and Plant Analysis. Soil Science Society of America, Inc., Madison, Wisconsin.

Duvineaud, P., and S. Denaeyer-DeSmet. 1973. Biological cycling of minerals in temperate deciduous forests. pp. 199-225 In: Reichle, D. E. (ed.), Analysis of Temperate Forest Ecosystems. Springer-Verlag, New York.

Egler, F. E. 1954. Vegetation science concepts. I. Initial floristic composition, a factor in old field development. Vegetatio 4:412-417.

Elton, C. 1927. Animal Ecology. Sidgwick and Jackson, London.

Epstein, E. 1972. Mineral Nutrition of Plants: Principles and Perspectives. John Wiley and Sons, New York.

Fales, S. L., and R. C. Wakefield. 1981. Effects of turfgrass on the establishment of woody plants. Agronomy Journal 73:605-610.

Farmer, R. E., Jr., M. Cunningham, and M. A. Barnhill. 1982. First-year development of plant communities originating from forest topsoils placed on southern Appalachian minesoils. Journal of Applied Ecology 19:283-294.

Foster, M. F., P. M. Vitousek, and P. A. Randolph. 1980. The effects of ragweed (Ambrosia artemisiifolia L.) on nutrient cycling in a 1st-year old-field. The American Midland Naturalist 103:106-113.

Fife, D. N., and E. K. S. Nambiar. 1982. Accumulation and retranslocation of mineral nutrients in developing needles in relation to seasonal growth of young radiata pine trees. Annals of Botany 50:817-829.

Garten, C. T. 1978. Multivariate perspectives on the ecology of plant mineral element compositions. The American Naturalist 112: 533-544.

Gerloff, G. C., D. D. Moore, and J. T. Curtis. 1964. Mineral content of native plants of Wisconsin. Wisconsin Agriculture Experiment Station Research Paper No. 14. 27 p.

Godo, G. H., and H. M. Reisenauer. 1980. Plant effects on soil manganese availability. Soil Science Society of America Journal 44:993-995.

Gray, D. H., and W. F. Megahan. 1981. Forest vegetation removal and slope stability in the Idaho batholith. USDA Forest Service, Intermountain Forest and Range Experiment Station, Research Paper INT-217. 23 p.

Grigal, D. F., and L. F. Ohmann. 1980. Seasonal change in nutrient concentrations in forest herbs. Bulletin of the Torrey Botanical Club 107:47-50.

Grime, J. P. 1981. The role of seed dormancy in vegetation dynamics. Annals of Applied Biology 98:555-558.

Grinnell, J. 1917. The niche relationships of the California thrasher. Auk 34:427-433.

Grinnell, J. 1928. Presence and absence of animals. University of California Chronicle 30:429-450.

Harcombe, P. A. 1977. Nutrient accumulation by vegetation during the first year of recovery of a tropical forest ecosystem. pp. 347-378 In: Cairns, J., K. L. Dickson, and E. E. Herricks (eds.), Recovery and Restoration of Damaged Ecosystems. University Press of Virginia, Charlottesville.

Haynes, R. J., and T. E. Ludecke. 1981. Effect of lime and phosphorus applications on concentrations of available nutrients and on P, Al and Mn uptake by two pasture legumes in an acid soil. Plant and Soil 62:117-128.

Hill, M. O., and P. A. Stevens. 1981. The density of viable seed in soils in forest plantations in upland Britain. Journal of Ecology 69:693-709.

Howard, G. S., and M. J. Samuel. 1979. The value of fresh-stripped topsoil as a source of useful plants for surface mine revegetation. Journal of Range Management 32:76-77.

Huntjens, J. L. M. 1971. Influences of living plants on immobilization of nitrogen in permanent pastures. Plant and Soil 34:393-404.

Hutchinson, G. E. 1958. Concluding remarks. Cold Spring Harbor Symposia in Quantitative Biology 22:415-427.

Interstate Mining Compact Commission. 1985. Annual Report, Year 1984. Lexington, Kentucky, 68 pp.

Iverson, L. R., and M. K. Wali. 1982. Buried viable seeds and their relation to revegetation after surface mining. Journal of Range Management 35:648-652.

Jarvis, S. C., and D. C. Whitehead. 1981. The influence of some soil and plant factors on the concentration of copper in perennial ryegrass. Plant and Soil 60:275-286.

Jordan, C. F. 1977. Distribution of elements in a tropical montane rain forest. Tropical Ecology 18:124-130.

Kennedy, H. E. 1981. Foliar nutrient concentrations and hardwood growth influenced by cultural treatments. Plant and Soil 63:307-316.

Khanna, P. K. 1975. Saisonalität der Flüsse von Stickstofformen in einem Buchen und einem Fichtenwald-Ökosystem. Mitteilgn. Bodenkundl. Gesellsh. 22:359-364.

Klopatek, J. M. 1978. Nutrient dynamics of freshwater riverine marshes and the role of emergent macrophytes. pp. 195-216 In: Good, R. E., D. Whigham, and R. L. Simpson (eds.), Freshwater Wetlands. Academic Press, New York.

Kramer, D. 1983. Genetically determined adaptations in roots to nutritional stress: correlation of structure and function. Plant and Soil 65:167-173.

Levine, S. H. 1977. Exploitation interactions and the structure of ecosystems. Journal of Theoretical Biology 69:345-355.

Levine, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, New Jersey.

Lamont, B. 1982. Mechanisms for enhancing nutrient uptake in plants, with particular reference to mediterranean South Africa and Western Australia. Botanical Review 48:597-689.

Likens, G. E., F. H. Bormann, N. M. Johnson, D. W. Fisher, and R. S. Pierce. 1970. Effects of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook Watershed Ecosystem. Ecological Monographs 40:23-47.

Lippert, R. D., and H. H. Hopkins. 1950. Study of viable seeds in various habitats in mixed prairie. Transactions of the Kansas Academy of Science 53:355-364.

Livingston, R. B., and M. L. Allessio. 1968. Buried viable seed in successional field and forest stands, Harvard Forest, Massachusetts. Bulletin of the Torrey Botanical Club 95:58-69.

Lodhi, M. A. K. 1977. The influence and comparison of individual forest trees on soil properties and possible inhibition of nitrification due to intact vegetation. American Journal of Botany 64: 260-264.

Marks, P. L. 1974. The role of pin cherry (Prunus pennsylvanica L.) in the maintenance of stability in northern hardwood ecosystems. Ecological Monographs 44:73-88.

Marks, P. L., and F. H. Bormann. 1972. Revegetation following forest cutting: mechanisms for return to steady-state nutrient cycling. Science 176:914-915.

Maser, C., J. M. Trappe, and R. A. Nussbaum. 1978. Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. Ecology 59:799-809.

McGrath, S. P., and I. H. Robinson. 1982. The influence of nitrogen source on the tolerance of Holcus lanatus L. and Bromus erectus Huds. to manganese. New Phytologist 91:443-452.

McNaughton, S. J., and L. L. Wolf. 1970. Dominance and niche in ecological systems. Science 167:131-139.

Megahan, W. F., N. F. Day, and T. M. Bliss. 1981. Landslide occurrence in the western and central Northern Rocky Mountain physiographic province in Idaho. Forest Soils and Land Use. Proc., C. T. Youngberg, ed. Fifth North American Forest Soils Conference, Fort Collins, Colorado, Aug. 1978, Colorado State University, Fort Collins.

Miller, W. F. 1966. Annual changes in foliar nitrogen, phosphorus, and potassium levels of loblolly pine (Pinus taeda L.) with site and weather factors. Plant and Soil 24:369-378.

Mugwira, L. M., S. M. Elgawhary, and A. E. Allen. 1980. Nitrate uptake effectiveness of different cultivars of triticale, wheat, and rye. Agronomy Journal 72:585-588.

Muller, R. N. 1978. The phenology, growth, and ecosystem dynamics of Erythronium americanum in the northern hardwood forest. Ecological Monographs 48:1-20.

Muller, R. N., and F. H. Bormann. 1976. Role of Erythronium americanum Ker. in energy flow and nutrient dynamics of a northern hardwood forest ecosystem. Science 193:1126-1128.

Munsell Color Company, Inc. 1954. Munsell Color Charts. Baltimore, Maryland.

Nambiar, E. K. 1976. Uptake of Zn^{65} from dry soil by plants. Plant and Soil 44:267-271.

Nambiar, E. K. 1977. The effects of drying of the topsoil and of micronutrients in the subsoil on micronutrient uptake by an intermittently defoliated ryegrass. Plant and Soil 46:185-193.

Nordin, A. 1977. Effects of low root temperature on ion uptake and ion translocation in wheat. Physiologia Plantarum 39:305-310.

Oosting, H. J., and M. E. Humphreys. 1940. Buried viable seeds in a successional series of old field and forest soils. Torrey Botanical Club Bulletin 67:253-273.

Ostman, N. L., and G. T. Weaver. 1982. Autumnal nutrient transfers by retranslocation, leaching, and litterfall in a chestnut oak forest in southern Illinois. Canadian Journal of Forest Research 12:40-51.

Ovington, J. D. 1968. Some factors affecting nutrient distribution within ecosystems. UNESCO, Natural Resources Research 5:95-105.

Parenti, R. L., and E. L. Rice. 1969. Inhibitional effects of Digitaria sanguinalis and possible role in old-field succession. Bulletin of the Torrey Botanical Club 96:70-78.

Parrish, J. A. D., and F. A. Bazzaz. 1982. Responses of plants from three successional communities to a nutrient gradient. Journal of Ecology 70:233-248.

Patten, B. C., and G. T. Auble. 1980. Systems approach to the concept of niche. Synthese 43:155-181.

Peters, E. J. 1968. Toxicity of tall fescue to rape and birdsfoot trefoil seeds and seedlings. Crop Science 8:650-653.

Rand, M. C., A. E. Greenberg, and M. J. Taras. 1976. Standard methods for the examination of water and wastewater. Fourteenth Ed. American Public Health Association, Washington, D.C.

Rice, E. L. 1974. Allelopathy. Academic Press, New York.

Rice, E. L. 1964. Inhibition of nitrogen-fixing and nitrifying bacteria by seed plants. I. Ecology 45:824-837.

Rice, E. L., and S. K. Pancholy. 1972. Inhibition of nitrification by climax ecosystems. American Journal of Botany 59:1033-1040.

Richards, T. W., W. C. McComb, D. H. Graves, and W. G. Vogel. 1984. Hardwood reforestation of surface-mined land. Final report of research control No. 23-770, University of Kentucky, Department of Forestry, Lexington, and USDA Forest Service, Northeastern Forest Experiment Station, Berea, Kentucky.

Riley, D., and S. A. Barber. 1971. Effect of ammonium and nitrate fertilization on phosphorus uptake as related to root-induced pH changes at the root-soil interface. Soil Science Society of America Proceedings 35:301-306.

Rothwell, F. M., and W. G. Vogel. 1982. Mycorrhizae of planted and volunteer vegetation on surface-mined sites. USDA Forest Service, Northeastern Forest Experiment Station, General Technical Report NE-66.

Rothwell, F., and C. Holt. 1978. Vesicular-arbuscular mycorrhizae established with Glomus fasciculatus spores isolated from the feces of cricetine mice. USDA Forest Service, Northeastern Forest Experiment Station, Research Note NE-259.

SAS Institute Inc. 1982. SAS User's Guide: Statistics, 1982 Edition. Cary, North Carolina: SAS Institute Inc.

Saif, S. R. 1983. The influence of soil aeration on the efficiency of vesicular-arbuscular mycorrhizaes. New Phytologist 95:405-417.

Schafer, W. M., G. A. Nielsen, and W. D. Nettleton. 1980. Minesoil genesis and morphology in a spoil chronosequence in Montana. Soil Science Society of America Journal 44:802-807.

Schmithüsen, J. 1968. Allgemeine Vegetationsgeographie. In: E. Obst and J. Schmithüsen (eds.), Lehrbuch der allgemeinen Geographie, pt. 4, 3rd ed. De Gruyter, Berlin.

Shoemaker, H. E., E. O. McLean, and P. F. Pratt. 1962. Buffer methods for determination of lime requirements of soils with appreciable amount of exchangeable aluminum. Soil Science Society of America Proceedings 25:274-277.

Sopper, W. E. 1975. Effect of timber harvesting and related management practices on water quality in forested watersheds. Journal of Environmental Quality 4:24-29.

Steel, R. G. D., and J. H. Torrie. 1980. Principles and Procedures of Statistics. 2nd ed. McGraw-Hill Book Company, New York.

Stroo, H. F., and E. M. Jencks. 1982. Enzyme activity and respiration in minesoils. Soil Science Society of America Journal 46:548-553.

Tacey, W. H., and B. L. Glossop. 1980. Assessment of topsoil handling techniques for rehabilitation of sites mined for bauxite within the jarrah (Eucalyptus marginata) forest of Western Australia. Journal of Applied Ecology 17:195-201.

Tamm, C. O., H. Holman, B. Popovic, and G. Wiklander. 1974. Leaching of plant nutrients from soils as a consequence of forestry operations. Ambio 3:211-221.

Tecator, Inc. 1976. Kjeltec System 1003 Distilling Unit. Manual. Herndon, Virginia.

Thompson, K., and J. P. Grime. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. Journal of Ecology 67:893-921.

Troll, C. 1968. Landschaftsokologie (English summary). In: R. Tuxen (ed.), Pflanzensoziologie und Landschaftsökologie. Ber. Symp. Int. Vergl. Vegetationskunde, Stolzenau/Weser 1963, 7:1-21.

Vail, J. A., and R. F. Wittwer. 1982. Biomass and nutrient accumulation in 10-year old eastern cottonwood, Virginia pine, and black locust plantations on eastern Kentucky mine spoil. pp. 237-242 In: D. H. Graves (ed.), 1982 Symposium on Surface Mining Hydrology, Sedimentology and Reclamation Dec. 5-10, University of Kentucky, Lexington.

van Andel, J., W. Ernst, and H. Nelissen. 1979. Mineralstoffkreislauf in populationen von kahlschlagarten in Beziehung zur sukzession. Verhandlungen der Gesellschaft für Ökologie 7:361-368.

van den Driessche, R. 1974. Prediction of mineral nutrient status of trees by foliar analysis. Botanical Review 40:347-394.

van der Valk, A. G., and C. B. Davis. 1976. The seed banks of prairie glacial marshes. Canadian Journal of Botany 54:1832-1838.

Warcup, J. H. 1957. Chemical and biological aspects of soil sterilization. Soils and Fertilizers 20:1-5.

Whittaker, R. H., S. A. Levin, and R. B. Root. 1973. Niche, habitat, and ecotope. The American Naturalist 107:321-338.

Woodwell, G. M., R. H. Whittaker, and R. A. Houghton. 1975. Nutrient concentrations in plants in the Brookhaven oak-pine forest. Ecology 56:318-332.

Wuenscher, J. E. 1969. Niche and specification and competitive modelling. Journal of Theoretical Biology 25:436-443.

APPENDICES

ROOT SYSTEMS DEVELOPMENT IN MICROPLOTS

Root Systems Functions

Roots, besides their obvious roles as parts of individual plants, have characteristics that are important in ecosystem stability and function. Plant roots stabilize surface soils and prevent erosion as well as lend stability to soil masses and prevent soil slips and slides. Gray and Megahan (1981) and Megahan et al. (1981) showed that roots of trees and shrubs played an important role in preventing landslides on steep northern Rocky Mountain slopes with coarse, shallow soils over bedrock. Bishop and Stevens (1964) also found tree roots to be important in stabilizing soil masses on steep slopes. Tap- and sinker roots resist slippage in planes parallel to the surface. Lateral roots resist slippage along vertical planes at the edges of potential slides.

The possible contributions of roots of herbaceous species to soil mass stability has not been studied to any extent. Large numbers of deep tap roots, even though more or less fleshy, should have some stabilizing effects. Strong lateral cohesion in surface soils should result from the extensive mat of roots formed in and below the topsoil in this study.

A multi-tiered root system has important effects on ecosystem nutrient cycling. Deep roots bring nutrients up from lower soil horizons. These are later released from plant shoots by leaching and mineralization of biomass. Shallow root systems pick these same ions

up and recycle them again when they are released by leaching and decay. Exploitation of different depths of soil by different species also lessens competition between those species.

General Observations

The observation of species rooting habits in this study, although not quantitative, gave some information that would be useful in choosing species to fill particular functions in ecosystem construction.

The topsoil and topsoil-spoil interface was very heavily exploited in all plots. The heaviest concentrations of root systems were found here forming a plane through the soil cube. Some roots reached the bottoms (about 50 cm depth) in all of the microplots. In general, rocks, clods, and spaces were important in allowing rapid penetration of roots into the spoil mass. Vertical rock surfaces in the spoils were frequently covered with root systems going to depth.

The reclamation treatment had very fine and diffuse root systems reaching the bottoms of the plots throughout the spoil mass. During the root washout procedure when the soils were saturated, this fine root mass was sufficient to keep the cube from collapsing after the plot sides had been removed.

The root systems exploiting the spoil mass were more extensive in the native species plots. The topsoil was heavily exploited, and tap roots and sinker roots of various species penetrated to the bottoms of all plots.

Root systems at greater depths did not appear to be as extensive in the native species plus grasses mix as in the native species alone, but roots did reach the bottoms of the plots. The surface soil root mass appeared to be slightly greater in this treatment than in the native species only plots. The additional topsoil root mass was contributed by the seeded grasses.

Treatment 4 had a well-exploited spoil mass. Roots of Chenopodium album and other species reached the bottoms of the plots.

Extensive fungal growth was noted in the soil and spoils of all plots but no fruiting bodies were found. Most of the mycelia were white or yellow and were concentrated around roots. Mycelial mats were found around some rock surfaces in the spoil as well as on spoil surfaces next to the plastic plot liners. Fungi were strongly associated with C. album roots in Treatment 4. No microscopic examination of roots was made to determine whether or not mycorrhizae had formed. In a seed bank study using similar methods and conditions. Farmer et al. (1982) found that many of the herbaceous species in a community established from forest soils spread over minespoils were endomycorrhizal. It is reasonable to assume that some of the soil fungi noted here were mycorrhiza.

Although topsoils used in Treatments 1 and 4 had been sterilized by methyl bromide, fungi may have been reintroduced to the plots. Maser et al. (1978) and Rothwell and Holt (1978) have found that mycorrhiza-forming fungi can be carried into an area by a number of different mammals including mice. Signs of mice were noted on several

plots so this vector could have been operative. Rothwell and Vogel (1982) found many of the native species grown in my study to be endomycorrhizal on various mined sites.

Root Development of Grasses

Both Digitaria ischaemum and D. sanguinalis had extensive, fine root systems. The majority of the root masses were in the topsoil and the top 10 cm of the spoils. Tan, delicate roots of both also penetrated to the bottoms of the plots.

The fine roots of Ergrostis curvula reached the bottom of several of the plots in the form of a white diffuse network following cracks and voids. The majority of the root mass was in the topsoil and the topsoil-spoil interface.

Festuca arundinacea roots very extensively exploited the surface soils. Some of the roots also reached the bottoms of the plots.

Lolium multiflorum and L. perenne had the heaviest surface soil root development of the grasses. Roots of one clone were washed out to a depth of 25 cm at 16 cm radius from the clone center. No roots of this species were found at any greater depth.

Panicum dicotomiflorum had a heavy root system exploiting all soil layers and reaching the bottoms of the plots.

Paspalum circulare and Tridens flavus roots systems reached depths of 30 and 25 cm respectively.

Root Development of Forbs

Acalypha virginica was predominantly a topsoil exploiter. A taproot usually penetrated to about 10 cm. The red roots of this species were very widespread and easy to trace in the topsoils. In Treatment 2, a root was traced completely across the plot from the stem's location near one edge.

Amaranthus hybridus had an extensive lateral root system from 20 cm taproot. The greatest concentration of roots was centered around 5 cm depth in the spoils.

Aster divaricatus roots were mostly confined to the top 10 cm of the spoils with a maximum depth of 15 cm. Rhizomes were found at the topsoil/spoil interface and in the top 5 cm of the spoil.

Chenopodium album taproots grew about 10 cm deep in the plots of Treatment 4. Lateral roots from the taproot extended out about 20 cm radius into the topsoil and the spoil. The greatest root concentration was in the topsoil/spoil interface. Strong, reticulate root systems originating from the lower portion of the taproot reached the bottoms of the plots.

Datura stramonium had a taproot about 10 cm long with many laterals in the region of the topsoil/spoil interface. These laterals eventually descended to about 25 cm at about 30 cm radius from the stem with a total length of about 50 cm.

Eupatorium purpureum had a branching root system that was primarily confined to the mid and upper part of the spoil profile. Roots were traced no lower than 30 cm.

Eupatorium rugosum and E. serotinum had coarse, branching root systems that reached the bottoms of the plots. E. rugosum roots were brown, those of E. serotinum were nearly white. Both of these species were important exploiters of the mid and lower levels of the spoils.

Helianthus decapetalus had a widespread lateral root system which predominantly exploited the top 15-20 cm of spoil. Some laterals were traced to a radius of about 55 cm from the stem. A few were found reaching the bottoms of the plots. H. microcephalus had a root system quite similar to that of H. decapetalus. In plot 21 of Treatment 2 the main roots had blackened tips at a depth of 16 cm as though they were entering a toxic zone, but other species did not exhibit this behavior.

Lactuca biennis had a strong, spreading root system of laterals from a taproot that extended to the bottom of the plot.

The roots of Lespedeza cuneata reached the bottoms of all plots in Treatments 1 and 3, even though the shoots were small in the former. The root system had delicate laterals in the top 10 cm of soil. Root nodules were mostly in the top 10 cm of soil and spoil.

Phytolacca americana had the largest taproot system of any species. Taproots reached the bottom of the plots in Treatments 2 and 3 with other laterals extending from the taproot at all levels. This species forms truly massive taproots in some spoils on surface mines.

The taproots of Robinia pseudo-acacia penetrated to about 35 cm. A widespreading lateral root system was traced as far as 45 cm radius from the stem in the spoil just below the topsoil. Some roots were nodulated to a depth of 15 cm.

In spite of a very small shoot size, yellow Rubus occidentalis taproots were traced to a depth of 20 cm.

Soutellaria ovata had a dense, fibrous root system in the topsoil layer and deeper roots that grew to the plot bottoms. Long, fleshy, white stolons extended across plots at the topsoil/spoil interface. Sometimes these stolons were also found 10-15 cm deep in the spoils.

Thick, fibrous root systems of Solidago flexicaulus extended to 40 cm.

Summary

The grasses and the native dicots produced overall different types of root systems. The roots of the grasses were fine and more heavily exploitative of the topsoil and upper soil. A sod was being formed in the topsoils that would have contributed greatly to resistance to surface erosion. Many of the native dicots had strong, heavy root systems that exploited the lower spoil levels that served to bind the spoil mass together vertically. Others had widespreading lateral roots systems that contributed a strong lateral stabilizing function. What individual roots lacked in strength was made up in numbers.

APPENDIX B

Table 20. Mean biomass (kg) per hectare and percent of total biomass in each taxa by treatment.

Species	Treatment 1		2		3		4	
	Biomass	%	Biomass	%	Biomass	%	Biomass	%
Acalypha gracilens					0.8	0.01		
A. rhomboidea			3.2	0.04	6.8	0.11	6.4	0.04
A. virginica			2.5	0.03	2.8	0.04		
Agrostis gigantea			104.3	1.27	9.0	0.14	4.0	0.03
Amaranthus hybridus					110.5	1.77		
Anemonella thalictroides			2.3	0.03	1.6	0.03		
Aristolochia serpentaria			0.1	-				
Aster divaricatus			47.2	0.57	35.2	0.56		
A. pilosus			36.3	0.44				
A. schreberi			1.5	0.02	1.2	0.02		
Aster sp.			4.8	0.06	4.2	0.07		
Bidens frondosa					39.9	0.64		
Bromus commutatus			1.0	0.01	23.2	0.37		
Carya cordiformis			0.6	0.01				
Chenopodium album							13,592.2	88.39
Cimicifuga racemosa			1.4	0.02				
Crotonopsis elliptica			3.2	0.04				
Cyperus esculentus			2.6	0.03				
Dactylis glomerata	75.4	1.36	59.7	0.73	43.5	0.69	3.4	0.02
Datura stramonium	108.4	1.96						
Digitaria ischaemum	1490.0	26.93	1138.3	13.83	1349.9	21.56	709.0	4.61
D. sanguinalis	358.3	6.48	35.6	4.27	179.8	2.87	143.9	0.94
Eleusine indica	0.9	0.01			1.7	0.03	0.2	-
Eragrostis curvula	745.4	13.47			1148.3	18.34	613.0	3.99
Erechtites hieracifolia			1965.4	23.88	437.8	6.97		
Erigeron canadensis			1.0	0.01			2.1	0.01
Euonymus atropurpureus					0.3	-		

Table 20 (continued)

Species	Treatment 1 Biomass	1 %	2 Biomass	2 %	3 Biomass	3 %	4 Biomass	4 %
Eupatorium purpureum			71.9	0.87	10.4	0.17		
E. rugosum			474.8	5.77	53.3	0.85		
E. serotinum			269.7	3.28	45.9	0.73		
Eupatorium sp.			8.1	0.10				
Festuca arundinacea	628.5	11.36	10.1	0.12	636.3	10.16		
Galium triflorum			5.2	0.06	0.5	0.01		
Galium sp.					0.1	-		
Geum sp.			0.6	0.01				
Hedeoma pulegioides			11.5	0.14	1.2	0.02		
Helianthus decapetalus			407.0	4.94	162.7	2.60		
H. laevigatus			3.9	0.05				
H. microcephalus			601.6	7.31	244.3	3.90		
Helianthus sp.			12.1	0.15				
Krigia sp.			0.3	-				
Lactuca biennis			53.3	0.65	2.7	0.04		
L. pulchella			11.9	0.14				
L. scariola					1.8	0.02		
Lactuca sp.			1.3	0.02				
Lespedeza cuneata	32.3	0.58			398.0	6.36	22.8	0.15
Liriodendron tulipifera			16.5	0.20	3.5	0.06		
Lolium multiflorum	1858.7	33.59			459.8	7.34		
L. perenne	147.2	2.66			482.8	7.71	5.0	0.87
Lolium sp.							3.1	0.03
Misc. Apiaceae			0.2	-	-	-		
Misc. Asteraceae			5.1	0.06	0.8	0.01		
Misc. Fabaceae			-	-	-			
Misc. Poaceae	12.8	0.23	3.2	0.04			2.2	0.01

Figure 20 (continued)

Species	Treatment 1		2		3		4	
	Biomass	%	Biomass	%	Biomass	%	Biomass	%
Miscanthus sinensis					5.1	0.08		
Miscellaneous sp.			4.4	0.04				
Monarda clinopodia			14.4	0.17	1.6	0.03		
Muhlenbergia schreberi	23.9	0.43			15.6	0.25	7.4	0.05
Oxalis stricta			0.7	0.01	0.3	-		
Oxalis sp.			-	-	-	-		
Panicum agrostoides					2.5	0.04		
P. dicotomiflorum	22.2	0.40	173.6	2.11	21.5	0.34	13.2	0.09
Paronychia canadensis			0.3	-				
Parthenocissus quinquefolia			1.4	0.02	1.6	0.02		
Paspalum circulare	7.7	0.14			1.4	0.02		
P. laeve							4.2	0.03
Physalis heterophylla			3.7	0.05	1.7	0.03		
P. pruinosa			4.1	0.05				
Phytolacca americana	9.1	0.16	2052.5	24.93	246.6	3.94	0.7	-
Plantago lanceolata	3.1	0.06	2.7	0.03	0.7	0.01		
Portulaca oleracea			0.7	0.01				
Pyrrhopappus carolinianus			0.5	0.01				
Ranunculus septentrionalis			2.8	0.03	-	-		
Rhus copallina							5.3	0.03
Robinia pseudo-acacia	3.8	0.07	49.5	0.60	3.7	0.06	1.9	0.01
Rubus allegheniensis			3.3	0.04	0.4	0.01		
R. occidentalis			12.7	0.15	0.2	-		
Rubus sp.			5.6	0.07	2.2	0.03		
Rumex acetosella							1.7	0.01
Sassafras albidum			2.0	0.02				
Scutellaria incana var. punctata			2.0	0.02	1.1	0.02		

Figure 20 (continued)

Species	Treatment 1 Biomass	1 %	2 Biomass	2 %	3 Biomass	3 %	4 Biomass	4 %
S. ovata			74.0	0.90	10.2	0.16		
S. serrata			9.1	0.11				
Scutellaria sp.			-	-				
Solanum carolinense					2.0	0.03		
Solidago flexicaulis			31.5	0.38	21.5	0.34		
Solidago sp.			1.3	0.06				
Stachys tenuifolia			1.9	0.02				
Strophostyles helvola					0.9	0.01		
Trifolium repens							0.2	-
Tridens flava	5.0	0.09						
Triticum aestivum					14.6	0.23		
Ulmus sp.			0.1	-				
Uniola latifolia							1.9	0.01
Uvularia perfoliata			0.7	0.01				
Viola sp.			40.2	0.49	5.4	0.09		
Vitis sp.			11.8	0.14	1.1	0.02		

VITA

Gary Leon Wade was born to Mr. and Mrs. Farris Wade in Centerville, Iowa, on March 26, 1948. He grew up in Seymour, Iowa, and attended the Seymour Community Schools from which he graduated in 1966.

He attended Iowa State University and in 1970 he received a Bachelor of Science degree with a major in botany and minors in zoology, chemistry and education. He entered graduate school in the same institution, but was drafted into the armed forces. He served in the United States Air Force from 1970 to 1974.

He entered The University of Tennessee, Knoxville, in 1975 and earned a Master of Science degree in Ecology in 1977. He reinrolled in the Graduate Program in Ecology at The University of Tennessee and received a Doctor of Philosophy degree in 1985.

He joined the U. S. Forest Service in 1981 where he is employed as a Botanist working in surface-mine reclamation research.

He is a member of the Ecological Society of America, American Association for the Advancement of Science, Tennessee Academy of Science, Kentucky Academy of Science, and American Society for Surface Mining and Reclamation.

He is married to the former María G. Padilla, Peoria, Arizona. They have three children, Ruth María, Anna María, and Frank David.