DIRECTING ECOLOGICAL RESTORATION: IMPACT OF ORGANIC AMENDMENTS ON ABOVE- AND BELOWGROUND ECOSYSTEM CHARACTERISTICS

A Dissertation

by

LORI ANN BIEDERMAN

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

May 2007

Major Subject: Rangeland Ecology and Management

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Approved by:

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ABSTRACT

Directing Ecosystem Restoration: Impact of Organic Amendments on Above- and Belowground Ecosystem Characteristics.

(May 2007)

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Increasing interest among restoration ecologists exists in developing strategies that stimulate biotic interactions and promote self-regulation in restored systems. These approaches should target above- and belowground organisms because they interact to regulate ecosystem pattern and process. In the following dissertation, I compare the ability of organic amendments to alter above- and belowground biological community structure and function to promote prairie establishment on Castle Drive Landfill in Garland, Dallas County, Texas. Treatments included altering the location of organic amendments in the soil profile, either applied to surface or incorporated, and varying the amount applied. Plant community composition, grass population dynamics, soil nutrient conditions, and soil biological parameters were monitored for three growing seasons.

Aboveground, the surface treatments were superior for the establishment of desired and undesired plant species. Plant density patterns can be attributed to the amelioration of physical conditions and the accidental burial of seed during incorporation. Grass population dynamics suggest that surface-amended plots supported establishment, but high-volume incorporated treatments were better for enhancing survival through seasonal and long-term drought. Belowground biological responses were affected by the plant community, and not by the amendment treatments. Soil microbial biomass and carbon mineralization potential were larger in those treatments with greater plant density. The structure of the nematode community suggests that decomposition in the surface-amended plots was directed through bacterial channels while decomposition in the incorporated plots was through fungal channels. It is likely that the higher rates of plant productivity in surface treatments stimulated root exudation, thereby favoring bacteria and the nematodes that feed on them. Treatment differences in decomposition pathway were attenuated after 17 months. The soil quality indicators, C_{mic}/C_{org}, $q\mathrm{CO}_2$, nematode family richness and nematode density, were not affected by the restoration treatments or plant density, but did increase over time. The results of this study suggest that restoration managers should direct their energies into establishing and promoting a high-quality plant community. This can be manipulated with amendments, but care is needed not to exceed thresholds within location treatments.

DEDICATION

To

Edward Cushing

and

Nancy Sather

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I would like to thank my committee chair, Dr. Steve Whisenant, and committee members Drs. Tom Boutton, David Briske, Jim Starr and Forest Robinson for their contributions and patience. Furthermore, without the encouragement of my parents, I would have never pursued this degree and I will be forever grateful for their support.

Special thanks to Grace Li and Diana Wall for providing nematode identification training and guidance. I appreciate your willingness to take me in and let me soak in everything nematode.

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TABLE OF CONTENTS

Page

ABSTRACT……………………………………………………………………..iii

DEDICATION………………………………………………………………......v

ACKNOWLEDGEMENTS……………………………………………………...vi

TABLE OF CONTENTS………………………………………………………vii

LIST OF FIGURES……………………………………………………………x

LIST OF TABLES……………………………………………………………...xii

CHAPTER

I INTRODUCTION……………………………………………………..1

II AMENDMENT TREATMENTS DIRECT PLANT COMMUNITY STRUCTURE AND FUNCTION, BUT NOT DIVERSITY, IN RESTORATION……………………...…………………………………5

Introduction……………………………………………………….5
Methods…………………………………………………………..7
Study area………………………………………………………..7
Restoration treatments ………………………………………….9
Measurement…………………………………………………14
Statistical analyses………………………………………14
Results…………………………………………………….......15
Removed plant density…………..……………………………..15
Desired species density……………………..…………….......15
Undesired species density…………………..……..................19
Diversity………………………………………….…………..……… 22
Discussion…………………………………….……...……....22
Diversity……………………………………..…...………..26
Individual species …………………………….....………..27
Reverse fertilization…………………………....…………...28
Conclusions and implications for restoration………..………29

III ORGANIC AMENDMENTS DIRECT GRASS POPULATION DYNAMICS IN RESTORATION……………………………………......30

CHAPTER Page

Introduction....30
Methods....33
Study area....33
Restoration treatments....34
Grass data collection....35
Soil temperature....36
Mid-day plant water potential....36
Statistical analysis....37
Results....38
Soil temperature....43
Mid-day plant water potential....43
Discussion....46
Recruitment....47
Seasonal drought....48
Mid-day plant water potential....50
Conclusions and implications for restoration....51

IV DIRECT AND INDIRECT EFFECTS OF AMENDMENT PLACEMENT ON SOIL CARBON AND NITROGEN DYNAMICS IN RESTORATION....52

Introduction....52
Methods....55
Study area....55
Restoration treatments....55
Reference sites....57
Seasonal peak aboveground biomass....58
Soil collection and analysis....58
Statistical analyses....61
Results....61
Seasonal peak aboveground biomass....61
Gravimetric water content and bulk density....65
Organic carbon and total nitrogen....65
Soil microbial biomass....69
Inorganic nitrogen pools....72
Potential nitrogen transformation rates....72
Carbon mineralization potential and qCO_2....74
$\delta^{13}C$ and $\delta^{15}N$ values of soils....78
Discussion....78
Direct amendment effects....80
Indirect amendment effects....81
Changes over time....82

CHAPTER Page

Nitrogen dynamics……………………………………………84
Conclusions and implications for restoration……….…………..85

V DEVELOPMENT OF SOIL FOOD WEB STRUCTURE AND FUNCTION: THE ROLE OF ORGANIC AMENDMENTS IN ECOLOGICAL RESTORATION ……………………………………...87

Introduction………………………………………….………..87
Methods……………………………………..…………..90
Study area……………………………….……………...90
Restoration treatments…………………………….…………91
Reference sites…………………………...……………..92
Soil collection …………………………….……………93
Nematode community indices……….………...…………94
Statistical analyses..……………..……………………..96
Results…………………………………………………...……98
Diversity and density…………….....……………………...…98
Trophic response……………….……………………...101
Functional indices……….……..……………………...104
Discussion…………………………………………………...108
Treatment effects…………….…………………………...108
Temporal changes……….…………………… …………109
Plant parasite changes……………………………..………...110
Implications for restoration………………...…………..…112
Conclusion ……………..……………….……………………..113

VI CONCLUSION..………....……………………………………..114

REFERENCES……………………….…………………………………………..117

VITA……………………………………………………………………………..140

LIST OF FIGURES

FIGURE Page

2.1 Monthly precipitation data for 2003, 2004, and 2005 and 30-year average from the Rockwall weather station, National Weather Service..……………………..10

2.2 *Helianthus annuus* L. and *Ambrosia trifida* L. density m^{-2} (mean ± SE, n=25) prior to removal by clipping in June 2003…………………………………………17

2.3 Desired species density m^{-2} by functional group in fall 2003 and spring and fall 2004 and 2005 (mean, n=50) by restoration treatment…………………….…….20

2.4 Undesired species density m^{-2} by functional group in fall 2003 and spring and fall 2004 and 2005 (mean ± SE, n=50) by restoration treatment……….……..21

2.5 Seasonal values of Simpson's index of diversity (mean ±SE, n=50) in 2003, 2004 and 2005 by restoration treatment..……..…………………………………23

2.6 Seasonal values of total and desired species richness (mean ±SE, n=50) in 2003, 2004 and 2005 by restoration treatment…………………………………25

3.1 Tiller density m^{-2}, total basal area cm^2 m^{-2}, plant density m^{-2} and average plant size (Basal area cm per plant) of all perennial grasses in the amendment treatments for the 2004 and 2005 growing season………………………………...40

3.2 Changes in tiller density m^{-2}, total basal area cm^2 m^{-2}, plant density m^{-2} and average plant size (Basal area cm per plant) of perennial grasses in the amendment location treatments over time in 2004 and 2005. …………..……...42

3.3 Plant density m^{-2} for *Bouteloua curtipendula* (a) and *Leptochloa dubia* (b) (mean ±SE) in the amendment treatments for the 2004 and 2005 growing seasons………………………………………………………..……………45

4.1 Seasonal peak aboveground biomass (mean ±SE, n=5) for the experimental treatments over time……………………………………………………………64

4.2 Soil bulk density (mean ± SE, n =5) for each experimental treatment over time…………………………………………………………………………...66

FIGURE Page

4.3 Soil organic carbon and soil total nitrogen concentrations (g kg^{-1}) and densities (g m^{-2}) for the experiment treatments (mean ±SE, n=5) in June 2003 and September 2005 and the Rosehill native prairie and restoration reference sites (mean ±SE, n =2) in September 2005……………………………...67

4.4 Soil C:N ratio (mean ± SE, n=5) for the experiment treatments in June 2003 and September 2005 and the native and attempted restoration reference sites (n =2) in September 2005……………………… …………………………68

4.5 Soil microbial biomass carbon (SMB-C) and nitrogen (SMB- N) (mean ± SE, n = 5) of each experimental treatment over time……………………..70

4.6 C_{mic}/C_{org} (mean ±SE, n=5) for the experiment treatments in June 2003 and September 2005 and the native and attempted restoration reference sites (n = 2) in September 2005……………………………………………………71

4.7 Ammonium (NH_4^+- N) and nitrate (NO_3^--N) availability (mean ±SE, n=30) of all experimental plots over time..…………………………………………….73

4.8 N-mineralization and nitrification potential (mean ±SE, n=5) by amendment amount for June 2003, March 2004 and June 2004………………………………..75

4.9 Carbon mineralization potential (a) and *q*CO2 values (b) (mean ±SE, n=5) of each experimental treatment over time…………………………………………77

4.10 δ^{13}C (a) and δ^{15}N (b) values of soil (mean ±SE, n=5) in the experiment treatments in June 2003 and September 2005, and the native and attempted restoration reference sites (n = 2) in September 2005……………………………..79

5.1 Nematode family richness (a), Simpson's index of dominance (b) and Shannon-Weaver index of family diversity (c) over time for the landfill experiment and the native and restored reference sites (mean ±SE, n = 2) in September 2004 and 2005…………………………………………………………99

5.2 Nematode density (mean ±SE, n = 30) by trophic group and total over time…….100

5.3 Nematode enrichment profiles (see Ferris and Bongers 2006) by restoration treatment (mean ±SE, n = 5) and reference areas (mean ±SE, n = 2)…………….102

5.4 Plant parasite and detritivore density in the experimental plots and reference areas in September of 2004 and 2005……………………………………………..103

FIGURE Page

5.5 Channel index (CI) (a) and Enrichment Index (EI) (b) of each location experimental treatment (mean ± SE, n=5) over time, and for the mean (mean ± SE, n=2) values for the native and restored prairie reference sites in September 2004 and 2005…………………………………………………...106

5.6 Nematode weighted faunal profiles (see Ferris et al. 2001) along axes of structure (SI) and enrichment (EI) in response to restoration treatments (mean ±SE, n = 5) and for reference areas (mean ±SE, n = 2)……………………107

LIST OF TABLES

TABLE Page

2.1 Pre-treatment (January 2003) soil characteristics of the experimental area at the Castle Drive Landfill, Garland, Texas, USA………………………….. 8

2.2 Pure live seeding rates (PLS) and commercial sources for the plant species in the seed mixes hand-planted in March 2003. …………………………………12

2.3 Rank Species that were among the ten most abundant with one or more fall sample period, their overall density and rank in abundance.……………….........16

2.4 Summary of fixed effects of ANOVA procedures for desired and undesired plant density m^{-2}………………………………………………………..…….....18

2.4 Summary of fixed effects of ANOVA procedures for total plant species richness and desired plant species richness………………………………………..24

3.1 Summary of fixed effects of the linear mixed model procedures for grass population characteristics for three sample periods in 2004 and 2005……………39

3.2. Summary of fixed effects of the linear mixed model procedures for plant density in 2004 population characteristics for *Bouteloua curtipendula* and *Leptochloa dubia* for three sample periods in 2004 and 2005. ……………………44

4.1 Summary of fixed effects of the linear mixed model procedures for the soil properties from eight sampling periods between June 2003 to September 2005…………………………………………………………………62

4.2 Summary of fixed effects of the linear mixed model procedures for the soil properties from June 2003 and September 2005…………………………………...63

4.3 Summary of fixed effects of the ANOVA procedures for potential nitrogen transformation rates for June 2003 to September 2004……………………………76

5.1 Summary of fixed effects of the linear mixed model procedures for the nematode community parameters from seven sampling periods between June 2003 to September 2005………………………………………………………97

CHAPTER I

INTRODUCTION

There is a need for restoration strategies that enable biotic interactions and promote the self-regulation of ecosystem processes (Harris and Hobbs 2001). This requires an understanding of how both the plant community and the soil ecosystem may be stimulated to ameliorate the site's physical conditions and regulate soil nutrient cycling and availability (Reever Morghan and Seastedt 1999, Blumenthal et al. 2003). In the following four chapters, I compare the ability of amendment treatments to alter both aboveground and belowground processes and facilitate recovery in restoration. These changes were monitored for three successive growing seasons to determine the relative success of these treatments over time. Specifically, I compared the ability of these treatments to initiate the establishment and function of southern mixed grass prairie vegetation on a landfill soil cap. These prairie ecosystems are dominated by C_4 native grasses and have high levels of belowground productivity with rich organic soils (Rice et al. 1998).

The amendment treatments used in this study consisted of different rates of a commonly available material that were altered in placement within the soil profile: surface-applied or incorporated. These treatments were intended to uniquely influence the physical and biological properties (Gill and Jalota 1996, Sanchez et al. 2000, Wher et al. 2005). Surface amendments moderate soil temperature and lessen moisture loss by

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This dissertation follows the style of Restoration Ecology.

reducing incident radiation on the soil surface (Tian et al. 1993, Price et al. 1998). Infiltration is also improved under surface mulches (Agassi et al. 1998).

Incorporation of amendments also benefits the soil's physical environment. Imbedded material slows evaporation of soil water by disrupting capillary networks (Gill and Jalota 1996). The incorporation of materials also reduces the shrink-swell capacity of clay soils, which can prevent water loss during periods of little rainfall by retaining the physical integrity of the soil's surface (Weindorf et al. 2006). Further, the material will itself retain moisture longer than those on the surface, and therefore can serve as a moisture reservoir (Beare et al. 1992).

The demography of the target plant species may be affected by amendment placement because differential plant morphology and access to soil resources will improve survival or accelerate growth. Plants respond to surface mulches by increasing root abundance and lateral growth at the surface, directly under the material (Chaudhary and Prihar 1974, Cotrufo 2006). Furthermore, surface amendments also create a more favorable microenvironment for seed germination and plant establishment (Winkel et al. 1991, Chambers 2000). The increased macroporosity in the incorporated treatment improves plant rooting depth and elongation (Gorenevelt and Grunthal 1998, Liang et al. 1999).

The composition and size of the soil food web is also affected by different locations of organic amendments. Surface material is physically separated from soil organisms and therefore, decomposes slowly (Beare et al. 1992, Tian et al. 1993). This amendment location also promotes a decomposition pathway dominated by fungi, which are tolerant of desiccation and can translocate materials within their tissue from the surface into the soil (Frey et al. 1999). Fungi and their consumers are more efficient at nutrient cycling than bacteria-dominated soil food webs (Fu et al. 2000, Bardgett et al. 2002) and as such, fungal-dominated pathways are often targets of restoration (Smith et al. 2003).

Incorporated amendments also influence the size and composition of the decomposer community. These materials are imbedded into the soil and have increased surface area exposure, which supports larger populations (Elliott et al. 1980, Killham et al. 1993). This location treatment also affects soil ecosystem structure by promoting organisms that respond rapidly to enrichment, such as bacteria and bactivorous fauna (Beare et al. 1992, Fu et al. 2000). These bacteria-dominated soil food webs increase the availability of nutrients and their rate of cycling (De Ruiter et al. 1993, Wardle et al. 2004).

To determine the effectiveness of these amendment treatments I compared their ability to increase the density and diversity of the plant community. I also monitored grass population dynamics over time to determine the amendments ability to effect plant survival. Belowground, I measured the changes in the soil nutrient pools and the size and composition of the soil food web. These belowground metrics include changes in soil carbon and nitrogen pools, the soil quality indicators qCO2 and C_{mic}/C_{org}, and the size and trophic distribution of the nematode community. I also measure two mechanisms that would explain treatment differences in plant performance and soil organism activity: soil temperature, which measures physical differences among treatments, and mid-day plant water potential, a physiological mechanism. Finally, I compared the nutrient storage and processes of the experiment with a nearby native prairie and an older restoration reference.

By comparing both above- and belowground biological responses, I sought to uncover the mechanisms behind the amendment treatments. This will help determine the appropriate application method and amendment amount that provides the most benefit in restoration.

CHAPTER II

AMENDMENT TREATMENTS DIRECT PLANT COMMUNITY STRUCTURE AND FUNCTION, BUT NOT DIVERSITY, IN RESTORATION

Introduction

Successful ecological restoration depends on the establishment and maintenance of desired plant species (Gillespie and Allen 2004). The degree of success depends on ability of the imposed treatments to enhance the physical environment during the initial stages of development when plant species within communities undergo the most challenges to their establishment and survival (Montalvo et al. 2002). This intervention in the physical environment is particularly important in severely disturbed sites where ecosystem function needs to be reinitiated (Whisenant 1999, Hobbs and Harris 2001).

Rapid development of the ecological functions associated with high plant density and diversity are often cited as important goals for restoration management (Palmer et al. 1997, Polley et al. 2005). High plant density physically protects the soil surface and promotes energy capture and nutrient retention (Dewald et al. 1996, Montalvo et al. 2002). Plant species diversity is not only aesthetically important (Sabre et al. 1996), but is desired for its potential contribution towards ecosystem services, such as high community productivity (Naeem et al. 2000, Wilsey and Potvin 2000, Tilman 2001), protection against invasion (Pokorny et al. 2005) or resilience in function following disturbance (Walker et al. 1999).

However, the achievement of high plant density and diversity in restoration is often limited by physical constraints. The application of organic amendments is a common restoration technique that can alter these constraints for improved plant success and community diversity. The physical advantages of organic amendments include increased moisture retention and a reduction of the magnitude of diurnal temperature change, thus lengthening the duration of water availability (Winkel et al. 1991, Zaongo et al. 1997, Chambers 2000, Petersen et al. 2004). Organic amendments can also alleviate high soil temperatures, improve low water availability and increase infiltration. Nutrient conditions are altered with amendments either through nutrient addition or microbial immobilization (Blumenthal et al. 2003, Corbin and D'Antonio 2004, Eschen et al. 2006).

The ability of amendments to direct physical qualities of the soil depends, in part, on its location within the soil profile: surface-applied or incorporated (Gill and Jalota 1996, Sanchez et al. 2000, Wher et al. 2005). Surface amendments moderate soil temperature and lessen moisture loss by reducing incident radiation on the soil surface (Tian et al. 1993, Price et al. 1998). This provides greater protection for plant seedlings and will enhance their emergence and survival (Winkel et al. 1991, Chambers 2000). Infiltration is also improved under surface mulches (Agassi et al. 1998). Plants respond to surface mulches by increasing root abundance and lateral growth at the surface, directly under the material (Chaudhary and Prihar 1974, Cotrufo 2006).

In contrast, the incorporation of amendments can improve physical conditions by disrupting capillary flow of soil water and slowing evaporation (Gill and Jalota

1996). Incorporated organic materials also reduce the shrink-swell capacity of clay soils and maintain soil moisture availability during periods of little rainfall through the maintenance of soil surface integrity (Weindorf et al. 2006). This creates and maintains macroporosity, which improves plant rooting depth and elongation (Gorenevelt and Grunthal 1998, Liang et al. 1999). Further, the incorporated material will itself retain moisture longer than those on the surface, and can therefore serve as a moisture reservoir during periods of low precipitation (Beare et al. 1992).

Because plant community structure may be affected by amendment placement, I monitored changes in both plant density and diversity over the first three years of this restoration. Specifically, I hypothesize that: (1) initial plant density, both desired and volunteer, would be greater in the surface treatments than in incorporated treatments. (2) incorporated amendments would enhance native plant diversity over surface-amended treatments (3) increasing the amount of amendment applied would enhance plant density and diversity in both location treatments.

Methods

Study area

This study was conducted on a 21-hectare portion of the Castle Drive Landfill in Garland, Dallas County, Texas (32° 93′ N, 96° 58′ W; elevation 165 m). In accordance with regulations by the Texas Commission on Environmental Quality, the landfill has a constructed clay cap 45 cm thick, which is designed to be impermeable to water seepage into the municipal garbage below. Overlaying this cap is a 26 to 35 cm composite of

Table 2.1. Pre-treatment (January 2003) soil characteristics of the experimental area at the Castle Drive Landfill, Garland, Texas, USA.

	Mean	**Standard error**
Particle size distribution		
Sand (%)	16	2
Silt (%)	41	4
Clay (%)	43	2
Bulk density (g cm^{-3})	1.45	0.01
pH	8.2	0
Organic carbon (mg kg^{-1} soil)	4800	200
Calcium (mg kg^{-1} soil)	57201	73
Magnesium (mg kg^{-1} soil)	476	19
Nitrate (mg kg^{-1} soil)	3	0.3
Total phosphorus (mg kg^{-1} soil)	23	5
Potassium (mg kg^{-1} soil)	336	3.8
Salinity (mg kg^{-1} soil)	315	31.8
Sodium (mg kg^{-1} soil)	362	15.9
Sulfur (mg kg^{-1} soil)	56	3

unconsolidated subsoil from an adjacent area and is a growing medium for the vegetation cover. Soil properties prior to treatment are listed in Table 2.1.

This area is in the Texas Blackland Prairie Ecoregion, which is dominated by tall- and mid-sized grasses with associated forbs (Diggs et al. 1999). The mean monthly low temperature (1 °C) occurs in January and the mean monthly high temperature (35.5 °C) is in July. The 30-year precipitation average is 999 mm and has a bimodal distribution, with the largest amounts of rain falling in May (134 mm) and October (116 mm). Annual precipitation was below average in 2003 (510 mm) and 2005 (474 mm). Although the total amount of precipitation was average during 2004, much of the rainfall fell in June and July (Fig. 2.1).

Restoration treatments

This experiment had six treatments in a 2 x 3 factorial completely randomized design. There were two amendment location treatments: surface applied and incorporated to 6 cm with a roto-tiller. There were three treatments that differed in the amount of material added: no amendment, a light amendment (765 g m^{-2}) and heavy amendment (1530 g m^{-2}). Each treatment occurred once in each of five replicate blocks, which occur along a 5% northeast slope. Alleyways (2 m wide) separated the 25 m^2 plots. The experimental area was disked three times to remove any previous vegetation before planting on March 12, 2003.

The amendment material used was untreated urban wood waste from the City of Garland Castle Drive Wood Recycling Facility. This material had a composition of

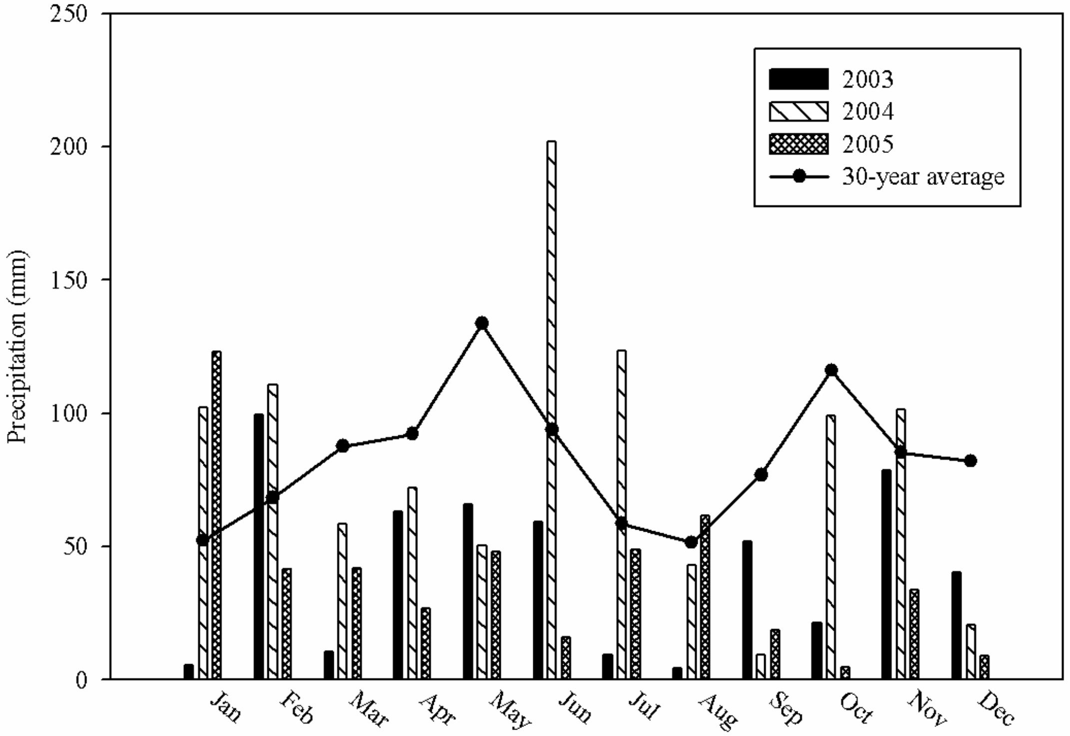


Figure 2.1. Monthly precipitation data for 2003, 2004, and 2005 and 30-year average from the Rockwall weather station, National Weather Service.

43.5% carbon, 0.45 % nitrogen, and a C:N ratio of 98:1. Amendment particle size distribution was 26 % of mass less than 1-cm^2, 17 % greater than 1-cm^2 but less than 5-cm^2, and 56% larger than 5 cm^2. The large, recalcitrant amendment material was chosen to address the issues associated with soil physical structure, such as compaction, but not create a dramatic pulse of nitrogen availability or immobilization (Whitford et al. 1989, Reid and Naeth 2005).

Seeds of native and naturalized grasses, legume and forb species typical of this region were acquired from two commercial vendors: Turner Seed Company and Native American Seed (Table 2.2). For the surface application treatments, the large and awned seeds were hand-spread followed by the use of a culti-packer (Brillion Farm Equipment, Brillion, Wisconsin) to firm the seedbed. The amendment was hand-spread over the seed bed at the three treatment amounts. In the incorporated treatments, the large and awned seeds were hand-sewn, followed by the application of the amendment. The material was then incorporated to 6 cm with a rototiller and the seedbed firmed with the culti-packer. In both location treatments, the final step was the hand-sewing of the small seeded species. The total pure live seed applied for all species was 2.1 g m^{-2}.

Aboveground stems of the large-leaved and abundant *Ambrosia trifida* L. (giant ragweed) and *Helianthus annuus* L. (annual sunflower) individuals were hand-clipped and removed from plots in June 2003 to minimize soil water loss during initial plant establishment. *Sorghum halepensis* (johnson grass), an aggressive invasive grass, was periodically treated throughout the experiment by individual wipe treatments of a

Table 2.2. Pure live seeding rates (PLS) and commercial sources for the plant species in the seed mixes hand-planted in March 2003. Nomenclature follows Correll and Johnston (1970).

awned seed mix	**Species**	**Common name**	**Variety**	**% pls**	**g pls m^{-2}**	**Source**
	Agropyron smithii	western wheat grass	Barton	50	0.05	Turner seed company
	Andropogon gerardi	big bluestem	Kaw	54	0.09	Turner seed company
	Aristida purpurea	purple three-awn		85	0.09	Native American Seed
	Bouteloua curtipendula	side-oats grama	Haskell	81	0.20	Turner seed company
	Buchlöe dactyloides	buffalo grass	Texoka	81	0.13	Turner seed company
	Elymus canadensis	canada wild-rye		56	0.06	Turner seed company
	Schizachyrium scoparium	little bluestem		53	0.09	Turner seed company
	Sorghastrum avenaceum	Indian grass	Lometa	71	0.08	Turner seed company
	Engelmannia pinnatifida	englemann daisy		80	0.17	Native American Seed
	Aster praealtus	Tall aster		80	0.01	Native American Seed
	Liatris mucronata	gay-feather		83	0.09	Native American Seed

Table 2.2. continued.

small seed mix	**Species**	**Common name**	**Variety**	**% pls**	**g pls m^{-2}**	**Source**
	Eragrostis trichodes	sand lovegrass	Bend	83	0.09	Turner seed company
	Leptochloa dubia	green sprangle top	van horn	90	0.15	Turner seed company
	Sporobolis asper	tall dropseed		60	0.06	Turner seed company
	Coreopsis lanceolata	lanceleaf coreopsis		86	0.09	Turner seed company
	Desmanthus illinoensis	Illinois bundle flower		94	0.05	Turner seed company
	Gaura lindheimeri	white gaura		73	0.02	Native American Seed
	Helianthus maximiliani	Maximillian sunflower	Aztec	87	0.05	Turner seed company
	Salvia coccinea	scarlet sage		90	0.07	Native American Seed
	Ipomopsis rubra	standing cypress		88	0.05	Native American Seed
	Cassia fasciculata	partridge pea	Comanche	82	0.18	Turner seed company
	Centaurea americana	basket flower		83	0.09	Native American Seed
	Coreopsis tintoria	golden wave		62	0.02	Native American Seed
	Dracopis amplexicaulis	clasping-leaf coneflower		82	0.04	Turner seed company
	Monarda citriodora	lemon mint		89	0.05	Turner seed company
	Rudbeckia hirta	black-eyed susan		83	0.02	Turner seed company

solution of one-third glyphosphate (N-phosphonomethyl glycine) and two-thirds water. All other unsown species were untreated during the experiment.

Measurement

Plant density and community composition was determined in August 2003, May 2004 and September 2004 and May and August 2005. All plants were identified and enumerated within the ten randomly placed 0.25-m^2 quadrats within each treatment plot ($n = 300$). Following data collection each plant species was assigned a season, spring or fall, based on its phenology and was only included in the analysis for that season.

Plant diversity was evaluated in several ways. Total and desired species richness, and Simpson's index of diversity ($D_j = 1- \Sigma(P_i)^2$) (Simpson 1949) was determined for each sample plot. Simpson's index of diversity is a measure of species evenness; values closer to one indicate that any two randomly chosen individuals will be of different species. In other words, larger values indicate that most species are rare within the plot and that there are only a few common species.

Statistical analyses

Treatment differences at each sample period were determined using ANOVA with amendment amount, location and their interaction as fixed terms and block as a random term. Bonferroni post-hoc tests were used to determine differences within response variables. Repeated measures analysis could not be used because the sample units were randomly chosen each sample period and are, therefore, not truly temporal replicates.

Results

Five species in the seed mixture failed to establish: *Agropyron smithii* Rydb. (western wheat grass)*, Elymus canadensis* L. (Canada wild-rye)*, Aster praeltus* Poir. (tall aster)*, Sporobolis asper* Michx. (tall dropseed) and *Salvia coccinea* Murr. (scarlet sage). In all the treatment plots, a total of 85 species (21 desired and 64 undesired) were identified. The ten most abundant species, their density and rank are listed in Table 2.3. There were no treatment differences in the density of individual forbs or legume species. Treatment differences in the density of individual perennial grass species are discussed in chapter III.

Removed plant density

During June 2003, the interaction of location and rate was significant for the density of *A. trifida* and *H. annuus* plants (Fig 2.2). In the control treatments, the incorporated treatment had a higher density of these plants, but the surface amendment had greater *A. trifida* and *H. annuus* density in the amended plots.

Desired species density

The grasses were the only functional group of the desired species that were affected by the amendment treatments (Table 2.4). In fall 2003 and fall 2005, the

Table 2.3. Species that were among the ten most abundant with one or more fall sample period, their overall density and rank in abundance. **Bold** indicates that the species were part of the seed mixture.

		2003		2004		2005	
Species	Common name	rank	density m^{-2}	rank	density m^{-2}	rank	density m^{-2}
Ambrosia psilostachya DC.	Western ragweed	15	0.08	10	1.09	-	0
Ambrosia trifida L.	Giant ragweed	10	0.49	3	10.95	11	0.09
Andropogon gerardi Vitman.	**Big bluestem**	**-**	**0.00**	**12**	**0.67**	**7**	**0.21**
Aristida purpurea Nutt.	**Purple three-awn**	**-**	**0.00**	**13**	**0.51**	**10**	**0.11**
Bouteloua curtpendula Michx.	**Sideoats grama**	**7**	**0.99**	**5**	**5.19**	**3**	**5.59**
Buchlöe dactyloides Nutt	**Buffalo grass**	**16**	**0.03**	**14**	**0.31**	**6**	**0.92**
Cassia fasciculata Michx.	**Partridge pea**	**12**	**0.24**	**7**	**2.92**	**9**	**0.13**
Croton monanthogynus Michx.	Prairie tea	3	1.63	9	2.13	-	0.00
Desmanthus illinoensis Michx.	**Illinois bundle flower**	**8**	**0.92**	**4**	**5.23**	**4**	**5.27**
Desmanthus leptolobus T. & G.	Prairie mimosa	1	3.69	2	14.83	2	18.35
Euphorbia maculata L.	Sidewalk doily	6	1.36	-	0.00	-	0.00
Euphorbia nutans Lag.	Eyebane	2	2.01	20	0.11	-	0.00
Helianthus maximiliani Schrad.	**Maximilian sunflower**	**11**	**0.47**	**8**	**2.41**	**12**	**0.05**
Ipomopsis rubra L.	**Standing cypress**	**9**	**0.60**	**18**	**0.19**	**-**	**0.00**
Iva annua L.	Marsh elder	4	1.59	1	34.68	1	18.43
Leptochloa dubia H.B.K.	**Green sprangle top**	**5**	**1.51**	**6**	**3.51**	**5**	**1.36**
Xanthocephalum dracunculoides DC.	Common broomweed	-	0.00	17	0.21	8	0.15

Location	*
Amount	n.s.
Location * Amount	*

* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$
n.s. not significant

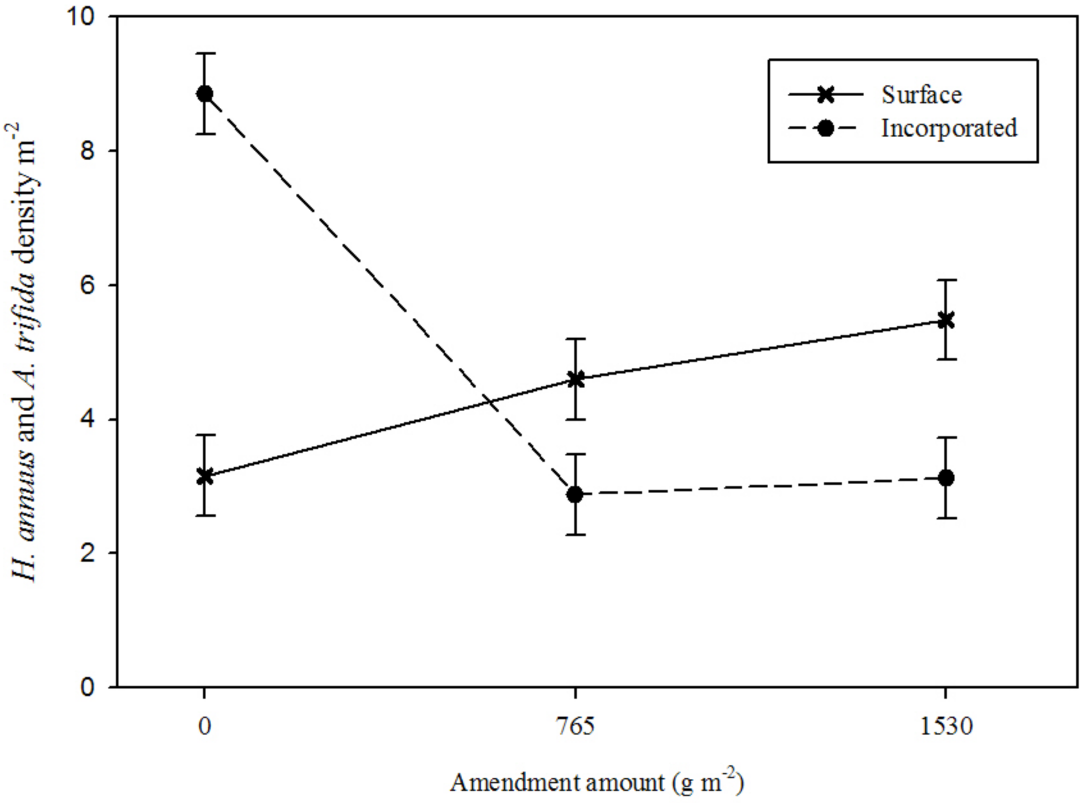


Figure 2.2. *Helianthus annuus* L. and *Ambrosia trifida* L. density m^{-2} (mean ± SE, n=25) prior to removal by clipping in June 2003.

Table 2.4. Summary of fixed effects of ANOVA procedures for desired and undesired plant density m^{-2}.

		Desired			Undesired		
		Forbs	Legumes	Grasses	Forbs	Legumes	Grasses
Fall 2003	Location	n.s.	n.s.	***	***	***	n.s.
	Amount	n.s.	n.s.	**	n.s.	*	n.s.
	Location * Amount	n.s.	n.s.	**	n.s.	**	n.s.
Spring 2004	Location	n.s.	n.s.	n.s.	***	*	***
	Amount	n.s.	n.s.	n.s.	n.s.	*	**
	Location * Amount	n.s.	n.s.	n.s.	n.s.	***	n.s.
Fall 2004	Location	n.s.	n.s.	***	n.s.	*	n.s.
	Amount	n.s.	n.s.	*	n.s.	n.s.	n.s.
	Location * Amount	n.s.	n.s.	n.s.	n.s.	**	n.s.
Spring 2005	Location	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Amount	**	n.s.	n.s.	n.s.	n.s.	n.s.
	Location * Amount	n.s.	n.s.	n.s.	n.s.	*	n.s.
Fall 2005	Location	n.s.	n.s.	***	n.s.	n.s.	n.s.
	Amount	n.s.	n.s.	*	n.s.	n.s.	n.s.
	Location * Amount	n.s.	n.s.	**	**	*	n.s.

* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$
n.s. not significant

interaction between rate and location was significant; the surface treatment was greater than the incorporated at the control and light amendment amounts, but the heavy location treatments overlapped. In fall 2004, the location and the amount, but not their interaction, were significant for the desired grasses. The surface treatments were greater than the incorporated, and the amended plots were significantly greater than the controls, but there were no differences between the amounts (Fig. 2.3).

In 2005, the spring-maturing forbs, such as *Monarda citriodora* Cerv. (lemon mint) and *Centaurea americana* Nutt. (basketflower), increased in density with application rate regardless of amendment location: heavy amendment treatment had the greatest forb density, followed by the light amendment treatment, then the control.

Undesired species density

The density of the undesired species was always equal to, or greater than, that of the desired species (Table 2.4). In the fall samples, both legumes and non-leguminous forbs responded to the restoration treatments (Fig. 2.4). The undesired non-leguminous forbs were greater in the surface plots than in the incorporated areas during fall 2003 and spring 2004. In fall 2005, the interaction between rate and location was significant for this group, with highest density in the incorporated-light treatment. The undesired legumes responded to the interaction between amendment location and amount at each time period. Undesired grasses were greater in the surface treatments than in the incorporated treatments. Amendment rate was also significant for this group, and the undesired grasses had higher densities in the control and heavy amendment plots.

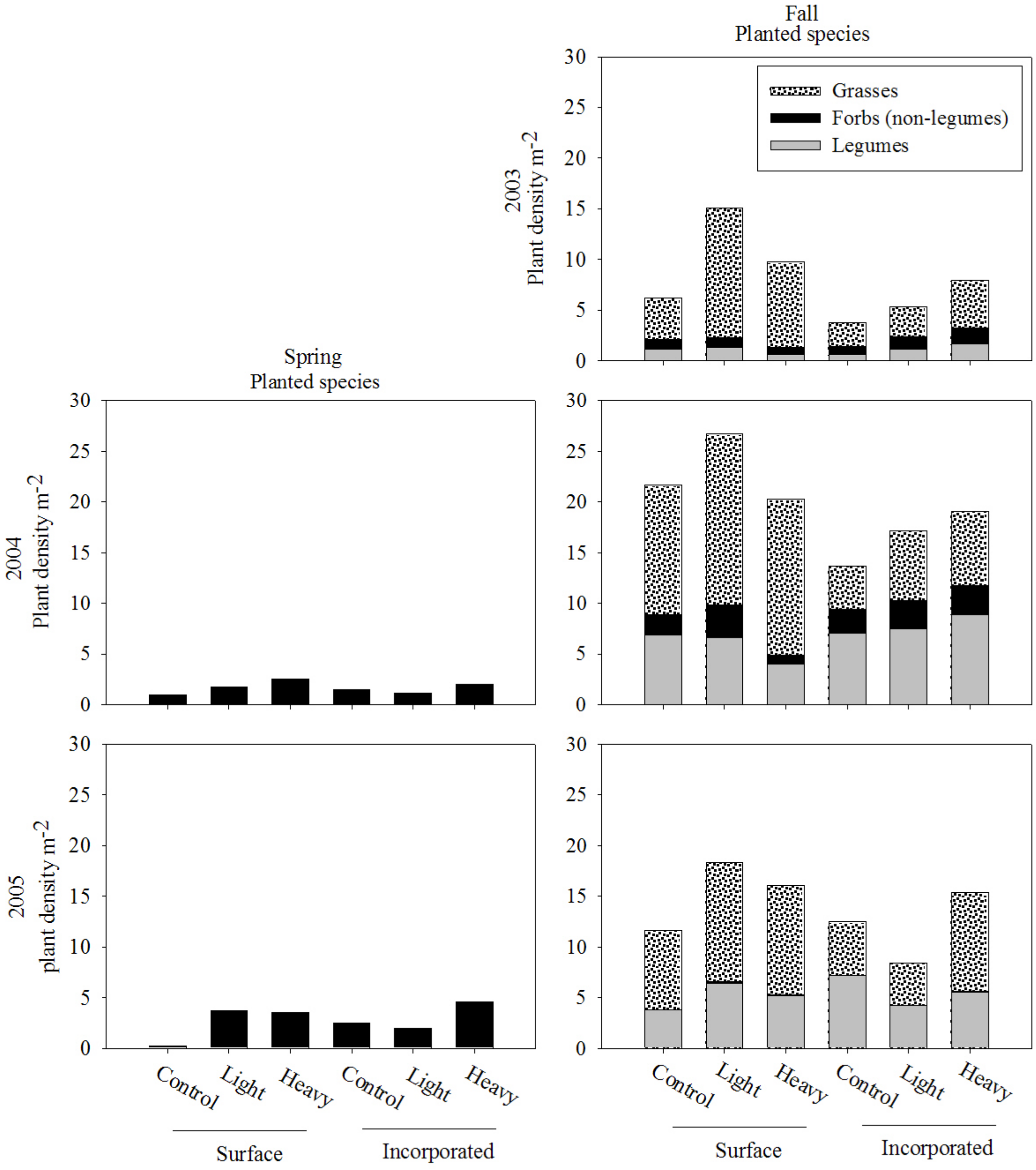


Figure 2.3. Desired species density m^{-2} by functional group in fall 2003 and spring and fall 2004 and 2005 (mean, n=50) by restoration treatment.

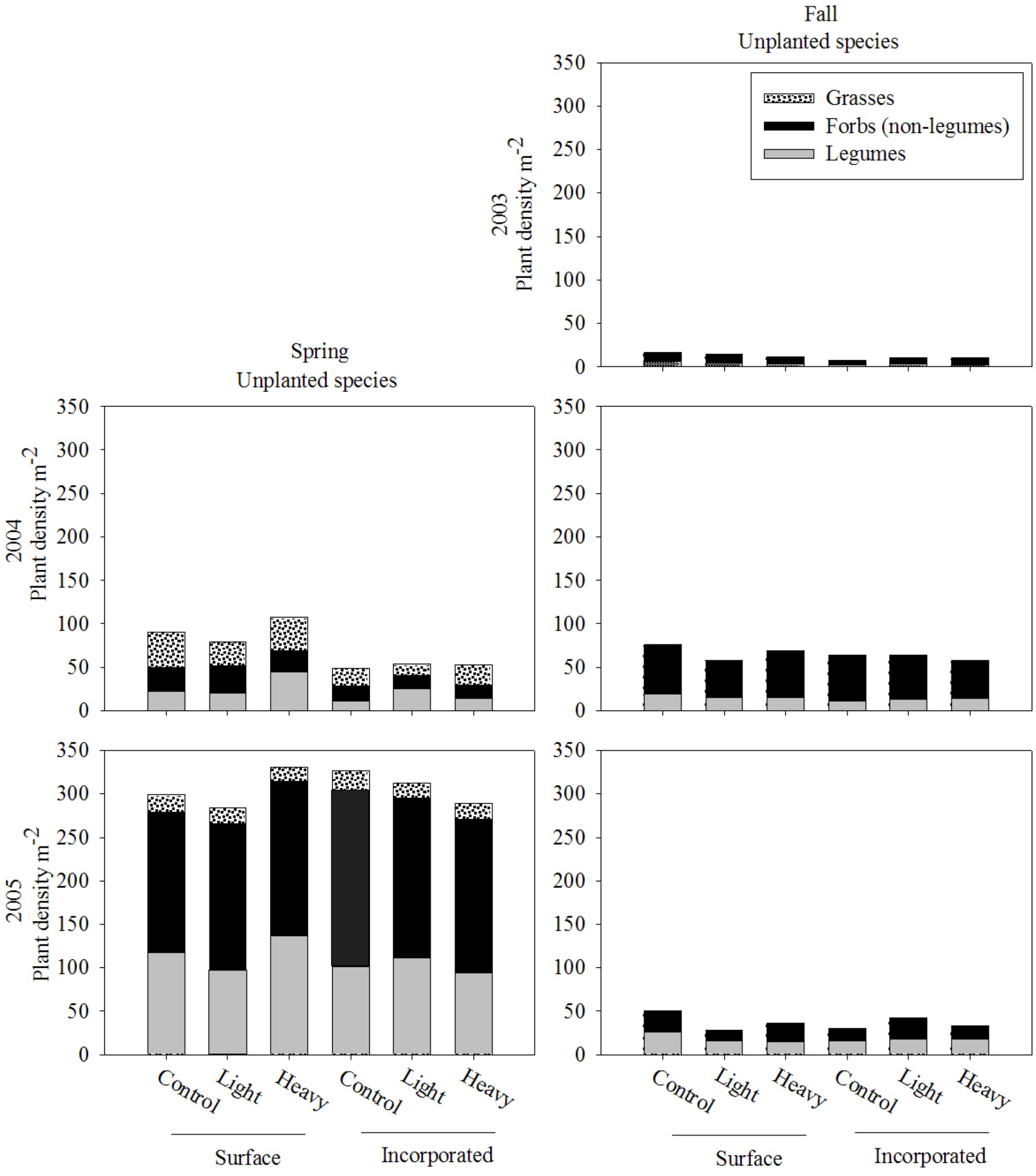


Figure 2.4. Undesired species density m^{-2} by functional group in fall 2003 and spring and fall 2004 and 2005 (mean ± SE, n=50) by restoration treatment.

Diversity

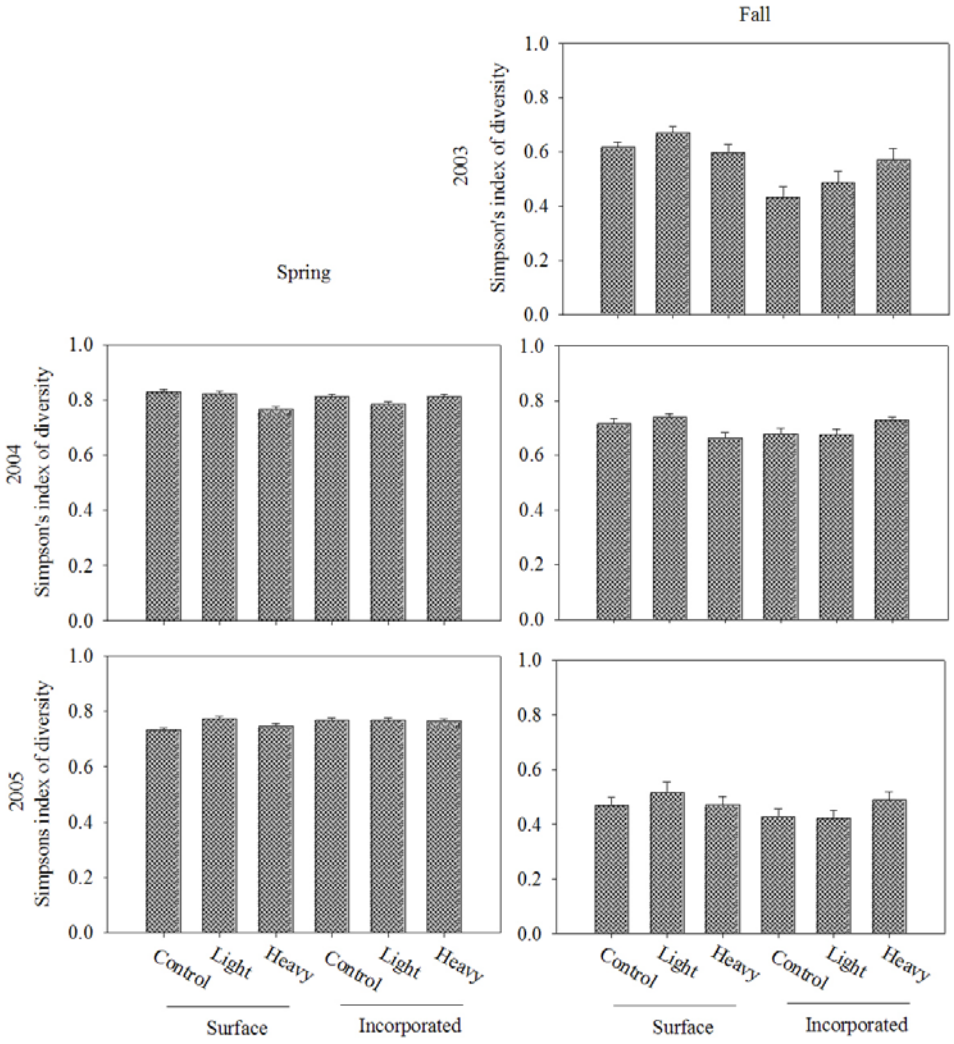
The interaction between location and amendment amount was always significant for Simpson's diversity index in the fall samples. The surface treatment had higher values than the incorporated treatments at the control and light amendment amounts. However, the surface-heavy and the incorporated-heavy treatments overlapped (Fig. 2.5). There were no treatment effects in Simpson's diversity index during the spring sampling periods.

There were significant interactions between location and amendment amount for total species richness in all sample periods in 2003 and 2004 (Table 2.5). The surface treatment was greater than the incorporated in the control and light amounts. The heavy location treatments overlapped. In spring 2005, there was a significant interaction, but there were no trends in the data. In fall 2005, only the location treatment was significant, where the surface treatments were greater than the incorporated ones (Fig. 2.6).

There were no significant treatment effects on desired species richness in fall 2003, but in 2004 the surface treatments had significantly higher desired species richness than the incorporated plots. In 2005 the interaction was significant, as the two heavy-amendment treatments overlapped in richness of desired species.

Discussion

The surface treatments were superior for the establishment of both desired and undesired species. There are several factors that may have contributed to the greater



	Fall 2003	Spring 2004	Fall 2004	Spring 2005	Fall 2005
Location	*	n.s.	n.s	n.s.	n.s.
Amount	n.s.	n.s.	**	n.s.	n.s.
Location * Amount	***	n.s.	***	n.s.	***

* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$
n.s. not significant

Figure 2.5. Seasonal values of Simpson's index of diversity (mean ±SE, n=50) in 2003, 2004 and 2005 by restoration treatment.

Table 2.5. Summary of fixed effects of ANOVA procedures for total plant species richness and desired plant species richness.

	Fall 2003		Spring 2004		Fall 2004		Spring 2005		Fall 2005	
	Total	Desired	Total	Desired	Total	Desired	Total	Desired	Total	Desired
Location	***	**	*	***	n.s.	*	n.s.	n.s.	**	**
Amount	*	n.s.	**	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Location * Amount	**	*	**	n.s.	**	n.s.	***	***	n.s.	*

* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$
n.s. not significant

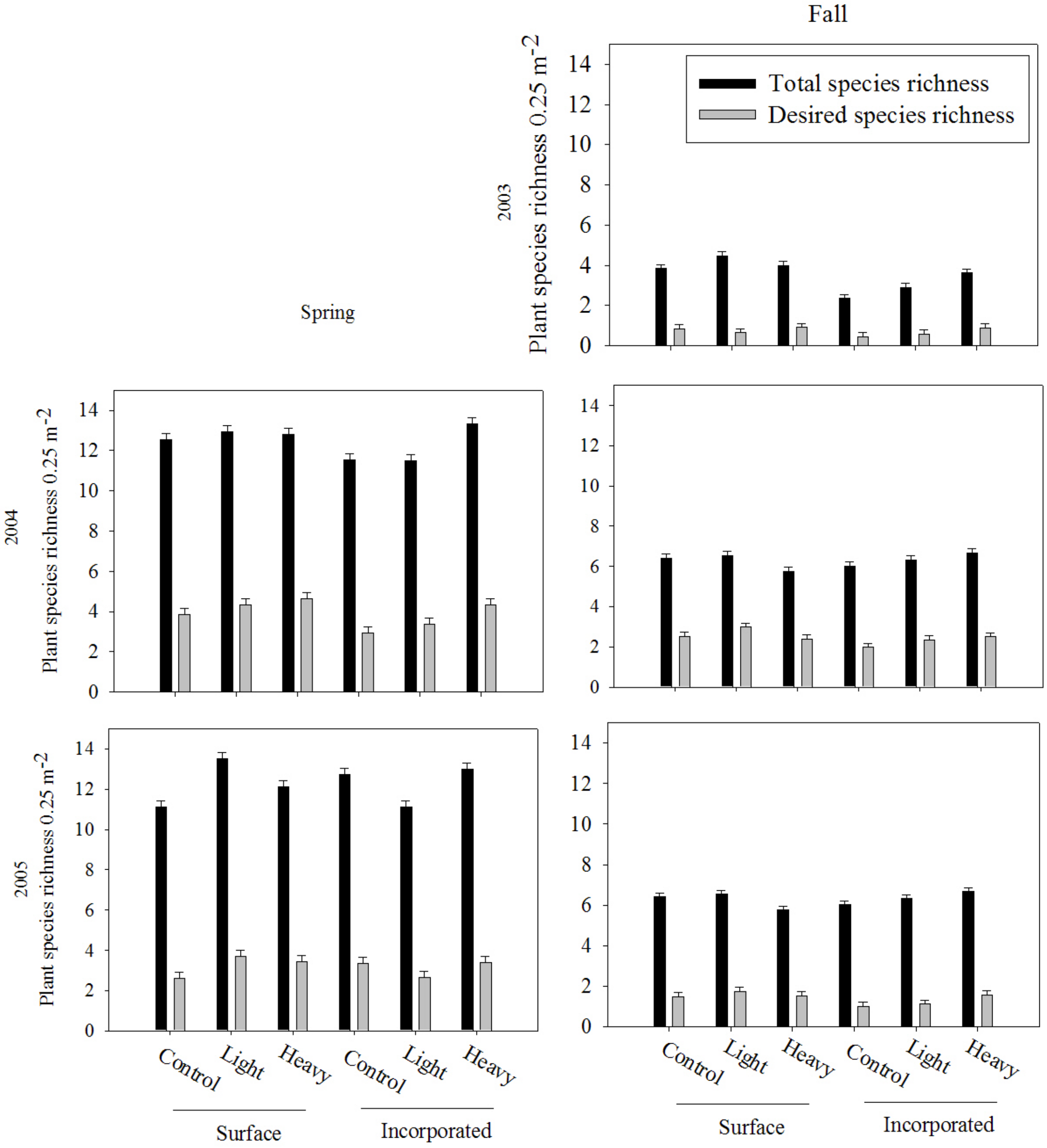


Figure 2.6. Seasonal values of total and desired species richness (mean ±SE, n=50) in 2003, 2004 and 2005 by restoration treatment.

plant density in the surface-amendment treatments, although their relative strength is not discernable from the data. First, there may have been reduced germination in the incorporation treatments as a result of deep burial of the awned seed mix during the incorporation procedure. This seed mix was dominated by the C_4 grasses component of the desired community (Table 2.2) and this oversight would have affected this group disproportionally. This mechanism, however, cannot explain treatment differences in the density of the undesired forbs and legumes. This seed would have been effectively mixed into the soil equally for all treatments during pretreatment disking.

Second, germination and early plant growth is enhanced by the surface amendment treatment. Surface amendments increase germination microsites and can enhance seedling emergence and survival (Aguilera and Lauenroth 1995, Chambers 2000, Petersen et al. 2004). Mulch application is particularly important for establishment in years with low precipitation (Noy-Meir and Briske 2002), as this site experienced in 2003. Furthermore, this mechanism can explain treatment density differences observed for both desired and undesired species. Early advantages in establishment can persist for several years (Montalvo et al. 2002, Fukami et al. 2005), as experienced for the desired C_4 grasses in this study.

Diversity

Plant species richness was generally low in all treatments. The failure to establish plant species diversity can be attributed to several causes, including low seed density (Montalvo et al. 2002) or incompatibilities between the species selected and site conditions. Sensitivity to conditions related to the landfill environment, such as gas diffusion or trace contaminants (Gilman et al. 1981, Marchiol et al. 2000) may also be a factor, but there was no evidence of plant toxicity.

The patterns of diversity are similar to those of plant density. The surface treatments generally were better for plant diversity, but at the highest rates of amendment, the location treatments overlapped. There is generally a rise in the diversity measures from 2003 to 2004 and a decline from 2004 to 2005, which corresponds to precipitation. Although drought can cause a loss of diversity through the local extinction of rare species (Tilman and Haddi 1992), it is unclear if this decline is permanent.

Individual species

There are three general categories of abundant individual plant species, which generally correspond to Grime's plant strategies (Grime 1979). First, the ruderal species were initially very dense, but dropped out over the course of the experiment (Table 2.3). These include *Ambrosia psilostachya* (western ragweed)*, Croton monanthogynus* (prairie tea)*, Euphorbia nutans* (eyebane)*,* and *Ipomopsis rubra* (standing cypress). These species may have declined because they were not as competitive as succession proceeded (Inouye et al. 1987) *H. maximiliani*, a late-successional perennial species also follows this pattern, but is responding to drought conditions in 2005.

Other abundant plant species generally fit within Grime's competitive plant strategy. The desired species *Cassia fasciculata, Desmanthus illinoensis,* and *L. dubia* and undesired species, *D. leptolobus, Iva annua*, and *Ambrosia trifida*. established large populations early and retained a relatively constant density throughout the experiment. Many of the desired grasses, *Andropogon gerardi, Aristida purpurea* (purple three-awn), and *Buchlöe dactyloides* (buffalo grass) not initially very dense, increased over the course of the experiment.

Reverse fertilization

Several studies have examined the utility of excess carbon treatments to create a nitrogen deficit through microbial immobilization, thus promoting late successional species in prairie restorations in former agricultural areas (Baer et al. 2003, Blumenthal et al. 2003, Smith et al. 2003). Although we added carbon to the soil, this phenomenon was not a factor in this study. There were no treatment differences in inorganic nitrogen levels over the first two years of the study (chapter IV), which suggests that the applied amendment was either too recalcitrant or in low enough quantities to stimulate the soil microbial community and immobilize nitrogen (Blumenthal et al. 2003, Eschen et al. 2006).

Also, the functional group responses to the amendments also suggest that immobilization of inorganic nitrogen was not significant in this study. C_4 grasses are generally not susceptible to nitrogen removal experiments (Eschen et al. 2006), but the density of this functional group was smaller in the incorporated treatments. In contrast, legumes, which are generally more competitive in soils low in available nitrogen (Ledgard and Steele 1992), had a higher density in the surface plots. Therefore, it is more likely that the higher plant density observed in the surface plots is a response to better establishment conditions. This supports the findings of Reid and Naeth (2005), who found that the amelioration of physical conditions can have a greater impact on initial plant community structure than changes in the nutrient environment.

Conclusions and implications for restoration

High plant density and diversity are often goals for restoration management, but the achievement of these goals is often limited by severe physical conditions. Organic amendments can ameliorate conditions and improve plant success or promote community diversity. In this study, I altered the location and amount of amendment and compared the ability of the treatments to establish and promote grasses through seasonal and long-term drought. I found that the amendment treatments were limited in their ability to direct these parameters. Plant density was greater in the surface amendment treatments. The burial of awned seeds during amendment incorporation was a likely contributor to the reduced density of desired C_4 grasses in these treatments, but this does not explain the observed differences in the densities of undesired forbs and legumes. Therefore, it is likely that both burial and improved conditions are responsible for treatment differences in plant density. Plant species diversity was similarly affected by the restoration treatments. These results suggest that surface treatments are superior to establishing vegetative cover. However, there is a relatively low threshold amount, where additional amendment will not result in greater plant density.

CHAPTER III

ORGANIC AMENDMENTS DIRECT GRASS POPULATION DYNAMICS IN RESTORATION

Introduction

Successful ecological restoration depends on the establishment, growth, and reproduction of plants within the target community (Gillespie and Allen 2004). The degree to which plant species successfully accomplish these life-history stages depends on the ability of the imposed treatments to ameliorate the physical stressors of the site, such as poor infiltration, high soil temperatures and low aggregate stability (Moloney 1990, Reid and Naeth 2005). This is particularly important during the initial stages of development when plant populations and communities undergo the most challenges to their establishment and survival (Montalvo et al. 2002). The resiliency of populations through these and other stressful periods, such as periodic drought, will improve the chances of restoration success.

Organic amendment application is a commonly used restoration treatment because these materials can alleviate the physical conditions that retard plant establishment and growth (Zink and Allen 1998, Petersen et al. 2004). This type of intervention can have a greater impact on plant community structure than other changes that occur with restoration, such as alteration of the nutrient environment (Reid and Naeth 2005). However, the mechanism behind the interaction of specific amendment attributes and plant population structure in restoration is unknown.

Perennial grasses are the dominant functional group in North American prairie ecosystems. Their population dynamics are driven primarily by the recruitment and mortality of tillers within individuals, rather than the generation of new individual plants from seed (Hartnett 1993, Aguilera and Lauenroth 1995). The processes of tiller recruitment and mortality are regulated by different processes. Tiller recruitment, both seasonal and inter-annual, is a plastic response to resource availability and that is regulated by both inter- and intra-specific competition (Cheplick 1997, Derner and Briske 1999). Tiller mortality, however, is driven by climate events, such as seasonal drought (Lapham and Drennan 1987, Butler and Briske 1988). Tiller survival through these events is dependent, in part, on the availability of water in the soil (Wher et al. 2005). Restoration treatments that can ameliorate site conditions and conserve moisture during dry periods will promote tiller survival (Briske and Butler 1989, Ewing 2002). Therefore, the ability of restoration treatments to promote establishment and ameliorate site conditions can be assessed by monitoring the population response of perennial grasses over time (Valverde and Pisanty 1999, Endels et al. 2005).

In this study, two qualities of organic amendments were manipulated: the location within the soil profile and the amount of amendment applied. The location of an organic amendment within the soil profile dictates its ability to influence the physical qualities of the soil (Gill and Jalota 1996, Sanchez et al. 2000, Wher et al. 2005). Surface amendments moderate soil temperature and lessen moisture loss by reducing incident radiation on the soil surface (Tian et al. 1993, Price et al. 1998). This provides greater protection for plant seedlings and will enhance their emergence and survival

(Winkel et al. 1991, Chambers 2000). Infiltration is also improved under surface mulches (Agassi et al. 1998). Plants respond to surface mulches by increasing root abundance and lateral growth at the surface, directly under the material (Chaudhary and Prihar 1974, Cotrufo 2006).

In contrast, the incorporation of amendments can improve physical conditions by disrupting capillary flow of soil water and slowing evaporation (Gill and Jalota 1996). Incorporated organic materials also reduce the shrink-swell capacity of clay soils and maintain soil moisture availability during periods of little rainfall through the maintenance of soil surface integrity (Weindorf et al. 2006). This creates and maintains macroporosity, which improves plant rooting depth and elongation (Gorenevelt and Grunthal 1998, Liang et al. 1999). Further, the incorporated material will itself retain moisture longer than those on the surface, and can therefore serve as a moisture reservoir during periods of low precipitation (Beare et al. 1992).

The demography of the target plant species may be affected by amendment placement because differential plant morphology and access to soil resources will improve survival or accelerate growth. To understand the consequences of these treatment differences for restoration, the following hypotheses were addressed: (1) initial total basal area, tiller density and plant density will be greater in the surface treatments compared to incorporated treatments. (2) these responses will increase linearly with amendment application rate for both treatments. (3) incorporated amendments will enhance tiller and plant survival through seasonal drought compared to surface treatments. Treatment differences in soil temperature were compared to estimate physical conditions among treatments. Maximum plant water stress, as measured by mid-day plant water potential, was also used as an integrated measure of water availability. This was done in a landfill remediation environment where there are many physical challenges, such as soil compaction and reduced infiltration, which limit plant establishment and survival.

Methods

Study area

This study was conducted on a 21-hectare portion of the Castle Drive Landfill in Garland, Dallas County, Texas (32° 93′ N, 96° 58′ W; elevation 165 m). In accordance with regulations by the Texas Commission on Environmental Quality, the landfill has a constructed clay cap 45 cm thick, which is designed to be impermeable to water seepage into the municipal garbage below. Overlaying this cap is a 26 to 35 cm composite of unconsolidated subsoil from an adjacent area that comprised the growing medium for the vegetation cover. Soil properties prior to treatment are listed in Table 2.1.

This area is in the Texas Blackland Prairie Ecoregion, which is dominated by tall- and mid-sized grasses with associated forbs (Diggs et al. 1999). The mean monthly low temperature (1 °C) occurs in January and the mean monthly high temperature (35.5 °C) is in July. The 30-year precipitation average is 999 mm and has a bimodal distribution, with the largest amounts of rain falling in May (134 mm) and October (116 mm). Annual precipitation was below average in 2003 (510 mm) and 2005 (474 mm).

Although the total amount of precipitation was average during 2004, much of the rainfall fell in June and July (Fig. 2.1).

Restoration treatments

This experiment had six treatments in a 2 x 3 factorial completely randomized design. There were two amendment location treatments: surface applied and incorporated to 6 cm with a roto-tiller. There were three treatments that differed in the amount of material added: no amendment, a light amendment (765 g m^{-2}) and heavy amendment (1530 g m^{-2}). Each treatment occurred once in each of five replicate blocks, which occur along a 5% northeast slope. Alleyways (2 m wide) separated the 25 m^2 plots. The experimental area was disked three times to remove any previous vegetation before planting on March 12, 2003.

The amendment material used was untreated urban wood waste from the City of Garland Castle Drive Wood Recycling Facility. This material had a composition of 43.5% carbon, 0.45 % nitrogen and a C:N ratio of 98:1. Amendment particle size distribution was 26 % of mass less than 1-cm^2, 17 % greater than 1-cm^2, but less than 5-cm^2 and 56% larger than 5 cm^2. The large, recalcitrant amendment material was chosen to address the issues associated with soil physical structure, such as compaction, but not create a dramatic pulse of nitrogen availability or immobilization (Whitford et al. 1989, Reid and Naeth 2005).

Seeds of native and naturalized grasses, legume and forb species typical of this region were acquired from two commercial vendors: Turner Seed Company and Native

American Seed (Table 2.2). For the surface application treatments, the large and awned seeds were hand-spread followed by the use of a culti-packer (Brillion Farm Equipment, Brillion, Wisconsin) to firm the seedbed. The amendment was hand-spread over the seed bed at the three treatment amounts. In the incorporated treatments, the large and awned seeds were hand-sewn, followed by the application of the amendment. The material was then incorporated to 6 cm with a rototiller and the seedbed firmed with the culti-packer. In both location treatments, the final step was the hand-sewing of the small seeded species. The total pure live seed applied for all species was 2.1 g m^{-2}.

Aboveground stems of the large-leaved and abundant *Ambrosia trifida* L. (giant ragweed) and *Helianthus annuus* L. (annual sunflower) individuals were hand-clipped and removed from plots in June 2003 to minimize soil water loss during initial plant establishment. *Sorghum halepensis* (johnson grass), an aggressive invasive grass, was periodically treated throughout the experiment by individual wipe treatments of a solution of one-third glyphosphate (N-phosphonomethyl glycine) and two-thirds water. All other unsown species were untreated during the experiment.

Grass data collection

In May 2004, five 0.5-m^2 permanent subplots were established within each treatment plot. Within each subplot, tiller number, plant density and basal area were measured for the established and desired grass species: *A* (big bluestem), *Aristida purpurea* Nutt. (purple three-awn), *B. curtipendula*, *Buchlöe dactyloides* (buffalo grass), *S. scoparium*, *S. avenaceum* and *Leptochloa dubia* H.B.K.(green sprangletop).

Bothriochloa ischaemum var. *songarica* Fisch. & Mey.(King ranch bluestem), an undesired invasive grass species, was also monitored. Grass measurement corresponded with maximum spring growth (May), the height of the summer dry period (August) and the expected resumption of cooler, wetter weather (late September/early October) in the second and third years of the restoration. Tillers and plants were counted only if they were alive; brown and brittle tillers were considered dead and not enumerated.

Soil temperature

Hobo H8 dataloggers (Onset Computer Corporation, Pocasset, Massachusetts) recorded ambient surface and shallow soil (7 cm) temperature in the surface treatments and in the incorporated-heavy treatment April 1, 2004 to September 30, 2004. The influence of the amendment treatments to buffer extreme heat (greater than 20º C) was estimated using the difference between the surface and buried temperature for a single daily temperature between 1:30 p.m. and 3:30 p.m. *Solenopsis invicta* (fire ant) damage resulted in loss of two monitors in incorporated-heavy treatment plots and one monitor in the surface-control treatment.

Mid-day plant water potential

Mid-day plant water potential was measured three times during the summer of 2004 with a pressure chamber (Soil Moisture Corp. Santa Barbara, CA). Two individual plants for each of three species, *B. curtipendula*, *Helianthus maximiliani* Schrad. (Maximilian sunflower), and *Desmanthus illinoensis* Michx. (Illinois bundle flower), were selected randomly from each plot. Water potential was determined using an individual non-flowering culm (*B. curtipendula*) or individual leaves (*H. maximiliani*, and *D. illinoensis*) from the selected plants.

Measurements were timed with rainfall events to capture maximum water stress. Sampling occurred on July 12, which was six days after a 5 mm rain event, July 26, which was 20 days after a 5 mm rain event and on August 22, which was 17 days after a 6 mm rain event. *D. illinoensis* was not measured during the final sampling because it had senesced.

Statistical analysis

All plant population data were transformed (square-root plus constant) to conform to the assumptions of normalcy and equality of variance. Back-transformed data are presented. Three sub-plots with large areas of *B. dactyloides* were excluded from analysis. In addition to community parameters, plant density of the two most abundant grasses, *B. curtipendula* and *L. dubia*, were also analyzed.

Data from each growing season were analyzed separately using repeated-measures analysis within the linear mixed models procedure (Piepho et al. 2003). I used Akaike's Information Criterion (AIC) to determine the optimal covariance structure, which was AR1 (Uzoh and Oliver 2006). The model included three fixed terms: amendment amount, location and time, as well as their interactions, and one random term: block (Piepho et al. 2003). The block effect of slope position was significant in most analyses and was, therefore, always included as a categorical random factor.

Bonferroni post-hoc tests were used to determine differences within response variables. Data were analyzed using SPSS 13.0.1 (SPSS Inc. Chicago, Illinois, USA). Significance was declared at the 0.05 level.

Soil temperature differences were analyzed with an ANOVA procedure with amendment amount and location and their interaction as fixed effects, the block of slope position as a random term, and ambient surface temperature as a covariate.

Results

In 2004, there was a significant interaction between amendment location and the amount applied for both tiller density (tillers m^{-2}) and total basal area (cm^2 m^{-2}). Table 3.1 provides a summary from the longitudinal analysis of the grass functional group for 2004 and 2005. These responses were larger in the surface-control and surface-light treatments compared to the incorporated-control and incorporated-light treatments (Fig 3.1). At the heaviest amendment amounts, however, the locations were similar.

Plant density in 2004 was greater in the surface treatments and there was an amendment effect (Fig. 3.1). The control plots had fewer plants than either of the plots with amendment, but there was no difference between the light- and heavy-amended plots for plant density. Average plant size (cm^2) was larger in the incorporated treatments.

Table 3.1. Summary of fixed effects of the linear mixed model procedures for grass population characteristics for three sample periods in 2004 and 2005.

	Tiller density (tillers m^{-2})	**Total basal area** (cm^{2} m^{-2})	**Plant density** (plants m^{-2})	**Average plant size** (cm^{2})
2004				
Location	***	**	***	***
Amount	**	n.s	***	n.s.
Time	***	*	***	***
Location * Amount	**	*	n.s.	n.s.
Location * Time	**	*	n.s.	n.s.
Amount * Time	n.s.	n.s.	n.s.	**
Location * Amount * Time	n.s.	n.s.	n.s.	n.s.
2005				
Location	***	*	***	*
Amount	***	**	***	n.s.
Time	***	***	***	***
Location * Amount	**	**	n.s.	n.s.
Location * Time	***	n.s.	n.s.	*
Amount * Time	n.s.	n.s.	n.s.	n.s.
Location * Amount * Time	**	n.s.	*	*

* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$
n.s. not significant

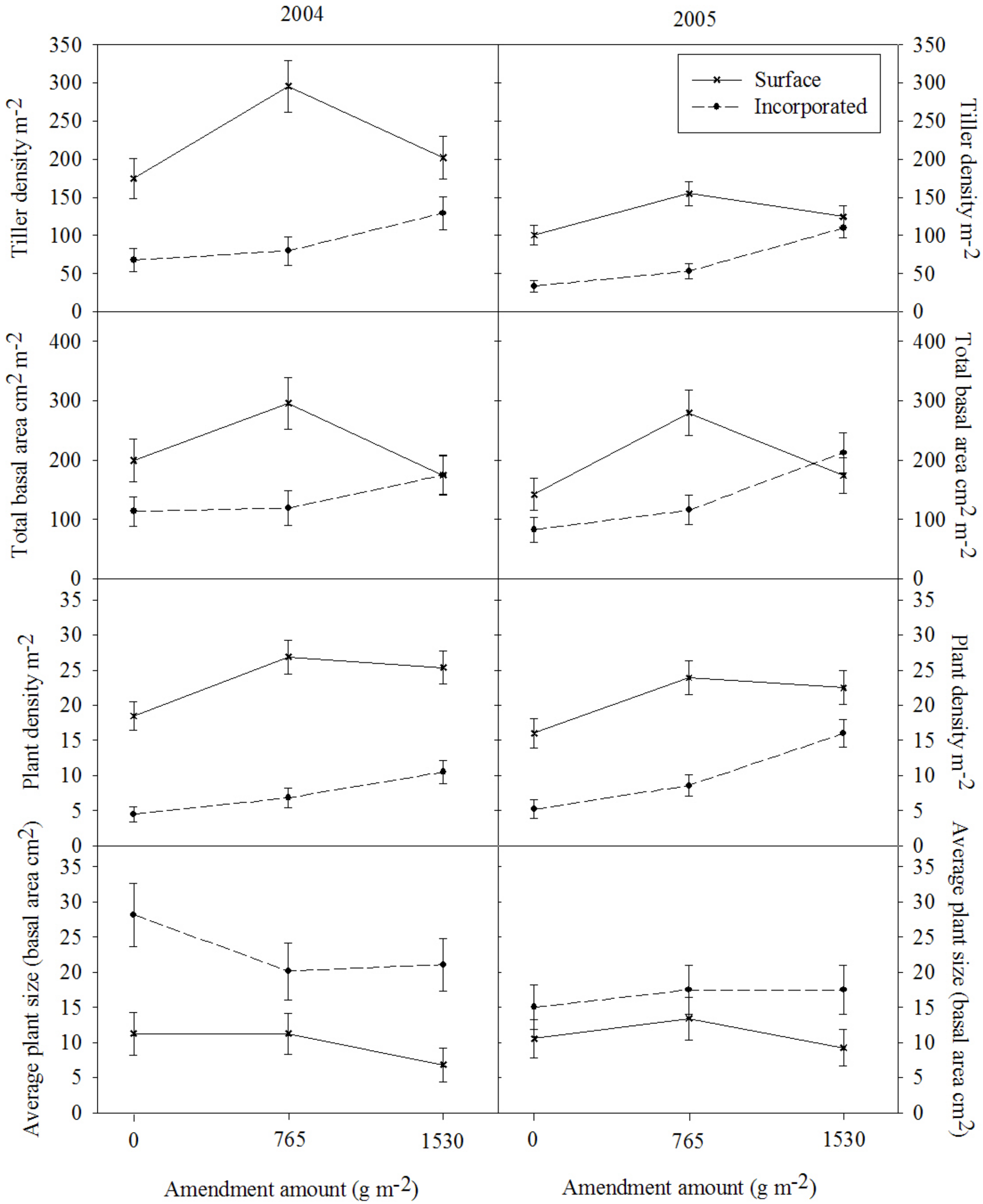


Figure 3.1. Tiller density m^{-2}, total basal area cm^2 m^{-2}, plant density m^{-2} and average plant size (Basal area cm per plant) of all perennial grasses in the amendment treatments for the 2004 and 2005 growing seasons.

Time was also a significant factor for the grass population parameters in 2004. There was an interaction between time and location for tiller density and total basal area (Fig. 3.2). In this case there were smaller decreases from June to August in the incorporated plots than in the surface plots, although tiller density was highest in the surface plots in October.

Until August 2005, the surface-light treatment had the highest tiller and plant density (Fig 3.2). However, in August and September 2005 this treatment converged with the surface-heavy and incorporated-heavy treatments, which resulted in a significant three-way interaction among rate, time and location for these variables. Average plant size (basal area per plant) also has a significant three-way interaction in 2005. In this case, there was no difference in the average size of the plants between the surface and the incorporated plots for August and September of 2005.

Total basal area had a significant interaction between amendment amount and location, which also resulted in the overlap of the incorporated-heavy treatment with the surface-light treatment. The main effect of time was also significant, and total basal area declined from June to August and stabilized in September.

B. curtipendula was the most abundant grass species comprising 37 ± 3% of the total plant density, 54 ± 3% of the tiller density and 52 ± 3% of the total basal area in May 2004. Because it was the dominant species, the dynamics of the entire grass community was dictated by *B. curtipendula.*

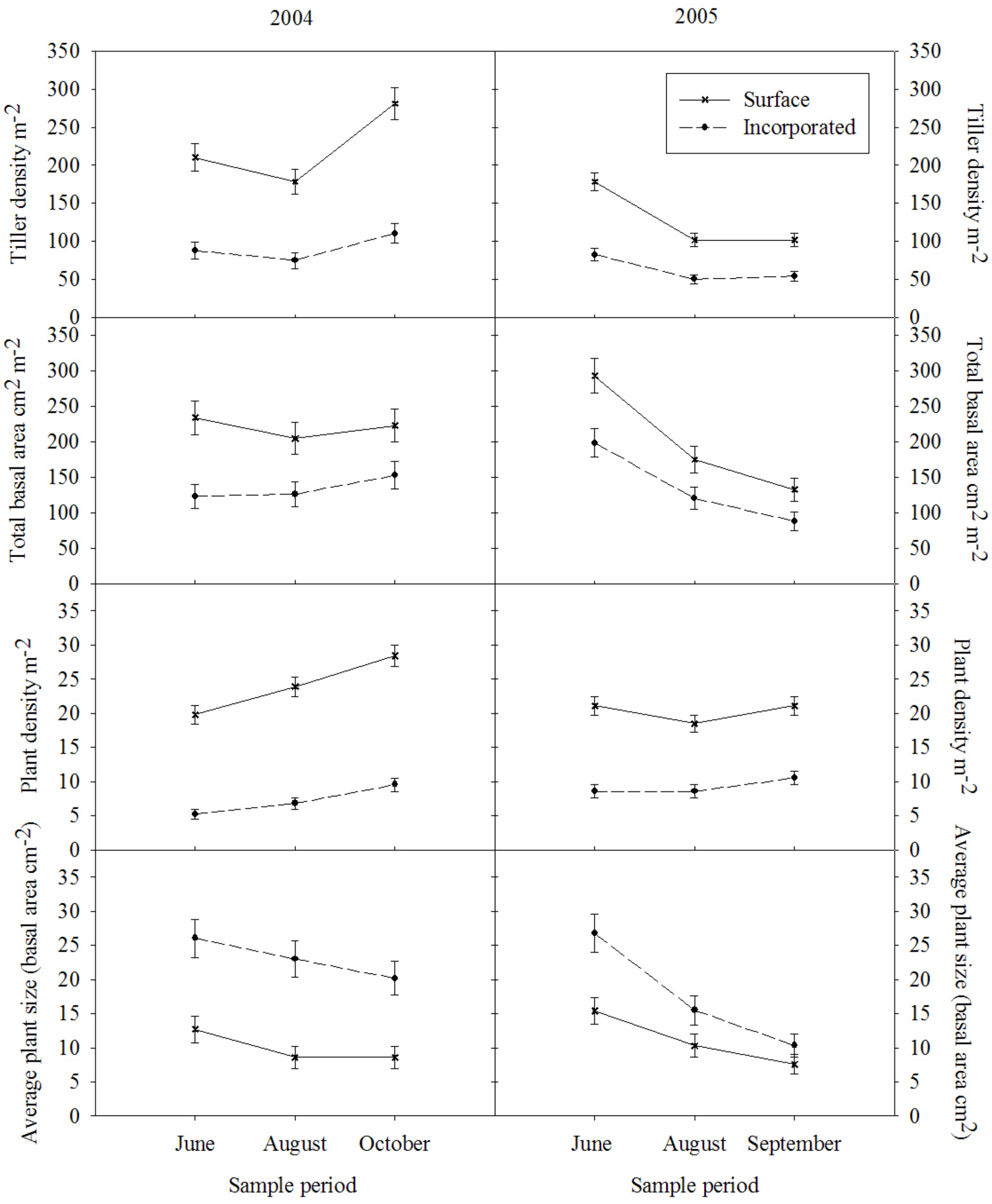


Figure 3.2. Changes in tiller density m^{-2}, total basal area cm^{2} m^{-2}, plant density m^{-2} and average plant size (Basal area cm per plant) of perennial grasses in the amendment location treatments over time in 2004 and 2005.

L. dubia was less abundant than *B. curtipendula*, but was the most abundant plant from the small seed mix. In May 2004 it was 40 ± 3% of the total plant density, 36 ± 3% of the tiller density and 34 ± 3% of the total basal area. In 2004, its plant density was significantly higher in surface treatments, but it did not change over time (Table 3.2 and Fig. 3.3).

Soil temperature

There was a greater difference between surface and soil temperature in the incorporated-heavy treatment (9.5 ± 0.1 ºC) than the surface-heavy treatment (8.4 ± 0.1 ºC). In an analysis of only surface-amended plots, the amount of amendment was significant: the control had the least difference between the surface and soil temperatures (5.9 ± 0.10 ºC), followed by the light amendment (6.6 ± 0.10 ºC) and the heavy amendment (8.3 ± 0.09 ºC).

Mid-day plant water potential

There were no treatment differences in mid-day water potential for *Helianthus maximiliani* at any of the sampling periods. The water potential for *H. maximiliani* was -0.87 ± 0.1 MPa on July 12, -1.13 ± 0.1 MPa on July 26, and -2.05 ± 0.3 MPa on August 22, 2004. There were also no treatment differences in mid-day water potential for *D.illinoensis* on July 12 (-1.19 ± 0.2 MPa) and for *B.curtipendula* on July 12 (-1.95 ± 0.1 MPa) and August 22 (-3.6 ± 0.1 MPa).

Table 3.2. Summary of fixed effects of the linear mixed model procedures for plant density in 2004 population characteristics for *Bouteloua curtipendula* and *Leptochloa dubia* for three sample periods in 2004 and 2005.

	Bouteloua curtipendula	***Leptochloa dubia***
	2004 plant density m^{-2}	**2004 plant density m^{-2}**
Location	***	***
Amount	***	n.s.
Time	***	n.s.
Location * Amount	*	n.s.
Location * Time	n.s.	n.s.
Amount * Time	n.s.	n.s.
Location * Amount * Time	n.s.	n.s.

* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$
n.s. not significant

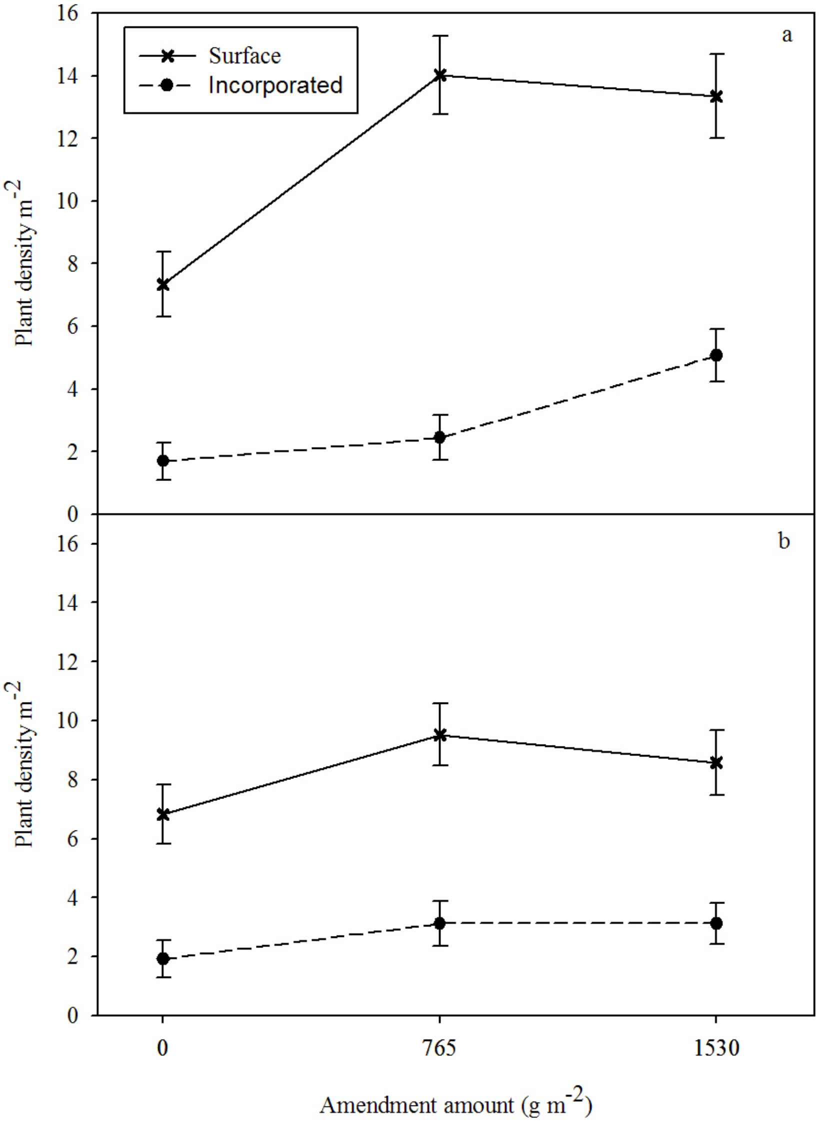


Figure 3.3. Plant density m^{-2} for *Bouteloua curtipendula* (a) and *Leptochloa dubia* (b) (mean ±SE) in the amendment treatments for the 2004 and 2005 growing seasons.

There were significant treatment differences in mid-day water potential for *Desmanthus illinoensis* and *B. curtipendula* on July 26, which was 20 days after a 5 mm rainfall. At this time, *D. illinoensis* responded to the rate of amendment application (Fig. 3.4a); its water potential was significantly greater in the heavy amendment treatment. However, there was no difference between the light amendment and the control. In contrast, water potential for *B. curtipendula* was greater in the control plots and lowest in the heavy amendment treatment (Fig. 3.4b). Amendment location was also significant for the *B. curtipendula* water potential. It was higher in the incorporated than the surface treatments.

Discussion

Effective ecological restoration management uses minimal inputs to improve growing conditions for the target plant community (Endels et al. 2005). The use of organic amendments is often used in restoration because it improves physical conditions of the site, including increased infiltration, reduced soil temperatures and greater aggregate stability (Moloney 1990). I monitored the population dynamics of the target functional group, perennial grasses, to determine the effectiveness of different amendment treatments over time. This will offer insight into the mechanisms behind the imposed restoration treatments and provide practitioners with the ability to tailor management strategies to specific site conditions and improve the chances for restoration success.

Recruitment

There were significant differences in grass plant density between the location controls, which received no amendment. This suggests that other factors, besides the amendment itself, were affecting the planted grasses. Indeed, the planting procedures may have resulted in reduced establishment in the incorporated treatments. The awned seed mix, which contained most of the grass species, was applied prior to amendment application and incorporation. This may have buried the seeds too deep within the soil profile and reduced establishment.

Although there were flaws in treatment implementation, there is some evidence that the surface treatments do improve conditions for grass establishment. *L. dubia,* which was part of the small seed mix sewn after incorporation, had greater plant density in the surface treatments in 2004. Therefore, it is likely that both mechanisms contributed to increased plant establishment in the surface treatments.

The interaction between amendment amount and location was significant for tiller density and total basal area in 2004. In these variables, the surface treatments were greater for the control and light amendment amounts, but the location treatments were similar at the highest amendment amount (Fig. 3.1). The response pattern of tiller density and total basal area within each location to amendment amount suggests that there may be threshold effects for amendment amount. In the surface treatment, amendment amounts greater than 765 g m^{-2} reduced the establishment of grasses. Excess amendments can reduce colonization space (Teasdale and Mohler 2000) or interfere with certain species' establishment through incompatibilities with seed structure (Facelli and Pickett 1991). In contrast, there is a linear increase with amendment amount in the incorporation treatment, which suggests that a threshold for grass basal area and tiller density has not been reached.

Soil temperature differences also suggest that the amount of amendment is important for ameliorating physical conditions. Within the surface treatments, the amount of amendment applied improves the insulation of the soil from extreme mid-day temperatures.

These initial patterns of tiller and plant density and total basal area are evident throughout the experiment, which is supported by Montalvo et al. (2002), who found that patterns of initial seedling establishment can last for several years.

Seasonal drought

There were dramatically different precipitation patterns in the two years of this study (Fig. 2.1). In 2004, there was an excess of growing season precipitation, particularly in June and July, with only a moderate seasonal drought in August. In 2005, there was a long-term regional drought. Seasonal grass population dynamics responded to these climatic events.

There was a significant interaction between location and time for tiller density and total basal area in 2004 (Fig 3.2). The decline in both of these parameters from June to August was smaller in the incorporated treatments than in the surface treatment. The increase in these parameters from August to September, however, was greater in the surface treatment. Plant density increased through continued recruitment throughout 2004. Average plant size decreased over this interval; and there were more, but smaller, plants at the end of the 2004 season.

In contrast, there was a continual decline through the 2005 growing season for total basal area and average plant size. Tiller populations declined from June to August, but stabilized after a few small rain events in September. The apparent increase in plant density in September 2005 is a result of assuming senescent individuals had died in August, but new tillers emerged from these individuals following the small rain events in early September.

In 2005, the tiller density and total basal area were similar in the incorporated-heavy, the surface-light and surface-heavy treatments. Despite its initial disadvantage in establishment, the incorporated-heavy treatment was able to obtain parity with the most successful treatment early in the restoration, the surface-light treatment.

Soil temperature differences indicate that the incorporated amendments were better at insulating the soil from extreme temperatures. This is contrary to the findings of Blumer (2000), who found that wood mulch applied on the surface was better at moderating soil temperature than incorporated wood mulch. However, other studies suggest that incorporated materials are superior for preserving soil moisture, which can protect the soil from temperature extremes. Incorporating materials disrupts upward capillary flow, which reduces its evaporation (Gill and Jalota 1996). The material itself retains moisture longer than those on the surface (Beare et al. 1992, Tian et al. 1993).

Finally, surface material may intercept precipitation during small events and prevent it from reaching the soil (Facelli and Pickett 1991).

There are several other possible mechanisms for improved tiller survival during drought in the incorporated treatments. These treatments had lower plant density, which may have reduced competition for resources. However, long-term grass population studies by Fowler (1995) suggest that density dependence is weaker than climatic factors in driving perennial grass populations. Furthermore, individual plants are larger in the incorporated treatments, which may have increased the accumulation of organic matter that can buffer drought conditions (Tongway and Ludwig 1997, Derner and Briske 1999). However, Shackleford (2005) did not find a relationship between basal area and drought resistance in short grass prairies.

Mid-day plant water potential

Treatment differences in mid-day plant water potential were only significant for the driest sampling period, suggesting that the amendment treatments do not influence plant water status until the soil is very dry. At this driest sampling period, the treatment differences in mid-day water potential for *D.illinoensis* and *B. curtipendula* were inconclusive, suggesting that other factors, such as intraspecific competition, may be affecting plant water status.

Conclusions and implications for restoration

Restoration treatments attempt to improve conditions for plant establishment and growth. Organic amendments are a commonly used in restoration, but the specific attributes that contribute to successful plant population dynamics in these circumstances are unknown. In this study, I altered the location and amount of amendment and compared the ability of the treatments to establish and promote grasses through seasonal and long-term drought. I found that surface application improved establishment, although the burial of seeds during amendment incorporation contributed to this treatment effect. This treatment also exceeded a threshold; amendment amounts greater than 765 g m^{-2} limited establishment. In contrast, grass establishment was lower in the incorporated treatments, but a threshold amendment amount was not reached. Furthermore, the incorporated-heavy treatment did improve survival through seasonal and long-term drought. The incorporated amendments also moderate soil temperature better than surface amendments.

This suggests that restoration managers need discretion when applying organic amendments. If the site requires rapid establishment of vegetative cover and its corresponding functions, then surface amendments are superior. However, there is a relatively low amount threshold. In contrast, incorporated amendments are superior at supporting established plant populations through stressful conditions and improve resilience. This treatment may be particularly useful when conditions for establishment are controlled, but long-term support is minimal. Furthermore, application rates may be greater in this treatment, although the threshold amount was not achieved.

CHAPTER IV

DIRECT AND INDIRECT EFFECTS OF AMENDMENT PLACEMENT ON SOIL CARBON AND NITROGEN DYNAMICS IN RESTORATION

Introduction

Soils in constructed sites are subject to removal, stockpiling and compaction. These activities damage soil structure through disruption of aggregates and the reduction of carbon stores through mineralization (Bloomfield et al. 1982, Harris et al. 1989). The biological components of the soil are also altered during these activities; soil microbial biomass is reduced, community composition is altered and there is a reduced capacity for nutrient cycling (Harris et al. 1993, Dmowska 2005, Ingram et al. 2005). Because the soil biota regulates ecosystem processes (Bardgett et al. 1999) and is a dynamic actor in plant succession (De Deyn et al. 2003, Reynolds et al. 2003, Partsch et al. 2006), strategies are needed to promote soil biota recovery and development following disturbance. This will facilitate plant growth and contribute to long-term recovery in these degraded sites (Zink and Allen 1998).

Some restoration treatments can have multiple long-term effects on the size, composition and activity of the soil biota (Boyle et al. 2005). One of the most effective treatments for manipulating soil biological activity is to alter the quantity and quality of organic residues in the soil, either by adding material or through changing the composition and biomass of cover plant species (Wardle et al. 1999b, Nahar et al. 2006). This is particularly important in severely disturbed areas, where organic inputs can be used to promote the development of soil microbial community and fauna, whose populations are limited by the lack of soil structure and organic energy resources (Whitford et al. 1989, Zink and Allen 1998).

The placement of amendments in the soil profile (incorporated or surface-applied) may be a particularly useful tool in restoration because it can affect the size, structure and activity of the soil biota in agricultural systems (Holland and Coleman 1987, Beare et al. 1992, Fu et al. 2000). However, it is unclear which placement may be more beneficial. Incorporating amendment material into the soil reduces soil bulk density and increases aeration which can improve root density and elongation (Gorenevelt and Grunthal 1998, Liang et al. 1999). Incorporation also increases the accessibility of amendment material to the soil organisms and, therefore, supports larger populations (Elliott et al. 1980, Killham et al. 1993). Soil food web structure is also affected by incorporating amendment because it promotes organisms that respond rapidly to enrichment, such as bacteria and bacteriophagous fauna (Beare et al. 1992, Fu et al. 2000). Soil food webs dominated by bacteria-channel decomposition increase the availability of nutrients and their rates of cycling (De Ruiter et al. 1993, Wardle et al. 2004).

Alternatively, surface-applied amendments may support restoration goals by promoting slower nutrient cycles that retain nutrients in the soil (Zink and Allen 1998). Surface-application of amendment materials, such as residue retention in no-till systems, typically supports smaller microbial populations and is slower to be utilized by soil organisms (Beare et al. 1992, Tian et al. 1993). The physical separation of amendment and soil biota alters soil food web structure by promoting fungal-channel decomposition because these organisms utilize hyphae to access carbon in the surface amendment, and to acquire nutrients in form the soil (Holland and Coleman 1987, Frey et al. 1999). Fungal-channel decomposition is also more efficient at nutrient cycling compared to bacteria-channel decomposition and, therefore, can enhance nutrient retention over time (Bardgett et al. 2002, Smith et al. 2003). Surface amendments can promote plant emergence and survival, however plant carbon inputs may overwhelm the amendment effects (Winkel et al. 1991, Chambers 2000).

Given that both amendment locations may positively impact the soil environment and contribute to ecosystem development, it is imperative that they be directly compared in a restoration setting over time. To do this, I measured both above- and belowground responses to the amendment treatments. Peak aboveground biomass, nutrient pool sizes (soil organic carbon and total nitrogen, soil microbial biomass, and inorganic N) and nutrient cycling rates (C-mineralization, potential nitrogen transformation rates) were quantified. I also compared the nutrient storage and dynamics of the landfill site with a nearby native prairie and an older restoration reference. By comparing these response variables across a series of restoration settings, I sought to uncover the mechanisms behind the amendment treatment effects to determine which would provide the most benefit in restoration.

Methods

Study area

This study was conducted on a 21-hectare portion of the Castle Drive Landfill in Garland, Dallas County, Texas (32° 93′ N, 96° 58′ W; elevation 165 m). In accordance with regulations by the Texas Commission on Environmental Quality, the landfill has a constructed clay cap 45 cm thick, which is designed to be impermeable to water seepage into the municipal garbage below. Overlaying this cap is a 26 to 35 cm composite of unconsolidated subsoil from an adjacent area and is a growing medium for the vegetation cover. Soil properties prior to treatment are listed in Table 2.1.

This area is in the Texas Blackland Prairie Ecoregion, which is dominated by tall- and mid-sized grasses with associated forbs (Diggs et al. 1999). The mean monthly low temperature (1 °C) occurs in January and the mean monthly high temperature (35.5 °C) is in July. The 30-year precipitation average is 999 mm and has a bimodal distribution, with the largest amounts of rain falling in May (134 mm) and October (116 mm). Annual precipitation was below average in 2003 (510 mm) and 2005 (474 mm). Although the total amount of precipitation was average during 2004, much of the rainfall fell in June and July (Fig. 2.1).

Restoration treatments

This experiment had six treatments in a 2 x 3 factorial completely randomized design. There were two amendment location treatments: surface applied and incorporated to 6 cm with a roto-tiller. There were three treatments that differed in the amount of material added: no amendment, a light amendment (765 g m^{-2}) and heavy amendment (1530 g m^{-2}). Each treatment occurred once in each of five replicate blocks, which occur along a 5% northeast slope. Alleyways (2 m wide) separated the 25 m^2 plots. The experimental area was disked three times to remove any previous vegetation before planting on March 12, 2003.

The amendment material used was untreated urban wood waste from the City of Garland Castle Drive Wood Recycling Facility. This material had a composition of 43.5% carbon, 0.45 % nitrogen, a C:N ratio of 98:1, a $\delta^{15}N$ of 1.67‰ and a $\delta^{13}C$ of -25.14‰. Amendment particle size distribution was 26 % of mass less than 1-cm^2, 17 % greater than 1-cm^2, but less than 5-cm^2 and 56% larger than 5 cm^2. The large, recalcitrant amendment material was chosen to address the issues associated with soil physical structure, such as compaction, but not create a dramatic pulse of nitrogen availability or immobilization (Whitford et al. 1989, Reid and Naeth 2005).

Seeds of native and naturalized grasses, legume and forb species typical of this region were acquired from two commercial vendors: Turner Seed Company and Native American Seed (Table 2.2). For the surface application treatments, the large and awned seeds were hand-spread followed by the use of a culti-packer (Brillion Farm Equipment, Brillion, Wisconsin) to firm the seedbed. The amendment was hand-spread over the seed bed at the three treatment amounts. In the incorporated treatments, the large and awned seeds were hand-sewn, followed by the application of the amendment. The material was then incorporated to 6 cm with a rototiller and the seedbed firmed with the culti-packer. In both location treatments, the final step was the hand-sewing of the small seeded species. The total pure live seed applied for all plant species was 2.1 g m^{-2}.

Aboveground stems of the large-leaved and abundant *Ambrosia trifida* L. (giant ragweed) and *Helianthus annuus* L. (annual sunflower) individuals were hand-clipped and removed from plots in June 2003 to minimize soil water loss during initial plant establishment. *Sorghum halepensis* (johnson grass), an aggressive invasive grass, was periodically treated throughout the experiment by individual wipe treatments of a solution of one-third glyphosphate (N-phosphonomethyl glycine) and two-thirds water. All other unsown species were untreated during the experiment.

Reference sites

Soil biological properties were characterized at the Rosehill Prairie Preserve, Rosehill Park, Garland Texas (32° 86′ N, 96° 59′ W), to provide a native undisturbed ecosystem as a point of reference. This area contains a small remnant (30 hectares) of upland vertisol tall grass prairie, dominated by the grasses *Schizachyrium scoparium* Michx. (little bluestem) and *Sorghastrum avenaceum* Michx. (Indian grass) (Bezanson 2000). It was acquired by the City of Garland in 1978 and has had no significant disturbance since that time (T. Frye, City of Garland Parks Department, *personal communication*), although there has been some encroachment by *Juniperus* L. (Juniper), *Rubus* L. (dewberry) species and *S. halepensis*. I also sampled a 28 hectare area adjacent to the Rosehill prairie that was restored to prairie vegetation in the early 1990s; however, it is currently dominated by an introduced C_4 grass, *Bothriochloa ischaemum* var. *songarica* Fisch. & Mey. (King Ranch bluestem), with some patches of *Bouteloua curtipendula* Michx. (side-oats grama).

Seasonal peak aboveground biomass

Seasonal peak aboveground biomass was collected from ten randomly placed 0.1-m^2 quadrats in November 2003, and in May and September of 2004 and 2005. The May samples included only the current year's winter grasses and forbs, which were excluded from the fall samples. The fall samples included only the current year's growth of summer forbs and grasses. These materials were dried at 60ºC for 48-72 hours. The plant materials were separated into grasses, legumes, and non-leguminous forbs and weighed to the nearest 0.01 gram (Briggs and Knapp 1995). The data was averaged to the plot level prior to statistical analysis.

The contribution to peak aboveground biomass of the *A. trifida* and *H. annuus* individuals removed in June 2003 was determined from collecting aboveground material from five randomly-placed 1-m^2 quadrats at the time of treatment and processing as above. These data were added to the seasonal peak aboveground biomass for the fall of 2003.

Soil collection and analysis

Soil samples were collected from the treatment plots in June and October of 2003 and March, June, and September of 2004 and 2005. Soils were also collected from the native prairie and restored area at Rosehill Park in Garland, Texas in September 2004 and September 2005. From each treatment plot, ten soil samples (0-10 cm) were collected and placed in a cooler for transport. Bulk density was determined for the upper 5 cm of soil using the core method with a correction for coarse fragments, including amendment material (Culley 1993). These soil samples were thoroughly mixed and sieved (4 mm) to remove amendment material, large roots and other course organic debris. Gravimetric water content was determined by drying soils at 105º C for 48 hours.

Soil organic carbon (SOC), soil total N (STN), δ^{13} C of SOC and δ^{15} N of STN were determined in June 2003 and September 2005 for the soils of the landfill experiment and in September 2005 for the reference soils. Sieved soils were dried at 60ºC and ground with a centrifugal mill (McCulley et al. 2004). Because the soils were calcareous, the soils were placed in a desiccator and exposed to an HCl atmosphere for 8 hours prior to combustion (Harris et al. 2001, Dai et al. 2006). Soils were analyzed using a Carlo Erba EA-1108 elemental analyzer interfaced with a Delta Plus isotope ratio mass spectrometer operating in continuous flow mode (ThermoElectron, Woburn, MA). The δ^{13} C values are reported relative to the international V-PDB standard by calibration through NBS-19 (Hut 1987, Coplen 1995), while δ^{15} N values are reported relative to atmospheric N_2 (Mariotti 1983) . Precision was <0.1 ‰ for δ^{13} C and <0.2‰ for δ^{15} N.

The chloroform fumigation-incubation method was used to determine soil microbial biomass carbon (SMB-C) (Horwath and Paul 1994). Twenty-five grams of sieved soil was placed in a 50-ml beaker and brought to 55% water holding capacity. This soil was fumigated with ethanol-free chloroform and incubated for 10 days in the dark at 25º C. Evolved CO_2 was captured in 3 ml of 2.0 M NaOH, and the amount of CO_2 absorbed by the alkali was determined by titration using 0.5 M HCl. SMB-C was calculated without subtracting a control and using a k_c value of 0.43 (Voroney and Paul 1984, Franzluebbers et al. 1999). The ratio of microbial to organic carbon (C_{mic}/C_{org}) was calculated as an index of readily metabolized organic carbon (Anderson and Domsch 1989, McCulley et al. 2004).

Carbon mineralization potential was determined from unfumigated soil over a 10-day incubation period under the same conditions as those for determining soil microbial biomass. The metabolic quotient (qCO_2), the conversion efficiency from available carbon to SMB-C, was calculated as the ratio of C-mineralization potential to SMB-C (Anderson and Domsch 1985, Wardle and Ghani 1995).

In 2003 and 2004, inorganic nitrogen was extracted from the soil before fumigation and from those incubated for SMB-C and carbon mineralization potential (McCulley et al. 2004). Three grams of dried soil was mixed with 30 ml of 1 M KCl and the filtered extract was analyzed for NH_4^+ -N and NO_3^- -N using a Technicon Auto Analyzer (Technicon Instrument Corporation, Tarrytown, N.Y). The pre-fumigation soils were used to determine available inorganic nitrogen. Soil microbial biomass-N (SMB-N) was calculated with a $K_N = 0.56$ (Harris et al. 1997). The rate of potential N-mineralization was determined using the difference between the incubated, unfumigated soils and the initial soil samples in NH_4^+ -N and NO_3^- -N (McCulley et al. 2004). The rate of nitrification was calculated using the difference between initial NO_3^- -N and incubated, unfumigated samples.

Statistical analyses

Gravimetric water content and potential nitrogen process rates data were analyzed with an ANOVA procedure with amendment amount, amendment location and their interaction, and slope position. Aboveground biomass, bulk density, SMB-C, SMBN, inorganic nitrogen, C-mineralization, $q\mathrm{CO}_2$, SOC, STN, C_{mic}/C_{org}, δ^{13} C and δ^{15} N data were analyzed with a repeated-measures analysis within the linear mixed models procedure (Tables 4.1 and 4.2) (Piepho et al. 2003). Akaike's Information Criterion (AIC) was used to determine the optimal covariance structure, which was AR1 (Uzoh and Oliver 2006). The model included three fixed terms: amendment amount, location and time, as well as their interactions, and one random term: block of slope position (Piepho et al. 2003). For all analyses, Bonferroni post-hoc tests were used to determine differences within response variables. Data were analyzed using SPSS 13.0.1 (SPSS Inc. Chicago, Illinois, USA). Significance was declared at the 0.05 level.

Results

Seasonal peak aboveground biomass

There was an interaction between location, rate and time for peak aboveground biomass (Fig. 4.1). The surface treatments had larger aboveground biomass in the fall of 2003 and 2004, and the incorporated treatments and the surface-control had greater biomass in the spring of 2004. There was no separation among treatments in 2005 because drought conditions limited plant growth.

Table 4.1. Summary of fixed effects of the linear mixed model procedures for the soil properties from eight sampling periods between June 2003 to September 2005.

	Bulk density	**Peak aboveground biomass**	**SMB-C**	**SMB-N**	**NH_4^+**	**NO_3^-**	**C-min**	**$q\mathbf{CO_2}$**
Location	**	*	**	**	n.s.	n.s.	***	n.s.
Amount	*	n.s.	***	**	n.s.	n.s.	***	n.s.
Time	***	***	***	***	***	***	***	***
Location * Amount	n.s.	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.
Location * Time	n.s.	**	n.s.	n.s.	n.s.	n.s.	n.s.	*
Amount * Time	n.s.	n.s.	n.s.	n.s.	n.s.	***	n.s.	**
Location * Amount * Time	n.s.	**	n.s.	n.s.	n.s.	n.s.	*	***

* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$
n.s. not significant

Table 4.2. Summary of fixed effects of the linear mixed model procedures for the soil properties from June 2003 and September 2005.

	SOC g kg^{-1}	**SOC g m^{-2}**	**TN g kg^{-1}**	**TN g m^{-2}**	**C_{mic}/C_{org}**	**$\delta^{13}C$**	**$\delta^{15}N$**
Location	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.
Amount	**	n.s	n.s.	n.s.	n.s.	n.s.	n.s.
Time	***	***	***	***	***	***	***
Location * Amount	n.s.	n.s	n.s.	n.s.	n.s.	*	n.s.
Location * Time	n.s.	n.s	n.s.	n.s.	n.s.	n.s.	n.s.
Amount * Time	n.s.	n.s	n.s.	n.s.	n.s.	n.s.	n.s.
Location * Amount * Time	n.s.	n.s	n.s.	n.s.	n.s.	n.s.	n.s.

* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$
n.s. not significant

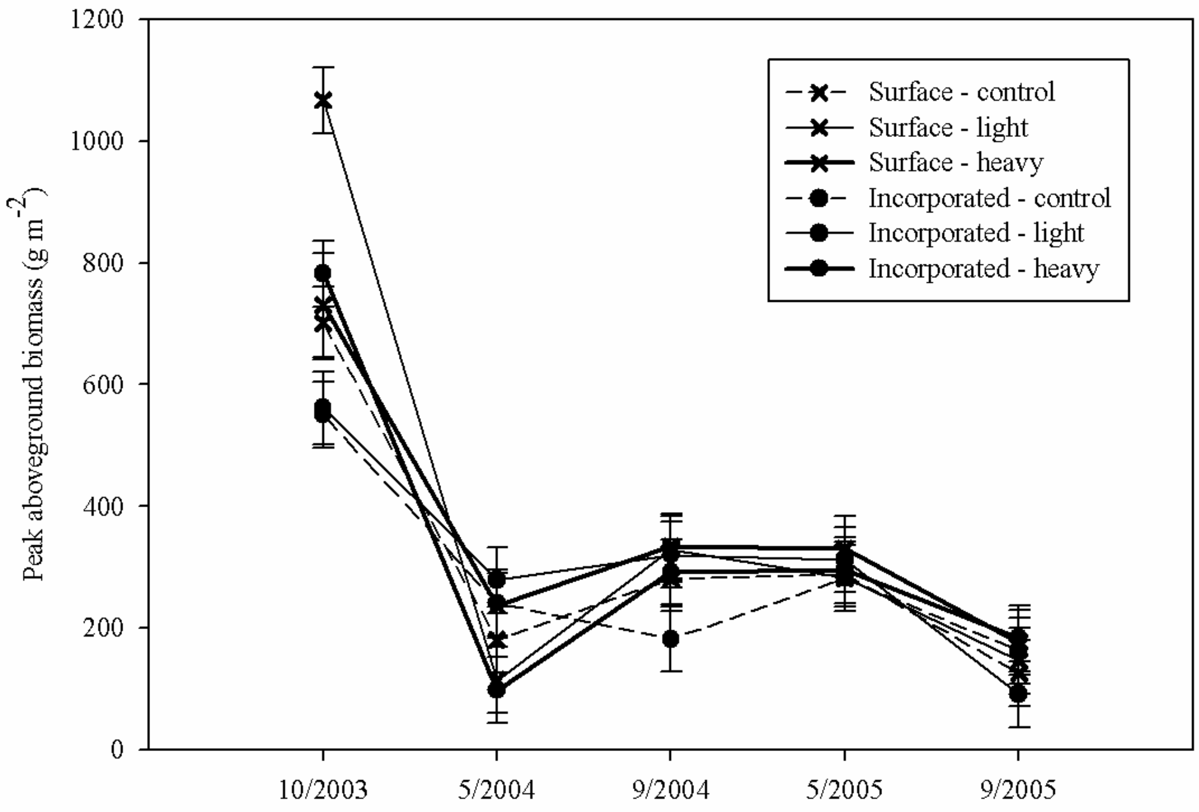


Figure 4.1. Seasonal peak aboveground biomass (mean ±SE, n=5) for the experimental treatments over time.

Gravimetric water content and bulk density

There were no treatment differences in gravimetric water content during any sampling period. Bulk density changed significantly over time (Fig. 4.2), with higher values during the first two sample periods and lower values thereafter. In June 2003, soil bulk density of the upper 5 cm was greater in the surface plots (1.5 ± 0.02 g cm^{-3}) than the incorporated plots (1.4 ± 0.02 g cm^{-3}).

Organic carbon and total nitrogen

The concentration of SOC (g C kg^{-1}) increased from June 2003 to September 2005 (Fig 4.3). In contrast the density of SOC (g C m^{-2}) decreased from June 2003 to September 2005, because the soil bulk density decreased. The restoration treatments also influenced SOC. Amendment application increased SOC concentration; it was greater in the treatments with the greatest amount of amendment and lowest in the control treatment. The density of SOC was altered by amendment location and was larger in the surface plots than the incorporated treatments.

The concentration of STN (g N kg^{-1}) increased from June 2003 to September 2005. Again, the decrease in bulk density was influential in the reduction of STN density (g N m^{-2}) from June 2003 to September 2005. The soil C:N ratio did not vary among treatments (Fig. 4.4).

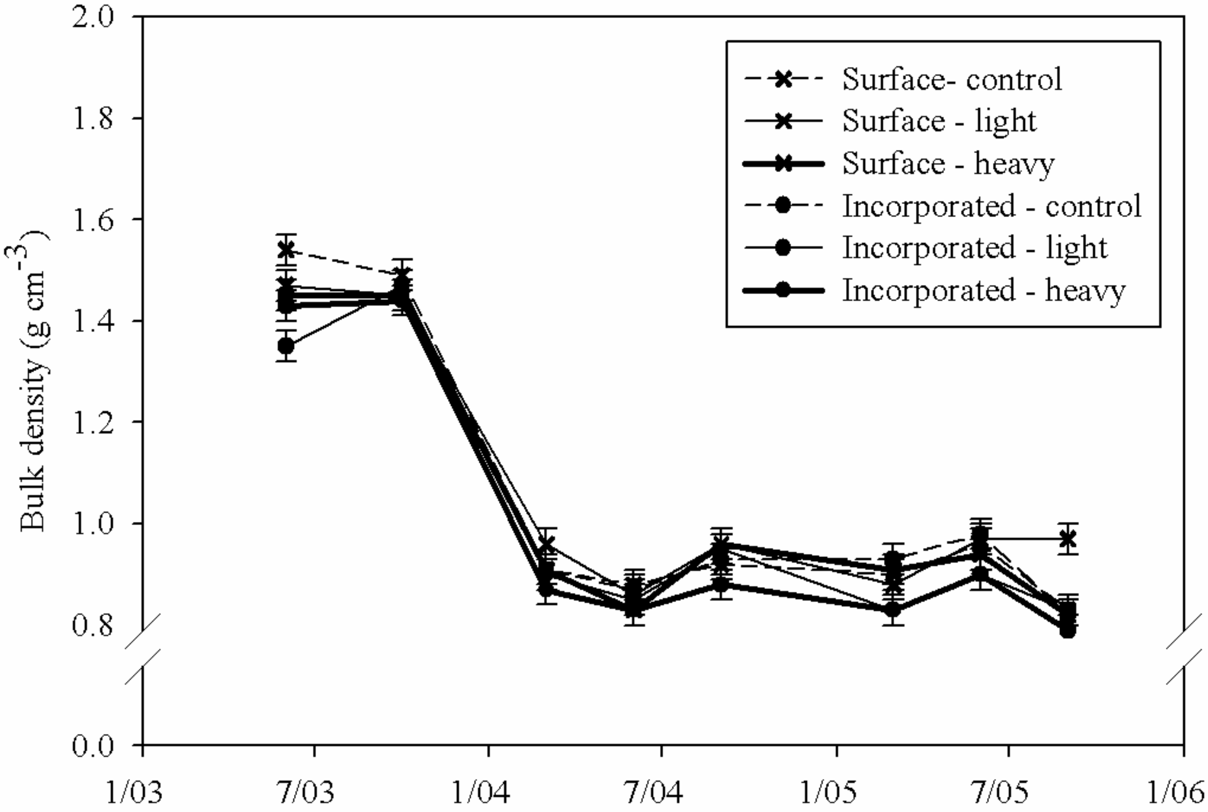


Figure 4.2. Soil bulk density (mean ± SE, n =5) for each experimental treatment over time.

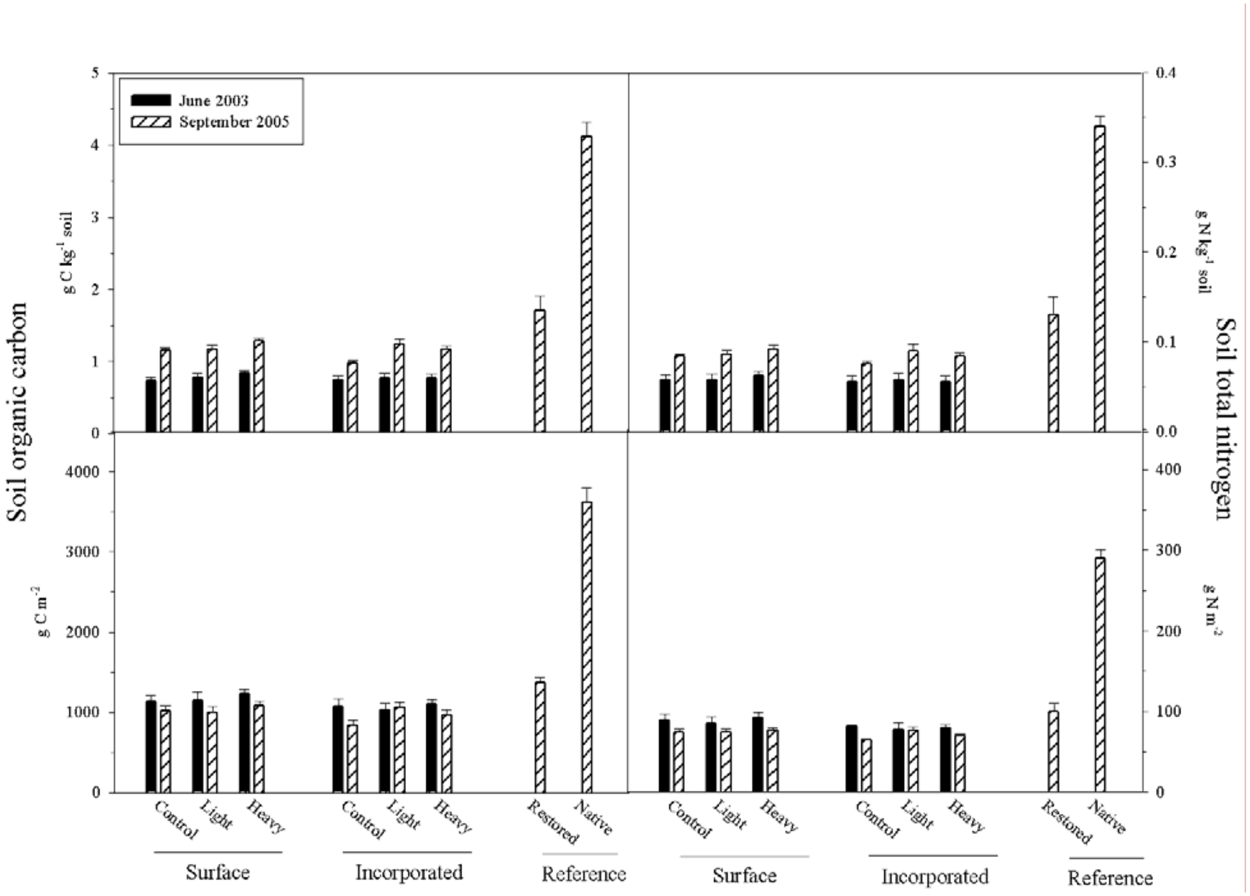


Figure 4.3. Soil organic carbon and soil total nitrogen concentrations (g kg^{-1}) and densities (g m^{-2}) for the experiment treatments (mean ±SE, n=5) in June 2003 and September 2005 and the Rosehill native prairie and restoration reference sites (mean ±SE, n =2) in September 2005.

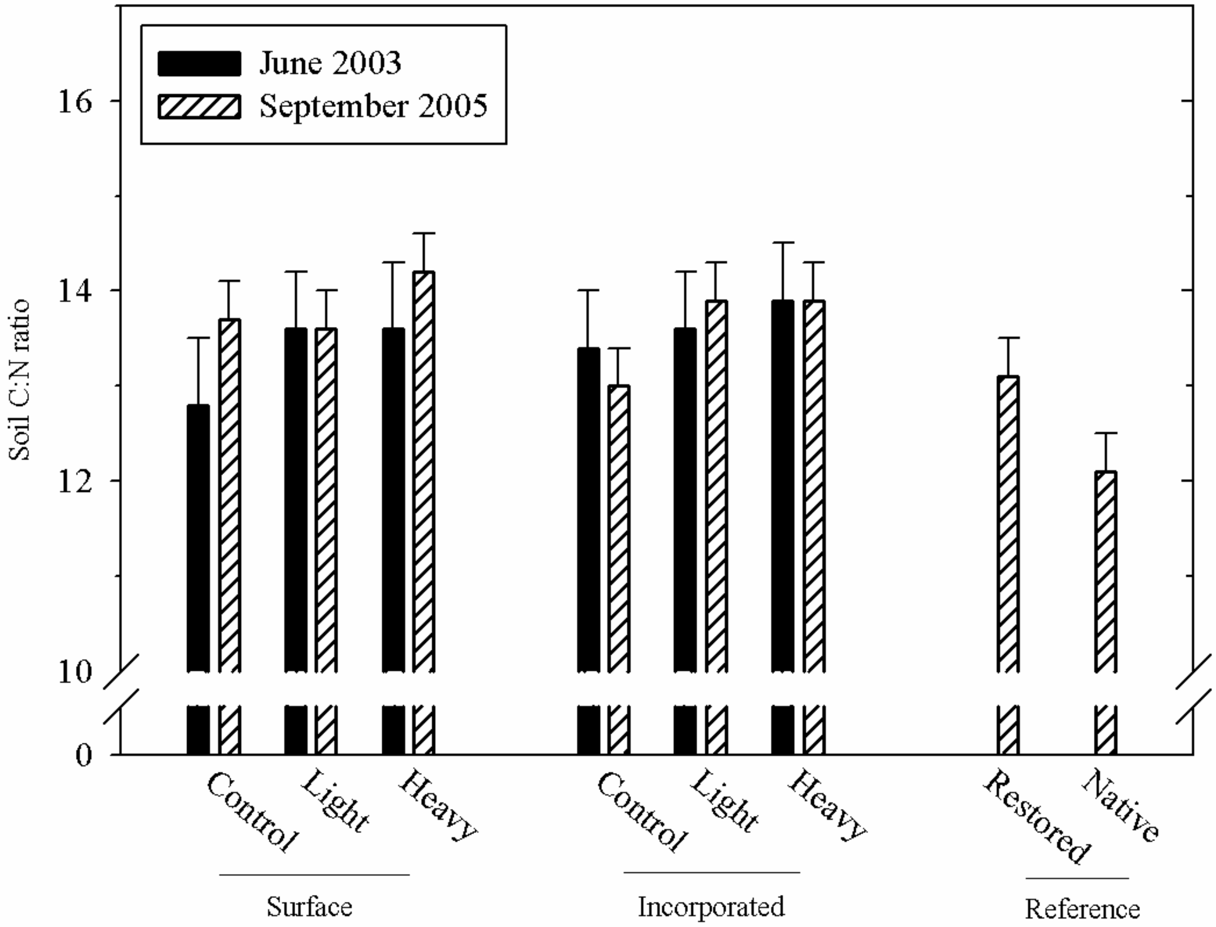


Figure 4.4. Soil C:N ratio (mean ± SE, n=5) for the experiment treatments in June 2003 and September 2005 and the native and attempted restoration reference sites (n =2) in September 2005.

The organic carbon and total nitrogen densities in the Rosehill restoration reference were similar to those in the experiment in September 2005. However, at this time the organic carbon and total nitrogen densities of the native prairie reference site were higher than either the experiment or the attempted restoration reference.

Soil microbial biomass

The interaction between location and amount was significant for SMB-C. SMB-C was greater in the surface-control and surface-light treatments, but there was no difference between the surface-heavy and the incorporated-heavy treatments (Fig 4.5).

SMB-N was greater in the surface treatments than the incorporated treatments (Fig. 4.5). In response to amendment amount, SMB-N was larger in amended plots, but there was no difference between the application amounts.

Time was a significant factor in the dynamics of SMB-C and SMB-N. These values generally increased throughout the experiment, even during drought conditions in 2005 (Fig. 4.5). The increase in SMB-N over time was less pronounced than that of SMB-C.

There were no treatment differences in ratio of SMB-C to the soil organic carbon (C_{mic}/C_{org}), but it did increase from 2003 to 2005 (Fig. 4.6). The C_{mic}/C_{org} in the reference restoration was similar to the experiment, but it was lower in the native prairie reference.

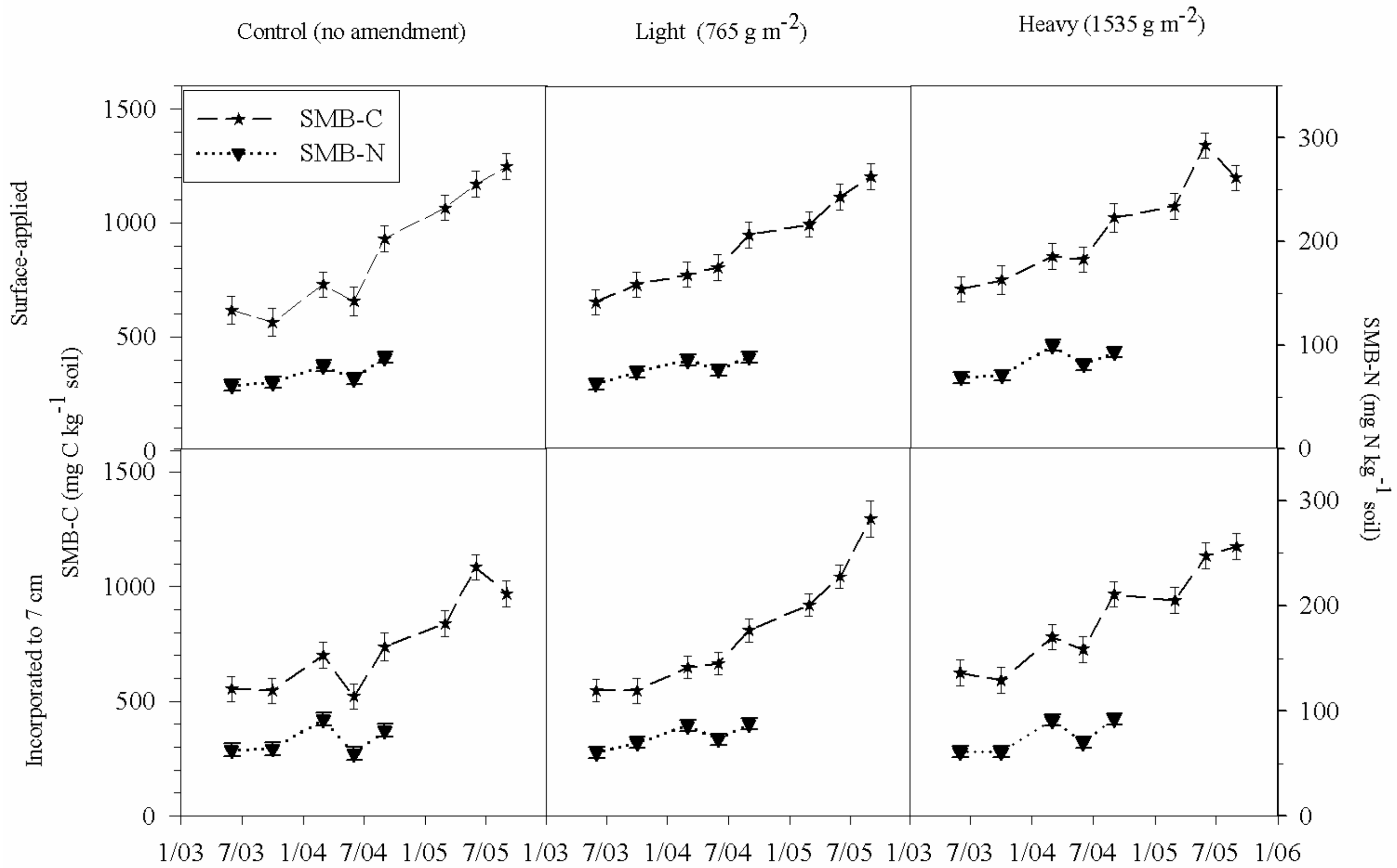


Figure 4.5. Soil microbial biomass carbon (SMB-C) and nitrogen (SMB- N) (mean ± SE, n = 5) of each experimental treatment over time.

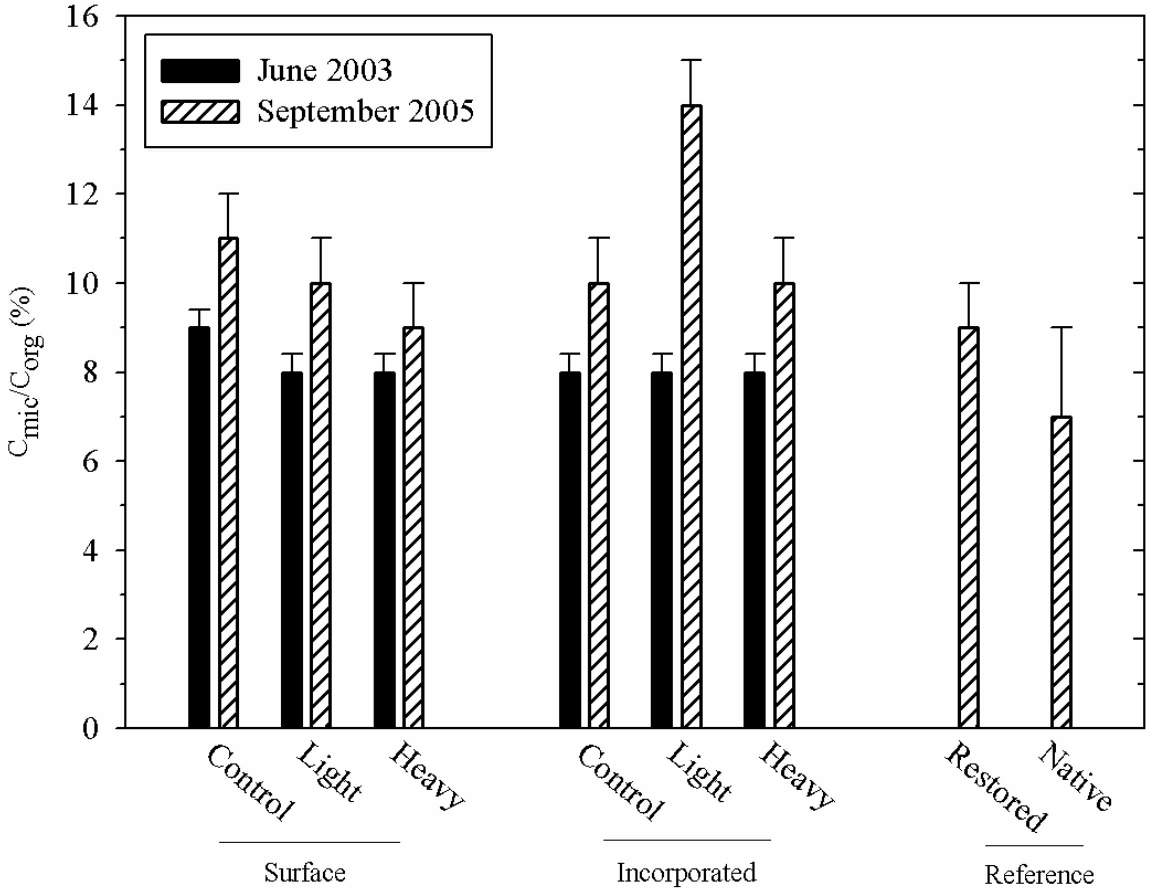


Figure 4.6. C_{mic}/C_{org} (mean ±SE, n=5) for the experiment treatments in June 2003 and September 2005 and the native and attempted restoration reference sites (n = 2) in September 2005.

Comparisons of SMB-C between the landfill experiment and the native and restored reference sites in September 2005 found that the restoration reference (1569.8 ± 91 mg C kg^{-1} soil) was slightly larger than the experimental plots. The native prairie SMB-C (2832 ± 209 mg C kg^{-1} soil) was more than twice the SMB-C of the experimental plots.

Inorganic nitrogen pools

There were no treatment differences in nitrate or ammonium concentrations in the soil; only time was significant (Fig. 4.7). However, when each time period was analyzed separately, the amount applied was important for nitrate concentration in March 2004. At this time, the heavy amendment treatment (1.72 ± 0.28 mg NO_3^--N kg^{-1} soil) had a significantly greater nitrate concentration than either the light (0.54 ± 0.28 mg NO_3^--N kg^{-1} soil) or control (0.47 ± 0.28 mg NO_3^--N kg^{-1} soil) application amounts.

Potential nitrogen transformation rates

There were no overall trends in the potential nitrogen transformation rates. When each time was analyzed individually, there were no treatment differences in either process during October 2003 (N-mineralization potential 1.1 ± 0.4 mg N kg^{-1} soil and nitrification potential 1.6±0.2 mg NO_3-N kg^{-1} soil) and September 2004 (N-mineralization potential 0.79 ± 0.42 mg N kg^{-1} soil and nitrification potential 0.44 ± 0.2 mg NO_3-N kg^{-1} soil). However, the nitrogen processes in the March and June samples had significant differences among the treatments. In both June 2003 and June 2004 the application amount created significant differences in both N-mineralization and

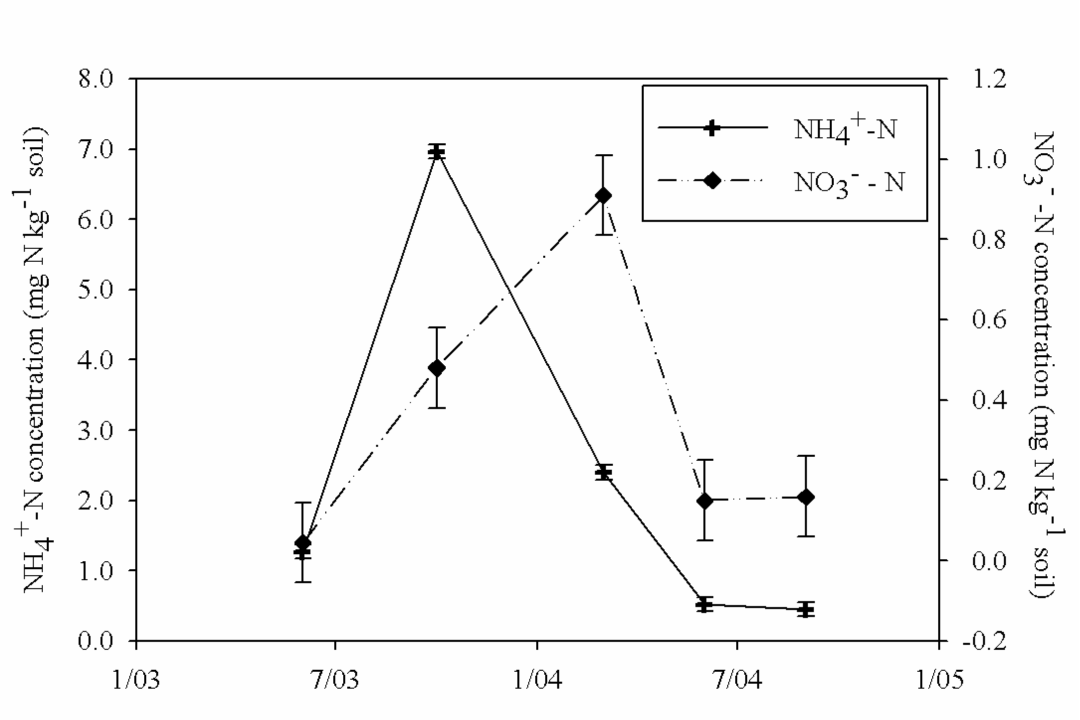


Figure 4.7. Ammonium (NH_4^+- N) and nitrate (NO_3^--N) availability (mean ±SE, n=30) of all the experimental plots over time.

nitrification potentials (Fig. 4.8). In all cases, there was a significantly lower rate in the heavy amended plots compared to the control and light amended plots. In 2005, however, N-mineralization potential in the control plot was intermediate between the light and heavy amended plots (Table 4.3).

In the March 2004, there was a significant interaction between amendment location and amount for both nitrogen processes. The control treatments of both locations had similar rates of nitrogen processes, but the amended incorporated plots were greater than the surface plots (Fig. 4.7).

Carbon mineralization potential and qCO_2

When averaged over time, the surface treatments had a significantly larger C-mineralization potential (30.3 ± 0.5 mg C kg^{-1} d^{-1}) than the incorporated treatments (27.3 ± 0.5 mg C kg^{-1} d^{-1}). In response to amendment amount, C-mineralization was lower in the control plots (25.7 ± 0.6 mg C kg^{-1} d^{-1}) than the amended plots: light (29.6 ± 0.6 mg C kg^{-1} d^{-1}) or heavy (31.0 ± 0.6 mg C kg^{-1} d^{-1}). Time was also a significant factor. C-mineralization values were generally similar from June 2003 and June 2004 and ranged from 16.9 to 25.3 mg C kg^{-1} d^{-1} (Fig 4.9). In contrast, values between September 2004 and September 2005 were greater and ranged from 28.3 to 46.6 mg C kg^{-1} d^{-1}. In September 2005, the C-mineralization of the attempted restoration reference was 24.0 ± 0.6 mg C kg^{-1} d^{-1} and that of the native prairie was 47.2 ± 3.2 mg C kg^{-1} d^{-1}.

The interaction between time and the treatments was significant for $q\mathrm{CO}_2$, but there were no obvious trends in this factor (Fig. 4.9). In 2005, the $q\mathrm{CO}_2$ for the

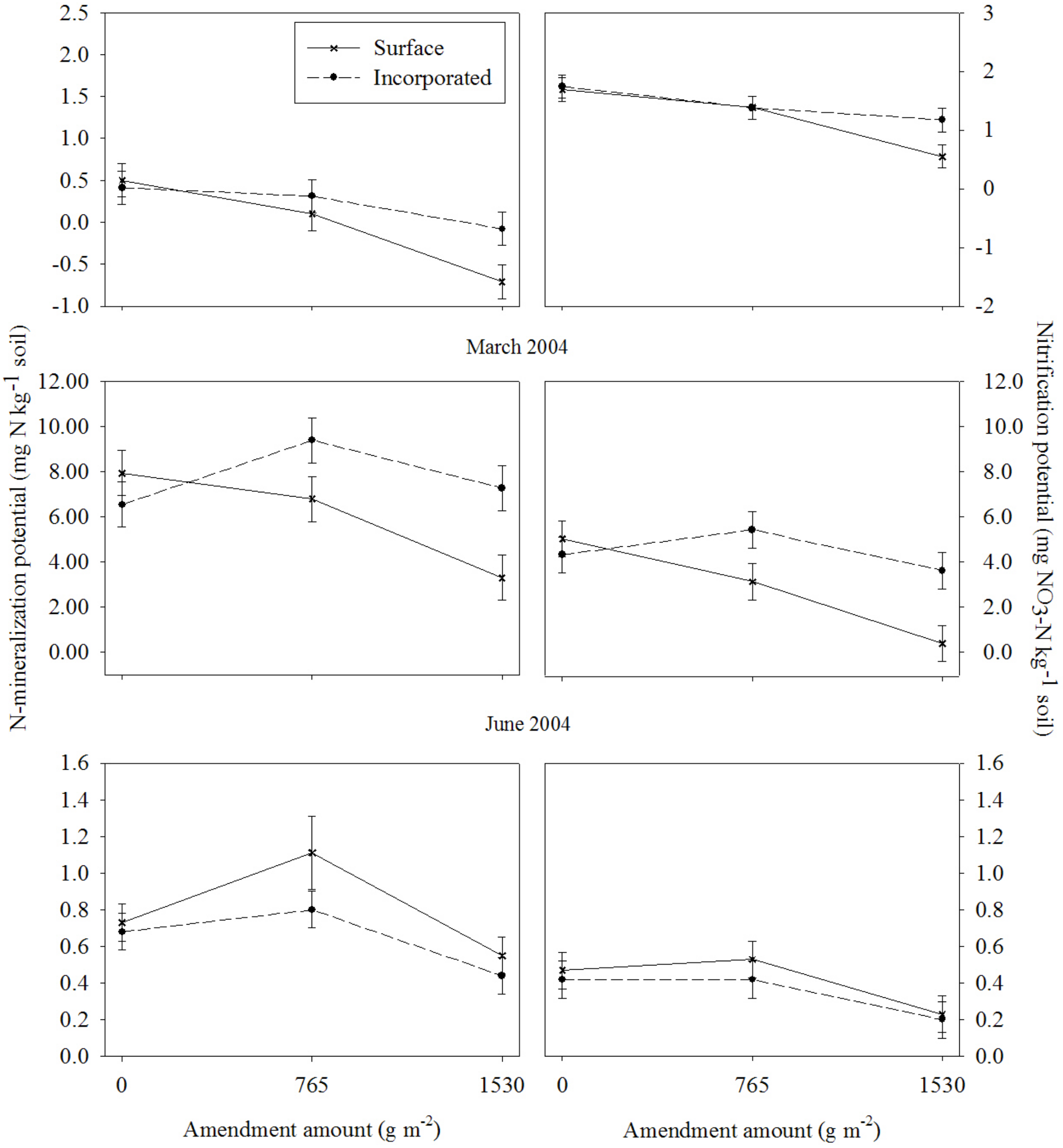


Figure 4.8. N-mineralization and nitrification potential (mean ±SE, n=5) by amendment amount for June 2003, March 2004 and June 2004.

Table 4.3. Summary of fixed effects of the ANOVA procedures for potential nitrogen transformation rates for June 2003 to September 2004.

N-mineralization potential	**Jun 03**	**Oct 03**	**Mar 04**	**Jun 04**	**Sep 04**
Location	n.s.	n.s.	*	n.s.	n.s.
Amount	**	n.s.	*	*	n.s.
Location * Amount	n.s.	n.s.	*	n.s.	n.s.

Nitrification potential	**Jun 03**	**Oct 03**	**Mar 04**	**Jun 04**	**Sep 04**
Location	n.s.	n.s.	*	n.s.	n.s.
Amount	***	n.s.	*	*	n.s.
Location * Amount	n.s.	n.s.	n.s.	n.s.	n.s.

* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$
n.s. not significant

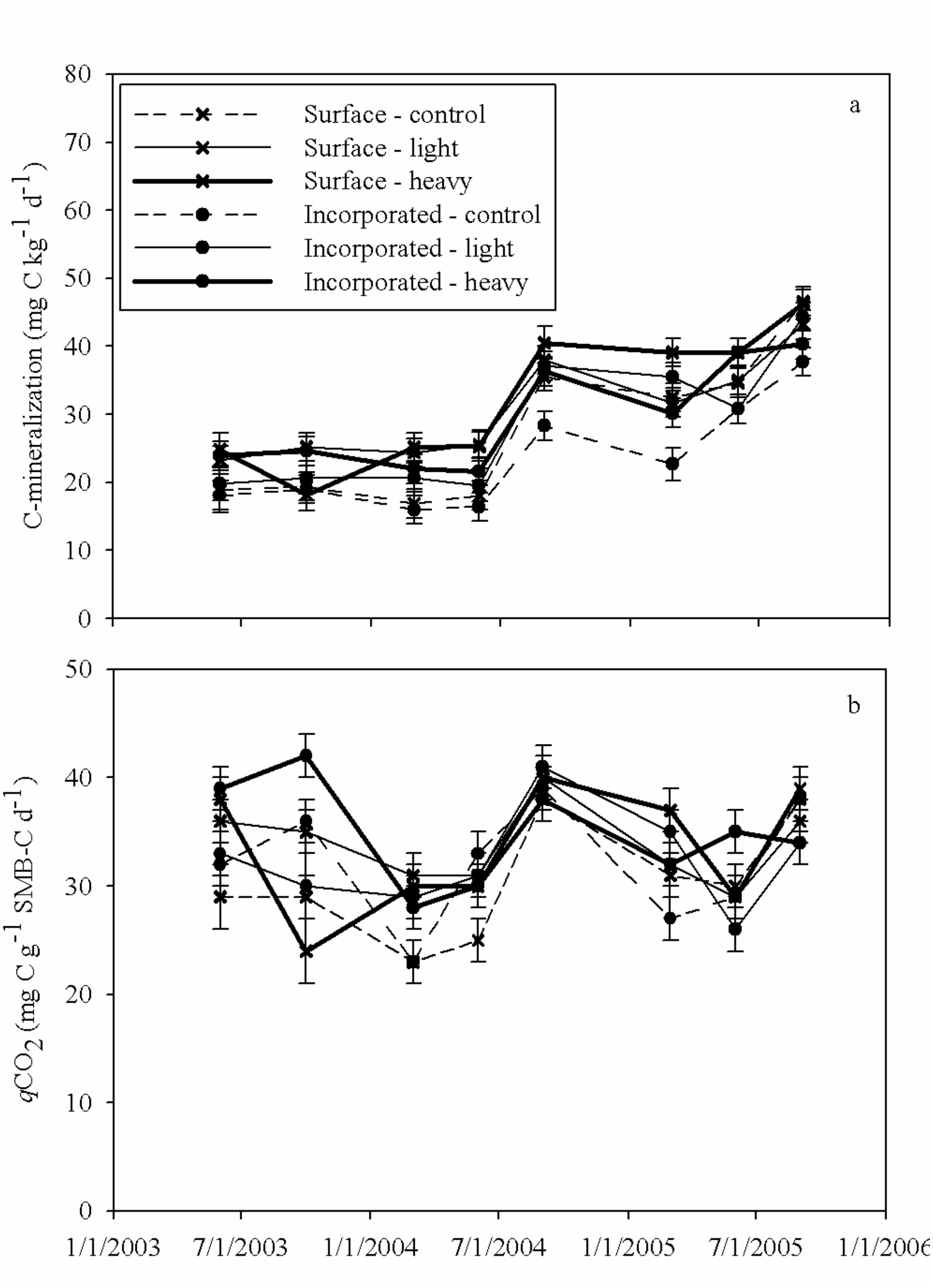


Figure 4.9. Carbon mineralization potential (a) and *q*CO2 values (b) (mean ±SE, n=5) of each experimental treatment over time.

attempted restoration reference was 15.34 ± 0.9 mg C g^{-1} SMB-C d^{-1} and the native reference had a *q*CO2 of 16.67 ± 0.1 mg C g^{-1} SMB-C d^{-1}.

$\delta^{13}C$ and $\delta^{15}N$ values of soils

The δ^{13}C of the surface soil decreased significantly from June 2003 to September 2005 (Fig. 4.9). There was also an interaction of the location and amount treatments, which finds larger δ^{13}C values in the incorporated-control compared to the surface control, but the incorporated treatments with amendment are more enriched with δ^{13}C.

Time was the only significant factor in the δ^{15} N of the surface soil (Fig. 4.10). This value was greater in 2003 than in 2005. When compared to the reference restoration and native sites in September 2005, the experimental restoration plots had larger δ^{15} N and more negative δ^{13}C values.

Discussion

The restoration treatments were only somewhat effective at altering the soil environment. Some aspects of the soil physical conditions (bulk density), but not others (GWC) were changed by the organic amendment treatments. There were treatment induced changes in seasonal peak aboveground biomass, but these differences varied over time. The soil biological responses were generally greater in treatments that resulted in larger aboveground biomass in the fall sampling periods, when many of the planted perennial species were at their peak. This suggests that the amendment

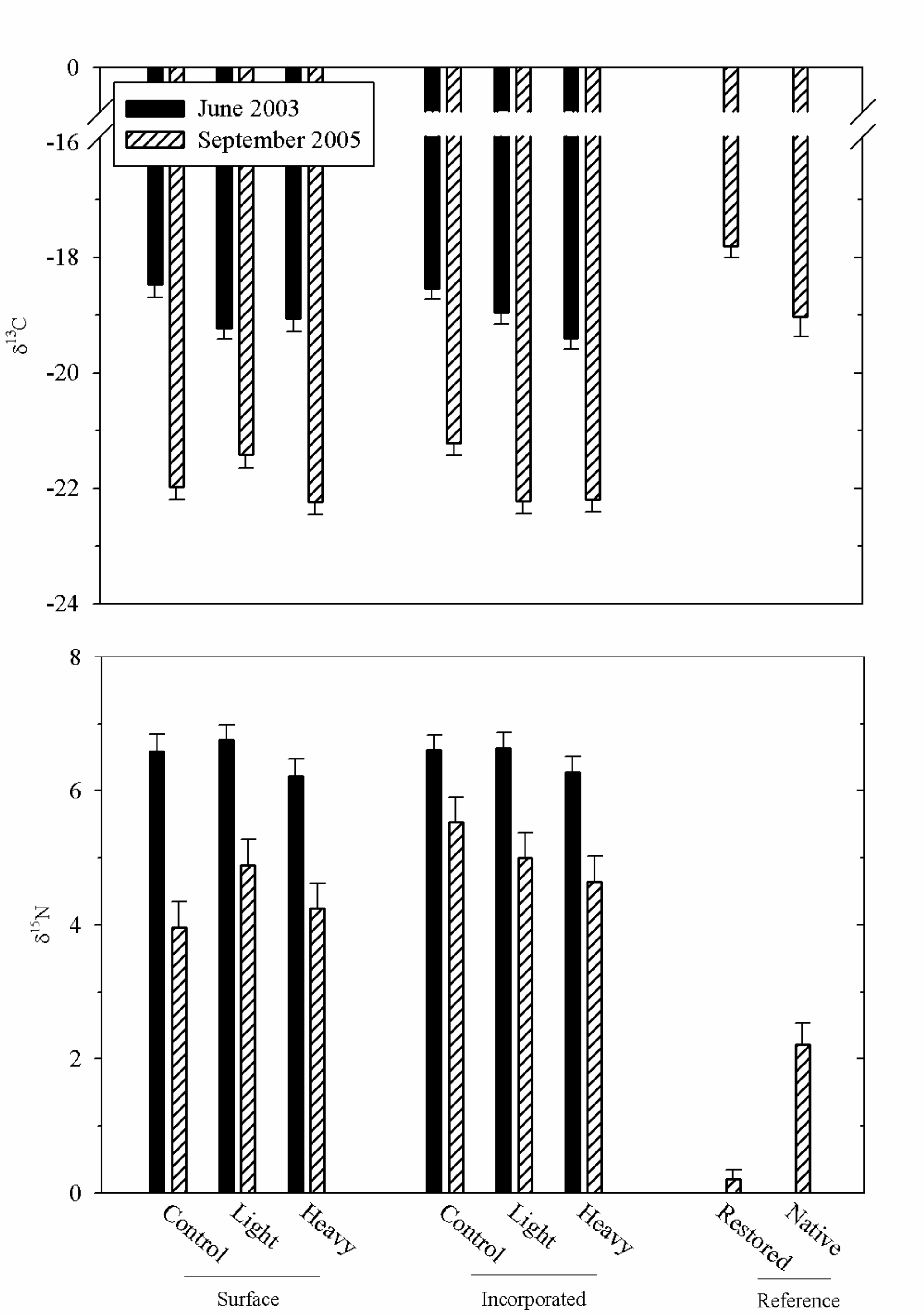


Figure 4.10. $\delta^{13}C$ (a) and $\delta^{15}N$ (b) values of soil (mean ±SE, n=5) in the experiment treatments in June 2003 and September 2005, and the native and attempted restoration reference sites (n = 2) in September 2005.

treatments did not affect the size and activity of the soil biota directly. Instead, these parameters were driven by the size and composition of the plant community.

Direct amendment effects

The incorporated treatments reduced bulk density in the first three months of the restoration, but these treatment differences were attenuated by October 2003. The bulk density of the top 5 cm in all the treatments declined over time and was similar to the reference areas by the end of the experiment. A reduction in bulk density following the addition of amendment, either to the soil surface or incorporated, is common in restoration (Kahn et al. 2000).

Peak aboveground biomass was affected by the amendment treatments, but the effect of the amendments was dependent on the season. The surface treatments and the incorporated-heavy had greater aboveground biomass in the fall sampling periods, which was dominated by species in the planting mix. There are several factors that contribute to these treatment differences in aboveground biomass, although their relative strength is not discernable from the data. Most likely, there was reduced germination in the incorporation treatments as a result of deep burial of the awned seed mix during the incorporation procedure. Alternatively, the surface amendments may have enhanced seedling emergence and survival by increasing germination microsites (Aguilera and Lauenroth 1995, Chambers 2000, Petersen et al. 2004). The protection conferred by mulch application is particularly important for establishment in years with low precipitation (Noy-Meir and Briske 2002), as this site experienced in 2003.

In contrast, the incorporated treatments and the surface-control had larger aboveground biomass in May 2004. The vegetation at this time was dominated by spring-blooming and winter annual plant species that were not in the seed mix. Long-term drought conditions limited plant biomass in September 2005 and there were no differences among treatments.

Indirect amendment effects

I anticipated that the incorporated treatments would have a larger soil microbial biomass because the material was imbedded in the soil and, therefore, more accessible to decomposers (Holland and Coleman 1987, Beare et al. 1992). Instead, SMB-C followed a similar pattern as the peak aboveground biomass in the fall sampling periods. It was greater in the surface and the incorporated-heavy treatments, than in the control- and light-incorporated treatments. Likewise, C-mineralization potential, a measure of microbial activity was greater in the surface-amended plots. Therefore, the amendment treatments, through the stimulation of plant productivity, acted indirectly on the soil community, rather than directly contributing to food sources (Wardle et al. 1993, Machulla et al. 2005, Potthoff et al. 2005).

The lack of a direct response to organic amendments by SMB or C-mineralization potential is supported by similar studies; Larsson et al. (1997) found that the addition of wood chips alone did not result an increase in the size of the soil microbial biomass over time. C-mineralization did not differentiate between surface and incorporation treatments in plots amended with wheat residue (Stott et al. 1986) or composted municipal solid waste (Agassi et al. 1998).

SOC was affected by the amendment treatments. Dissolved organic carbon or small fragments derived from the amendments may have contributed to the increase in SOC concentration with amendment rate. The greater aboveground biomass response in the surface treatments may have contributed to the greater SOC density in the surface treatments.

$\delta^{13}C$ was reduced in areas with added amendment and this reduction was greater in the incorporated treatments (Fig. 4.10). This value would be reduced through greater carbon inputs from C_3 sources: the amendment material (-25.14‰), C_3 forbs and C_3 grasses (Boutton 1996). The incorporated-control treatment had the highest $\delta^{13}C$ value because it lacked amendment and had the lowest plant response.

Changes over time

SMB-C doubled over the first 3 years and SMB-N increased 41% over the first 2 growing season of this restoration. This rapid increase is similar to other studies that find significant increases in the active pools of C and N over short periods of restoration management (Insam and Domsch 1988, Potter et al. 1999, Baer et al. 2002, Camill et al. 2004), and suggests that this site is not at an equilibrium with production inputs (Zak et al. 1994). As expected, the SMB-C at the landfill site, was lower than both the restored and native Rosehill grasslands. Levels of SMB observed in this study are within the range of other restoration projects in the blackland prairie ecoregion (Blaisdell 2001).

SOC and STN concentrations increased slightly over the experiment, but decreases in bulk density caused SOC and STN density to decrease slightly. These nutrient pools are large relative to annual inputs and losses, and consequently change on decadal time scales following restoration, succession or management changes (Larsson et al. 1997, McLauchlan et al. 2006). For example, Baer et al. (2002) found only a slight increase in total C and N density over a 12-year chronosequence of restored prairies. Comparisons with the reference sites support this. The Rosehill restored reference had somewhat larger concentrations of SOC and STN than the experimental site, but both of these sites had much lower values than the native prairie (Fig. 4.3). The native prairie site had SOC and TSN levels similar to other native sites in the Texas blackland prairie (Blaisdell 2001), but is slightly lower in SOC than other Texas prairies sampled by Potter et al. (1999).

The ratio of SMB-C to SOC, C_{mic}/C_{org}, is an indicator of soil quality and typically decreases over time as the carbon pools in the soil become more recalcitrant (Insam and Domsch 1988, Wardle 1993). In this study, however, this ratio increased with time, suggesting that the SMB-C and/or the SOC pools have not reached equilibrium. This could have resulted from the new plants and amendment treatments providing new available carbon for the microbes, when there was no substrate available initially. This trend is congruent with other restorations in the blackland prairie ecoregion; Blaisdell (2001) found that C_{mic}/C_{org} continued to increase during the first 20 years of restoration before it declined.

There was a significant increase in C-mineralization potential between June and September 2004 (Fig. 4.9). This increase may indicate an improved the balance between soil predator and prey organisms, which through succession may have shifted the soil microbial community to a younger, more active community (Insam and Haselwandter 1989).

The $q\mathrm{CO}_2$ values of the landfill restoration were greater than those of the reference soils in September 2005, which suggests that the experimental site may be experiencing stressors beyond typical early successional communities. The $q\mathrm{CO}_2$ of the reference soils were within the range of other native and restored prairies in the Texas blackland prairie ecoregion (Blaisdell 2001). However, $q\mathrm{CO}_2$ has been criticized as an soil quality indicator because it does not differentiate between the metabolic response to stress, which is chronic, and periodic disturbance events (Wardle and Ghani 1995). Blaisdell (2001) found that this variable was a poor indicator of soil quality following restoration.

Nitrogen dynamics

The amount of amendment applied and the carbon input from vegetation were both responsible for differences in the rates of N-mineralization potential and nitrification potential. The magnitude of these processes, however, is related to the amount and quality of litter present in the soil during incubation and are not necessarily associated with the amount of available inorganic nitrogen (Ehrenfeld 2003). This is the case for this experiment; plots with the heaviest amendment amount also had the lowest rates of nitrogen transformations in the spring and summer samples. There was also a location effect in the potential N-mineralization and nitrification during March of the second year (Fig. 4.7). The surface treatments had reduced potential rates of N-mineralization and nitrification, which suggests that the larger SMB found in this treatment was immobilizing the available nitrogen (Hassink et al. 1994). This suggests that the applied amendment was either too recalcitrant or in low enough quantities not to immobilize nitrogen in the soil microbial community (Blumenthal et al. 2003, Eschen et al. 2006).

Conclusions and implications for restoration

The capacity for soil to store and process carbon and nitrogen are disrupted or lost during degradation and construction. These processes are critical for ecosystem functioning and must be reestablished for restoration to succeed over time. In this study, I altered the amount and location of amendments within the soil profile and monitored their ability to promote aboveground biomass, soil organic carbon, total nitrogen and soil microbial biomass, as well as its activity. These treatments were successful at directing some physical aspects of top soil layer and some aspects of the vegetation, either through divergence in site conditions or through differences in seed burial. The changes observed in the size and activity of the soil biological parameters were not directly related to the amendment treatments. Instead, the soil community differences were driven by changes in vegetation.

The soil nutrient pools did increase over time and by the end of the study, the landfill site had similar SMB-C as the restoration reference site, which was approximately ten years older. The restored reference site had very poor plant community development, which further emphasizes the need to maintain high-quality vegetation for continued improvement of soil ecosystem function. Therefore, rather than directly targeting the soil biota, restoration managers should direct efforts to the establishment and promotion of the proper plant community. Further study is necessary to determine if the amendments assist in the development of feedbacks between plants and the soil community and the promotion of soil ecosystem redundancy.

CHAPTER V

DEVELOPMENT OF SOIL FOOD WEB STRUCTURE AND FUNCTION: THE ROLE OF ORGANIC AMENDMENTS IN ECOLOGICAL RESTORATION

Introduction

There is increasing interest among restoration ecologists in developing strategies that will stimulate biotic interactions and promote the self-regulation of ecosystem processes in restored systems (Whisenant 1999, Hobbs and Harris 2001). The soil food web is essential to many ecosystem processes, such as the regulation of soil nutrient cycling and availability (Reever Morghan and Seastedt 1999, Blumenthal et al. 2003), the development of improved soil structure (Caravaca et al. 2006) and improved plant productivity and diversity (Linden et al. 1994, Wardle et al. 1999a, Verschoor 2002, De Deyn et al. 2003). Further, the development of complex soil biotic communities that are similar to undisturbed systems should require fewer inputs than managed systems, because of increased diversity and redundancy in function (Smith et al. 2003). The failure to consider belowground biota can reduce the probability of restoration success (Verschoor 2002, Korb et al. 2004, Diaz et al. 2006), however, there are currently few restoration strategies that directly target and manage the development of the soil food web.

The soil food web can be limited in severely disturbed areas by the lack of soil structure and organic energy sources (Whitford et al. 1989, Zink and Allen 1998). The application of organic amendments to the soil alleviates these conditions by providing a carbon substrate for the soil microbial community, altering soil nutrient status, and creating pore networks that facilitates interaction (Nahar et al. 2006). Amendment addition also improves other aspects of the restoration environment that promotes plant community development. It can protect the soil surface from erosive forces, retain soil moisture and moderate surface temperatures (Winkel et al. 1991, Chambers 2000).

Studies in agro-ecosystems have demonstrated the location of the organic amendment within the soil profile, surface-applied or incorporated at depth, can affect the size, structure and activity of the soil food web (Tian et al. 1993). Incorporation increases the surface area exposure of the amendments to the decomposer community, and therefore supports larger populations and can have a more immediate impact on soil nutrient status (Beare et al. 1992). Incorporation of organic material also increases the habitable pore space for soil fauna, which can increase nutrient mineralization (Elliott et al. 1980, Freckman and Baldwin 1990, Ritz and Trudgill 1999). Incorporated material supports larger populations of bacteria and bacteriophagous organisms because they can respond rapidly to resource enrichment (Beare et al. 1992, Fu et al. 2000).

Surface-application, such as residue retention in no-till agroecosystems, is slower to be utilized by soil food web (Beare et al. 1992, Tian et al. 1993). This amendment location also promotes decomposition through the fungal decomposition channel. Fungi are tolerant to desiccation and can translocate materials within their hyphal tissue from the surface into the soil (Frey et al. 1999). A decomposition channel dominated by fungi and their consumers is often the target of restoration because it is more efficient at nutrient cycling than a bacteria channel food web (Bardgett et al. 2002, Smith et al. 2003). Fungi are more efficient than bacteria at converting substrate carbon into new tissue, and their tissue is more resistant to decay (Sylvia et al. 1999).

In this study, I compare the ability of organic amendments to direct soil food web development and stimulate natural ecosystem function in a restoration setting. To do this, I monitored the development of the nematode community over three growing seasons to determine the rate and direction of change. Nematodes are a useful indicator of soil food web development. They are the most numerous soil mesofauna and are found in all ecosystems (Ritz and Trudgill 1999). Nematodes occupy all consumer trophic levels within the soil food web and, therefore, one can infer ecosystem function from their community structure (De Ruiter et al. 2005). Their populations react quickly to disturbance (Bongers 1999) and can be used to differentiate the effects of management practices (Freckman and Ettema 1993, Neher and Campbell 1994). On a practical level, they are easy to extract from the soil, require very little specialized equipment, and identification to family is relatively easy (Coleman et al. 1999, Ritz and Trudgill 1999). There are also numerous indices available to assess the structure and function of the nematode community (Bongers 1990, Ferris et al. 2001).

Specifically, I hypothesize that the addition of organic material will accelerate the development of the soil food web, creating greater density and diversity of soil nematodes in all trophic levels. The rate of response will be greater in plots where the material is incorporated, as this creates closer contact with the soil, and therefore more rapid decomposition. Imbedded material also increases the availability of pore space for grazing (Gorres et al. 1999).

Further, I expect that the location of the organic amendments within the soil profile will influence the decomposition pathway and this will be detectable in the nematode profiles: surface application will promote fungal channel decomposition and incorporated treatments will support decomposition through the bacteria channel of the soil food web.

Methods

Study area

This study was conducted on a 21-hectare portion of the Castle Drive Landfill in Garland, Dallas County, Texas (32° 93′ N, 96° 58′ W; elevation 165 m). In accordance with regulations by the Texas Commission on Environmental Quality, the landfill has a constructed clay cap 45 cm thick, which is designed to be impermeable to water seepage into the municipal garbage below. Overlaying this cap is a 26 to 35 cm composite of unconsolidated subsoil from an adjacent area and is a growing medium for the vegetation cover. Soil properties prior to treatment are listed in Table 2.1.

This area is in the Texas Blackland Prairie Ecoregion, which is dominated by tall- and mid-sized grasses with associated forbs (Diggs et al. 1999). The mean monthly low temperature (1 °C) occurs in January and the mean monthly high temperature (35.5 °C) is in July. The 30-year precipitation average is 999 mm and has a bimodal distribution, with the largest amounts of rain falling in May (134 mm) and October (116 mm). Annual precipitation was below average in 2003 (510 mm) and 2005 (474 mm).

Although the total amount of precipitation was average during 2004, much of the rainfall fell in June and July (Fig. 2.1).

Restoration treatments

This experiment had six treatments in a 2 x 3 factorial completely randomized design. There were two amendment location treatments: surface applied and incorporated to 6 cm with a roto-tiller. There were three treatments that differed in the amount of material added: no amendment, a light amendment (765 g m^{-2}) and heavy amendment (1530 g m^{-2}). Each treatment occurred once in each of five replicate blocks, which occur along a 5% northeast slope. Alleyways (2 m wide) separated the 25 m^2 plots. The experimental area was disked three times to remove any previous vegetation before planting on March 12, 2003.

The amendment material used was untreated urban wood waste from the City of Garland Castle Drive Wood Recycling Facility. This material had a composition of 43.5% carbon, 0.45 % nitrogen and a C:N ratio of 98:1. Amendment particle size distribution was 26 % of mass less than 1-cm^2, 17 % greater than 1-cm^2 but less than 5-cm^2, and 56% larger than 5 cm^2. The large, recalcitrant amendment material was chosen to address the issues associated with soil physical structure, such as compaction, but not create a dramatic pulse of nitrogen availability or immobilization (Whitford et al. 1989, Reid and Naeth 2005).

Seeds of native and naturalized grasses, legume and forb species typical of this region were acquired from two commercial vendors: Turner Seed Company and Native

American Seed (Table 2.2). For the surface application treatments, the large and awned seeds were hand-spread followed by the use of a culti-packer (Brillion Farm Equipment, Brillion, Wisconsin) to firm the seedbed. The amendment was hand-spread over the seed bed at the three treatment amounts. In the incorporated treatments, the large and awned seeds were hand-sewn, followed by the application of the amendment. The material was then incorporated to 6 cm with a rototiller and the seedbed firmed with the culti-packer. In both location treatments, the final step was the hand-sewing of the small seeded species. The total pure live seed applied was 2.1 g m^{-2}.

Aboveground stems of the large-leaved and abundant *Ambrosia trifida* L. (giant ragweed) and *Helianthus annuus* L. (annual sunflower) individuals were hand-clipped and removed from plots in June 2003 to minimize soil water loss during initial plant establishment. *Sorghum halepensis* (johnson grass), an aggressive invasive grass, was periodically treated throughout the experiment by individual wipe treatments of a solution of one-third glyphosphate (N-phosphonomethyl glycine) and two-thirds water. All other unsown species were untreated during the experiment.

Reference sites

Soil biological properties were characterized at the Rosehill Prairie Preserve, Rosehill Park, Garland Texas (32° 86′ N, 96° 59′ W), to provide a native undisturbed ecosystem as a point of reference. This area contains a small remnant (30 hectares) of upland vertisol tall grass prairie, dominated by the grasses *Schizachyrium scoparium* (little bluestem) and *Sorghastrum avenaceum* (Indian grass) (Bezanson 2000). It was acquired by the City of Garland in 1978 and has had no significant disturbance since that time (T. Frye, City of Garland Parks Department, *personal communication*), although there has been some encroachment by *Juniperus* (Juniper), *Rubus* (dewberry) species and *S. halepensis*. I also sampled a 28 hectare area adjacent to the Rosehill prairie that was restored to prairie vegetation in the early 1990s; however, it is currently dominated by an introduced C_4 grass, *Bothriochloa ischaemum* var. *songarica* (King Ranch bluestem), with some patches of *Bouteloua curtipendula* (side-oats grama).

Soil collection

Soils were collected from the treatment plots on October 2003 and March, June, and September of 2004 and 2005. From each treatment plot, ten soil samples (1-10 cm) were randomly collected and bulked. In September 2004 and September 2005, soils were also collected from the native prairie and a restoration at Rosehill Park in Garland, Texas. All soil samples were placed in a cooler for transport and were extracted within 24 hours of collection (Coleman et al. 1999).

Baermann funnels were used to extract nematodes from a 50 g aliquot of soil. This technique is well-suited to extracting nematodes from fine-textured soils because it produces a clean sample for identification and enumeration. However, it requires active movement of nematodes and is therefore biased against larger, slower moving nematodes and sedentary plant ectoparasites (Freckman and Baldwin 1990). Further, populations may be enhanced by eggs hatching or the death of individuals from anoxia over the 3-day extraction period (Freckman and Baldwin 1990).

The Baermann funnel procedure was modified to ensure collection of nematodes along the funnel sides (J. Starr, *personal communication*). In this procedure, funnel water is completely replaced every 24 hours. At each replacement, nematodes were concentrated using a 25 µm sieve and then held in a beaker. After 72 hours, extracted nematodes were preserved in 5% formalin. I identified and enumerated all nematodes in each sample using an inverted microscope using a gridded field at 40x magnification. Gravimetric water content was determined for each soil sample to express nematode densities by soil dry weight (per 100 g of soil).

Nematode community indices

Nematode communities were evaluated using several different indices that evaluate community structure and function. These indices included: family richness, the Simpson index of dominance ($D = 1/ \Sigma p_i^2$) and Shannon-Weaver index of diversity ($H' = \Sigma p_i \ln p_i$) (Shannon and Weaver 1949, Simpson 1949).

Trophic groups were assigned to nematode families according to Yeates et al. (1993). Root-tip feeders were placed in the fungal feeders group (Forge et al. 2003). Enrichment profiles, or trophic triangles, were generated to illustrate the flow of carbon through the soil food web (Yeates et al. 1993, Ferris and Bongers 2006). This scheme allows one to interpret the quality of organic inputs and the structural response of the food web food source (Fig. 5.3)(Ruess and Ferris 2004, Ferris and Bongers 2006). Rapid turnover in nematode populations and ephemeral carbon resources is typical of the “fast-ephemeral” region. The “slow-sustained” region is characterized by conservative processes that retain nutrients in the system (Ruess and Ferris 2004).

The Total Maturity index (ΣMI) was used to characterize the successional stage of entire soil nematode communities (Bongers 1990, Yeates 1994). This index assigns each nematode family a ‘c-p value’ based on its reproductive capacity and response to disturbance: 1 for rapid colonizers to 5, for persisters. This index for each sample is calculated using the formula $\Sigma MI = \Sigma v_i f_i$, where v_i is the c-p value of the i^{th} taxa, and the f_i is the frequency of the i^{th} taxa in the sample (Bongers 1990).

Ferris et al. (2001) extended the trophic group concept and the maturity index into a single tool to evaluate the soil community, the weighted faunal analysis system. This qualitative evaluation technique characterizes the nematode community using three indices: channel, enrichment and structure (Ferris et al. 2001). The channel index evaluates the relative importance of the fungal versus bacterial decomposition pathways and is more reliable than the ratio of fungivores to bacteriophagous nematodes (Ruess 2003). The channel index is calculated as: $CI = 100 (k_e Fu_2)/ ((k_e Ba_1) + (k_e Fu_2))$, where Ba_1 and Fu_2 are the percentage of opportunistic bacteria and fungal grazers, respectively, and k_e represents the enrichment rankings of each of these guilds.

Within the weighted faunal analysis system the enrichment index considers nematode groups that respond to increased resource availability (Ferris et al. 2001). This index is calculated as: $EI = 100 (e/(e+b))$, where $b = \Sigma k_b n_b$ and $e = \Sigma k_e n_e$ and k is the weight given to each guild and n is the density of nematodes within that guild.

The structure index assesses the degree of maturation of the food web by emphasizing nematode guilds that require stability for increased population growth. Over time, this index characterizes succession within the soil fauna (Ferris et al. 2001). The structure index is calculated as: SI =100 (s/(s+b)), where $b= \Sigma k_b n_b$ and $s= \Sigma k_s n_s$ and k is the weight given to each guild and n is the density of nematodes within that guild.

Statistical analyses

Initial statistical analysis showed no significant block effects due to slope position and, herefore, this was removed from subsequent statistical analyses. Data were analyzed with a repeated-measures analysis within the linear mixed models procedure (Tables 5.1) (Piepho et al. 2003). Nematode density data were log-transformed to meet assumptions of normality and equality of variance; back-transformed data are presented. Index and percentage values were not transformed. Akaike's Information Criterion (AIC) was used to determine the optimal covariance structure, which was AR1 (Uzoh and Oliver 2006). The model included three fixed terms, amount, location and time, as well as their interactions (Piepho et al. 2003). Least Squares Difference post-hoc tests were used to determine differences within response variables. Data were analyzed using SPSS 13.0.1 (SPSS Inc. Chicago, Illinois, USA). Significance was declared at the 0.05 level. Table 5.1

Table 5.1. Summary of fixed effects of the linear mixed model procedures for the nematode community parameters from seven sampling periods between June 2003 to September 2005.

	Family richness	**D**	**H'**	**ΣMI**	**Channel index**	**Enrichment index**	**Nematode density**
Location	n.s.	n.s.	n.s.	n.s.	***	*	n.s.
Amount	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.
Time	***	***	***	*	***	***	***
Location * Amount	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Location * Time	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.
Amount * Time	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Location * Amount * Time	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$
n.s. not significant

Results

Diversity and density

A total of 22 families were identified throughout the experiment. Bacterivorous families included Alaimidae, Cephalobinae, Monhysteridae, Plectidae, and Rhabditidae. Fungivorous families included Aphelenchidae, Aphelenchoididae, Anguinidae, and Leptonchidae. Omnivorous families included Dorylaimidae and Noriidae. Root-hair feeding taxa included Psilenchidae, and Tylenchidae. Plant parasitic families included Belondiridae, Heteroderidae, Hoplolaimidae, Longidoridae, Meloidogyniae, Neotylenchidae, Paratylenchidae, and Pratylenchidae. Predatory taxa included Monochidae. Family richness ranged from 7 to 18 families in each sample.

There were no treatment effects on family diversity, dominance or richness, although these indices varied significantly over time. Both the Simpson and Shannon-Weaver indices were lowest in June 2004, when the samples were dominated (45%) by a single family of plant parasitic nematodes (Hoplolaimidae) (Fig. 5.1). Although there was a spike in these diversity indices in September 2004, they remained relatively unchanged throughout 2005, when there was limited rainfall and soil activity was low. Family richness increased throughout the experiment, and was the highest in June and September 2005. Nematode family richness and Shannon-Weaver diversity were greater in the native and restored reference prairie than in the experimental site (Fig. 5.1).

The total density of nematodes 100 g^{-1} of soil varied significantly over time, with each sampling period being significantly different than the others, except for March and September 2005 (Fig. 5.2). When averaged over time, the surface mulch treatment had

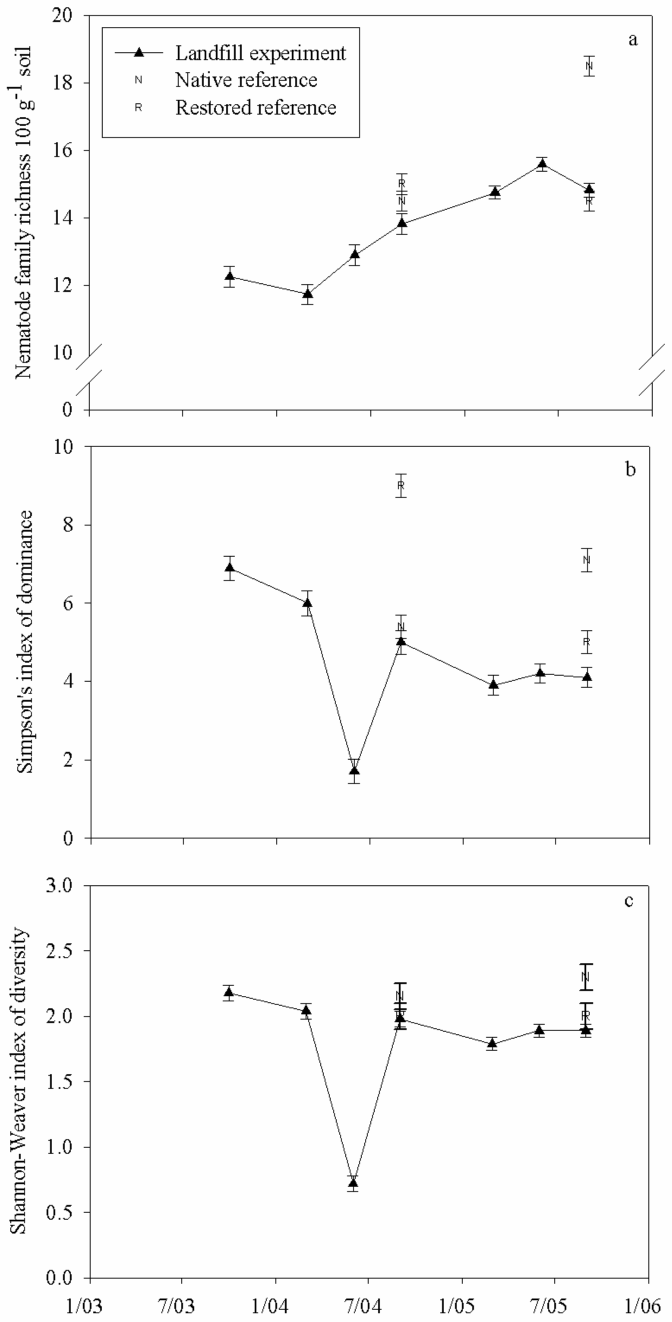


Figure 5.1. Nematode family richness (a), Simpson's index of dominance (b) and Shannon-Weaver index of family diversity (c) over time for the landfill experiment and the native and restored reference sites (mean ±SE, n = 2) in September 2004 and 2005.

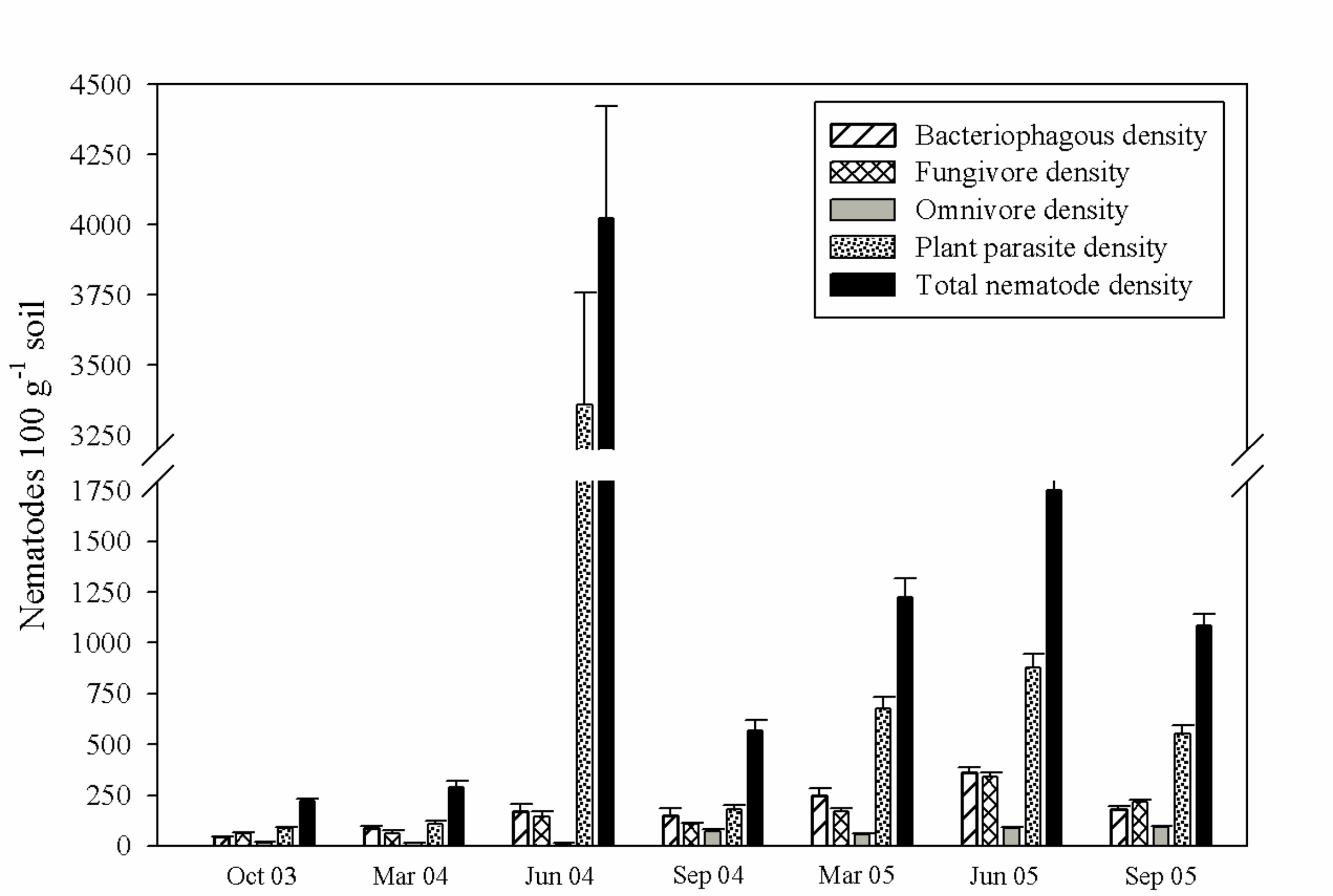


Figure 5.2. Nematode density (mean ±SE, n = 30) by trophic group and total over time. Values were averaged across all treatment combinations.

higher nematode density 100 g^{-1} soil than the incorporated treatments, but t-tests did not find any differences within any individual sample time. With the exception of the high populations in June 2004, there was an annual increase in seasonal nematode densities. Plant parasitic nematodes were the dominant trophic group at each sampling period and comprised over 50% of the total nematode population in June 2004 and throughout 2005.

Trophic response

In the Enrichment profiles (triangles), the treatment groups converge and largely remain over time in the “compromised” area, with the exception of March 2004, when the incorporated-heavy treatment fell into the “fast-ephemeral” area (Fig. 5.3). In contrast, both the native and restored references are within the “slow and sustained” area in September 2004 and September 2005.

Total nematode population size at the landfill site is lower than the native reference prairie, and similar or slightly larger than total populations at the restored reference site (Fig. 5.4). The native and restored reference samples had a greater percentage of detritivores (omnivores, bacteriophagous and fungivores and root-tip feeders) than the landfill experiment in the Septembers of 2004 and 2005. Plant parasite populations were also much lower in these areas compared to the landfill experiment.

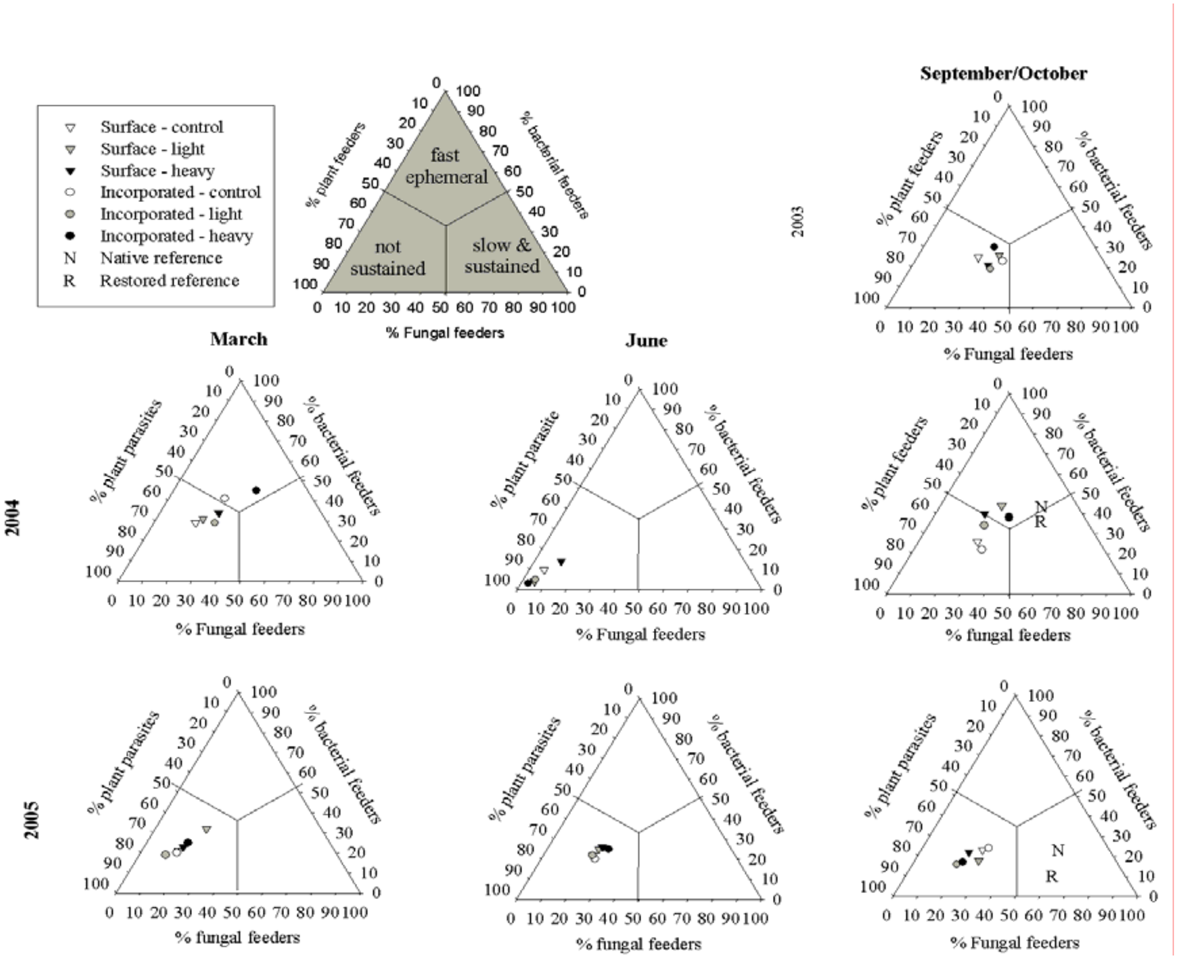


Figure 5.3. Nematode enrichment profiles (see Ferris and Bongers 2006) by restoration treatment (mean ±SE, n = 5) and reference areas (mean ±SE, n = 2).

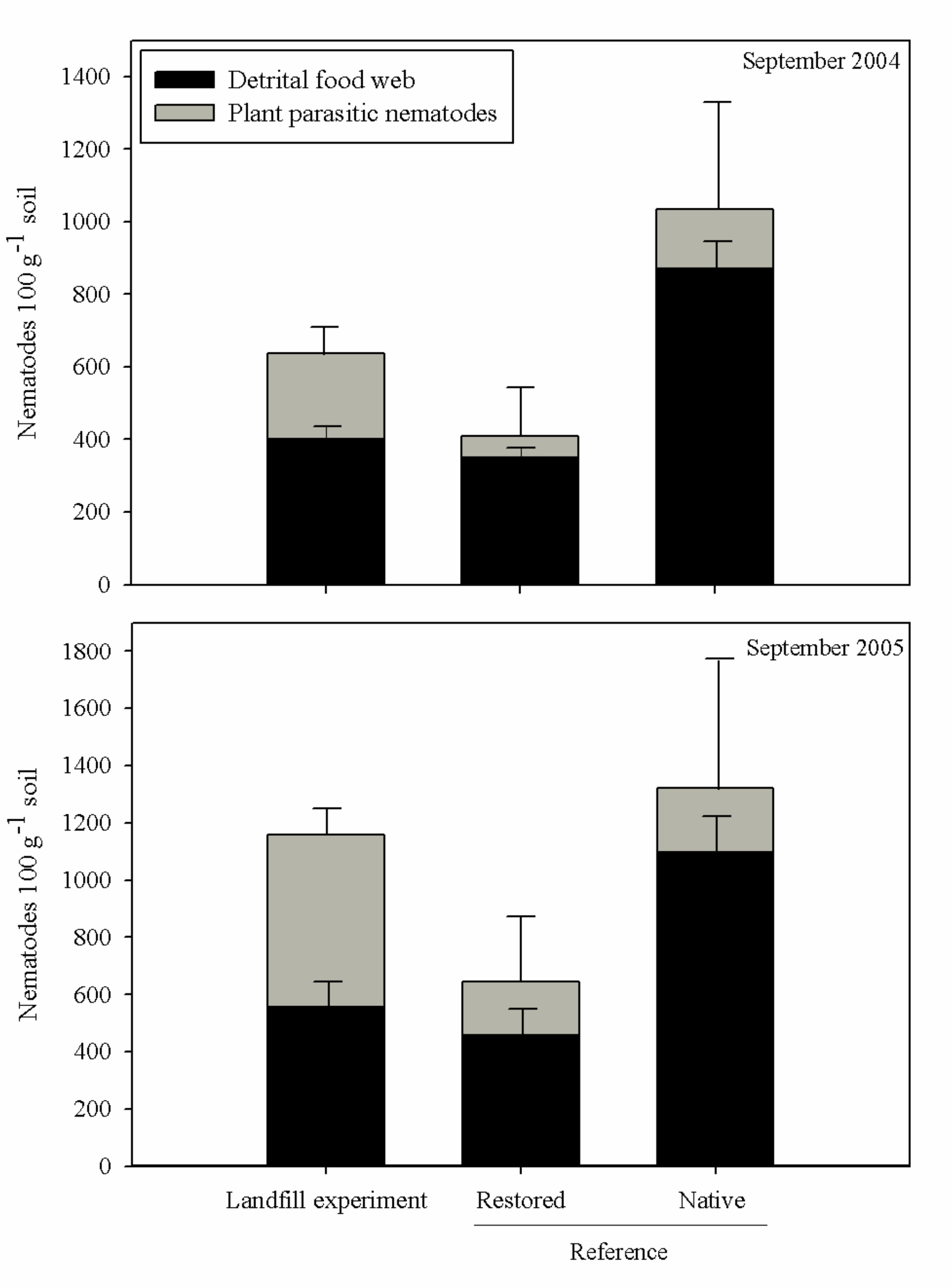


Figure 5.4. Plant parasite and detritivore density in the experimental plots and reference areas in September of 2004 and 2005.

Although the percentage of plant parasitic nematodes increased in both areas from 2004 to 2005, this was still much lower than the experimental area. The restored reference had a larger percentage of omnivores (19% in 2004 and 24% in 2005) than either the native reference area (7% both years) or the landfill experiment (1 - 14%).

Functional indices

The applied treatments had no effect on the total maturity index (ΣMI). This value changed over time, but was only significantly different in June 2004 and September 2005, when it increased to 2.9. Otherwise, this value remained between 2.6 to 2.7 during the course of the experiment. The increase during June 2004 was due to an increase in the population density of nematodes in the Hoplolaimidae family (45% of total nematodes), which have a c-p value of 3, which influenced the average. In September 2005, this value was elevated because of Hoplolaimidae populations were again high (48%). The elevated omnivore (c-p value of 4) populations (9% of total population) also contributed to the higher ΣMI value in September 2005.

In general, the ΣMI values of the reference sites were similar to the experimental sites. The native reference prairie had a maturity index value of 2.5 ± 0.3 in September 2004 and 2.6 ± 0.01 in September 2005. The restored reference site had a maturity index value of 2.8 in September 2004 and 3.3 ± 0.1 in September 2005.

When averaged over time, the channel index distinguished among amendment locations. The incorporated treatments have a higher channel index, which translates into having a fungal decomposition pathway. This treatment effect attenuated after June 2004, when channel index values of the location treatments converge (Fig. 5.5a). The interaction between time and location was significant for the enrichment index, which distinguished among amendment locations and after June 2004, this treatment effect was also no longer apparent (Fig. 5.5b). Amendment rate was also significant for Enrichment index with the control plots having significantly lower values (54 ± 1.3) than either the light (58.4 ± 1.3) or heavy (58 ± 1.3) amendment treatments.

When illustrated using the weighted faunal analysis system established by Ferris et al. (2001), the plots were grouped by location treatments in October 2003, where the incorporated plots were in the undisturbed/stable quadrant and the surface plots were in the low to moderate disturbance quadrant (Fig. 5.6). In March 2004, light amendment treatments were unchanged, but the incorporated-heavy treatment moved into the stressed quadrant In June 2004, the treatments with the greatest grass response, the surface-light, surface-heavy, and the incorporated-heavy (chapter II), fell into the high disturbance/enriched quadrat. The treatments converged in the low to moderate disturbance quadrant in September 2004 and remained in this quadrant until it moved to the undisturbed quadrant in September 2005.

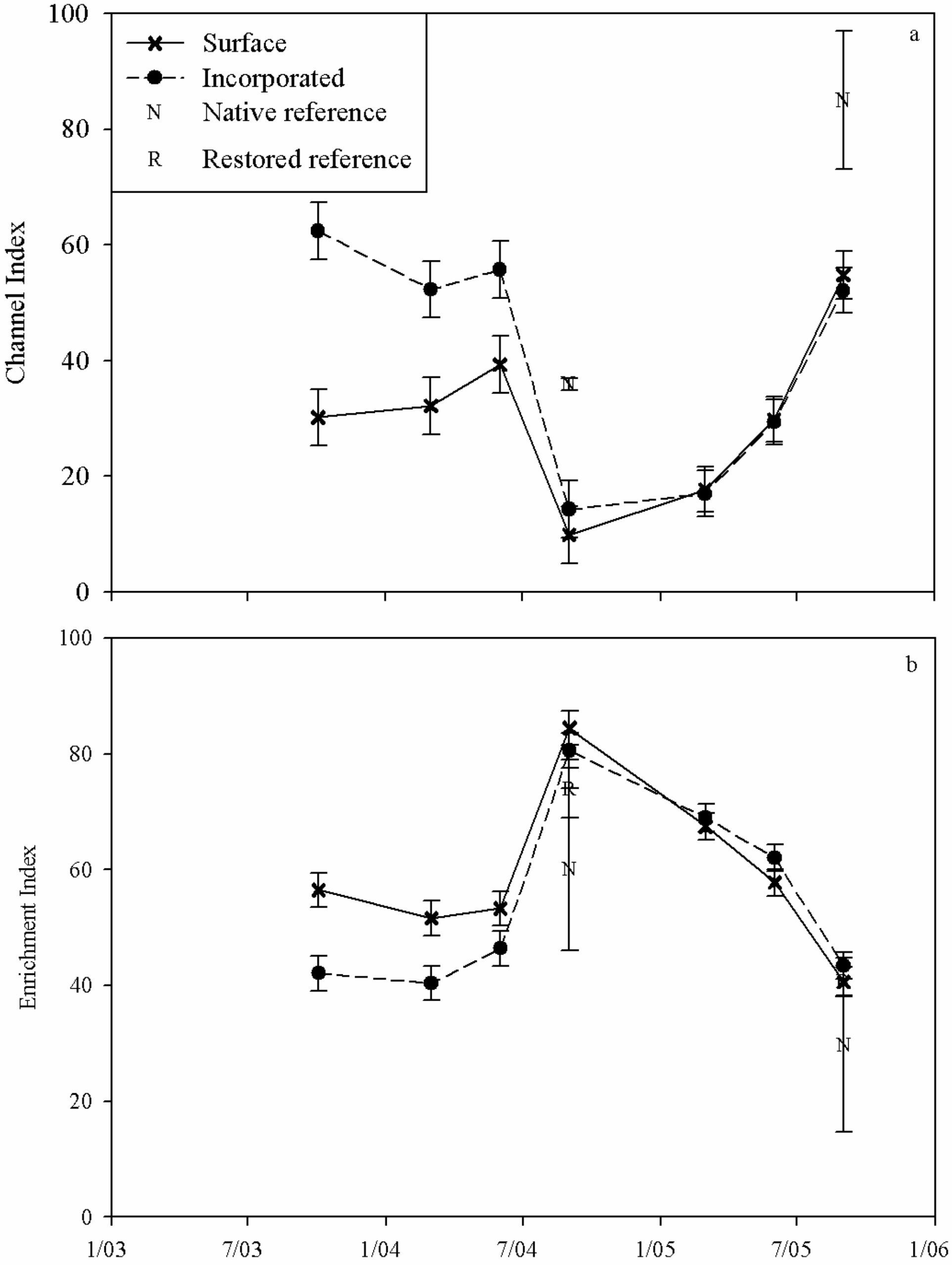


Figure 5.5. Channel index (CI) (a) and Enrichment Index (EI) (b) of each location experimental treatment (mean ± SE, n=5) over time, and for the mean (mean ± SE, n=2) values for the native and restored prairie reference sites in September 2004 and 2005.

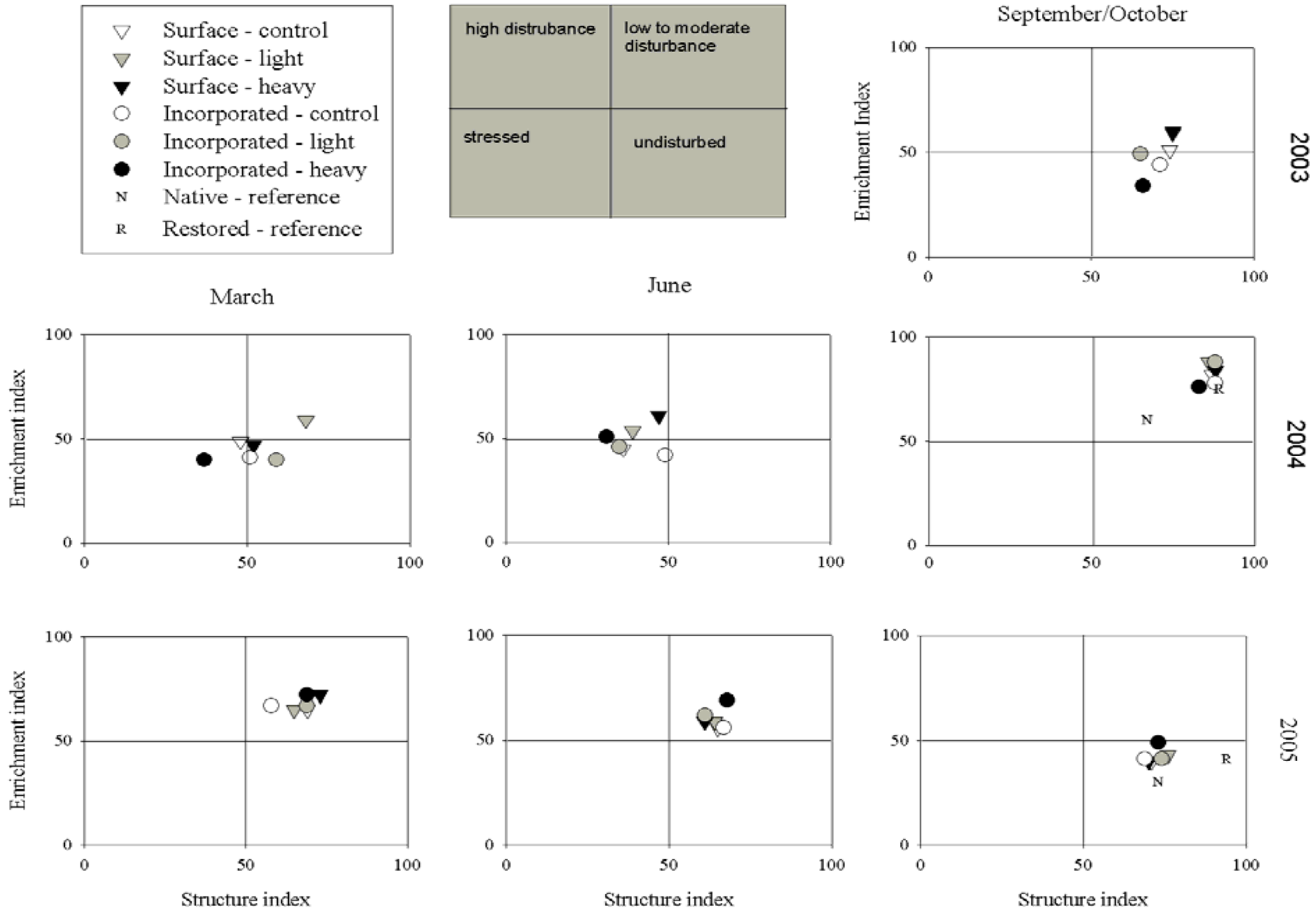


Figure 5.6. Nematode weighted faunal profiles (see Ferris et al. 2001) along axes of structure (SI) and enrichment (EI) in response to restoration treatments (mean ±SE, n = 5) and for reference areas (mean ±SE, n = 2).

Discussion

Treatment effects

The organic matter necessary to fuel the soil ecosystem in ecological restoration can be supplied by plants or as organic amendments to the soil. The quality and size of those carbon inputs constrains the activity of the soil food web by limiting energy and nutrients (Fontaine et al. 2003). This study attempted to direct the development of the soil food web in a restoration by supplying organic matter to different locations in the soil profile. In this study, the amendment treatments did not influence nematode density, diversity or trophic complexity.

There were treatment-induced differences in decomposition channel, but the response was opposite of expectations. Plots with surface-applied organic amendments had a lower channel index value and a higher enrichment index, indicating that the bacterial decomposition channel was dominant (Ferris et al. 2001). High enrichment index values are indicative of higher levels of available resources (Ferris and Matute 2003). The fungal decomposition channel was greater in the plots where organic amendments were incorporated into the soil, as indicated by the higher channel and lower enrichment index values.

The dominance of the soil decomposition channels may be related to treatment differences in plant establishment. Plants exude labile carbon that is easily utilized by bacteria and the density of bacterivores correspond with plant growth (Ferris et al. 1998, Viketoft et al. 2005). In this study, the surface-applied treatments had a greater plant density (27.7 ± 3.2 plants m^{-2} in October 2003) and had a higher enrichment index, indicating bacteria-dominated decomposition. Limited plant establishment in the incorporated plots (15.4 ± 3.2 plants m^{-2} in October 2003) may have forced the soil food web to use the imbedded amendment material, which is predominantly decomposed by fungi (Sylvia et al. 1999).

The differences in the decomposer food web were evident early in the restoration. This supports Belnap et al. (2005), who found rapid changes in the soil fauna following invasion of an exotic annual into native grass stands. In contrast, other studies suggest that it takes time for relationships between soil fauna and resources to develop following restoration or other management (Wardle et al. 1995, Ettema et al. 1998, Li et al. 2006). Korthals et al. (2001) found that the detrital food web structure was unresponsive to management changes.

Temporal changes

Although there were few treatment effects due to amount and placement of organic amendments, soil food web complexity did develop and change over time. Family richness increased through the experiment (Fig. 5.1b) and there was an annual increase in spring and fall seasonal total nematode density (Fig. 5.2). In September 2005, the landfill experiment was within the range of nematode density found at the native and restored reference sites (Fig 5.4). This suggests that landfill contamination (e.g. noxious gases), which has been found to adversely affect the population size of soil animals in other studies (Wong et al. 1992), was minimal.

There was little variation among treatments or over time in the Total Maturity Index (ΣMI). This index appears to be the most useful when comparing responses to the enrichment of readily available nutrient sources, such as the application of fertilizer or highly labile organic matter (Ferris et al. 2004). Subtle changes in management, like those promoted by ecological restoration practices, are less likely to create changes in this index. The lack of differentiation between the experiment with the native and restored reference site underscore this. Likewise, there was no differentiation among treatments for either the Weighted Faunal Profiles (Ferris et al. 2001) or Enrichment Profiles (trophic triangles) (Ferris and Bongers 2006) after June 2004.

Increases in the channel index from September 2004 to September 2005 (Fig. 5.5a) indicate that the fungal decomposition channel increased in dominance. This shift may indicate succession towards a food web similar to prairie ecosystems, which are fungal dominated (Todd 1996, Smith et al. 2003). Alternatively, this shift may indicate drought-induced changes in soil community structure, as there are similar shifts in these indices at the reference sites (Fig. 5.5).

Plant parasite changes

The most unusual aspect of this study is the high density of plant parasites, in particular members of the Hoplolaimidae family. This portion of the soil food web increased dramatically in June 2004. It also dominated the soil food web throughout 2005, when drought conditions prevailed (Fig. 5.3). Plant parasite populations in the landfill experiment were also much larger than either of the reference sites (Fig 5.4).

The dominant herbivorous nematode was the spiral nematode (Hoplolaimidae family). This nematode family is associated with tallgrass prairie ecosystems (Todd 1996). The body structure of this family is energetically efficient and is, therefore, advantageous in low nutrient ecosystems (Verschoor 2001). These herbivores are generalists and can infect exotic species that have otherwise escaped from specific indigenous belowground enemies (van der Putten et al. 2005).

The high herbivore densities were unexpected because large populations of plant-parasitic nematodes are not well-documented in restoration projects concerned with primary succession. Instead, there is an expectation that the detrital-feeding organisms arrive earlier in succession because “their table is set early”; community development is supported by indigenous carbon sources rather than plant inputs (Bongers 1990, Hodkinson et al. 2002). For example, low levels of plant parasitism were observed in reclaimed Polish ash dumps (Dmowska 2005). Stanton and Krementz (1982) found lower densities of plant parasites on reclaimed mines than on nearby native sites. Wasilewska (1994) found the ratio of detritivores to plant parasites was higher in younger meadows and older meadows had a greater proportion of plant parasites.

Deteriorating environmental conditions, such as drought, can promote high densities of plant parasites or the dominance of a single family (Wasilewska 1997, Murray et al. 2006). Drought increases soil food web dependence on plant-derived carbon by limiting decomposition (Elliot et al. 1988). Drought also increases plant stress and its vulnerability to parasitism (Verschoor 2001).

Disproportional grazing on plant species by the plant parasites may also shift plant community composition (Kardol et al. 2005, Whiles and Charlton 2006). In this case, the soil food web may be promoting the desired C_4 grasses. Early successional forbs and C_3 grasses are of higher nutritional quality and are less well-defended than late successional species (Grime 2001), and therefore, are generally favored by herbivores. Uneven consumption of plants leads to succession towards species that are better defended and are of lower nutritional quality (Scott et al. 1979, Hobbie 1992). Belowground herbivory, like aboveground grazing, can enhance secondary succession through disproportional consumption (Olff et al. 2000, Verschoor 2002, De Deyn et al. 2003, Schadler et al. 2004). These negative interactions can also enhance succession in earlier stages of ecosystem development (Kardol et al. 2006), such as mine reclamation (Hohberg 2003).

Implications for restoration

The soil food web is essential for ecosystem function. It can influence the rate and direction of ecosystem processes, such as nutrient cycling, because its organisms feed directly on the microbial community (Wardle 1999, Hodkinson et al. 2002). Belowground herbivores, such as nematodes, can control primary production (Scott et al. 1979) and plant community composition (De Deyn et al. 2003). However, the rate of succession for aboveground and belowground components of the ecosystem are not parallel because the constituent organisms have different dispersal capabilities (Kardol et al. 2005). Therefore, restoration ecologists need to develop techniques that specifically target and promote these organisms.

Conclusion

There is a need to manage the soil food web in order to optimize restoration success (Stanton and Krementz 1982, Hohberg 2003, Todd et al. 2006). The quality and size of carbon inputs, supplied by plants or organic residues, constrains the activity of the soil food web by limiting energy and nutrients (Fontaine et al. 2003). This study attempted to direct the development of the soil food web in a restoration by supplying organic matter to different locations in the soil profile. The location treatments did direct soil food web development in the first seventeen months of the restoration by promoting a bacteria channel food web in the surface treatments and a fungal dominated food web in treatments where the amendment was incorporated. However, the effects were opposite of expectations and were attenuated following high levels of plant parasitism in June 2004. Other aspects of the soil food web, such as nematode population size and family diversity, were not affected by the restoration treatments.

The high levels of generalist plant parasites in June 2004 and throughout 2005 may be preferentially infecting early successional forbs and exotic grasses, thus promoting succession to the better defended C_4 grasses. Further study is necessary to determine if the high population densities of plant parasitic nematodes observed at this site are typical in prairie restoration, and to determine how they may be manipulated to direct the outcome of plant competition at the community level.

CHAPTER VI

CONCLUSION

In this dissertation, I compare the ability of restoration treatments to alter both above- and belowground structure and function for processes and promote recovery. The treatments used in this project included altering the amount of organic amendment and its placement in the soil profile: applied to the soil surface or incorporated. I hypothesized that the surface-applied material would improve conditions for plant establishment and increase plant density, but that the incorporated treatments would promote plant survival through periods of stress and would promote plant diversity. I also expected that the size and composition of the soil food web would be greater in plots with incorporated amendments, because more of the material would be exposed to the soil biota. It was expected that the magnitude of these responses would increase with the amount of amendment applied.

The hypotheses for the plant community were largely supported; surface treatments improved plant establishment and diversity, especially the grass component of the seed mixture. The surface amendment improved conditions for germination and seedling survival, but errors in the implementation of the incorporated treatments buried the awned seed, including the grasses, to such a depth that it reduced establishment. Furthermore, the threshold for amendment amount was exceeded in the surface treatments, which had no improvement in grass establishment after 765 g m^{-2}.

The incorporated treatments were better at maintaining grass populations though drought conditions and buffering the soil from temperature extremes than the surface treatment. The threshold for amendment amount was not reached in the incorporated treatment.

The size and activity of the soil biota, however, did not adhere to expectations. Instead, soil microbial biomass and C-mineralization were greater in those treatments with higher plant density, particularly the grass component of the plant community. The location treatments also directed soil food web development in the first seventeen months of the restoration by promoting a bacteria channel food web in the surface treatments and a fungal dominated food web in treatments where the amendment was incorporated. However, the effects were opposite of expectations and were attenuated following high levels of plant parasitism in June 2004. Other aspects of the soil food web, such as nematode population size and family diversity, and other soil qualities, such as inorganic nitrogen levels, were not affected by the restoration treatments.

These results suggest that restoration managers should direct their energies into establishing and promoting a high-quality plant community to initiate overall ecosystem integrity. This can be manipulated with amendment treatments, but discretion in amount of amendment applied is required. If rapid plant establishment is required, then surface amendments are superior. However, if the amount threshold is low for the species to be established then excess amendment will reduce establishment. In contrast, incorporated amendments are superior at supporting established plant populations through stressful conditions and improve resilience. This type of treatment may be particularly useful when conditions for establishment are controlled, but long-term support is minimal. Further, there is a higher, but unknown, amount threshold. Therefore, it is critical for managers to understand which factor will limit success at the specific restoration site, conditions for establishment or long-term support, and tailor treatments accordingly.

The most intriguing part of this study was the high population density of plant parasitic nematodes. It is unclear how this was affecting the vegetation. The landfill experiment had a much greater density of plant parasitic nematodes than either of the reference areas. In contrast, its soil microbial biomass was smaller than the reference areas, and the size of the detrital food web was similar to the restoration reference. These data suggest that carbon may be moving through different pathways in the soil food web. Further research is needed to uncover their function in restoration and determine if their populations can be manipulated for use in directing plant community composition.

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