RESTORATION OF DEGRADED LAND: A COMPARISON OF STRUCTURAL AND FUNCTIONAL MEASUREMENTS OF RECOVERY

by

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ABSTRACT

The main goals of this study were to document the structural and functional recovery of differently restored areas, to understand better the relationship between the two, and to determine which types of measurements are best for assessing restoration success. To address these questions, an experimental system was created through topsoil removal and subsequent restoration in a blocked, completely randomized design using two levels of soil amendment (with or without 10 kg of leaf mulch per m^2) and three levels of seeding treatment (no seed, a standard reclamation mix, and an alternative, wildflower dominated reclamation mix). All measurements were designed to document responses due to restoration treatment in comparison to adjacent, undisturbed, reference sites.

Vegetation structure in amended sites, as measured by total vegetation cover and species richness, recovered to levels similar to references within the two years of the study. Plant community composition did not develop similarity to references in any experimental treatments. Both soil amendment and seeding type affected cellulose decomposition rates, with amended plots showing higher decomposition rates than unamended, and seeded plots exhibiting higher rates than unseeded. Enzyme activities were largely determined by soil amendment, but the reference plots consistently had higher enzymatic activity. Amended sites exhibited significant increases over time in soil respiration, reaching or surpassing the rates observed in reference areas. Methane oxidation rates were generally increased in disturbed plots compared to undisturbed references due to increased atmospheric diffusion into the soil. Amended areas exhibited depressed rates relative to unamended, and seeding level had no significant effect on methane oxidation. Over all measurements, restoration of ecosystem function was most facilitated by the addition of the soil amendment. Seeding treatment significantly altered the resultant plant community, which may have substantial, long-term consequences for succession. The inclusion of functional parameters into restoration assessment provides for better overall information concerning ecosystem performance and may add to the ability to predict long-term success of restoration efforts.

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Science is a process of thinking that has developed to the point that a huge body of individuals now make up the "scientific field". At the root level, however, are still the individual people who require much more than just a hypothesis and an experimental design in order to live a rewarding life. I have been wonderfully blessed with a loving family that has supported me in countless ways as I explore the world. Now, I am doubly blessed because Tricia Turner has allowed me to explore the world along with her. Her love and support throughout this degree program has perhaps been its own, best reward. Thank you.

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JUDGING RESTORATION SUCCESS: OVERVIEW AND EXPERIMENTAL DESIGN

Introduction

The relationship between human society and natural systems has changed dramatically since the agricultural and industrial revolutions. As human population pressures have increased the demand on ecological systems, efforts have been made to "fix" the impacts that society causes. Over time, the science of restoration ecology has responded and developed into a more established field (Cairns and Heckman 1996, Hobbs and Norton 1996). Bradshaw (1983) has stated that restoration ecology is the acid test for understanding ecosystems, since it is necessary to understand something before it can be put back together. This statement is at the root of the scientific interest in ecological restoration, considering that community- and ecosystem-level theories are perhaps best tested in a manipulative context (Jordan et al. 1987). However, from a practical standpoint, Earth contains very few areas that have not been altered in some way by human activities (Cairns 1995). The industrial activities of the 19th and 20th centuries, while offering innumerable gains to society, effectively began an uncontrolled, manipulative experiment on the biosphere level (Farvar and Milton 1972). Society is beginning to realize that repairing the damage already done to its ecological support system is necessary, especially since this same support system must also be used to better the human condition. Restoration ecology is the outgrowth of this realization.

Before restoration can become a well integrated part of the economy, some normative, standards-based methods must be developed for judging the effectiveness of restoration practices. Similar to the field of engineering, ecological restoration must become a robust practice with substantial oversight and redundancy. This mandate calls for ecological research that will clarify the ramifications of human impacts on ecological systems. This dissertation research addresses the problem of how to judge effectively the success of a restoration project. Ecological systems such as upland forests or wetlands have a recognizable structure that is often the final goal of restoration attempts. However, the underlying function of the system and its relation with its surrounding landscape are also of major concern in restoration projects. These ecological functions are the basis for all ecosystem services, which are an essential component of human society's life support system (Cairns 1996, Ehrlich and Mooney 1983, Westman 1977).

The goal of this study was to determine the relationship between structural and functional measurements of ecosystems for estimating the effectiveness of ecological restoration. The study traces the initial recovery of disturbed old field systems that were restored using different seed mixes and soil amendment levels. Throughout the first 2 years of recovery, both structural and functional measurements were made in the recovering areas as well as in adjacent, undisturbed reference areas.

Defining Restoration

In a field encompassing as many disciplines as restoration ecology, an unequivocal definition of goals and directions is necessary. Restoration ecology can be defined as the

scientific study of human-facilitated recovery processes. From the discussion in the literature on this topic, two main emphases have developed: goal-oriented restoration that focuses on the science of reconstructing functioning ecological systems, and process-oriented restoration that deals with the integration of ecological principles and human social systems. Rather than splitting the field, this dichotomy clarifies the scientific and social nature of restoration ecology and further emphasizes that both factors must be considered equally.

The National Research Council (NRC 1992) illustrates a goal-oriented definition of restoration: "the return of an ecosystem to a close approximation of its condition prior to disturbance." While attractively simple at first, this definition presents two questions that are at the core of restoration ecology. First, what frame of reference should be used as the predisturbance condition? A true predisturbance condition almost never exists; some approximation must be chosen, which is often difficult in areas of extreme disturbance (e.g., urbanized landscapes). Second, what comparisons should be made between recovering and reference areas? This issue is at the root of this study; the choice of ecosystem characteristics can manifestly change the outcome of the comparison.

A paramount value of a goal-oriented definition of restoration is its emphasis on restoring a self-maintaining and/or self-perpetuating ecosystem (i.e., restoring dynamic processes characteristic of all mature ecosystems which, over long periods of time, become characterized by ecologically acceptable structure and function despite species turnover). Another emphasis is the integration of a restored patch into the larger ecological landscape in which it occurs. Difficulty

in defining such phrases as “acceptable structure and function” or “integration into the surrounding landscape” adds to the task of restoration ecologists. However, only by addressing, defining, and meeting such stringent goals will restoration ecologists be able to judge their success objectively.

The goal-oriented NRC definition provides a starting point for objective research into the design of ecological restoration. However, this definition does not address many of the causes underlying the need for restoration. A process-oriented definition of restoration shifts the emphasis from replication of predisturbance condition and allows restoration to encompass all actions necessary to ensure the return of a natural ecological state. Jackson and colleagues (1995) define restoration as "the process of repairing damage caused by humans to the diversity and dynamics of indigenous ecosystems." This concept places the goal-oriented tenets of ecosystem reconstruction and the judgment of ecological integrity into an applied perspective that concentrates on facilitating recovery without requiring historical comparisons.

For the purposes of this dissertation, as in most practical applications of the term, restoration integrates components of both definitions. The term will primarily be used in the process-oriented context to depict the remediative activities undertaken, but these activities are meant to bring about a larger, goal-oriented restoration. The main difference in this situation is the choice of the goal. Using the NRC definition, the restoration goal in this study area should be an oak and hickory dominated hardwood forest. To better approximate the time scales that are most often applied in practical situations, the restoration goal for this study will be the condition

of the study site immediately before the experimental disturbance. By choosing this goal, the study can objectively compare the disturbed and undisturbed areas, thereby allowing conclusions to be drawn that are not possible in naturally occurring situations (i.e., situations where the disturbance event is not experimentally controlled).

Judging Restoration Success

Perhaps the most pressing problem when studying the recovery of a disturbed area is the choice of a frame of reference for judging success. This frame of reference is evident in many of the problems inherent in defining the term restoration and the goals of a restoration project. The predisturbance state of an area is often unknown, as most disturbance events are not preceded by thorough ecological surveys (Cairns 1991). In many situations, such as the tall grass prairie of the Great Plains, it is difficult to find any of the predisturbance ecosystem. Furthermore, restoration to such predisturbance states is usually unattainable due to the dynamic state of natural systems; vegetative and faunal communities constantly change over time so that the complexity of events that precipitated a particular condition can never be reconstructed (Pickett and Parker 1994).

In practical situations, however, it is important to select some reference area, however imperfect, to facilitate baseline studies and the monitoring of success (Aronson et al. 1995). Therefore, most restoration projects pursue an approximation of predisturbance condition that is congruent with the current surrounding landscape. Thus, judging restoration success by assessing

return to approximate predisturbance condition is highly dependent on which component of the system is studied. This dependency can be shown by the conflicting results generated by studies that focus on different structural components as indicators of ecological recovery (Hutson 1990, Bhatt and Soni 1992, Holl and Cairns 1994).

To address this problem, Aronson and colleagues (1993a, b) move beyond single component comparisons to a matrix of measurements that document the structural and functional recovery of disturbed systems. This synthetic approach incorporates measures, called vital ecosystem attributes, of current and potential future plant structure, faunal relationships, soil condition, water and nutrient availability, and microsymbiont effectiveness to create a more inclusive picture of the recovering landscape. The present study uses an approach similar to that of Aronson and colleagues by aiming to compare structural and functional measurements in disturbed and undisturbed areas. The lack of predisturbance information in restoration situations dealing with natural disturbances makes this type of comparison impossible in most cases. However, because this research includes an artificial, homogeneous disturbance with undisturbed, adjacent reference plots, direct comparisons can be made between disturbed and undisturbed areas.

General Methods and Experimental Design

This study has been conducted entirely on an experimental field plot study site located adjacent to the Virginia Polytechnic Institute and State University (VPI&SU) debris landfill at the

intersection of Route 460 and Prices Fork Road, Blacksburg, Virginia. The soils can be classified as Ernest series, fine-loamy, mixed, mesic Aquic Fragidults with some characteristics of the Groseclose series, fine-loamy, mixed, mesic Typic Hapludults. The experimental area had been a hay field for at least 20 years before the beginning of the study.

On July 22, 1994, the first 20 cm of soil were removed from the site. The area was then plowed to approximately 50 cm and disked. These processes effectively removed the vegetational community and the majority of the root biomass; the following two months showed no regrowth on the site. Thirty, 4-m x 4-m experimental plots were marked off, separated by 1-m walkways. The walkways were mulched, tilled, seeded with tall fescue, and rolled to establish a homogeneous buffer strip around all of the plots. The walkways were mowed every week throughout the growing season during the study period. Using a randomized complete block design (two soil amendment treatments x three seeding treatments x five blocks, blocked against edges), treatments were completely installed on September 30, 1994 (Figure 1.1). The soil amendment treatments were either with or without 10 kg (field wetness) of decomposed leaf mulch/m^2. Two seed mixtures were chosen. The "standard" mixture was based upon the revegetation mixture used at the Roanoke Regional Landfill, chosen because of its known ability to colonize waste areas (Sabre 1994). The "meadow" mixture was originally designed as an alternative revegetation mixture that emphasized wildlife habitat provision on surface mined areas (Heckman et al. 1996). The seeding treatments are summarized in Table 1.1. None of the plots received any inorganic fertilization treatments so as to limit the experimental design complexity.

Table 1.1 - Experimental seeding treatments.

Treatment	Species Name	Common Name	Seeding Rate (# PLS/m^2)
"Standard" Mix	*Festuca arendinacea*	Ky31 fescue	570
	Lespedeza cuneata	Sericea lespedeza	412
	Lolium multiflorum	Annual ryegrass	634
	L. perenne	Perennial ryegrass	634
	Agrostis alba	Red top	665
	Secale cereale	Abruzzi ryegrass	190
	Coronilla varia[*]	Crownvetch	63
"Meadow" Mix	*Centaurea cyanus*	Bachelor's button	222
	Coreopsis lanceolata	Lance-leaved coreopsis	222
	C. tinctoria	Plains coreopsis	222
	Echinacea purpurea	Purple coneflower	127
	Helianthus annuus	Sunflower	127
	Hesperis matronalis	Dame's rocket	127
	Lupinus perennis	Perennial lupine	63
	Oenothera speciosa	Evening primrose	222
	Rudbeckia hirta	Black-eyed Susan	222
	Silene armeria	Catchfly	349
	Andropogon gerardii	Big bluestem	317
	Panicum virgatum	Switchgrass	317
	Schizachrium scoparius	Little bluestem	317
	Trifolium pratense[*]	Red clover	317

[*] Legumes were not inoculated with symbiotic bacteria

Four reference plots were established in an undisturbed area immediately adjacent to the degraded area. Table 1.2 lists the nomenclature that will be used throughout this document for referring to the experimental and reference plots.

Table 1.2 - Summary of abbreviations used to refer to the experimental and reference plots.

Abbreviation	Plot description
None, none	No soil amendment, no seeding treatment
None, std	No soil amendment, seeded with the "standard" reclamation mixture
None, mead	No soil amendment, seeded with the "meadow" mixture
Amd, none	With soil amendment, no seeding treatment
Amd, std	With soil amendment, seeded with the "standard" reclamation mixture
Amd, mead	With soil amendment, seeded with the "meadow" mixture
Reference	Undisturbed reference

Observations of the experimental plots began in March 1995. Each plot was divided into usage zones to ensure that any destructive sampling would not interfere with other sampling methods (Figure 1.2). The structural measurements included plant community observations (per species % cover, total vegetative cover, species richness), total soil combustible matter by loss on ignition, and total soil moisture by dried weight loss. Functional measurements included system respiration by sealed chamber incubation, CH_4 flux by sealed chamber incubation, and cellulose decomposition rate using weight loss of artificial cellulose substrates over time. Soil enzyme activity levels for beta-glucosidase and dehydrogenase were also measured and can be considered either functional or structural measurements. Details on the individual assays are provided in the following chapters.

The goals of this research were to document the structural and functional recovery of the differently restored areas, to understand better the relationship between the two, and to

determine which measurements or what combination between the two are best for judging restoration success. This information is necessary for designing future restoration projects that are optimized for economic and ecological efficiency.

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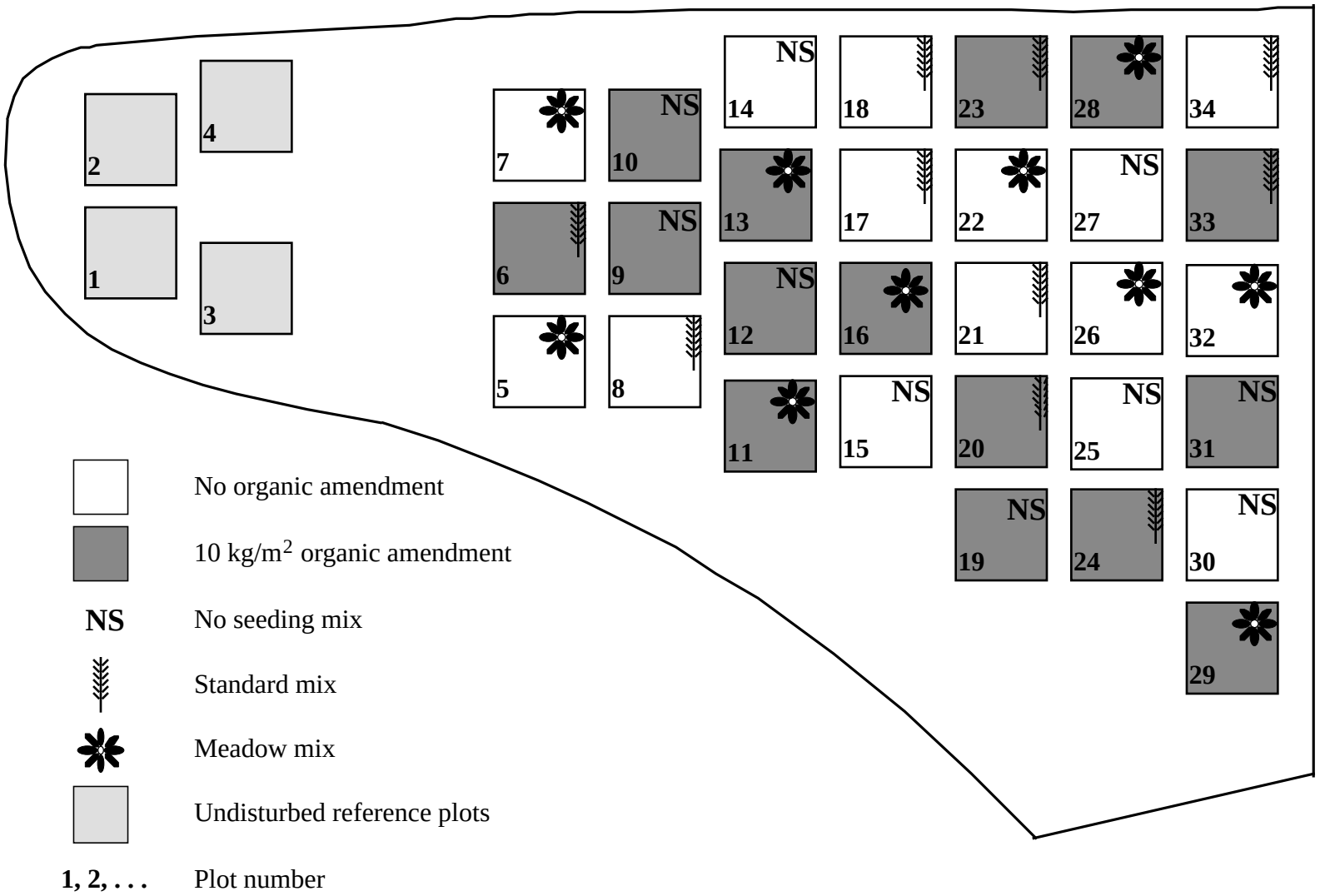

Figure 1.1 - Schematic drawing of the study site with the experimental design

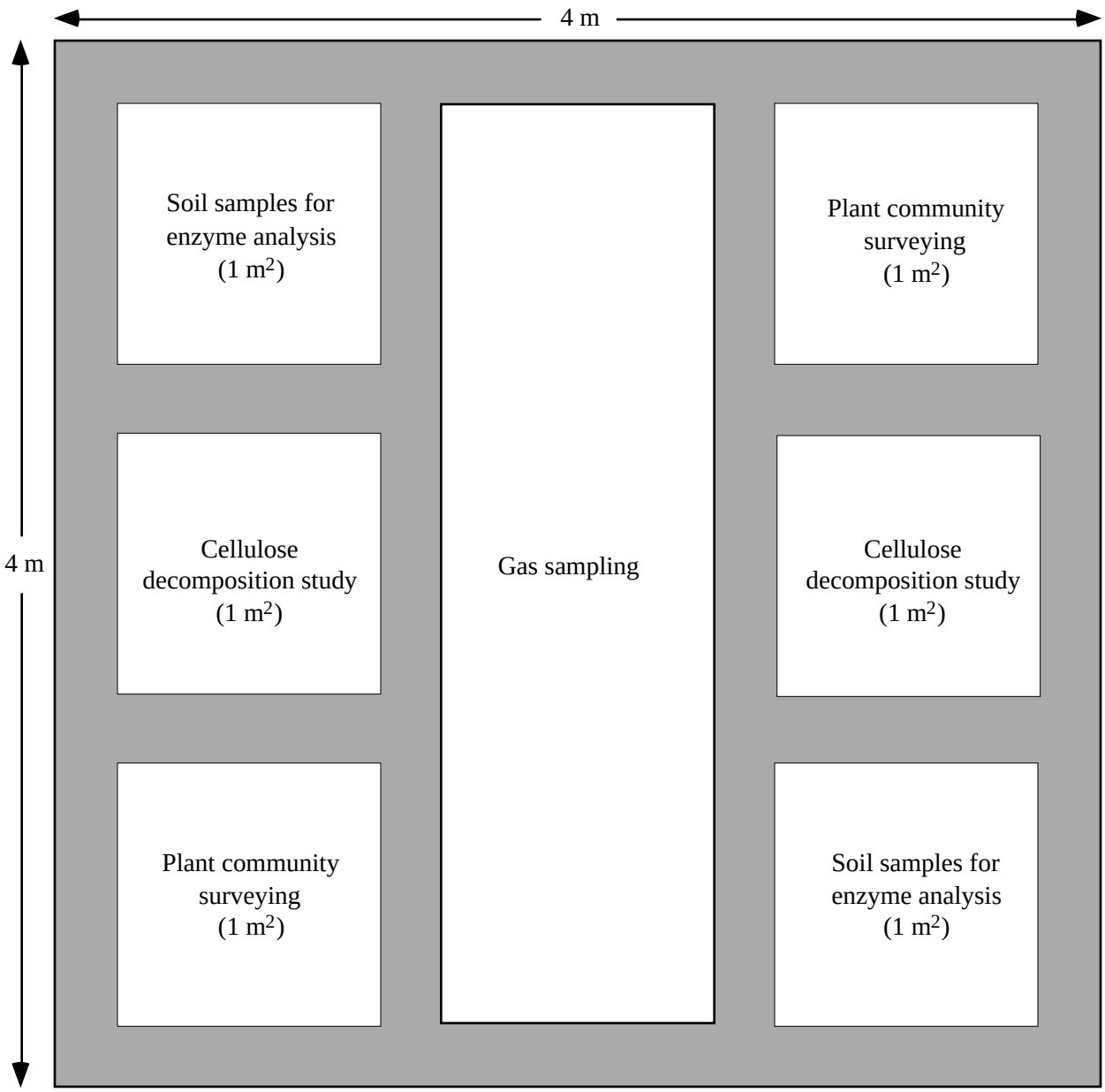

Figure 1.2 - Schematic drawing of field plot usage divisions

Chapter 2

VEGETATIONAL DYNAMICS IN DIFFERENTLY RESTORED TERRESTRIAL COMMUNITIES

Introduction

Restoration ecology in terrestrial systems is often viewed as a vegetation science with its genesis in a wide array of investigations that range from research on succession conducted by Aldo Leopold at the University of Wisconsin, Madison Arboretum to Gifford Pinchot's pioneering work in conservation forestry. This botanical perspective emphasizes the importance of plant communities as structural components of ecosystems. Plants are by far the most important means of primary production, and, therefore, the recovery of an adequate plant community is central to any plan for restoring degraded land (Hobbs and Norton 1996). Although primary productivity is arguably the most prominant ecological function of plants, the specific structure of plant communities can play crucial roles in controlling ecosystem development. This factor makes community composition an area of special concern for restoration ecologists (Drake 1990, Chapman and Younger 1995, Heckman and Cairns 1997).

Common goals for vegetation establishment in restoration situations usually include the establishment and maintenance of sufficient ground cover to control erosion, a degree of resistance to invasion by exotic colonizers, and low maintenance costs (Luken 1990). Many restoration efforts, especially those intended only to satisfy regulatory requirements, aim specifically at solving short-term problems. These efforts can have considerable consequences on

the long-term successional trajectory of the site. The introduction of *Pueraria lobata* (kudzu) to control erosion on road cuts provides an excellent example of unexpected, negative, long-term consequences. *Pueraria* exhibits an amazing capacity for overtaking and choking out other vegetation (Frankel 1989, Carter et al. 1989). The introduction of this plant, which began with the best of intentions, satisfied its original goals, but also effectively halted succession.

The potential for drastic consequences, such as in the case of kudzu, emphasizes the importance of focusing on the relationship between revegetation and the desired final plant community. In a restoration situation, initial revegetation decisions need to be made with future succession in mind. This stipulation does not mean that each situation must be uniquely designed. Economic realities do not allow for the custom tailoring of revegetation mixes to each specific site; standardized mixtures are a necessity (Gilman et al. 1985, Hill and Grim 1977). Intelligent design of standard mixtures, however, can satisfy long- and short-term goals by taking successional processes into account. Primary revegetation mixtures should be composed of pioneer species with a shorter life span and high rate of turnover to allow for replacement by later successional species that are longer lived and more resistant to turnover (Leps 1987).

The goals of this research were to use these precepts for judging the restorative success of the six treatment combinations installed in the expermental design when compared to the undisturbed reference plots (see Chapter 1). Specific goals were to document the community characteristic of each treatment combination, to observe the changes in plant community over time as the plots recovered from the initial disturbance, and to compare the recovering

Table 2.1 - Hypothesis statements for plant community structure observations.

Number	Hypothesis
1	Revegetation mixture and soil amendment status will be strong determinants of the speed at which the experimentally disturbed plots regain total cover and species richness.
2	Revegetation mixture and soil amendment will determine the rate of colonization by pioneer species for the disturbed plots.
3	Plots revegetated with the wildflower/grass mixture will maintain a higher level of diversity than the standard seeded plots.

communities with the adjacent, undisturbed reference plots. Specific hypothesis statements are shown in Table 2.1. All observations are meant to distinguish those restoration treatments promoting a plant community that provides adequate cover, the lack of a tendency to hinder succession, and an overall similarity to the predisturbance plant community.

Methods

Field methods

Two subsamples per plot were taken from the plant community in each experimental plot on a monthly basis from April until August 1995 and from April until October 1996. Total percent cover and cover of individual species were estimated using the relevé method with 1.0-m^2 quadrats (Mueller-Dombois and Ellenberg 1974). The quadrats were fixed in two locations in the

experimental plot 0.25 m from the edge and independent of sampling areas for the other analyses (see Figure 1.2). Importance of individual species was assessed using relative cover estimates and were converted to van der Maarel's scale of cover classes, a modification of the Braun-Blanquet method (Table 2.2) (Jongman et al. 1995).

Plants were identified to the species level as their development throughout the year allowed. Individual plants not identifiable were given a pseudotaxon until identification was possible later in the year. Nomenclature follows Radford et al. (1968) and Wofford (1989).

Soil physical measurements

Measurements of soil moisture and soil weight lost on ignition (a measurement of soil organic matter) were taken concurrent with monthly vegetation sampling, monthly soil enzyme

Table 2.2 - Cover scale of Braun - Blanquet, extended to a combined cover/abundance scale by Barkman et al. (1964) and recoded by van der Maarel (1979) (from Jongman et al. 1995).

Braun-Blanquet Symbol	Cover (%)	Barkman Symbol	Cover (%)	van der Maarel's Scale
		r	rare	1
		+	few	2
1	< 5	1	many	3
		2m	abundant	4
2	5 to 25	2a	5 - 12.5	5
		2b	12.5 - 25	6
3	25 to 50	3		7
4	50 to 75	4		8
5	> 75	5		9

assays, and all weekly or biweekly gas sampling dates (see Chapters 3 and 4). Three, 1.5 x 10-cm soil samples were removed from each experimental plot using a soil probe and mixed in one sample bag. Moisture content was determined by calculating the weight lost after a 24-hr drying period at 100°C. Soil organic matter lost on ignition was estimated by calculating the total weight loss of dry soil after ignition at 550°C for 4 hr (Ohtonen et al. 1994). This measurement includes not only the humic soil organic matter, but the whole organic content of soil. For the purposes of this dissertation, "soil organic matter" or "organic matter lost on ignition" are defined as the whole soil organic content as measured by this method. Soil nutrients were analyzed from soils sampled in March 1997. Analyses for soil pH, P, K, Ca, Mg, Mn, and Zn were conducted by the Soil Testing and Plant Analysis Laboratory of the Cooperative Extension Service at VPI&SU.

Numerical analyses

Treatment effects on species richness and total percent cover were analyzed using analysis of variance (ANOVA). Seed mixture and soil amendments were main effects. The experimental design included edge as a blocking factor to account for possible edge effects. One-way ANOVA was used to test for differences between treatment combinations and the reference plots. Tukey's HSD test was used for multiple comparison tests. All statistical analyses were performed using the Minitab statistical analysis package (Minitab, Inc.).

Changes in vegetational community composition over time were analyzed using principal components analysis (PCA) of the van der Maarel's cover class by site matrix. The PCA used

the correlation matrix based on variance in plant abundance and composition. For each sampling date, principal components were calculated and correlated with the individual species cover class values. The dominant taxa for each sampling date were chosen by correlation with the first two principal component axes ($r > 0.5$ was used as the criterion for importance). The analysis was then repeated using only the dominant taxa. To quantify change in plant community over time, Euclidean distance was calculated between treament combinations. The average positions of group means in the PCA ordination space approximates these Euclidean distances (Dunn and Sharitz 1987).

Results

Table 2.3 shows means, medians, and ranges for all community structure variables and soil physical parameters over all vegetation sampling dates and treatment groups. Table 2.4 summarizes the soil nutrient data for all treatment combinations. Vegetational community

Table 2.3 - Means, medians, and ranges of vegetational community and soil physical data.

Variable	Units	Mean	Median	Range
Species richness (VSR)	#	7.42	8	0 to 18
Average total cover (ATC)	%	54.5	47.5	1 to 100
Soil moisture (H2O)	%	16.83	16.79	6.26 to 28.75
Soil weight lost on ignition (LOI)	%	3.12	2.84	0.42 to 11.16

Table 2.4 - Summary of soil nutrient data for all treatment combinations (mean ± SD). Values followed by the same letter are not significantly different using Tukey's HSD with a family error rate of 0.5 (individual error rate = 0.00366).

Treatment Combination	pH	ppm P	K	Ca	Mg	Zn	Mn
None, none	5.82 ± 0.16a	23.2 ± 13.39a	52.8 ± 11.8a	1449 ± 177a	172 ± 28.4a	7.76 ± 4.36a	25.8 ± 5.89a
None, Std	5.96 ± 0.05ab	21.6 ± 4.56a	64.8 ± 17.5a	1545 ± 196a	184 ± 36.9a	8.56 ± 1.89a	35.2 ± 13.11ab
None, Mead	5.88 ± 0.08ab	16.8 ± 1.38a	59.2 ±14.8a	1478 ± 104a	179 ± 34.4a	6.96 ± 2.13a	24.16 ± 4.42a
Amd, None	6.668 ± 0.08c	30.4 ± 8.29ab	147.2 ±15.6b	2947 ±330b	451 ± 36.3b	10.16 ± 1.66a	56.64 ± 6.45c
Amd, Std	6.32 ± 0.13c	36.8 ± 5.21ab	145.6 ±20.3b	3072 ± 293b	446 ± 34.7b	9.52 ± 3.24a	62.0 ± 4.52c
Amd, Mead	6.56 ± 0.11c	31.2 ± 8.19ab	164 ±37.7b	3100 ± 575b	441 ± 56.7b	11.44 ± 5.74a	56.8 ± 10.4c
Reference	6.05 ± 0.06bc	40.0 ± 3.27b	123.0 ± 26.4b	2054 ± 160ab	342 ± 47.8b	12.9 ± 3.55a	45.1 ± 8.27b

structure on all experimental plots was significantly different than reference plots at the beginning of 1995. Figures 2.1 and 2.2 show the trends in average total cover over 1995 and 1996. Average total cover was highly correlated with time since disturbance (r = 0.99). By May 1996, the amended and seeded sites had developed an average total cover indistinguishable from the reference plots. By June 1996, all amended sites had developed a cover similar to the reference areas.

The "amd, mead" plots started with higher species richness than the reference plots due to the high diversity of the seed mixture itself (Figure 2.3). Species richness showed less of a correlation with time since disturbance (r = 0.72). All plots showed similar richness values on at least one sampling date, with the later dates showing little or no differences between treatments (Figure 2.4).

Table 2.5 summarizes the significance of experimental treatments and design elements over time. On all sampling dates, subsampling and blocks had no significant effect on either average cover or species richness. Soil amendment and the seed mix treatment were highly significant factors in determining both average total cover and species richness. Both factors became considerably less important for determining species richness as time progressed.

Soil organic matter lost on ignition and soil moisture over 1995 and 1996 are shown in Figures 2.5 and 2.6. The apparent increase in organic matter over 1995 is probably an artifact of the small sampling size as it does not appear in the more frequent soil measurements in Chapters 3 and 4. Analysis of covariance with organic matter lost on ignition and soil moisture showed

Table 2.5 - Summary of two-way ANOVA p-values for treatment effects and interactions.

Factor	3/95	5/95	6/95	7/95	8/95	5/96	6/96	7/96	8/96	10/96
Average Cover										
Amendment	***	***	***	***	***	***	***	***	***	***
Seed Mix	***	***	***	***	*	***	*	***	***	***
Amendment * Seed Mix	***	ns	ns	ns	*	ns	ns	ns	ns	ns
Sp. Richness										
Amendment	-	***	***	***	***	***	*	**	ns	ns
Seed Mix	-	***	***	***	*	*	ns	ns	ns	ns
Amendment * Seed Mix	-	ns	***	***	ns	ns	*	***	*	ns

ns = p>0.05, *p<0.05, **p<0.001, ***p<0.0001

Table 2.6 - Summary of analysis of covariance of soil organic matter and soil moisture with average total cover and species richness.

Factor	6/95	7/95	8/95	5/96	6/96	7/96	8/96	10/96
Average cover								
Org. matter	ns	ns	ns	ns	ns	*	ns	*
Moisture	ns	ns	ns	ns	ns	*	ns	*
Sp. Richness								
Org. matter	ns	ns	ns	ns	ns	ns	ns	ns
Moisture	ns	ns	ns	ns	ns	ns	ns	ns

ns = $p>0.05$, *$p<0.05$

little to no explanatory capacity for these variables. Significant covariation was only seen in July and October of 1996 (Table 2.6).

Figures 2.7 and 2.8 show locations of the experimental and reference plots along the first two axes of PCA ordination space. A complete list of species and their prevalence in each treatment combination is given in Appendix 1. The PCA ordination axis 1 explained an average of 34.8% of the variance, and axis 2 explained an average of 20.8% (55.6% total). The main trend over the 2-year study period shows the “meadow” seeded sites tend towards being farthest from the reference plots while the non-seeded sites tend to be the most similar to the references.

Amendment with soil organic matter generally amplifies this tendency. Similarity, or closeness, of sites is quantified in Table 2.7 using average Euclidean distances between treatment combinations for 1995 and 1996.

Table 2.7 - Average Euclidean distances between treatment combinations for monthly averaged species compositional structure over 1995 and 1996.

1995	None, None	None, Rec	None, Mead	Amend, None	Amend, Rec	Amend Mead
None, Rec	5.97 ± 0.31					
None, Mead	6.22 ± 0.53	8.32 ± 0.45				
Amend, None	7.02 ± 0.46	8.93 ± 0.43	8.98 ± 0.64			
Amend, Rec	10.33 ± 0.44	5.80 ± 0.30	11.45 ± 0.47	10.78 ± 0.54		
Amend, Mead	10.91 ± 0.85	11.73 ± 0.72	6.68 ± 0.34	11.01 ± 1.19	12.85 ± 0.63	
Reference	9.44 ± 1.00	10.91 ± 0.83	10.90 ± 1.13	9.27 ± 0.78	13.47 ± 0.87	13.87 ± 1.22

1996	None, None	None, Rec	None, Mead	Amend, None	Amend, Rec	Amend Mead
None, Rec	6.79 ± 0.24					
None, Mead	7.58 ± 0.10	9.33 ± 0.22				
Amend, None	7.03 ± 0.27	8.59 ± 0.16	9.39 ± 0.23			
Amend, Rec	10.98 ± 0.23	8.11 ± 0.41	12.00 ± 0.26	11.39 ± 0.45		
Amend, Mead	11.90 ± 0.44	12.47 ± 0.38	6.14 ± 0.31	11.37 ± 0.71	13.47 ± 0.40	
Reference	10.51 ± 0.60	10.69 ± 0.58	12.45 ± 0.55	11.83 ± 0.45	13.54 ± 0.54	15.07 ± 0.46

A total of 69 species was found across all experimental and reference plots during the study period. A complete listing of species by treatment combination is given in Appendix 1. Table 2.8 summarizes the germination and growth of the seeded species in both "standard" and "meadow" mixtures. The undisturbed reference plots were dominated by grasses including sheep's fescue (*Festuca ovina*), green foxtail (*Setaria viridis*), sweet vernal grass (*Anthozanthum odoratum)*, and redtop (*Agrostis alba*). Also included were a number of herbaceous dicots common to old fields such as Queen Anne's lace (*Daucus carota*), English plantain (*Plantago lanceolata*), and yellow wood-sorrel (*Oxalis stricta*). Experimental plots with no amendment and no seeding (none, none) were characterized by a number of weedy annuals and perennials, including tall goldenrod (*Solidago altissima*), frost aster (*Aster pilosa*), lesser stichwort (*Stellaria*

Table 2.8 - Summary of germination and importance of seeded species across unamended and amended plots. Importance is defined as making up more than 1% of the average community composition over the entire study period.

Treatment	Species Name	Germination		Importance	
		Unamended	Amended	Unamended	Amended
"Standard" mix	*Festuca arendinacea*	*	*	*	*
	Lespedeza cuneata	*	*	*	
	Lolium multiflorum				
	L. perenne	*	*	*	*
	Agrostis alba	*			
	Secale cereale	*	*	*	*
	Coronilla varia	*	*	*	*
"Meadow" mix	*Andropogon gerardii*				
	Centaurea cyanus	*	*	*	*
	Coreopsis lanceolata	*	*	*	*
	C. tinctoria	*	*	*	*
	Echinacea purpurea	*	*		
	Helianthus annuus	*	*		
	Hesperis matronalis	*	*	*	*
	Lupinus perennis	*	*	*	*
	Oenothera speciosa		*		
	Panicum virgatum				
	Rudbeckia hirta	*	*	*	*
	Schizachrium scoparius				
	Silene armeria	*	*	*	*
	Trifolium pratense	*	*	*	*

gramania), winter cress (*Barbarea vulgaris*), and red fescue (*Festuca rubra*). Plots with no amendment but seeded with the "standard" mixture ("none, std") were dominated by the planted species KY-31 tall fescue (*Festuca arendenaciea*), Abruzzi ryegrass (*Secale cereale*), perennial ryegrass (*Lolium perenne*), and white clover (*Trifolium repens*). Important invading species in

the unamended, "standard" seeded plots included frost aster (*Aster pilosus*) and tall goldenrod (*Solidago altissima*). Unamended plots planted with the "meadow" mixture ("none, mead") were typified by planted species such as lance-leaved coreopsis (*Coreopsis lanceolata*), bachelor's button (*Centaurea cyanus*), catchfly (*Silene armeria*), and black-eyed Susan (*Rudbeckia hirta*). These sites were commonly invaded by frost aster (*Aster pilosus*) and ox-eyed daisy (*Chrysanthemum leucanthemum*).

Those sites that were not planted, but were amended with decomposed leaf mulch ("amd, none"), were dominated by white clover (*Trifolium repens*), wild lettuce (*Lactuca* spp.), frost aster (*Aster pilosus*), tall goldenrod (*S. altissima*), and green foxtail (*S. viridis*). The amended plots that were seeded with the "standard" mixture ("amd,std") were clearly dominated by crown vetch (*Coronilla* varia), which averaged over 70% coverage in the last months of 1996. Other planted species that were important components of the amended "standard" seeded community included Ky-31 tall fescue (*Festuca arendenacia*), Abruzzi ryegrass (*Secale cereale*), perennial ryegrass (*Lolium perenne*), and sericea lespedeza (*Lespedeza cuneata*). No invading species made up more than 5% of the total community for this treatment combination. The amended plots planted with the "meadow" mixture ("amd,mead")were characterized by the planted species, such as lance-leaved coreopsis (*Coreopsis lanceolata*), red clover (*Trifolium pratense*), black-eyed Susan (*Rudbeckia hirta*), bachelor's button (*Centaurea cyanus*), and dame's rocket (*Hesperis matronalis*). Similar to the "amd,std" plots, no invading species made up more than 5% of the total community.

Discussion

Early successional stages were marked by widely dispersed pioneer species exploiting the community niches left empty by the disturbance (Myster and Pickett 1994, Connell and Slatyer 1977, Luken 1990). The goal of any restoration project must be to accelerate this process by (a) increasing the colonization rate by providing suitable seed source and/or (b) decreasing the decolonization rate or failed colonizations by removing impediments to colonization (Harris et al. 1996, Hobbs and Norton 1996). When judging restoration success, it is necessary to weigh the merit of any restoration efforts in comparison to the successional processes that would take place regardless of any human intervention. In this study, the plots "none, none" plots served as the successional controls and the benchmark with which the restoration treatments could be compared. Within this context, the addition of soil amendment is the primary factor in accelerating initial colonization. Amended plots showed a rate of cover increase 1.5 times that of unamended plots (Table 2.9, Figure 2.9). These plots exhibited vegetation essentially equal to the reference sites less than 2 years (approx. 600 days) after the disturbance and revegetation activities.

The plant community as represented by the PCA ordinations does not show a similar recovery however (Figures 2.7, 2.8). After 2 complete years of recovery, the experimental plots show very little similarity to the reference plots compositionally. This is not surprising since the experimental seedings were not designed to mimic the predisturbance community, a situation

Table 2.9 - Summary of recovery of total average cover by treatment combination..

Treatment Combination	Slope (rate of recovery)	r^2
None, None	0.078	0.97
None, Rec	0.1	0.96
None, Mead	0.096	0.92
Amend, None	0.146	0.94
Amend, Rec	0.152	0.97*
Amend, Mead	0.148	0.96*

* Linear regression performed on data series truncated after reaching 100% cover.

which is most often observed in reclamation (Cairns 1989). A more interesting statistic, which is of more concern for future succession, is the ability of the different restoration treatments to allow for successful new colonizing species. Species richness values were highly similar across treatment combinations, but sites seeded with the "standard" seeding mixture were largely dominated by crown vetch (*Coronilla varia*), which represented 70 - 80% of the total cover of "amd, std" plots during the later months of the study. This dominance of a single species impedes species turnover and can effectively halt or significantly slow succession. Conversely, "amd, none" plots developed a community composed entirely of pioneer colonizers from the surrounding landscape. This increased cover in amended plots may also be due to a seed bank contained in the decomposed leaf mulch amendment.

Another issue of increasing concern is the homogenization of plant communities over large regions. Of all species observed across all experimental and reference plots, 58% were not originally part of the flora of the Blue Ridge province (Wofford 1989). This problem has been thoroughly investigated (McKnight 1991, Dudgeon 1992) but has had few solutions suggested (e.g., Tucker and Richardson 1995). One step towards ameliorating the situation would be to regionalize standard revegetation mixtures so that they are composed entirely of native plants. The "standard" mixture used in this study, based upon the Roanoke Regional Landfill revegetation mixture, was made up entirely of introduced species. The "meadow" mix, although designed to be more consistent with the southwestern flora, contained six introduced species of a total fourteen. Regionalized, native revegetation mixtures could slow the spread of cosmopolitan species and help to maintain local community heterogeneity.

Conclusions

Vegetation structure is a primary concern in all restoration efforts and must play an important role in judging restoration success. General structural parameters, such as total plant cover and overall species richness, can easily recover from disturbance within 2 years with the aid of soil amendment and, to a lesser extent, reseeding with either of the revegetation mixtures studied. None of the experimental treatments in this study enhanced recovery of community composition similar to the reference areas. Of greater concern, the "standard" seeded areas exhibited single species dominance, which will severely impede further succession.

Direct comparison of vegetation structure to the predisturbance or reference structure is not a useful measurement of restoration success in the first 2 years after restoration efforts using the treatments in this study. Measurements of species turnover may prove to be better end-points for early assessments of success. In nearly all situations, a longer period of time is necessary before robust conclusions can be made concerning the recovery of the plant community.

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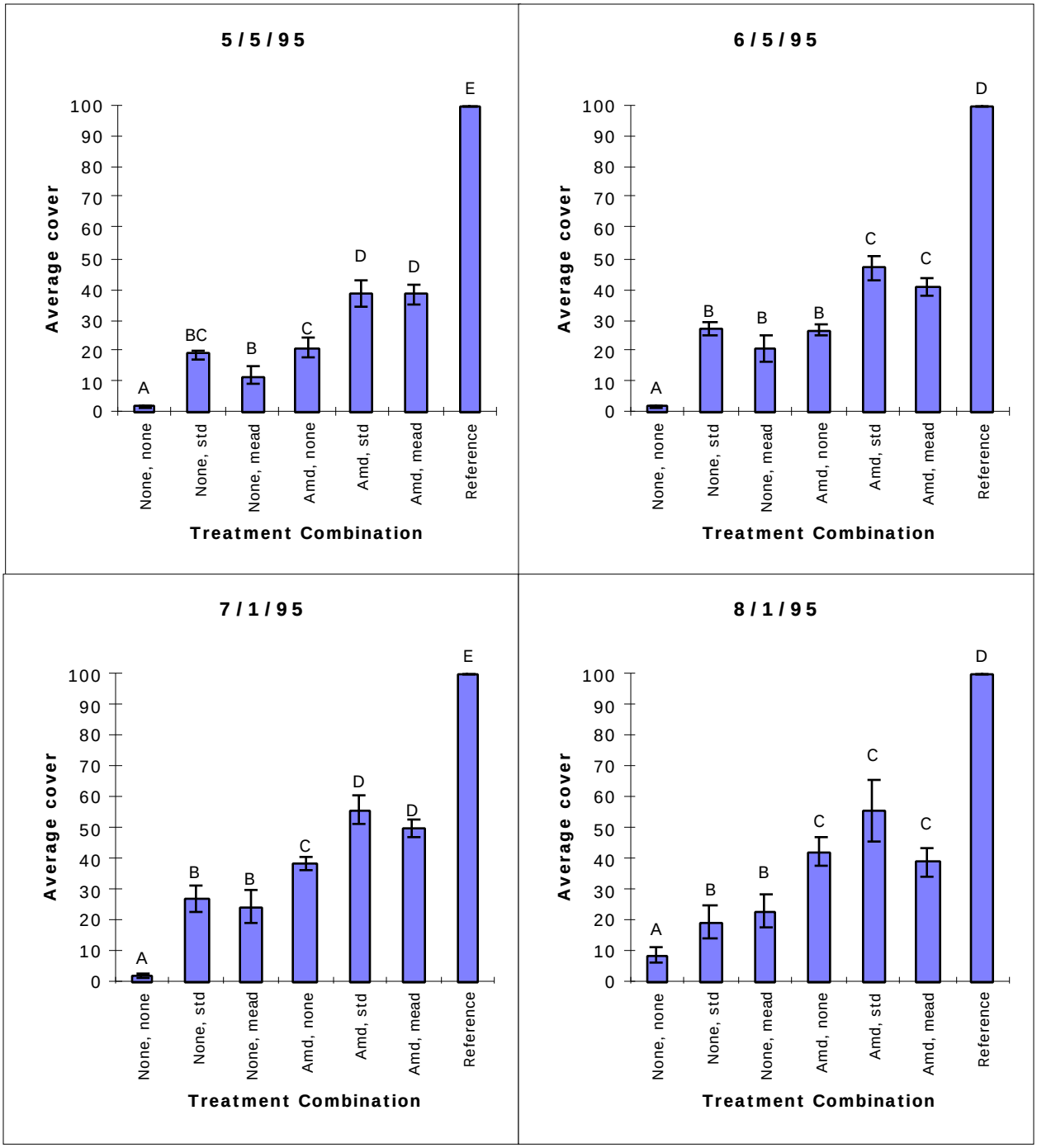

Figure 2.1 - Average percent vegetational cover by treatment combination for 1995. Error bars represent one standard error. Columns that do not share a common letter are considered significantly different using Tukey's HSD with a family error rate of 0.05 (individual error rate 0.00339).

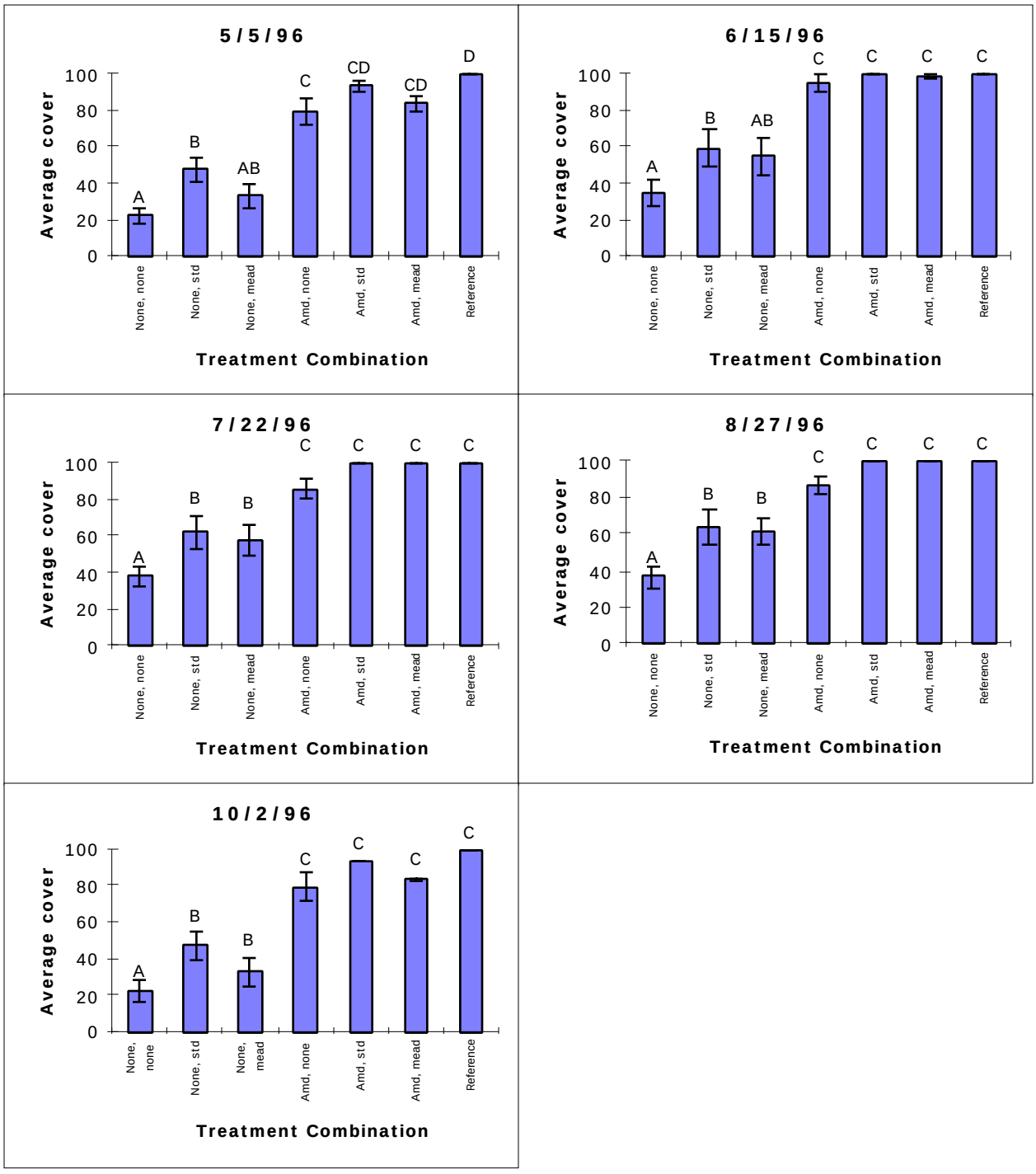

Figure 2.2 - Average percent vegetational cover by treatment combination for 1996. Error bars represent one standard error. Columns that do not share a common letter are considered significantly different using Tukey's HSD with a family error rate of 0.05 (individual error rate 0.00339).

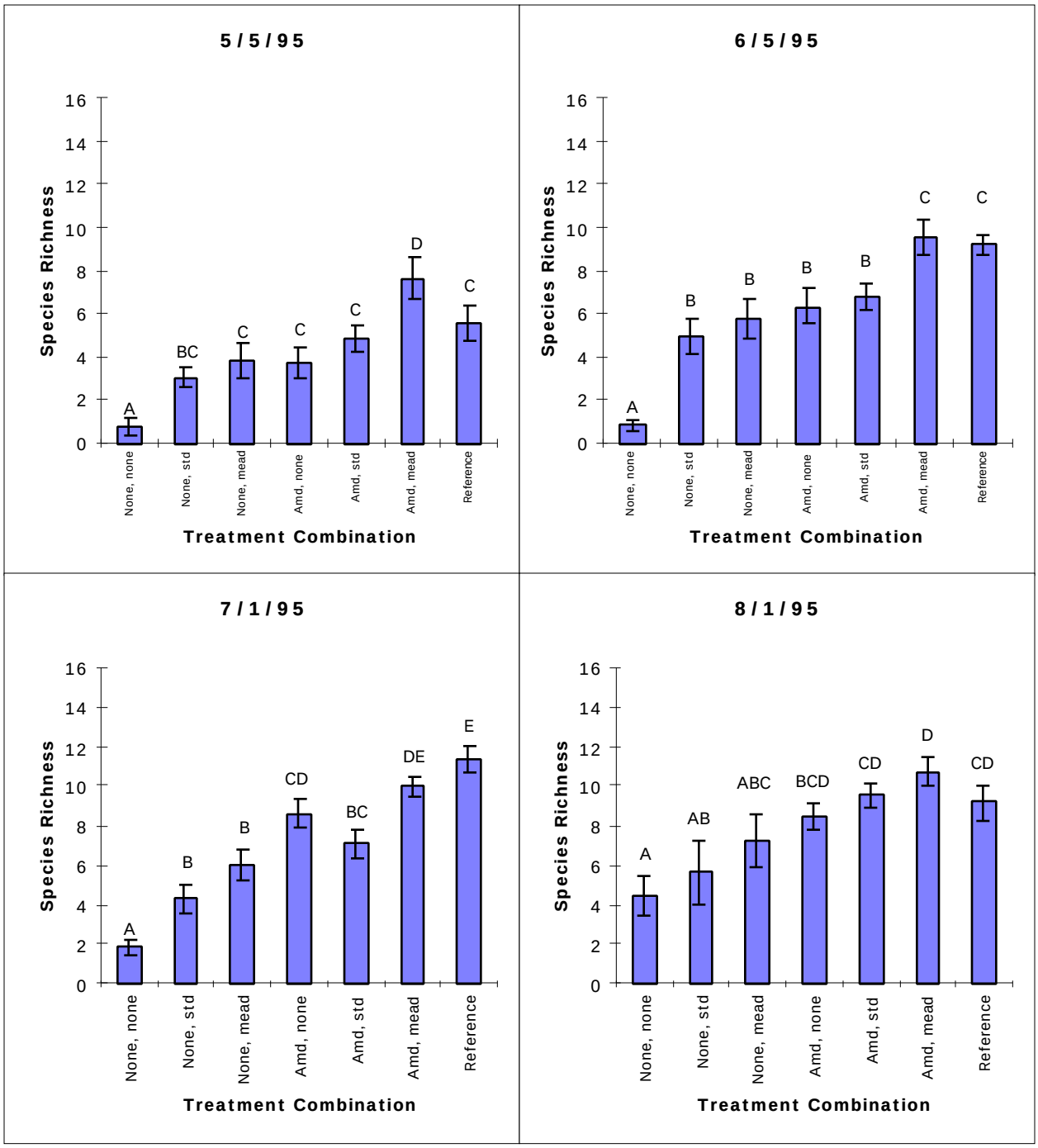

Figure 2.3 - Species richness by sampling date for 1995. Error bars represent one standard error. Columns that do not share a common letter are considered significantly different using Tukey's HSD with a family error rate of 0.05 (individual error rate 0.00339).

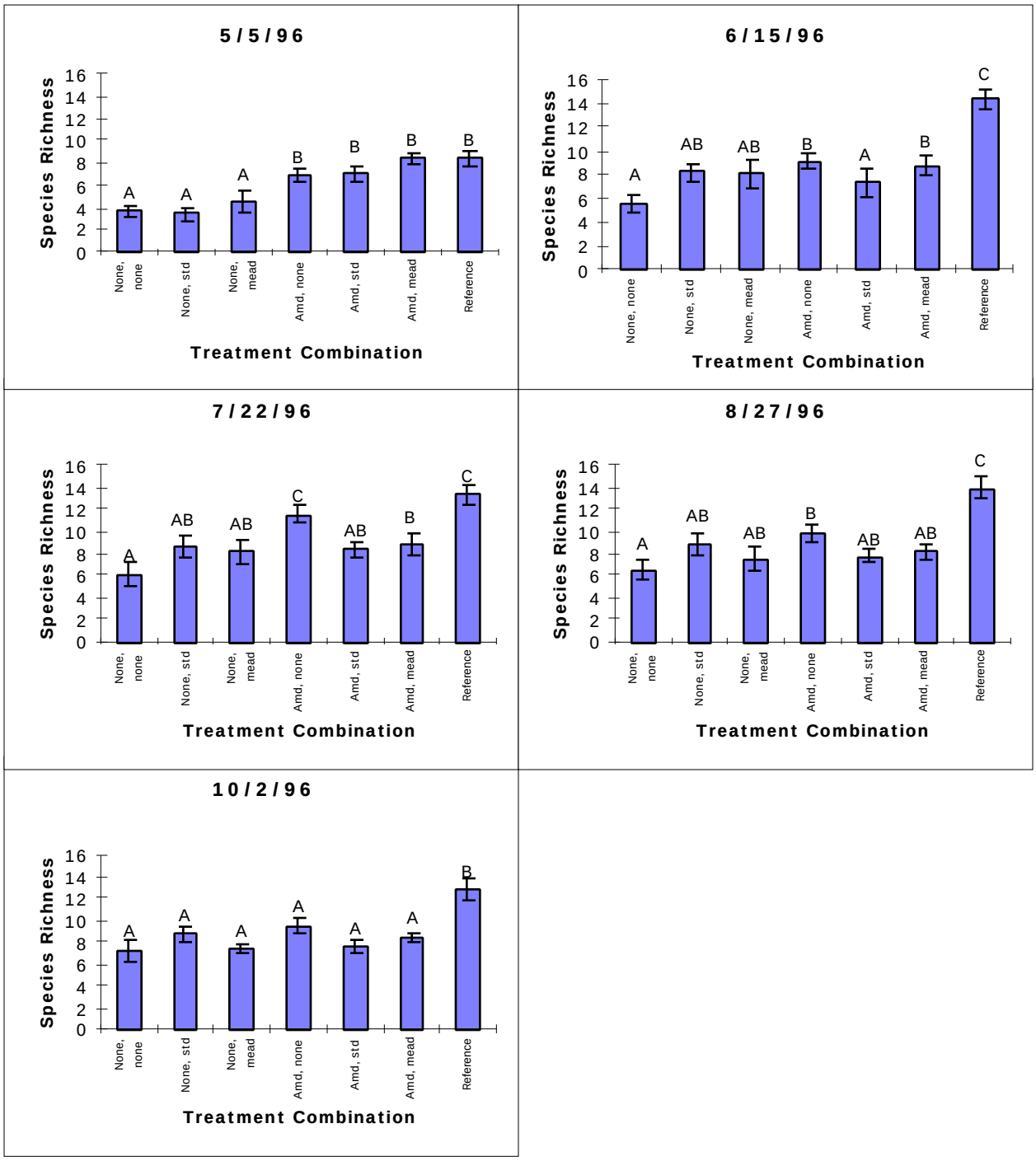

Figure 2.4 - Species richness by sampling date for 1996. Error bars represent one standard error. Columns that do not share a common letter are considered significantly different using Tukey's HSD with a family error rate of 0.05 (individual error rate 0.00339).

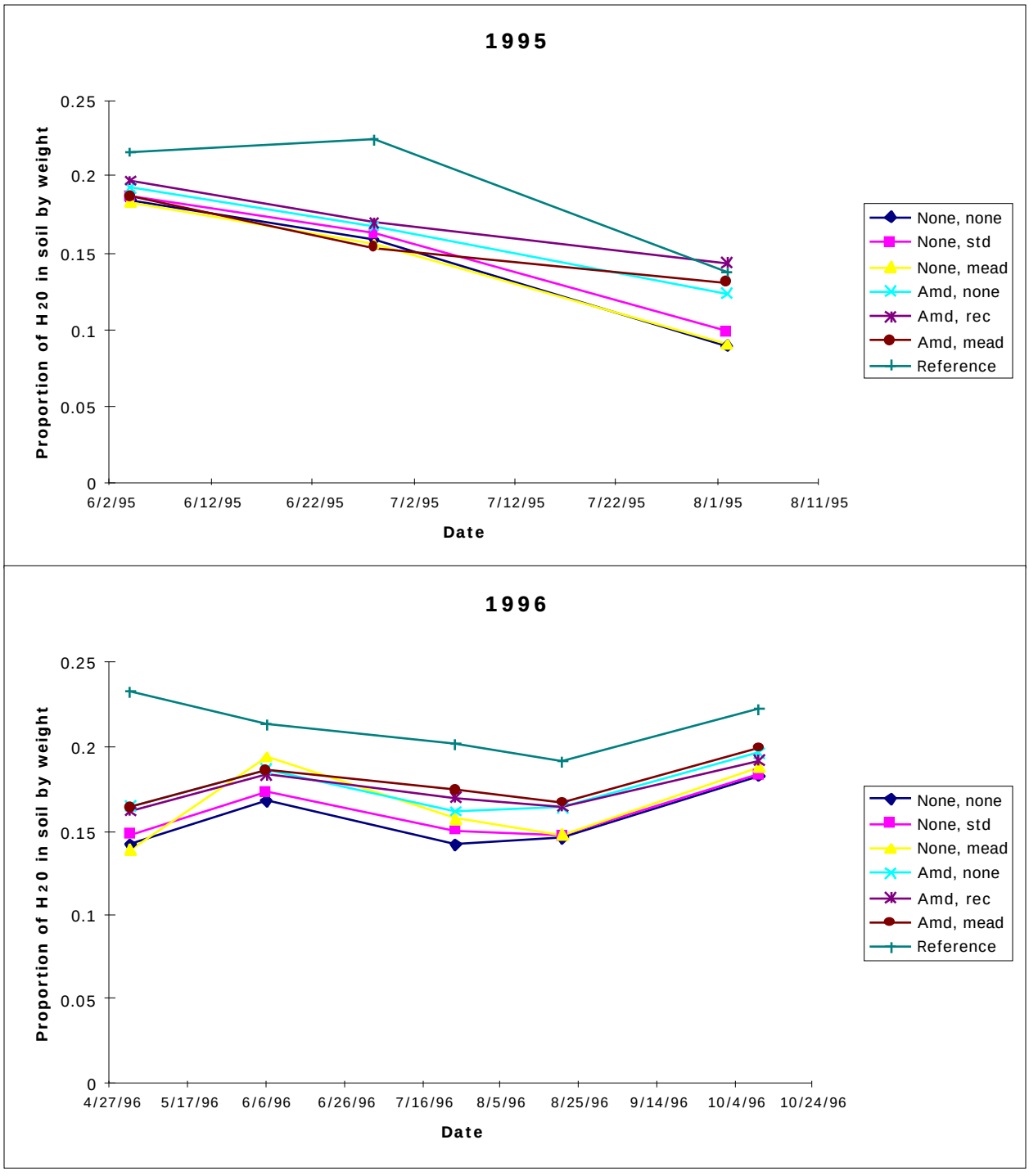

Figure 2.5 - Average soil moisture as a proportion of soil weight for 1995 and 1996 by treatment combinations.

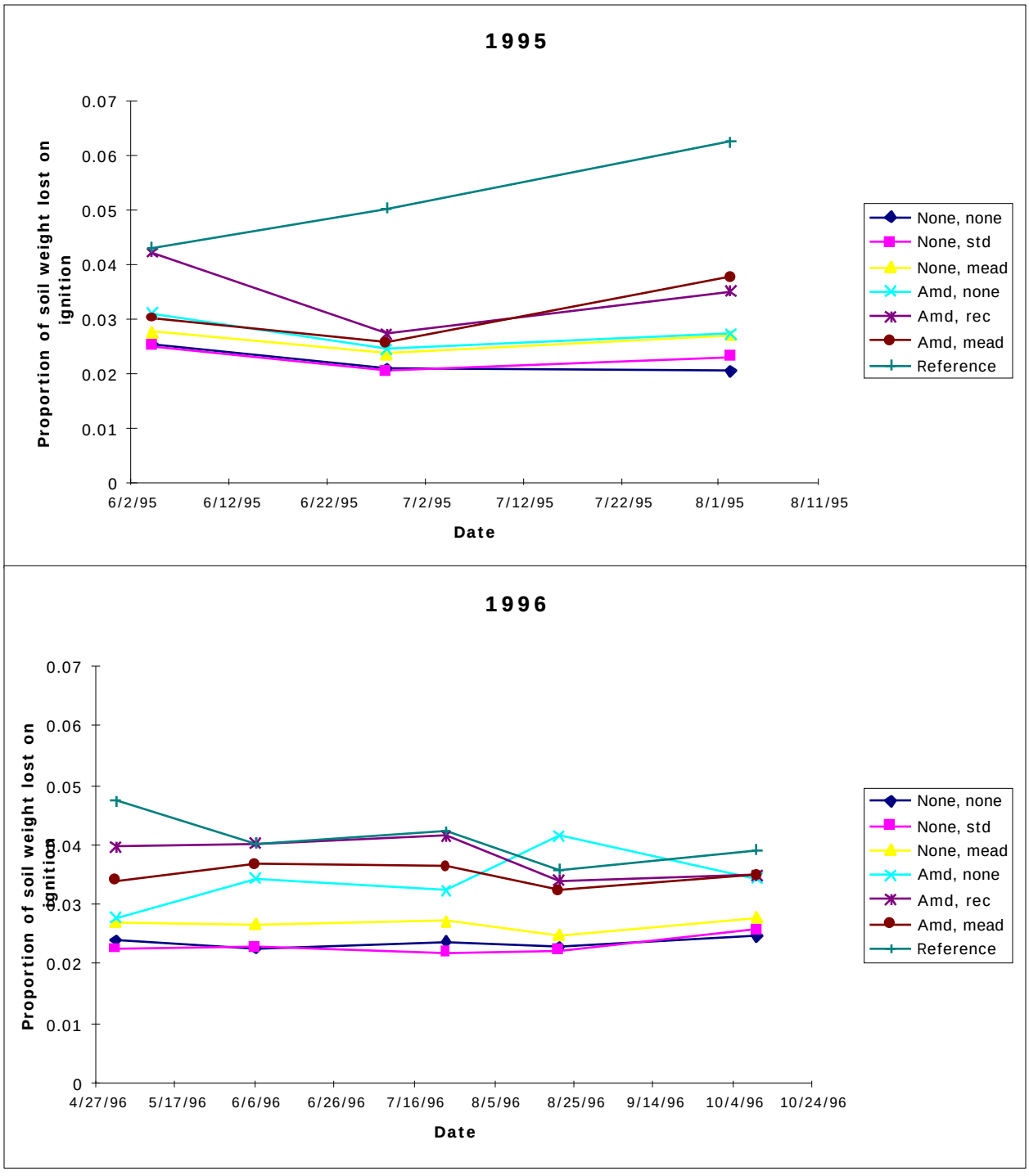

Figure 2.6 - Average soil organic matter estimated as the proportion of soil weight lost on ignition for 1995 and 1996 by treatment combinations.

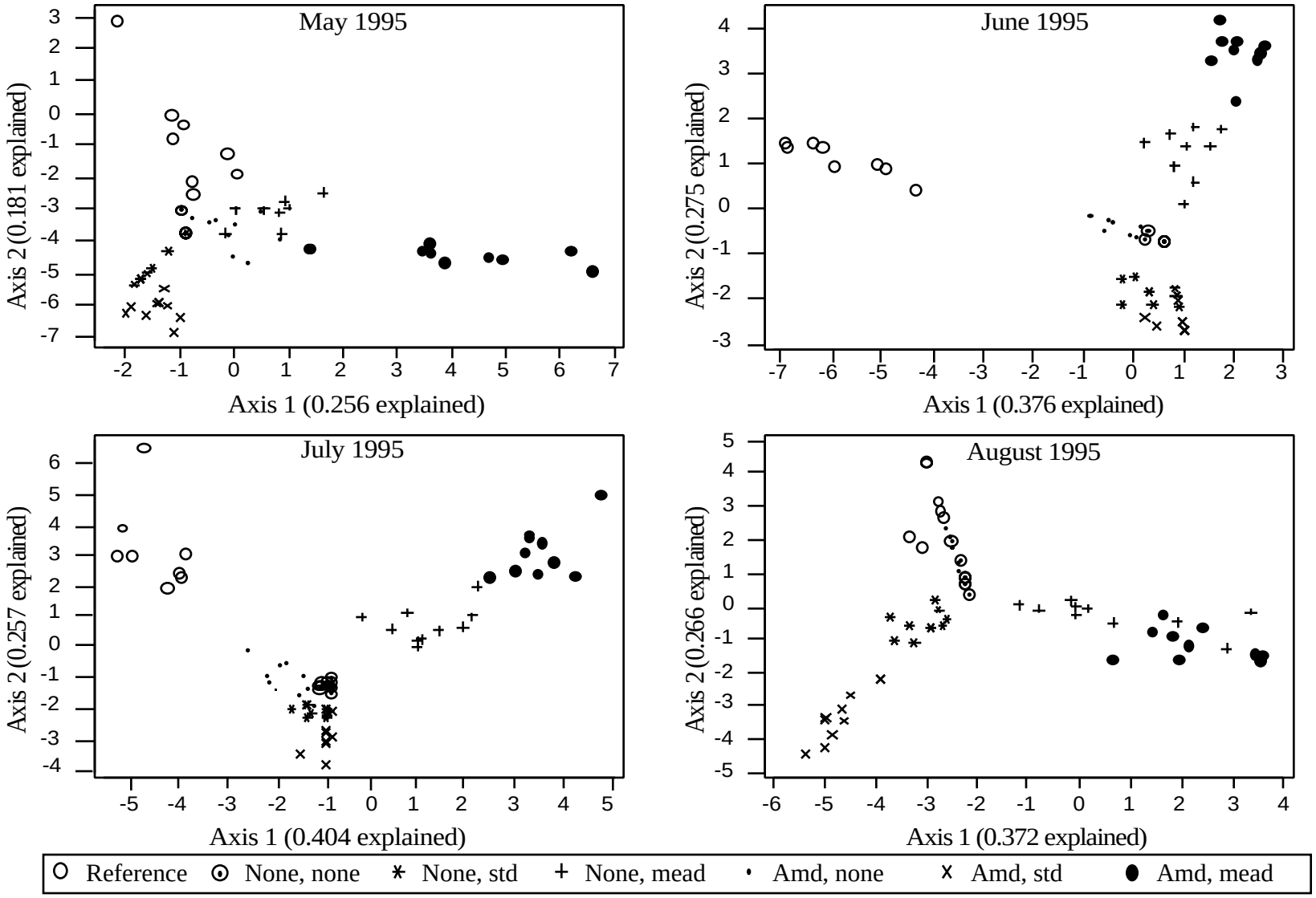

Figure 2.7 - Principal components ordination of site by species community structure matrix for four sampling dates in 1995.

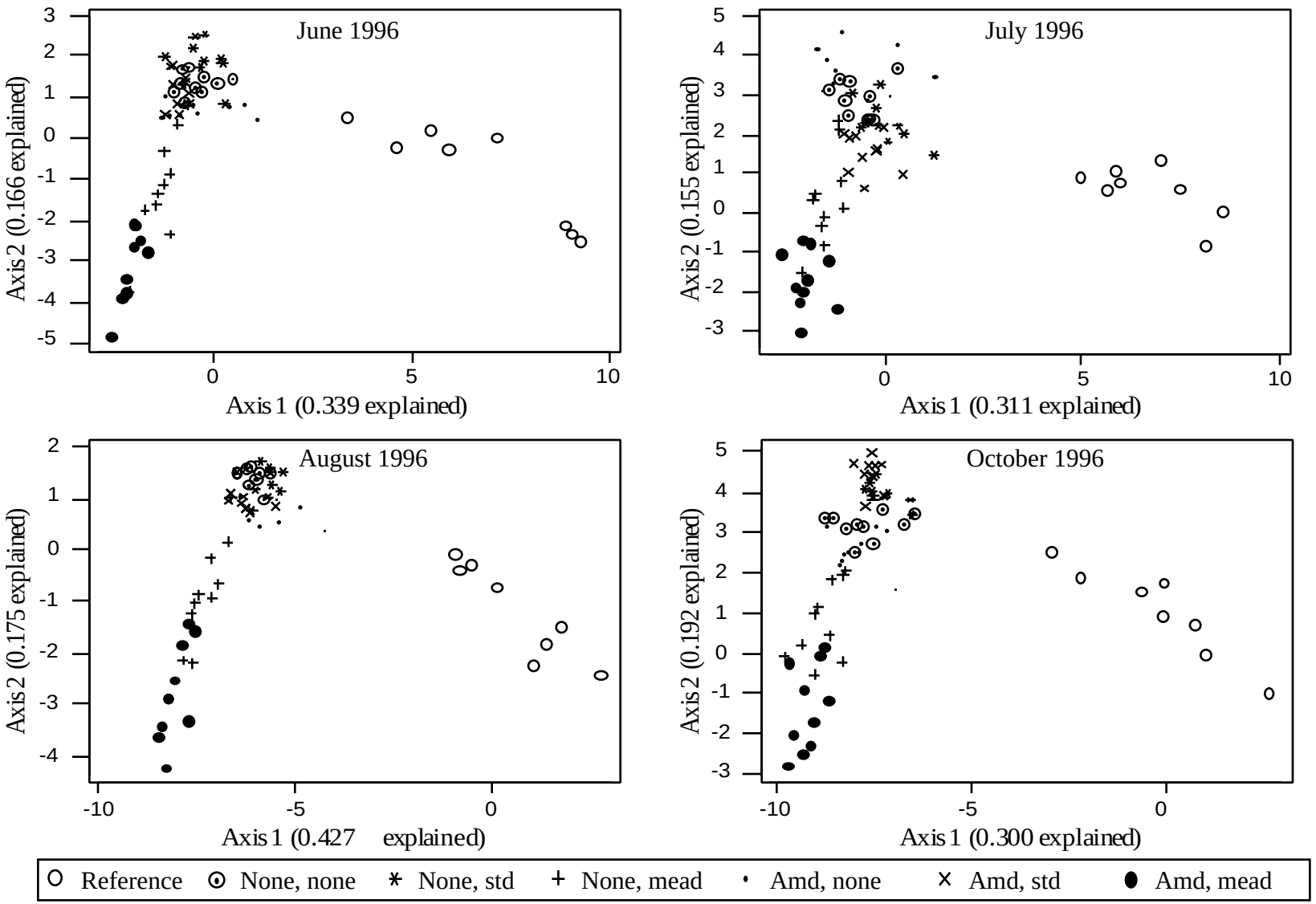

Figure 2.8 - Principal components ordination of site by species community structure matrix for four sampling dates in 1996.

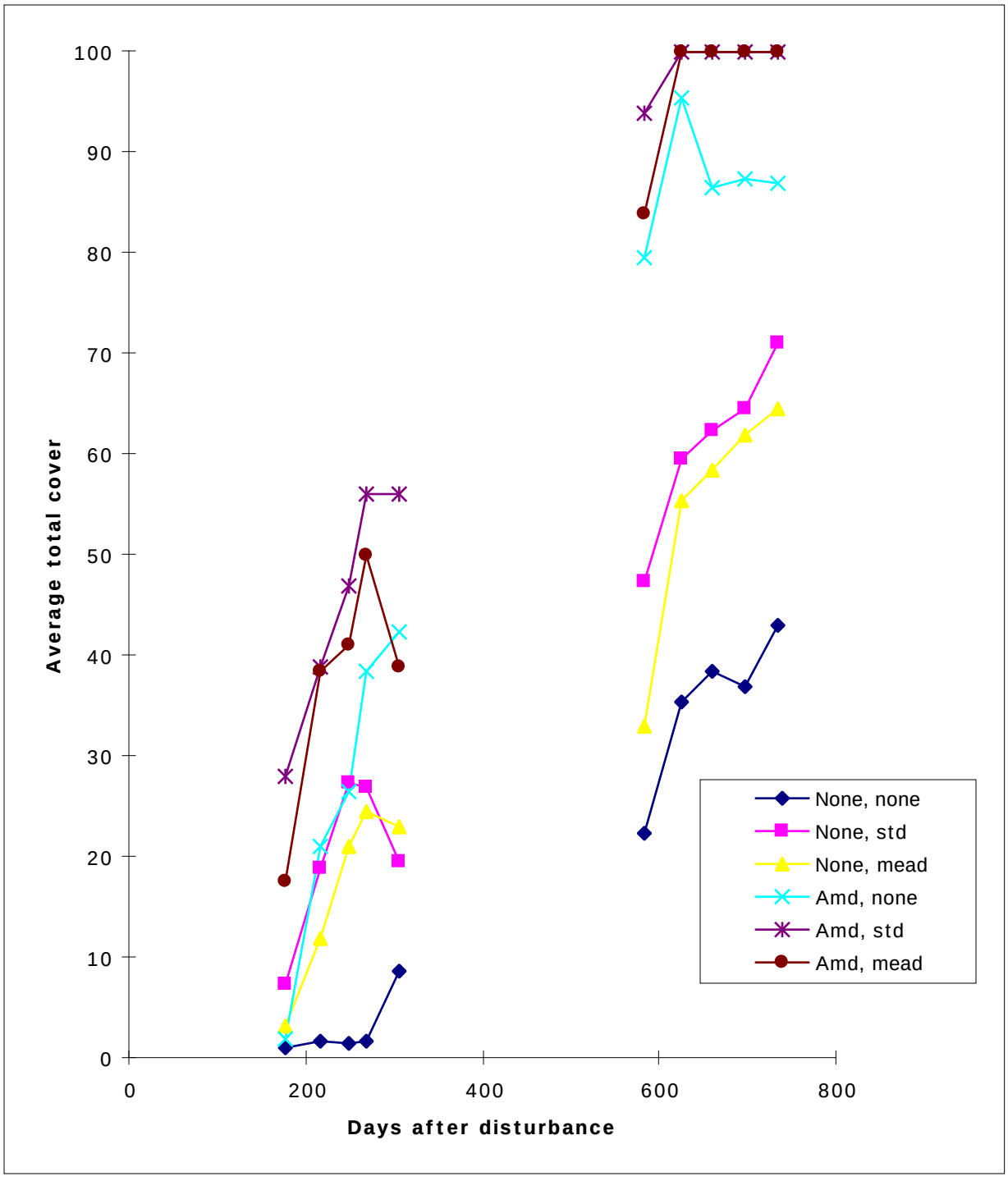

Figure 2.9 - Summary of average total cover over time to show the performance of the restoration treatments based upon this recovery measurement.

Chapter 3

CELLULOSE DECOMPOSITION DYNAMICS AND SOIL ENZYME ACTIVITIES IN RECOVERING OLD-FIELD COMMUNITIES

Introduction

Despite the importance of soils in the restoration and recovery of damaged ecosystems, they have received much less attention than plant communities. This oversight may be due to the regulatory and societal view of restoration, where most emphasis is on initiating plant growth on damaged sites. Many of the most important energy and nutrient fluxes in ecosystems are mediated in the soil (Raich and Schlesinger 1992). Any attempt to restore degraded land must, therefore, make careful consideration of soil system recovery (Harris et al. 1996, Aronson et al. 1993, Ruzék 1994). This consideration entails a process similar to restoring the plant community: the community of microorganisms in the soil must be restored to a state that functions like the predisturbance community. The primary function that was focused upon for this research was cellulose decomposition since it integrates a great deal of biological activity (Coleman et al. 1983) and is a vital link in the cycle of energy through an ecosystem (Wiegert 1988).

The rate at which cellulose is decomposed in a system can be considered a direct measurement of biological activity and energy flow in soil (Bienkowski 1990). Depressed cellulose decomposition capacity has been shown to be a limiting factor in ecosystem development in a number of situations. Surface mined areas often exhibit a low decomposition

activity which, in turn, can be linked to poor soil development and low nutrient turnover (Lawrey 1977). Pollutional gradients have also been shown to alter decomposition rates as they limit microbial growth in soil (Ohtonen et al. 1994).

Closely linked to decomposition capacity, soil microbial enzyme activities have been used to estimate terrestrial system recovery and relationships between disturbed areas. Because of the dependence of cellulose decomposition on the presence of specific enzyme systems at adequate levels, soil enzymes are a useful indicator of biological activity and decomposition capacity. Measurements of soil enzymes are actually indirect measures of soil microbial activity; enzymes present in the soil have their genesis as extracellular secretions and/or products from lysed cells (Tabatabai 1982). Bentham et al. (1992) and Harris and Birch (1989) have shown that it is possible to characterize ecosystem restoration and development with a group of soil microbiological and physico-chemical measurements. Harris et al. (1996) have taken this further by showing a successional relationship between soil microbial community development as measured by enzyme activities and plant community development. For the current research, two enzyme systems, dehydrogenase and beta-glucosidase, were assayed as functional components of the recovering systems because of their broad involvement in decompositional processes (Eivazi and Tabatabai 1990, Tabatabai 1982).

Dehydrogenases catalize a broad range of microbial oxidation reactions, including those involved in fermentation and respiration; therefore, their activity level can be used as a good estimate of overall microbial activity in soil (Skujins 1976, Ohtonen 1990). There are several

specific dehydrogenase pathways and, therefore, measurements of dehydrogenase activity represent an average activity (Tabatabai 1982). Soil dehydrogenase enzyme activity has been linked to the progress of post-stress succession in the revegetation of abandonded agricultural fields (Pancholy and Rice 1973). Decreased dehydrogenase activity has also been linked to industrial disturbance of soil (Rowell and Florence 1993). Recovery of the dehydrogenase pathways in soils is a key step towards restoration of soil system functionality (Harris and Birch 1990).

Soil dehydrogenase activity has been shown to correlate significantly ($r = 0.95$) to beta-glucosidase activity in soils (Garcia et al. 1994). Beta-glucosidase is member of the glycosidase group of enzymes, including cellulase and amylase, that catalyze the hydrolysis of different glycosides. Beta-glucosidase, responsible for catalyzing the hydrolysis of beta-D-glucopyranosides, is the rate-limiting enzyme in microbial cellulose degradation and the most sensitive enzyme of the cellulase complex to phenolic-humic inhibition (Busto et al. 1995, Fauci and Dick 1994). In cellulose decomposition, beta-glucosidase is primarily involved in hydrolysis of the maltose subunits left after cellulase cleaves them from the cellulose chain. Glucosidase activity is highly sensitive to heavy metal pollutants, fertilizers, and components of industrial and municipal wastes (Eivazi and Zakaria 1993). Overall activity of beta-glucosidase is generally dependent upon the level of soil organic matter available and is highly correlated with cellulose decomposition rate (Eivazi and Zakaria 1993, Frankenberger et al. 1983).

Table 3.1 - Hypothesis statements for cellulose decomposition rate and enzyme activity assays.

Number	Hypothesis
1	Experimentally disturbed sites will show decreased decomposition rates and enzyme activities when compared to undisturbed references.
2	Sites amended with organic matter will exhibit greater similarity to reference plots than unamended sites, as measured by decomposition rates and enzyme activities.
3	Sites seeded with the “standard” or “meadow” revegetation mixtures will exhibit greater similarity to reference plots than unseeded sites. The two revegetation mixtures will not exhibit different effects on either decomposition rate or enzyme activities.

The goals of this study were to determine the rates that cellulose is decomposed in the differently restored plots, the correlation of decomposition rates and soil microbial enzyme activities, and the change in decomposition rates and enzyme activity levels in relation to the undisturbed reference areas over the course of the study period. The hypotheses are listed in Table 3.1. The experimental design used to test the hypotheses is described in Chapter 1.

Methods

Field and laboratory methods

Cellulose decomposition rate

Cellulose decomposition was estimated using filter paper circles (99.7% alpha-cellulose paper) as artificial decomposition substrates (Swift et al. 1979, Yin et al. 1989). This approach is superior to using natural leaf substrates in this situation because of the different plant communities present in the differently restored plots. An artificial cellulose substrate negates any interactions that may have arisen due to the selection of substrate material that may have been present in one community but not in another.

In March 1995 and 1996, 24 sets of 6 disks of Whatman #1 filter paper (5.5 cm; total set weight, 1.21 ± 0.02 g) were arranged in each experimental plot (see Figure 1.2). The sets for 1995 were enclosed in plastic citrus bags with a 0.5-cm mesh. The bags set out in the plots with low total vegetative cover exhibited a high degree of deterioration due to sunlight, which resulted in a high amount of lost samples. The sets for 1996, therefore, were enclosed in galvanized hardware cloth of 0.8-cm mesh. This arrangement provided for a lower number of lost samples.

Beginning in April of each year, three sets of filter paper were removed from each plot on a monthly basis. The filter paper was removed from its enclosure and hand washed in tap water to remove large chunks of debris. Cleaned samples were dryed at 100°C for at least 24 hr,

weighed, ashed at 550°C for 2 hr, and weighed again. The percentage of cellulose remaining was calculated from the ash-free dry weight and the initial weight of the samples.

Dehydrogenase activity level

Dehydrogenase assays began in June 1995 and continued through November of that year. Assays for beta-glucosidase began in June 1996 and both assays continued on a monthly basis through November 1996. For each sampling date, three soil cores of approximately 10 cm depth were taken from each plot (Eivazi and Zakaria 1993). The three soil cores were mixed to make one aggregate sample per plot. A part of each resulting sample was immediately weighed and placed in a drying oven for 24 hr. The remainder of the sample soil was finely chopped and left to air dry for 36 hr (Tabatabai 1982). After the interval, each sample was sieved to 2 mm.

Dehydrogenase activity was measured using the Lenhard method (Lenhard 1956, Tabatabai 1982). This method is based on the dehydrogenase mediated conversion of 2, 3, 5-triphenyltetrazolium chloride (TTC) to the red product 2, 3, 5-triphenyl formazan (TPF) by removing two electrons and two hydrogen atoms. Ten grams of each seived soil sample were mixed thoroughly with 0.1 g of $CaCO_3$. A 3-g subsample of this was placed in a test tube to which was added 1 ml of 1.5% TTC solution and 1 ml of distilled water. Tubes were stoppered and incubated at 37°C for 24 hr. After the incubation interval, methanol was used to wash samples from each test tube and through a cotton-blocked funnel. The washing/filtration process continued with each sample until the red color of the TPF was no longer present in the sample

soil. Each filtrate was collected volumetrically. Light absorbance of the filtrate was measured at 485 nm using a Perkin-Elmer Lambda 6 spectophotometer. The concentration of TPF in each sample was determined by comparing the observed absorbance with a standard absorbance curve built from known concentrations of TPF in methanol.

Beta-glucosidase activity level

Field methods for assaying beta-glucosidase activity level were identical to those for dehydrogenase activity level (see above). Beta-glucosidase activity was measured in the laboratory using the Eivazi method (Eivazi and Tabatabai 1990, Tabatabai 1982). This method was included in the study because of the low variance it exhibits. It is based on beta-glucosidase hydrolyzing nitrophenyl-beta-D-glucoside (PNG) to remove the glucose subunit, leaving only p-nitrophenol (pNP), which is yellow in color. One gram of each seived soil sample was placed in a 50-ml Erlenmeyer flask. Four milliliters of modified universal buffer (pH 6.1), 1 ml of 0.025 M PNG solution, and 0.025 ml of toluene were added to each flask. Flasks were swirled and then placed in a 37°C incubator for 1 hr. After the incubation interval, 1 ml of 0.5M $CaCl_2$ and 4 ml of THAM buffer (pH 12) were added to each sample. The resulting suspension was filtered through a folded Whatman No. 3 filter paper. Light absorbance of the filtrate was measured at 410 nm using a Perkin-Elmer Lambda 6 spectophotometer. The concentration of pNP in each sample was determined by comparing the observed absorbance with a standard absorbance curve built from known concentrations of p-nitrophenol in THAM buffer.

Soil physical measurements

Soil organic matter lost on ignition and soil moisture was measured at each sampling date as described in Chapter 2. Soil temperature was measured using a soil thermometer (Forestry Supply Co.) inserted to a depth of 15 cm. On two dates, soil temperature was measured across all plots, and differences between plots were insignificant compared to warming over time during the sampling period. Soil temperature was, therefore, measured in three random plots at the beginning and end of the sampling period. The average temperature over these plots during the sampling period was then recorded. Soil nutrients were assayed as described in Chapter 2.

Numerical analyses

Activity levels for both dehydrogenase and beta-glucosidase were calculated on a per gram of air dried soil basis. Analysis of variance was used to test for block and treatment effects. One-way analysis of variance was used to test for differences between treatment combinations and reference plots. Tukey's HSD test was used for multiple comparison tests. Variance due to laboratory techniques was tested with one-way analysis of variance on data sets produced from the same sample over three concurrent days.

Decomposition rates were calculated using linear regression on the pooled subsamples for each plot against time of exposure. Two-way analysis of variance was used to test for block and treatment effects on the calculated decomposition rates. One-way analysis of variance with

Tukey's HSD multiple comparison test was used to compare treatment combinations and reference plots.

Covariance of enzyme activity levels and decomposition rates with soil organic matter, soil moisture, and soil temperature was tested using two-way analysis of covariance. Correlation of all measurements was documented using Pearson's correlation.

Results

Table 3.2 shows the overall means, medians, and ranges for enzyme activities, decomposition rates, and soil physical parameters over the entire sampling period. Soil nutrient data are shown in Table 3.3. Pearson's correlation coefficients for pairwise comparisons of all variables are shown in Table 3.4. Table 3.5 shows average values for all variables across all treatment groupings. Soil and air temperature in 1995 and 1996 are shown in Figure 3.1. Soil moisture was highest in reference plots for nearly all dates (Figure 3.2). Amended plots were generally moister than unamended plots, but not as moist as reference plots. The same trends held for soil organic matter lost on ignition. Amended plots had more organic matter than unamended, but less than the references (Figure 3.3).

Cellulose decomposition over time is shown for 1995 and 1996 in Figure 3.4. Relative differences between treatment groupings and combinations should only be made within each year. Between year comparisons are probably confounded by the methodological differences between the two years. In 1995, reference areas appear to show higher decomposition rates than all

Table 3.2 - Means, medians, and ranges of decomposition, enzyme activity, and soil physical data.

Variable	Units	Mean	Median	Range
Dehydrogenase activity (DHD)	mg TPF/kg/hr	30.5434	24.5347	0.2346 to 130.5722
Beta - glucosidase activity (GLC)	mg pNP/kg/hr	25.2171	21.5308	2.4399 to 120.6856
Decomposition rate (DEC)	mg cellulose/d	- 4.214	- 3.989	- 0.845 to - 8.88
Soil moisture (H2O)	%	17.64	17.75	6.25 to 25.79
Soil weight lost on ignition (LOI)	%	3.09	2.89	1.6 to 6.33
Soil temperature (TEMP)	°C	18.06	20	8 to 23

Table 3.3 - Summary of soil nutrient data for all treatment combinations (mean ± SD). Values followed by the same letter are not significantly different using Tukey's (family error rate of 0.5).

Treatment Combination	pH	ppm					
		P	K	Ca	Mg	Zn	Mn
None, none	5.82 ± 0.16a	23.2 ± 13.39a	52.8 ± 11.8a	1449 ± 177a	172 ± 28.4a	7.76 ± 4.36a	25.8 ± 5.89a
None, std	5.96 ± 0.05ab	21.6 ± 4.56a	64.8 ± 17.5a	1545 ± 196a	184 ± 36.9a	8.56 ± 1.89a	35.2 ± 13.11ab
None, mead	5.88 ± 0.08ab	16.8 ± 1.38a	59.2 ±14.8a	1478 ± 104a	179 ± 34.4a	6.96 ± 2.13a	24.16 ± 4.42a
Amd, none	6.668 ± 0.08c	30.4 ± 8.29ab	147.2 ±15.6b	2947 ±330b	451 ± 36.3b	10.16 ± 1.66a	56.64 ± 6.45c
Amd, std	6.32 ± 0.13c	36.8 ± 5.21ab	145.6 ±20.3b	3072 ± 293b	446 ± 34.7b	9.52 ± 3.24a	62.0 ± 4.52c
Amd, mead	6.56 ± 0.11c	31.2 ± 8.19ab	164 ±37.7b	3100 ± 575b	441 ± 56.7b	11.44 ± 5.74a	56.8 ± 10.4c
Reference	6.05 ± 0.06bc	40.0 ± 3.27b	123.0 ± 26.4b	2054 ± 160ab	342 ± 47.8b	12.9 ± 3.55a	45.1 ± 8.27b

Table 3.4 - Pearson's correlation coefficients for overall averages of decomposition rate, enzyme activities, and soil physical parameters (abbreviations same as in Table 3.2).

	DEC	LOI	H2O	DHD
LOI	-0.632			
H2O	-0.620	0.881		
DHD	-0.644	0.825	0.776	
GLC	-0.679	0.868	0.779	0.945

Table 3.5 - Average values with standard deviations for all variables by treatment groupings (abbreviations and units same as in Table 3.2).

Grouping	DHD	GLC	DEC	H2O	LOI
Unamended	20.10 ± 10.09	14.88 ± 9.39	-3.29 ± 0.55	0.150 ± 0.033	0.024 ± 0.004
Amended	32.10 ± 16.03	31.82 ± 13.21	-4.98 ± 0.67	0.164 ± 0.032	0.035 ± 0.009
Unseeded	23.53 ± 11.96	20.60 ± 12.20	-3.91 ± 1.18	0.157 ± 0.036	0.029 ± 0.008
Standard seed	25.85 ± 12.63	24.00 ± 14.59	-4.17 ± 1.09	0.158 ± 0.032	0.029 ± 0.008
Meadow seed	28.91 ± 17.46	25.44 ± 15.47	-4.32 ± 0.93	0.171 ± 0.039	0.035 ± 0.011
Reference	55.21 ± 24.33	52.11 ± 23.48	-4.78 ± 0.35	0.202 ± 0.035	0.044 ± 0.009

experimental treatments except the amended but unseeded plots. In 1996, decomposition in amended plots proceeded at a higher rate than in references, while unamended plots had rates lower than reference plots (Table 3.6). Generally, amended plots exhibited a significantly higher decomposition rate than unamended plots and seeding treatment had no significant effect (Table 3.7). Both soil organic matter and soil moisture were moderately correlated with decomposition rate ($r = 0.63$).

Soil dehydrogenase activities across all treatment combinations are summarized in Figure 3.5 and 3.6a,b. Dehydrogenase activity exhibited a high level of variance, which decreased the power for multiple comparisons. On the first three sampling dates in 1995, all experimental plots showed lower activity than the reference plots. A similar relationship developed for 1996, with the amended plots beginning to show activities more similar to reference levels. This trend is reflected in the analysis of variance summarized in Table 3.8 as the amended plots showing

Table 3.6 - Summary of cellulose decomposition by treatment combination using linear regression to calculate actual decomposition rates.

Treatment combination	Mean rate* (mg cellulose/day)	r^2
None, none	- 4.504 a	0.89
None, std	- 5.144 ab	0.90
None, mead	- 5.202 ab	0.88
Amd, none	- 6.403 bc	0.94
Amd, std	- 7.602 c	0.90
Amd, mead	- 7.648 c	0.90
Reference	- 5.728 ab	0.94

* Rates followed by the same letter were found significantly different using Tukey's HSD test with a family error rate of 0.05.

Table 3.7 - Summary of two-way ANOVA p-values for treatment effects on cellulose decomposition and p-values from analysis of covariance with soil organic matter lost on ignition and soil moisture.

Factor	1995	1996
Amend	***	***
Seed mix	ns	*
Amend * Seed mix	*	ns
LOI	ns	ns
H2O	ns	ns

ns = $p>0.05$, *$p<0.05$, *** $p<0.001$

marginal significance in predicting dehydrogenase activity. Soil organic matter lost on ignition and soil moisture were both marginally significant covariates on some sampling dates but not over the

entire sampling period (Table 3.9). Both soil organic matter and soil moisture were moderately correlated with dehydrogenase activity (r = 0.82, 0.77, respectively).

Soil beta-glucosidase activity was highly correlated to dehydrogenase activity (r = 0.95). It showed similar relationships between treatment combinations but exhibited lower within treatment combination variance (Figure 3.7a,b). Therefore, as 1996 progressed, amended plots were often indistinguishable from reference plots. From June through August, it was possible to discern significant differences between seeded sites with soil amendment and all other experimental sites. This suggests an interaction between soil amendment and seeding, although such an interaction was not found to be statistically significant (Table 3.8). Soil amendment was

Table 3.8 - Summary of two-way ANOVA p-values for treatment effects on soil enzyme activities.

Factor	6/95	7/95	8/95	11/95	3/96	4/96	5/96	6/96	7/96	8/96	9/96	10/96
Dehydrogenase												
Amendment	*	ns	ns	*	*	*	ns	**	ns	*	*	ns
Seed mix	ns	ns	ns	ns	ns	ns	ns	**	ns	ns	ns	ns
Amendment * Seed mix	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
ß-glucosidase												
Amendment	-[1]	-	-	-	ns	***	***	***	***	***	***	***
Seed mix	-	-	-	-	ns	ns	ns	ns	ns	ns	ns	ns
Amendment * Seed mix	-	-	-	-	ns	ns	ns	ns	ns	ns	ns	ns

ns = p>0.05, *p<0.05, **p<0.01, ***p<0.001
[1]Beta-glucosidase not measured in 1995

highly significant in predicting beta-glucosidase activity (Table 3.8). Similar to soil dehydrogenase activity, soil organic matter lost on ignition and soil moisture were moderately correlated with decomposition (r^2 = 0.75, 0.60 respectively) and were significant covariates on some dates but not across the entire sampling period (Table 3.9).

Discussion

The primary hypothesis of this research was that the removal of the top 20 cm of soil would alter the decomposition rates and enzyme activities as compared to the undisturbed reference areas. The data support this hypothesis and show markedly lower decomposition rates and enzyme activity levels in the restoration control plots (the "none, none" treatment combination) relative to the references. Similar results have been seen in studies of industrial

Table 3.9 - Summary of analysis of covariance of organic matter lost on ignition and soil moisture with enzyme activities.

Factor	6/95	7/95	8/95	11/95	3/96	4/96	5/96	6/96	7/96	8/96	9/96	10/96
Dehydrogenase												
LOI	ns	*	ns	ns	ns	ns	ns	ns	*	*	ns	ns
H2O	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns
ß-glucosidase												
LOI	-[1]	-	-	-	ns	ns	*	ns	ns	*	ns	ns
H2O	-	-	-	-	ns	ns	**	ns	ns	ns	ns	ns

ns = p>0.05, *p<0.05, **p<0.01

[1]Beta-glucosidase not measured in 1995

construction and surface mining effects (Rowell and Florence 1993, Gonzalez-Sangregorio et al. 1991, Tate 1985).

Aside from physical weathering, cellulose decomposition is largely a microbial process (Kjoller and Struwe 1989). In disturbed areas, soil microbial communities exhibit a marked decrease in all types of functional groups (Vasquez et al. 1993, Segal and Mancinelli 1987, Fresquez et al. 1986, Lindemann et al. 1984). This decline is matched in functional enzyme levels and microbial activity in general (Bolton et al. 1993, Sinsabaugh et al. 1991, Nadler and Steinberger 1993, Insam and Domsch 1988). Soil enzyme activities can further be limited by nutrient limitations, latent pollutants, low organic matter, and low soil moisture. All of these are often characteristics of disturbed areas (Rowell and Florence 1993, Eivazi and Tabatabai 1990). Table 3.10 compares the activity levels observed in this study with those found in studies of other systems. The experimental disturbance in the current study decreased both soil moisture and organic matter (Table 3.5), which may provide the best explanation for the decreased decomposition rate and enzyme activities observed.

Soil amendment was expected to accelerate cellulose decomposition rates and enzyme activities, making amended plots more similar to the undisturbed references. This hypothesis was supported by the significant treatment effects for the soil amendment found with analysis of variance. Increased cellulose decomposition rates were observed in treatments that also exhibited higher activities for dehydrogenase and beta-glucosidase enzymes, two components of the

microbially mediated system that oxidizes organic matter. These increases are probably most dependent upon the favorable microbial growing conditions caused by the increased soil moisture and soil organic matter in the amended plots (Bardgett et al. 1995, Eivazi and Zakaria 1993). Both measures were not statistically significant using analysis of variance but were significantly correlated with enzyme activity ($r = 0.63$)

Most of the previous studies documenting the association between vegetation and soil enzymes and cellulose decomposition rate are in agricultural or forested systems (e.g., Sethi et al. 1990, Cochran 1991, Piene and Van Cleve 1977). Many of these studies show a close correlation between the vegetative community and soil biological activity. However, this association is slower to develop and, therefore, may not be present in early successional communities. In such

Table 3.10 - Comparison of enzyme activity levels observed in the current study with activity levels from other systems (mean ± SD).

Study system	Dehydrogenase (mg TPF/kg/hr)	Beta-glucosidase (mg pNP/kg/hr)	Reference
Restored old fields			
Unamended	20.10 ± 10.09	14.88 ± 9.39	Current study
Amended	32.10 ± 16.03	31.82 ± 13.21	Current study
Reference	55.21 ± 24.33	52.11 ± 23.48	Current study
Wheat fields	13.83	-	Sethi et al. 1990
Sludge amended soil	-	42 ± 17.5	Eivazi and Zakaria 1993
Beech forest soil	-	16.7 ± 6.5	Rastin et al. 1988
Agricultural soils	-	106.8 ± 40.04	Eivazi and Tabatabai 1990
Bare desert soils	2.7 ± 2.13	-	Garcia et al. 1994

systems, simply the presence of any vegetative community may be the most important plant effect on soil activity (Yin et al. 1989). In the current study, no differences were noted in decomposition rate or enzyme activity due to the different seeding mixtures.

Enzyme activity levels decreased while relative variance increased towards the end of each sampling year. This change may be due to the disassociation of the microbial community as the seasons changed from summer to winter. Such community shifts are important to identify because of their ability to confound comparisons between sites (Rastin et al. 1988).

In the broader context of ecological restoration and society, restoration of soils is not only essentially invisible to the public, but the attributes are exceedingly difficult to standardize and measure by regulatory agencies. It is difficult to overestimate the importance of regulatory requirements in most ecological restoration efforts. Restoration efforts involving surface mines, highway construction, and landfilling frequently involve establishing a bond ensuring that if the land owner goes bankrupt, the restoration will continue. The time limits on most bonds are usually only 5 to 10 years, so the tendency is to attempt restoration of comparatively large vegetation, as opposed to focusing on the development of a healthy soil system. This often leads to soil fertilization that may benefit short-term plant growth but will not facilitate long-term ecological self maintenance. Increased attention to sustainable development has called attention to the services provided by ecosystems. When these are given substantial attention, soils become of considerable importance in the restoration process.

Conclusions

Recovery of a functional soil microbial community can be facilitated by the addition of organic amendment in the soil. This treatment improves the conditions for microbial growth by increasing the organic substrate quality and soil moisture. In terms of restoration assessment, cellulose decomposition rate and soil microbial enzyme activity levels are useful in separating differently restored sites and do not exhibit a return to the level of undisturbed reference areas within 2 years. Because of their importance in biological energy and nutrient cycling, measurements of the soil microbial community could be very useful in assessing the state of recovery in disturbed and restored ecosystems.

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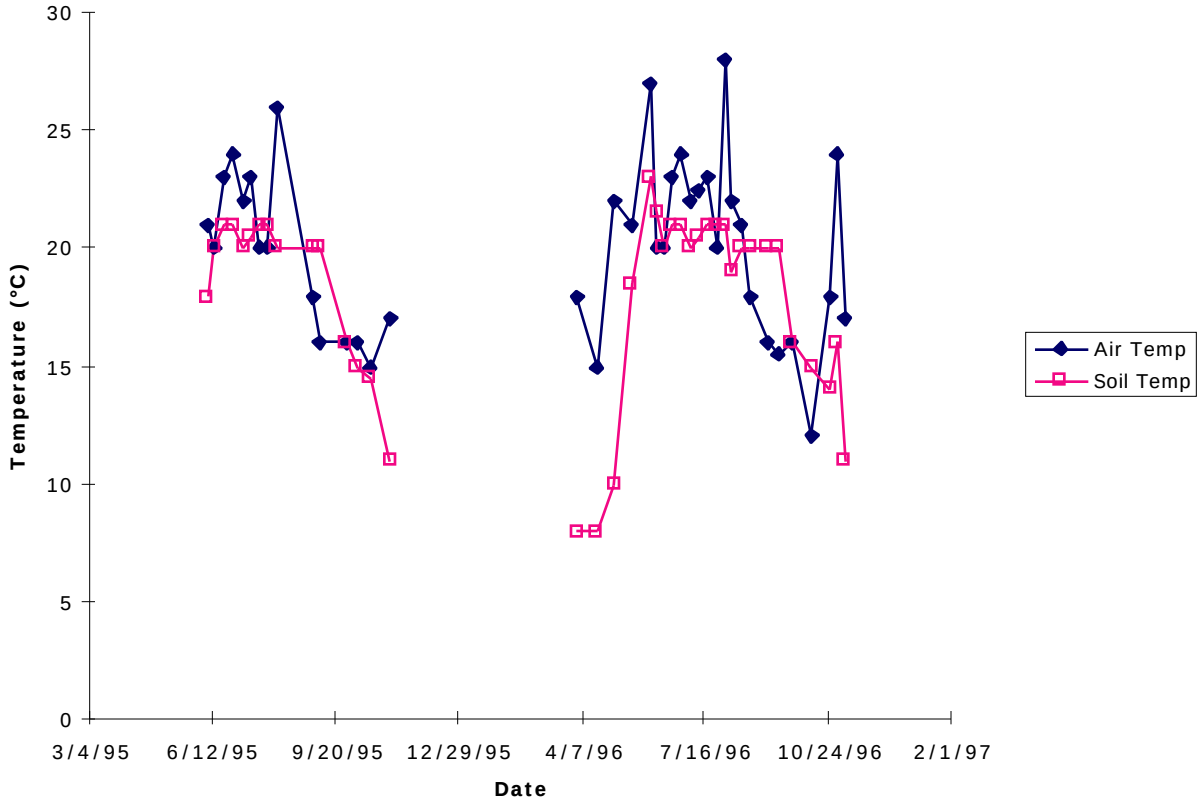

Figure 3.1 - Air and soil temperatures for 1995 and 1996.

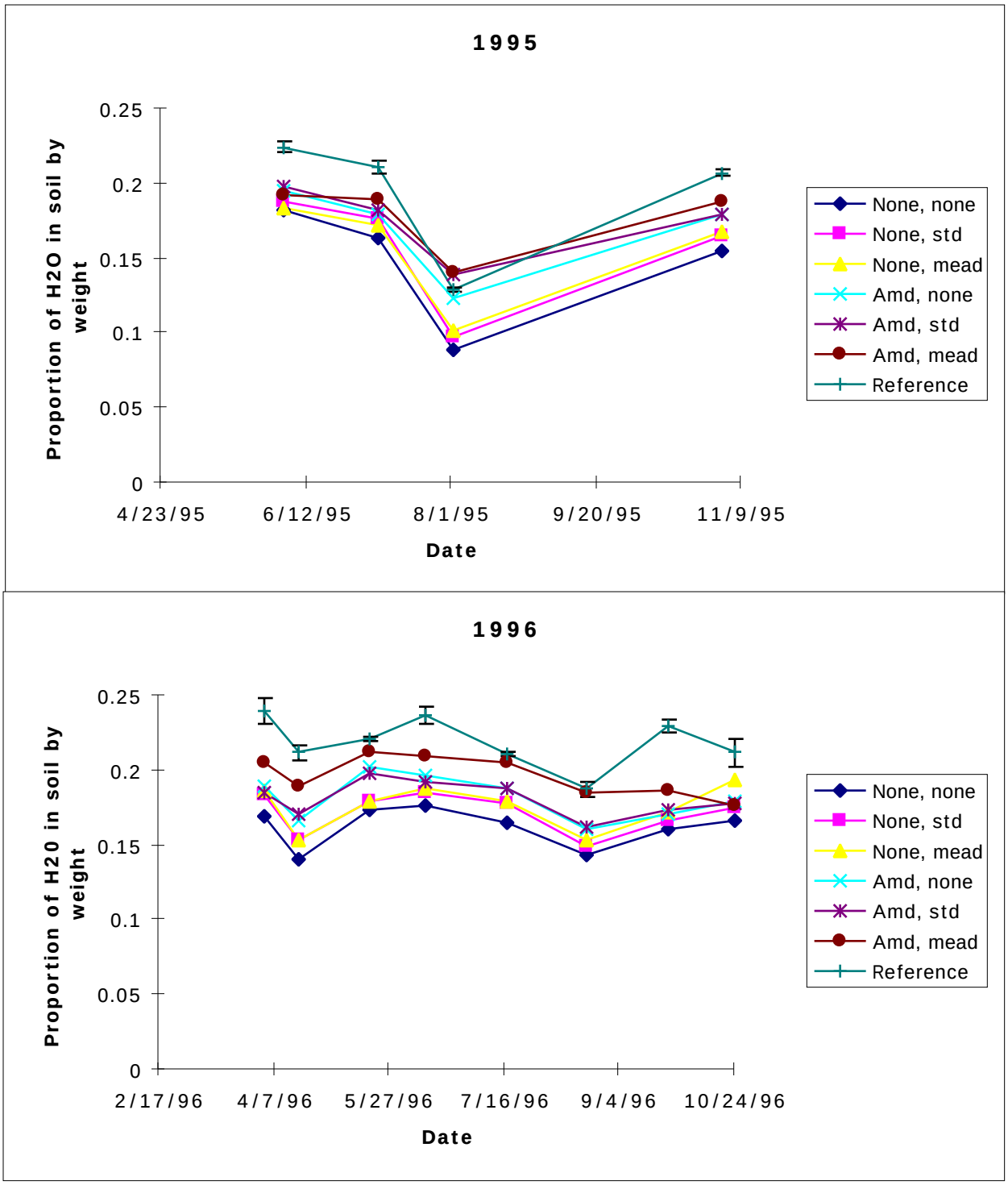

Figure 3.2 - Average soil moisture as a proportion of soil weight for 1995 and 1996 by treatment combinations. Error bars on the reference series represent one standard error.

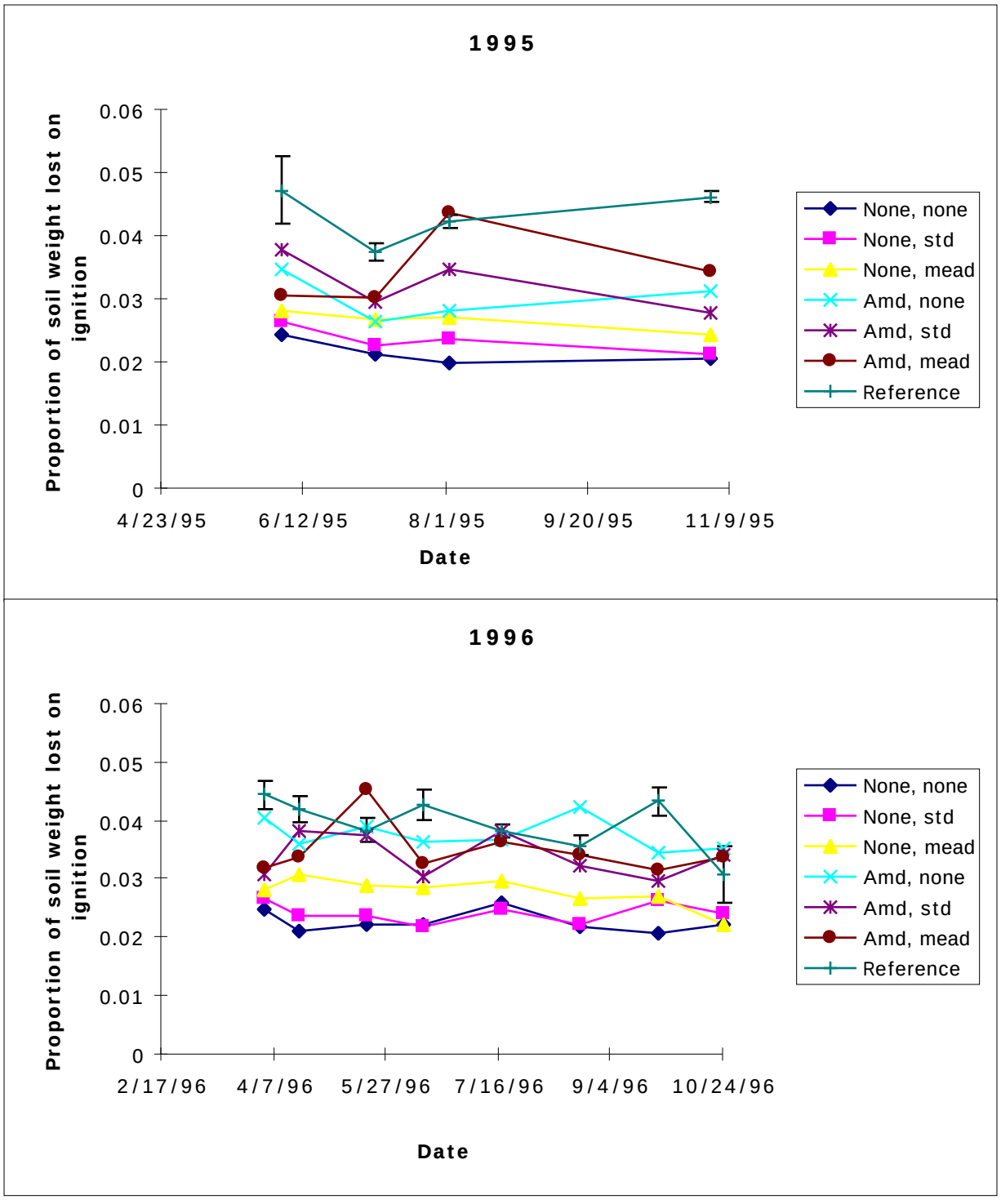

Figure 3.3 - Average soil organic matter estimated as the proportion of soil weight lost on ignition for 1995 and 1996 by treatment combinations. Error bars on the reference series represent one standard error.

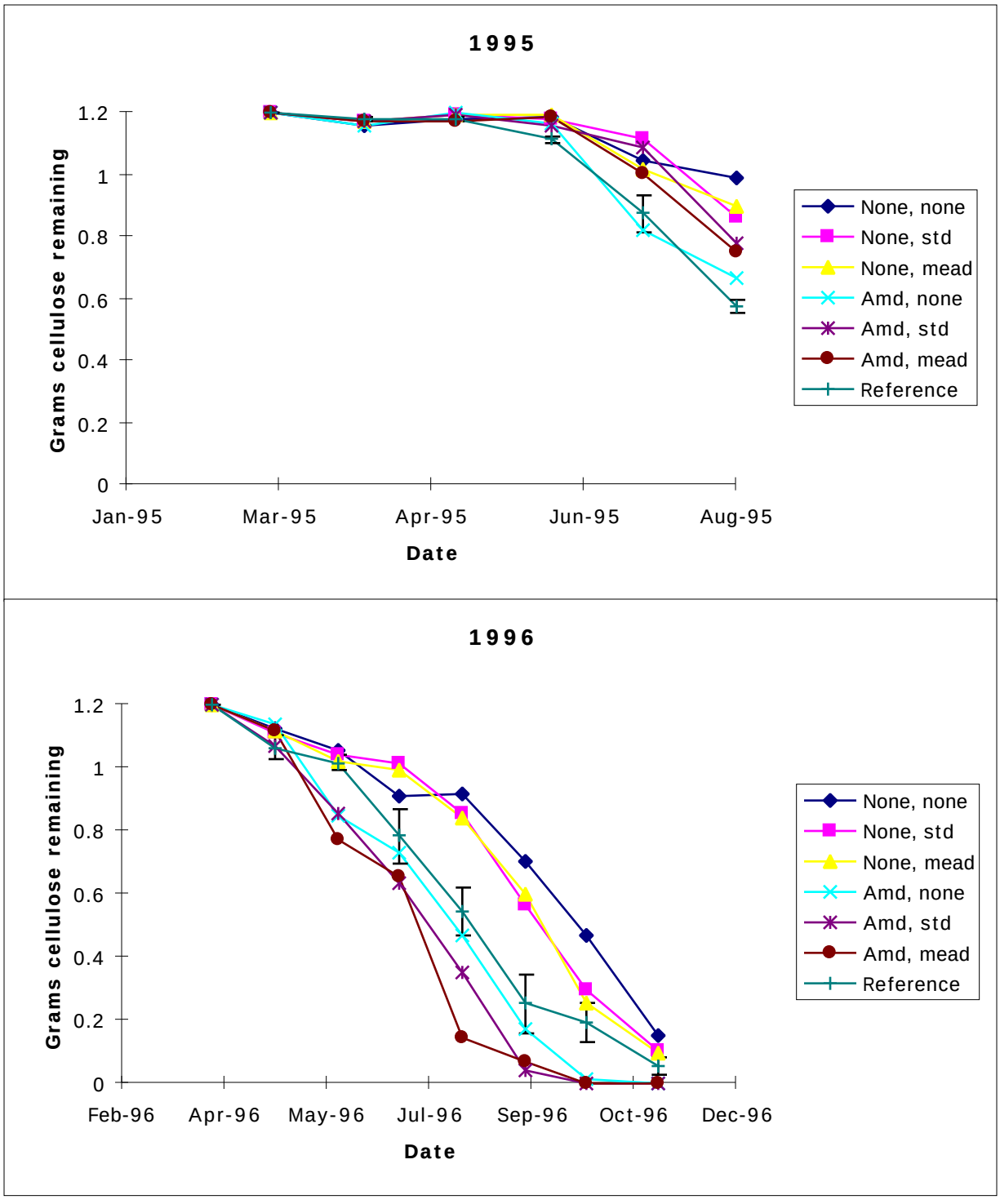

Figure 3.4 - Cellulose decomposition over time in 1995 and 1996. Error bars on the reference series represent one standard error.

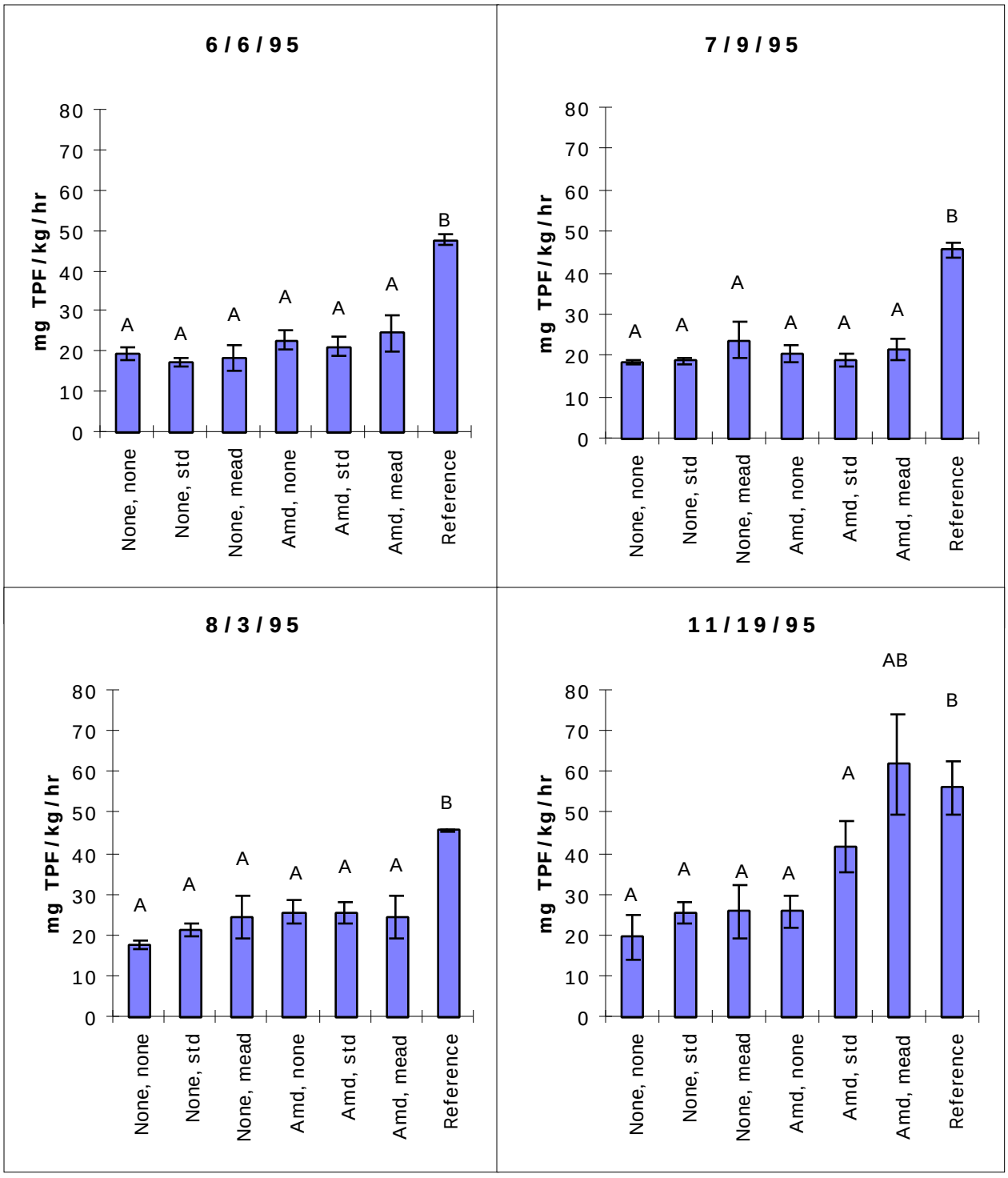

Figure 3.5 - Dehydrogenase activity by treatment combination in 1995. Error bars represent one standard error. Columns that do not share a common letter are considered significantly different using Tukey's HSD with a family error rate of 0.05 (individual error rate of 0.00366).

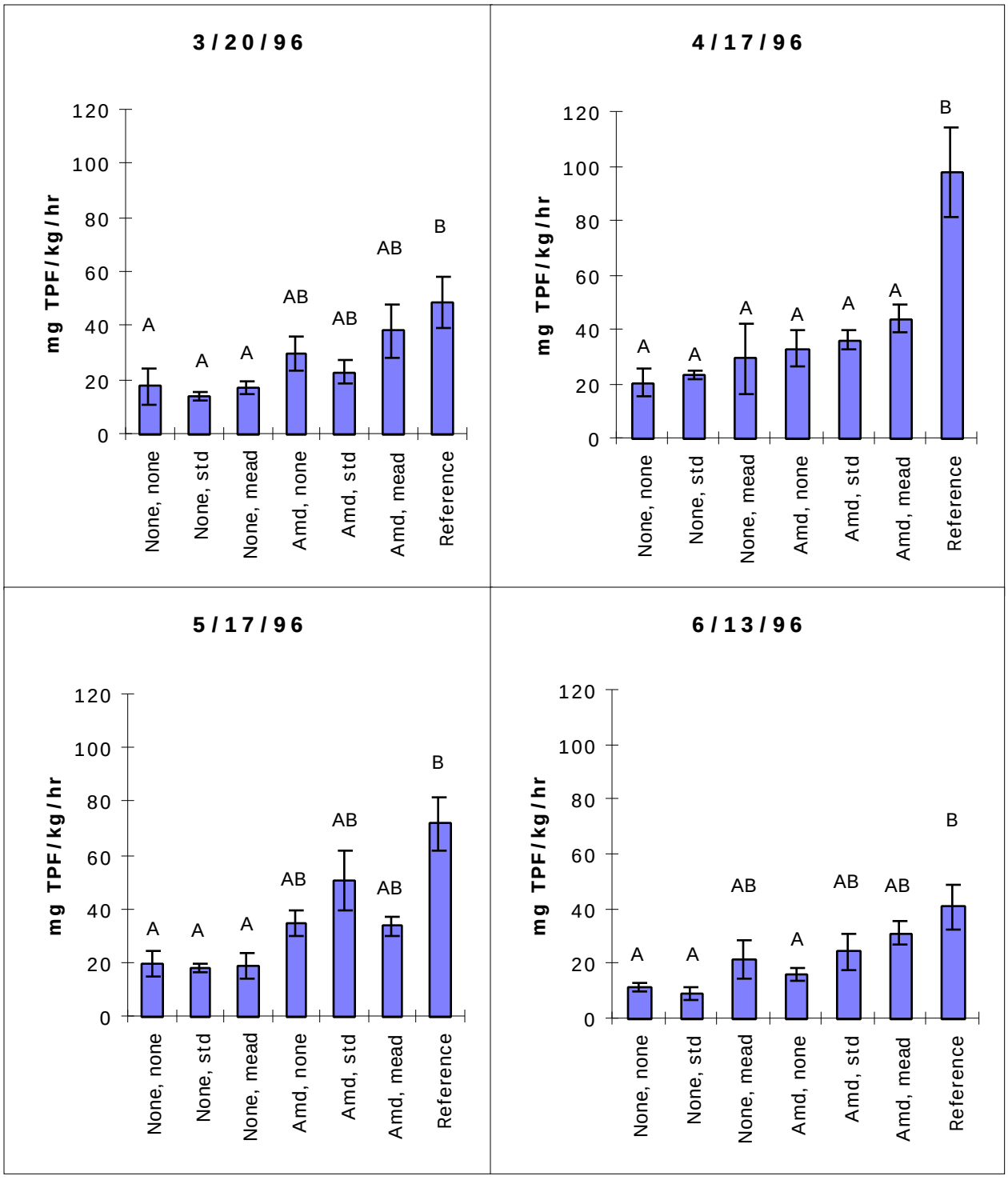

Figure 3.6a - Dehydrogenase activity by treatment combination in the first four sampling dates of 1996. Error bars represent one standard error. Columns that do not share a common letter are considered significantly different using Tukey's HSD with a family error rate of 0.05 (individual error rate of 0.00366).

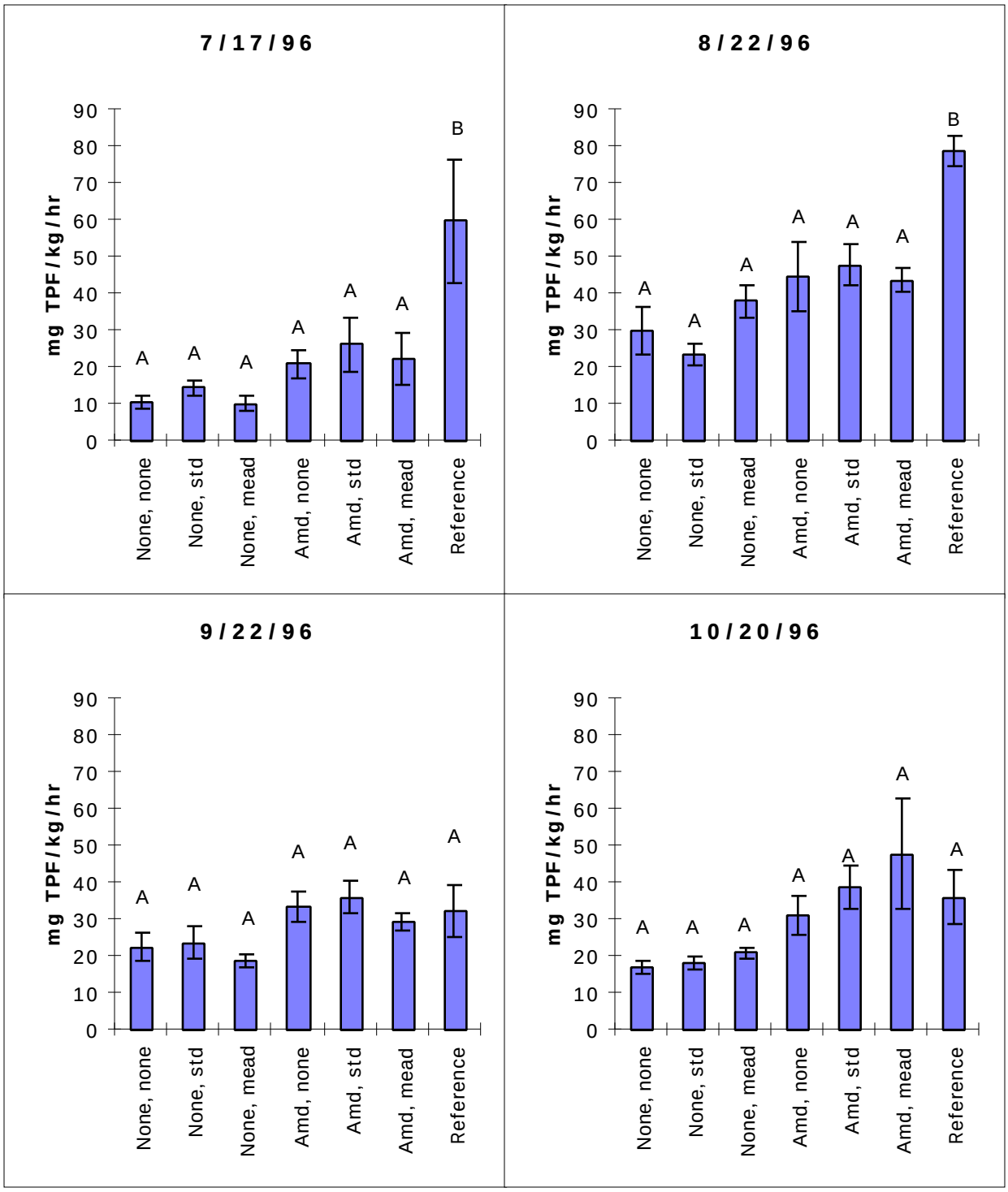

Figure 3.6b - Dehydrogenase activity by treatment combination in the last four sampling dates of 1996. Error bars represent one standard error. Columns that do not share a common letter are considered significantly different using Tukey's HSD with a family error rate of 0.05 (individual error rate of 0.00366).

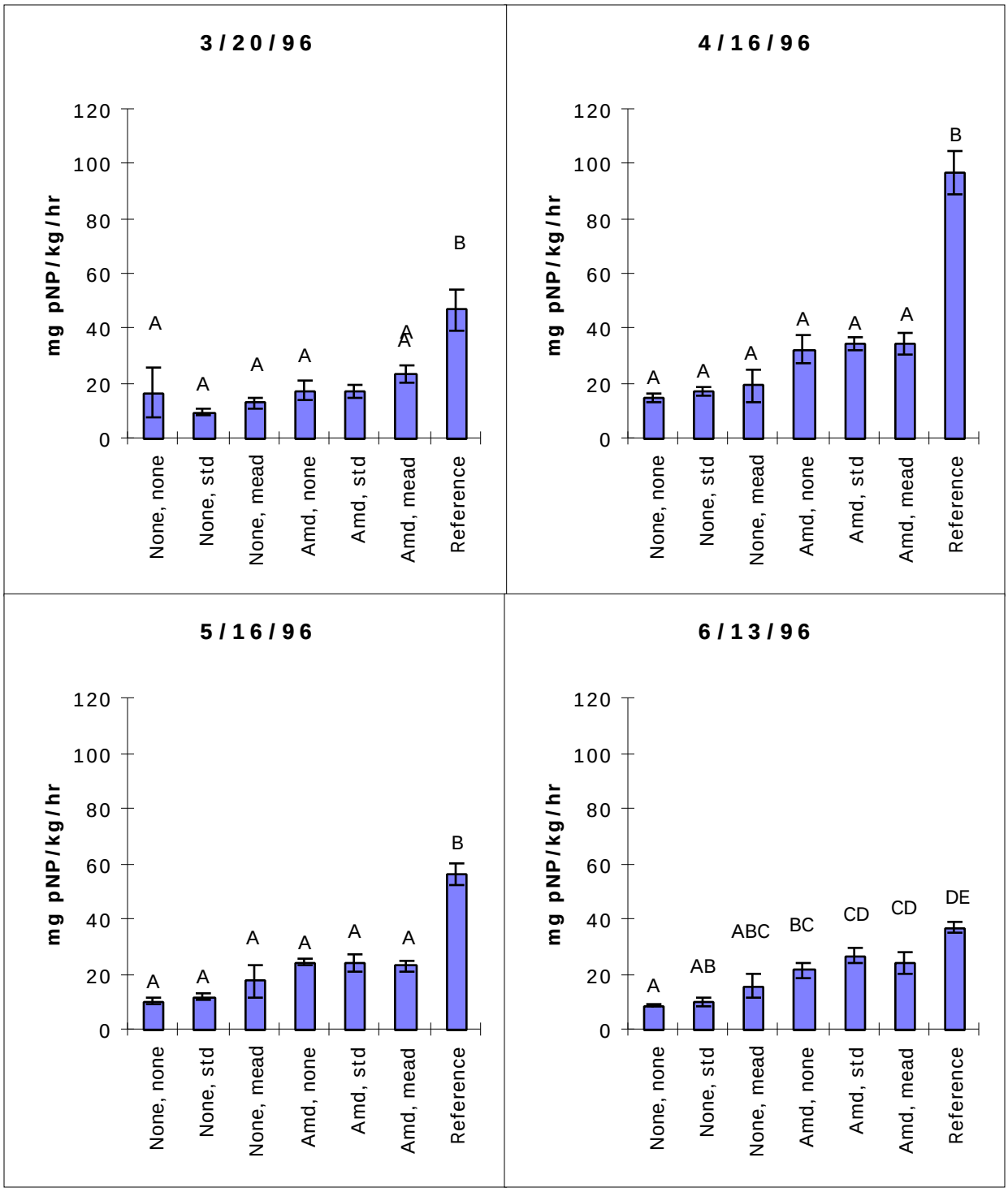

Figure 3.7a - Beta-glucosidase activity by treatment combination in the first four sampling dates of 1996. Error bars represent one standard error. Columns that do not share a common letter are considered significantly different using Tukey's HSD with a family error rate of 0.05 (individual error rate of 0.00366).

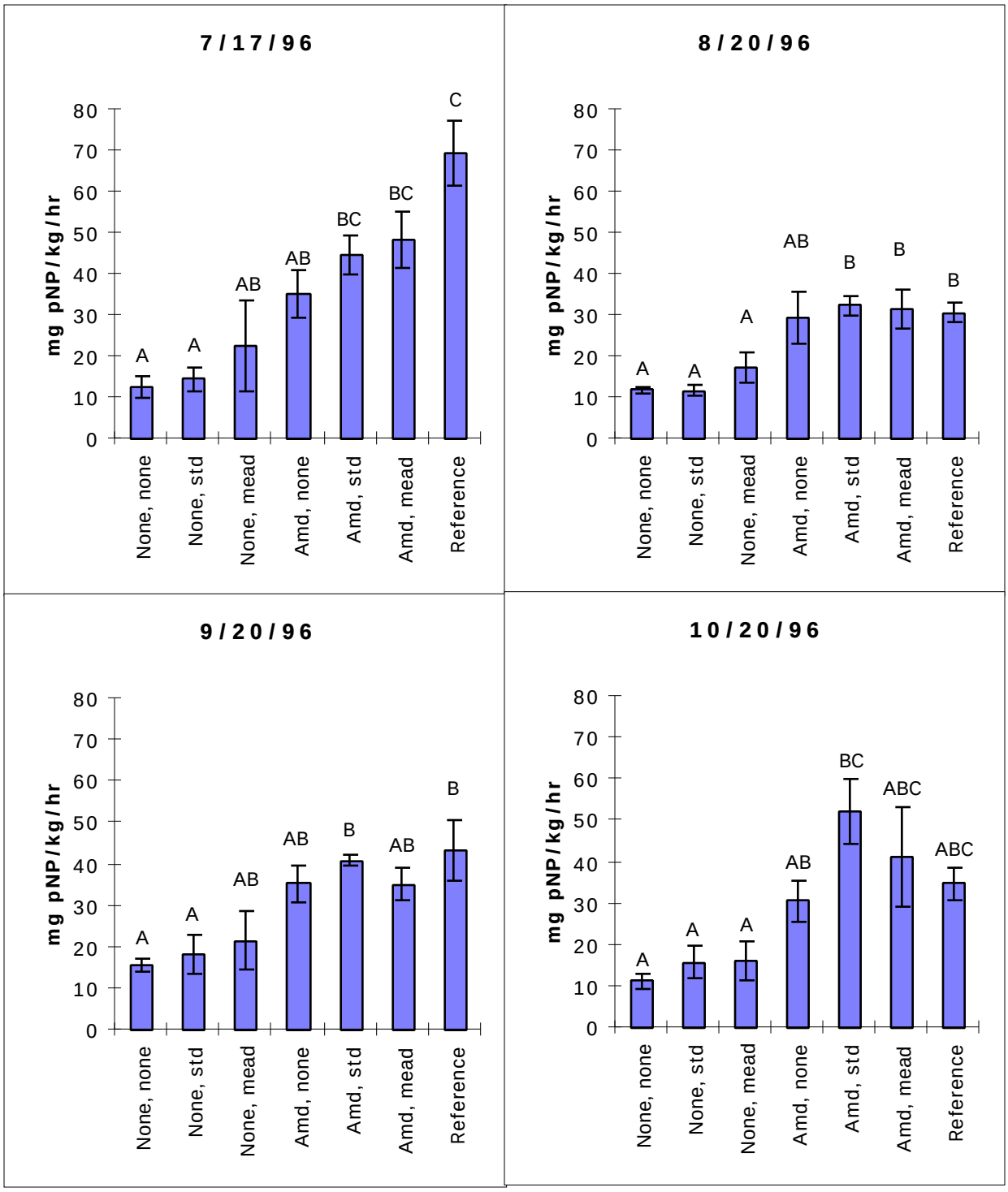

Figure 3.7b - Beta-glucosidase activity by treatment combination in the last four sampling dates of 1996. Error bars represent one standard error. Columns that do not share a common letter are considered significantly different using Tukey's HSD with a family error rate of 0.05 (individual error rate of 0.00366).

Chapter 4

IMPLICATIONS OF RESTORATION TECHNIQUE UPON RECOVERY OF SOIL / ATMOSPHERE GAS EXCHANGE

Introduction

To ennsure ecological sustainability, ecosystem integrity must be maintained at a level that allows for proper functioning and therefore, provision of ecosystem services. From toxicological response studies, it is known that ecosystem structure can be maintained while the constituent organisms are in poor health, thereby altering the ecosystem functions (Karr 1991, Cairns and Pratt 1995). Because of this dynamic nature of all ecological processes, many indices of restoration success have been criticized for their emphasis on ecosystem structure (Cairns and Niederlehner 1993). However, even if a dynamic, time-based measure of specific ecosystem functions would provide a more complete and accurate picture of restoration success, the fact remains that ecological functions are more resource intensive to define and measure. The effects of disturbance to ecosystem functions are becoming more apparent across regional boundaries as human population pressures increase the utilization of ecosystem services (e.g., Brown 1995). The benefits to a functional approach towards restoration assessment are obvious when maintenance of global ecosystem services is acknowledged as the overall restoration goal (Cairns 1995). Two functional parameters of upland terrestrial ecosystems that may be potential measurements of restoration success are the recovery of methane oxidation capacity in soils and the recovery of soil respiration rates, which reflect overall soil microbial activity.

Recent increases of radiatively active atmospheric trace gases are an indication of a functional alteration in the interaction between human and natural systems. Collectively known as greenhouse gases, the net global effects from these increases have been subject to much public debate. It is prudent to better understand the natural processes involved in regulating atmospheric gas balance and the effect human society is having on this regulatory capability. Ecological restoration of degraded lands offers a unique opportunity to study these interactions. Degradation of an area's ecological assemblage effectively provides a blank slate on which to observe ecological functioning as the system recovers. This allows extrapolation of the system's effect on landscape-level processes such as trace gas flux.

The concentration of methane in the atmosphere, a greenhouse gas with eleven times the heat retaining capacity of carbon dioxide (Dueñas et al. 1994), has been increasing for at least the past century and has contributed 17% of the total global warming over the past 10 years (IPCC 1990, 1992). The main sources of atmospheric CH_4 are rice fields, wetlands, biomass burning, ruminants, landfills, natural gas production, and coal mining (Denmead 1991). Temperate forested upland soils often harbor methane-oxidizing bacterial communities with a CH_4 uptake of up to 3.17 mg CH_4-C/m^2/day; global consumption rates in these systems may be up to 9.3 Tg CH_4-C/yr (Steudler et al. 1989). Grassland soils typically exhibit lower consumptions rates in a range of 0.15 to 1.45 mg CH_4-C/m^2/day. Over all upland terrestrial systems, this removal accounts for 5 - 10% of global methane uptake, while oceans make up the major global sink (Adamsen and King 1993). Methane oxidation is dependent upon methanotrophic soil

microorganisms, including the genera of *Methylomonas, Methylobacter, Methylococcus, Methylosinus,* and *Methylocystis* (Topp and Hanson 1991, Bédard and Knowles 1989). The effect of disturbance and subsequent recovery of methane oxidation capacity have been studied for hurricanes blowdowns (Bowden et al. 1993), forest clear cutting (Steudler et al. 1991), and agricultural systems (Kruse and Iversen 1995, Mosier et al. 1991, Hansen et al. 1993).

System respiration is an ecological function that is easily identified since CO_2 consumption and egress are central to energy transfer in practically all life. Perhaps for this reason, methodologies for soil respiration have been well documented and implemented for a variety of purposes (Anderson 1982). Carbon dioxide production from soil can be used as a general measure of microbial activity (Insam and Domsch 1988, Mathes and Schriefer 1985). Soil respiration is a major component of the global carbon budget with an estimated input of 50-75 Pg C/yr (Raich and Schlesinger 1992, Houghton and Woodwell 1989), which is 10-15 times the input due to fossil fuel burning in 1980 (Marland and Rotty 1984). Although an important part of global cycles, recovery of soil respiration after physical disturbance may be more important as an indicator of ecosystem functioning. High biological activity can be used as an indirect index of the nutrient cycling (Rowell and Florence 1993). The recovery of microbial community activity, therefore, is a good measurement of restoration success because a high nutrient use efficiency is a characteristic of mature ecosystems (Odum 1969).

The goals of this study were to test for the effects of soil amendment and revegetation treatments on soil respiration rate, the effects of these treatments on methane oxidation rate, and

Table 4.1 - Hypothesis statements for soil respiration and methane oxidation rate assays.

Number	Hypothesis
1	Experimentally disturbed sites will show decreased soil respiration and methane oxidation rates as compared to the undisturbed reference plots.
2	Sites amended with organic matter will exhibit greater similarity to reference plots than unamended sites, as measured soil respiration and methane oxidation rates.
3	Sites seeded with the "standard" or "meadow" revegetation mixtures will exhibit greater similarity to reference plots than unseeded sites. The two revegetation mixtures will not exhibit different effects on soil respiration or methane flux.

the change in these measurements in relation to the undisturbed reference areas over the course of the study period. The hypotheses are listed in Table 4.1 The experimental design used to test the hypotheses is described in Chapter 1.

Methods

Field methods

Soil system respiration and methane uptake were quantified simultaneously using closed equilibration chambers anchored to the soil surface (Mosier et al. 1993, Hutchinson and Mosier 1981) (Figure 4.1). The chambers are 9 cm tall by 20.4 cm in diameter (total volume, 2.92 L). The chambers mated to a docking collar that was submerged to a depth of 10 cm in the soil. Each chamber was fitted with a 0.25-inch (7 mm) Swage-lok sampling port and a 0.125-inch (3.5 mm)

pressure equilibration tube. Due to difficulties in the manufacturing of the chambers and docking collars, only 28 collars were available. Therefore, one block was deleted from the experimental design, resulting in a two by three completely randomized block design with four blocks, blocked against edge. The vegetation within the collars was trimmed to a height of 10 cm to allow for the chambers to mate unhindered by tall plants (A.R. Mosier, personal communication). To account for the trimming effect, the docking collars were shifted after every two sampling periods to a new location in the field plot.

On a weekly or semi-weekly basis, flux measurements were conducted using a 30-minute incubation period; gas samples were taken from the chambers at time 0, 15, and 30 minutes. Sampling usually began at 0800 hours. Three separate incubation periods were used to allow for reasonable logistics for taking samples and switching chambers (one period for plots # 1 - 10, a second for plots # 11 - 19, a third for plots # 20 - 28). Chambers were waved vigorously over the docking collar at least five times before docking for homogenizing atmospheric gas concentrations at ground level prior to sampling. Time zero samples were taken from two to three chambers per incubation period and accounted for each treatment type. Samples were taken with a 35-ml polypropylene syringe fitted with a gas-tight stopcock and #25 needle. Samples were stored immediately after sampling in an insulated cooler and stored in this manner until analyzed. Analysis took place within 24 hr of sampling. Soil and air temperatures were taken at the beginning and end of each sampling period. Values for each were averaged and recorded. Soil samples were taken on each gas sampling date as discussed in Chapter 2.

Laboratory methods

Gas samples were analyzed for CO_2 and CH_4 content on an SRI 8000 gas chromatograph using a thermal conductivity detector (TCD) for CO_2 and a flame-ionization detector (FID) for CH_4. The detectors were mounted in-line with the non-destructive TCD first to allow simultaneous measurement of CO_2 and CH_4. The gas chromotograph was equipped with Poropak-Q column and run at 105°C with He carrier gas at 20 ml/min. Ten-milliliter samples were injected through a Valco sampling valve with a 2-ml sampling loop. A water-tube manometer on the sampling valve exhaust loop ensured that injection onto the column was delayed until internal and external (laboratory) pressures equilized. Barometer readings were taken at each analysis period for use in calculating injection volumes. This setup allowed for a precise 2-ml injection with a minimum of operator error.

A standard curve for CO_2 and CH_4 concentrations was created by using known concentrations of pure gas diluted in Argon. A tank of compressed air was tested against this standard curve for CO_2 and CH_4 concentrations and then used as the standard to which all gas samples were compared (A.R. Mosier, personal communication). The standardized air was injected multiple times at the beginning of each analysis period to establish linearity on the detectors and after each tenth sample injection to account for baseline changes in the gas chromatograph due to shifts in laboratory temperature, pressure, and humidity. Gas concentrations were calculated using a sliding, interpolative scale between two injections of the

known standard gas. Thus, the calculation was proportionally weighted towards the proximate standard injection.

Numerical analyses

The closed chamber method for gas flux evaluation imposes a perturbation on gas exchange rates throughout the sampling period due to the changing concentration of gases inside the incubation chamber. This disturbance can result in a nonlinear change in gas concentrations over the sampling period. For this reason, gas fluxes were calculated using both linear and non-linear models (Hutchinson and Livingston 1993). The three linear models were based upon gas concentrations at each of the three sampling times,

$$Flux = F\,(C_{30} - C_{15}) \qquad [1]$$

$$Flux = F\,(C_{15} - C_{0}) \qquad [2]$$

$$Flux = \frac{F\,(C_{30} - C_{0})}{2} \qquad [3]$$

where F is a factor converting the flux units from ppm/chamber area/15 minutes to $gC/m^2/hr$,

$$Flux = \frac{(\text{Ambient Pressure})(\text{Chamber Volume})(12\text{g/mol C})(4\text{ time units})}{(8.314)(\text{Temp in K})(\text{Chamber Area})(1{,}000{,}000)} \qquad [4]$$

The nonlinear model used was developed from diffusion theory and proposed by Matthias et al. (1978) and Hutchinson and Mosier (1981).

$$Flux = \frac{F\,(C_{15} - C_0)^2}{(2C_{15} - C_{30} - C_0)} \ln\left[\frac{C_{15} - C_0}{C_{30} - C_{15}}\right] \qquad [5]$$

The flux calculation was chosen for each sample based upon a decision algorithm that determines the linearity of the concentration curve.

Analysis of variance was used to test for treatment effects. One-way analysis of variance was used to test for differences between treatment combinations and reference plots. Tukey's HSD test was used for multiple comparison tests. Covariance of CO_2 and CH_4 flux with soil organic matter, soil moisture, and soil temperature was tested using two-way analysis of covariance. Correlation of all measurements was documented using Pearson's correlation.

Results

Table 4.2 shows the means, medians, and ranges of soil gas flux and the soil physical parameters observed over the entire study period. Soil nutrients are summarized in Table 4.3. Soil temperatures over 1995 and 1996 are shown in Figure 3.1 (see Chapter 3). Figures 4.2 and 4.3 show soil moisture and soil organic matter lost on ignition for both study years. No soil gas flux or soil physical parameters were highly correlated, although the difference in relative correlation between the two gas fluxes and other variables is interesting (Table 4.4). Soil respiration and methane oxidation rates were not highly correlated ($r = -0.31$). Soil respiration was moderately correlated with soil and air temperature ($r = 0.62$), while methane oxidation showed low correlation with soil and air temperature ($r = -0.40, -0.21$, respectively). Soil

Table 4.2 - Means, medians, and ranges of soil respiration, methane flux, and soil physical data.

Variable	Units	Mean	Median	Range
Net CO_2 flux (CO2)	mg CO_2-C/m^2/hr	169.59	152.29	12.81 to 555.31
Net CH_4 flux (CH4)	mg CH_4-C/m^2/hr	- 0.00765	- 0.00763	- 0.0511 to 0.0268
Soil moisture (H2O)	%	16.19	16.55	4.38 to 48.75
Soil weight lost on ignition (LOI)	%	3.19	2.88	0.08 to 12.02
Soil temperature (STEMP)	°C	18.06	20	8 to 23
Air temperature (ATEMP)	°C	20.05	20	12 to 28

Table 4.3 - Summary of soil nutrient data for all treatment combinations (mean ± SD). Values followed by the same letter are not significantly different using Tukey's(family error rate of 0.5).

Treatment Combination	pH	ppm					
		P	K	Ca	Mg	Zn	Mn
None, none	5.82 ± 0.16a	23.2 ± 13.39a	52.8 ± 11.8a	1449 ± 177a	172 ± 28.4a	7.76 ± 4.36a	25.8 ± 5.89a
None, Std	5.96 ± 0.05ab	21.6 ± 4.56a	64.8 ± 17.5a	1545 ± 196a	184 ± 36.9a	8.56 ± 1.89a	35.2 ± 13.11ab
None, Mead	5.88 ± 0.08ab	16.8 ± 1.38a	59.2 ±14.8a	1478 ± 104a	179 ± 34.4a	6.96 ± 2.13a	24.16 ± 4.42a
Amd, None	6.668 ± 0.08c	30.4 ± 8.29ab	147.2 ±15.6b	2947 ±330b	451 ± 36.3b	10.16 ± 1.66a	56.64 ± 6.45c
Amd, Std	6.32 ± 0.13c	36.8 ± 5.21ab	145.6 ±20.3b	3072 ± 293b	446 ± 34.7b	9.52 ± 3.24a	62.0 ± 4.52c
Amd, Mead	6.56 ± 0.11c	31.2 ± 8.19ab	164 ±37.7b	3100 ± 575b	441 ± 56.7b	11.44 ± 5.74a	56.8 ± 10.4c
Reference	6.05 ± 0.06bc	40.0 ± 3.27b	123.0 ± 26.4b	2054 ± 160ab	342 ± 47.8b	12.9 ± 3.55a	45.1 ± 8.27b

Table 4.4 - Pearson's correlation coefficients for gas flux and soil physical variables (abbreviations same as in Table 4.2).

	CO2	CH4	H2O	LOI	STEMP
CH4	- 0.314				
H2O	0.072	0.547			
LOI	0.019	- 0.134	- 0.430		
STEMP	0.623	- 0.404	- 0.153	- 0.085	
ATEMP	0.616	- 0.212	0.004	- 0.124	0.511

moisture was moderately correlated with methane oxidation rate (r = 0.55) but not with CO_2 production (r = 0.07). Soil organic matter was not correlated with either gas flux rate.

Average gas fluxes across the entire study period for each treatment grouping are shown in Table 4.5. In general, soil respiration was highest in the undisturbed reference plots. Amended sites showed higher respiration rates than unamended sites but did not reach the same level as the undisturbed reference sites. This effect is reflected in the significance of the amendment treatment as a predictor of CO_2 production as tested by two-way analysis of variance (Table 4.6). The effect of seeding treatment on soil respiration was slightly significant (during 5 of 12 months) and generally showed a higher CO_2 production rate for the "standard" seeded plots.

Table 4.5 - Average CO_2 and CH_4 fluxes ± one standard error by treatment grouping.

Treatment Grouping	CO_2 flux (mg CO_2-C/m^2/hr)	CH_4 flux (mg CH_4-C/m^2/hr)
Unamended	130.37 ± 19.12	- 0.00922 ± 0.00250
Amended	186.27 ± 25.53	- 0.00723 ± 0.00266
No seeding	143.58 ± 28.95	- 0.00827 ± 0.00294
Standard seeding	175.06 ± 30.94	- 0.00698 ± 0.00351
Meadow seeding	156.32 ± 26.97	- 0.00943 ± 0.00300
Reference	237.22 ± 52.70	- 0.00351 ± 0.00515

Table 4.6 - Summary of two-way ANOVA p-values for treatment effects and interactions on $C0_2$ and CH_4 flux.

Factor	6/95	7/95	8/95	9/95	10/95	4/96	5/96	6/96	7/96	8/96	9/96	10/96
CO2 Flux												
Amend	**	*	*	ns	*	***	***	***	***	**	*	*
Seed mix	*	ns	ns	ns	ns	**	ns	ns	ns	*	**	**
Amend * Seed mix	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	**
CH4 Flux												
Amend	ns	ns	*	*	*	ns	ns	***	*	*	*	ns
Seed mix	ns	ns	ns	ns	ns	***	**	ns	ns	ns	*	*
Amend * Seed mix	*	ns	*	ns	ns	***	**	ns	ns	*	***	ns

ns = $p>0.05$, *$p<0.05$, **$p<0.01$, ***$p<0.001$

All reference and experimental plots showed the capacity to oxidize and generate methane at some point over the study period. The general trend shows the reference plots with a lower methane oxidation capacity than the disturbed, experimental plots (Table 4.5). Amended plots showed an overall tendency towards lower methane oxidation rates than unamended plots. Soil amendment had a significant effect on methane oxidation capacity, showing significance in two-way analysis of variance for 7 of 12 sampling dates (Table 4.6). Seeding treatments differed slightly in methane uptake capacity, with significance on only 4 of 12 dates. The general trend was for "standard" seeded plots to show lower methane oxidation rates than unseeded or "meadow" seeded plots.

Average monthly soil respiration for 1995 and 1996 is shown in Figures 4.4 and 4.5a,b separated by treatment combination. The general trend shows reference plots to be significantly different than disturbed experimental plots during 1995 until the onset of late summer and fall. The same trend continued in 1996, with amended plots beginning to show significant differences from unamended plots also. Through 1996, plots that were amended and seeded with the "standard" seeding mix showed the highest respiration rates of all experimental plots, with rates equal to or surpassing the undisturbed references during later summer months.

Average monthly methane oxidation rates for 1995 and 1996 are shown in Figures 4.6 and 4.7a,b and are separated by treatment combination. Few differences between experimental plots were observed during 1995. The main differences were between reference and experimental plots, with reference plots showing lower consumption rates and sometimes averaging a net production of CH_4 in some months. Consumption rates show a wide variance during the later months of 1995. Methane production in reference plots and consumption in experimental plots continued in the early parts of 1996. Again, few differences between reference and experimental plots can be seen throughout the rest of the year until the later months when high variance between treatment combinations was observed. Discernable trends due to amendment or seeding levels are difficult to discern through 1996.

Discussion

Removal of the top 20 cm of topsoil significantly altered soil respiration and methane oxidation rates throughout both years of the study. Soil respiration was significantly reduced in all experimental treatments at the beginning of the study. Two years later, at the end of 1996, the restoration treatment control (the "none, none" treatment combination) was still significantly different from the undisturbed reference plots. Soil respiration is a broad, integrative measurement of biological activity. Without any restoration effort, the disturbed systems in this study did not exhibit the ability to recover their soil biological activity to a level similar to the predisturbance state within 2 years.

In amended sites, however, soil respiration rates recovered to the point that they were indistinguishable from reference sites during much of 1996. This is most likely due to the additional organic matter, which increases the total energy available for the microbial community (Johnson et al. 1995). In this study, soil respiration did not show a correlation with soil organic matter lost on ignition ($r = 0.019$). This unexpected result is probably because the soil amendment and most of the increased biological activity were in the uppermost soil layers (< 5 cm deep) while the soil samples were 10 cm deep. Soil moisture did not correlate with respiration either, which has been documented in previous studies (Mathes and Schriefer 1985, Rochette et al. 1991).

The choice of revegetation mixture did not account for a significant effect on soil respiration rate according to two-way analysis of variance. Over the entire study period,

however, there was a trend towards a higher respiration rate for the “standard” seeded plots. Based upon earlier studies, it would be expected that soil respiration would vary depending upon the associated plant community (Buyanovsky et al. 1986, Raich and Schlesinger 1992). This study shows that 2 years of recovery after disturbance is enough time for vegetation to begin its alteration of the soil microbial environment, but not enough time for the soil community to adapt fully to the associated vegetation.

Methane oxidation rates observed in this study exhibited a high variance, with all soils ranging from net production to net consumption of methane. The moderately high correlation of soil methane flux and soil moisture ($r = 0.547$) is due to the importance of soil moisture in limiting the porosity and diffusion rates of atmospheric gases into the soil (Harris et al. 1982, Whalen and Reeburgh 1990). Therefore, during wetter periods, it is possible for upland soils to generate methane anaerobically. In other words, lower total vegetative cover and soil organic matter of the disturbed plots make for dryer soils with higher diffusion rates and, consequently, higher methane uptake rates. This effect is limited when soils become too dry to support the methanotropic community, at which point methane uptake sharply declines (Mosier et al. 1991).

The main observable effect on methane flux found in this study was the increase in the consumption rate in all experimentally disturbed soils. This was observed in both 1995 and 1996 and was most definite in early spring and late fall. This result is similar to what has been observed in hurricane blowdowns (Bowden et al. 1993) and cultivated soils (Kruse and Iversen 1995). The general effect of soil amendment on soils was to suppress methane uptake rate

compared to the unamended plots. On average, amended soil exhibited 77% of the unamended soil methane uptake capacity, although variances were high. This may be caused by the increased porosity found in the soils due to the organic amendment. The negative correlation between organic matter lost on ignition and methane flux ($r = - 0.134$) may indicate that the increased organic matter improves atmospheric diffusion into the soil. The unamended soils were very hard-packed, clayey soils that would exhibit lower gaseous permeability. Another possible contributing factor is the increased nutrients in the amended soil (Table 4.3). Fertilization has been shown to decrease methane oxidation rates substantially in a wide variety of soil types (Steudler et al. 1989, Hütsch et al. 1993, 1994, Nesbit and Breitenbeck 1992). Inhibition due to increased N availability is of specific interest and will be assessed for this study when that information is available (NO_3-N content in the experimental plot soils is currently being analyzed, but is unavailable at the time of this writing). Revegetation mixture showed no significant effects. This result follows from previous observations showing soil diffusion and N availability to be the primary determinants in methane oxidation

In comparison to previously reported rates for methane oxidation, those observed in this study are much lower than those reported for forest areas and similar to those observed in grasslands (Table 4.7). This follows the global trend of uptake rates in different ecosystems where relative rates taken from published values are grasslands < tropical forest < subtropical broadleaf savannah < tundra < temperate forest. The importance of methane uptake in these

Table 4.7 - Comparison of CO_2 and CH_4 flux rates observed in this study with flux rates from other systems (mean ± SE).

Study System	Soil Respiration (mg CO_2-C/m^2/hr)	Methane Flux (mg CO_2-C/m^2/hr)	Reference
Old fields recovering from mechanical disturbance			
Unamended	130.37 ± 19.12	- 0.00922 ± 0.00250	Current study
Amended	186.27 ± 25.53	- 0.00723 ± 0.00266	
No seeding	143.58 ± 28.95	- 0.00827 ± 0.00294	
Standard seeding	175.06 ± 30.94	- 0.00698 ± 0.00351	
Meadow seeding	156.32 ± 26.97	- 0.00943 ± 0.00300	
Reference	237.22 ± 52.70	- 0.00351 ± 0.00515	
Temperate woodland	250 ± 63.75	- 0.06875 ± 0.012	Crill 1991
Temperate forest			Bowden et al. 1993
Control	63.8 ± 4.5	- 0.049 ± 0.003	
After hurricane	62.3 ± 1.9	- 0.052 ± 0.005	
Subalpine meadow	-	- 0.012 ± 0.0043	Mosier et al. 1993
Shortgrass prairie			Mosier et al. 1991
Native	-	0.0108 ± 0.0045	
Fallow	-	0.0075 ± 0.0033	
Wheat planted	-	0.0054 ± 0.0025	

different soils must be understood to quantify its role in global methane budgets and greenhouse gas effects (Tyler 1991).

Conclusions

The effect of mechanical disturbance and subsequent restoration on soil respiration and methane oxidation rate can be observed and interpreted in terms of a restoration assessment

relative to a reference condition. In this study, respiration rates were consistently higher in reference areas throughout the observation period. Furthermore, the standard reclamation mixture appears to show the highest degree of recovery in total respiration over two years. Soil respiration rates are useful in determining the overall biological activity in restored soils and is important for determining functional recovery from disturbance and the ability for restored systems to cycle energy and nutrients satisfactorily. Soil methane flux is less dependent upon overall biotic activity and therefore less useful for assessing restoration progress. However, its global ramifications for biogeochemical cycles make it an vital end-point for determining the cross-landscape effects of a restored ecosystem.

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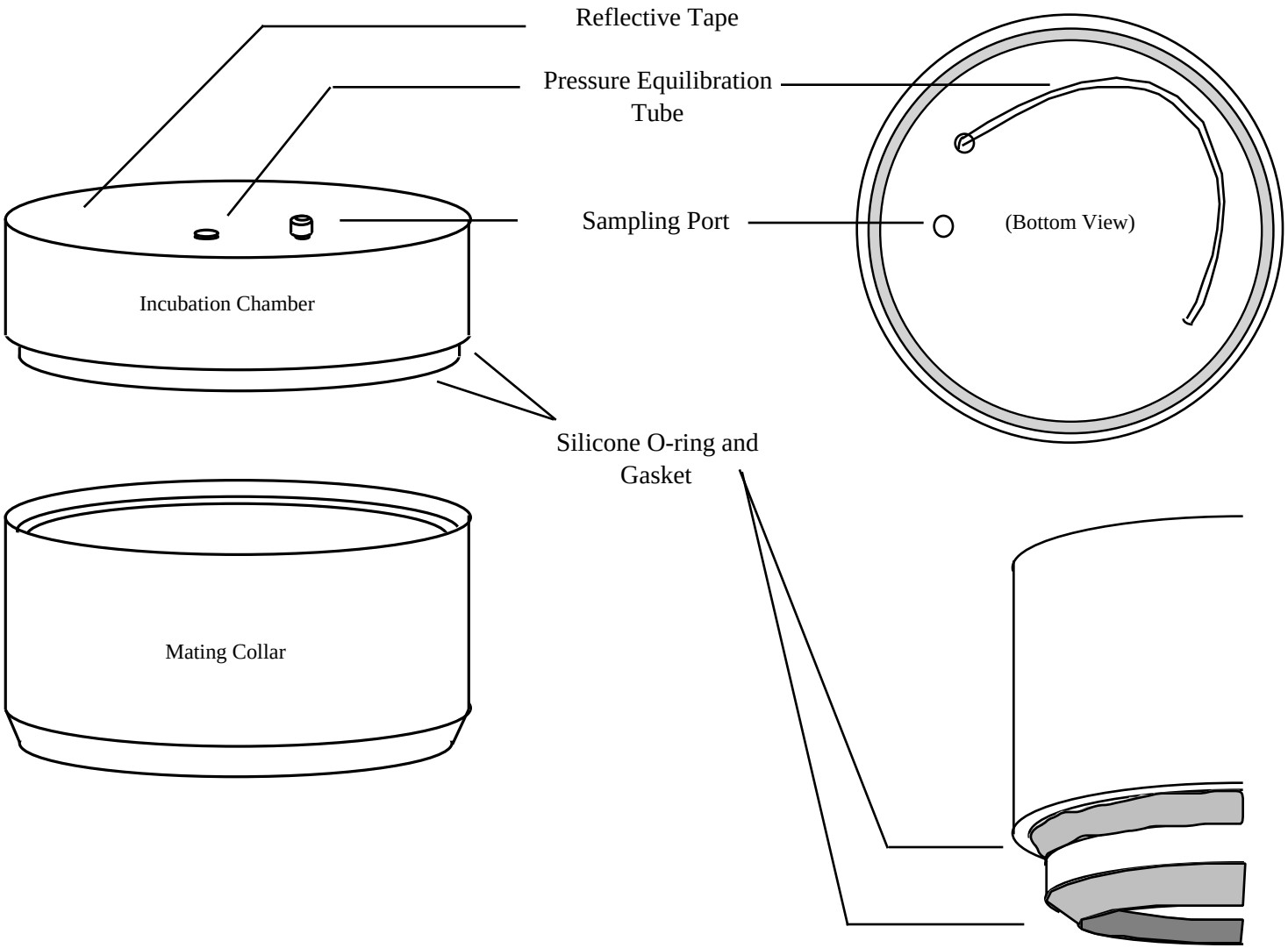

Figure 4.1 - Schematic drawing of the closed incubation chambers for soil / atmospheric gas flux calculation

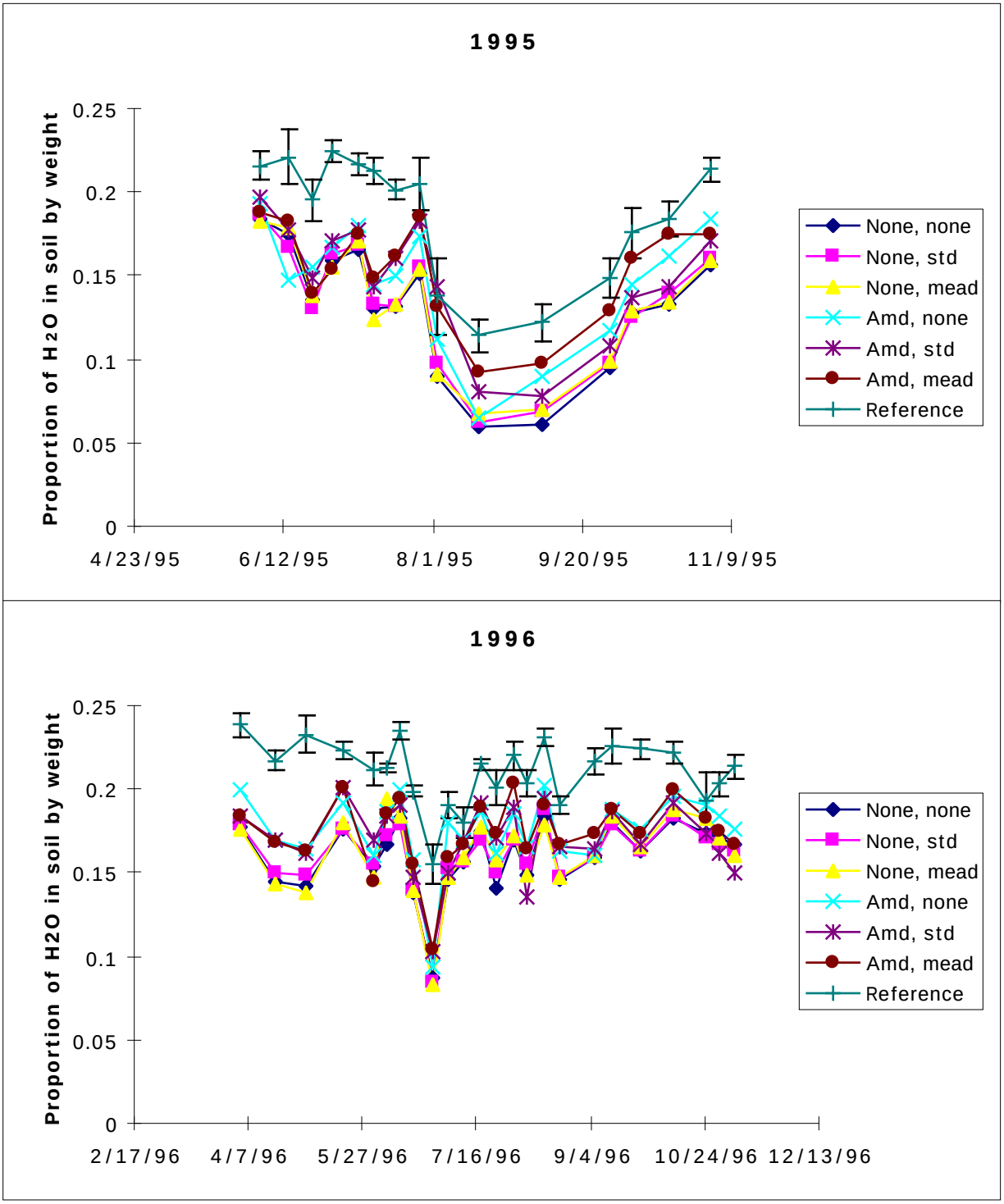

Figure 4.2 - Average soil moisture for all treatment combinations in 1995 and 1996. Error bars on the reference data series represent one standard error.

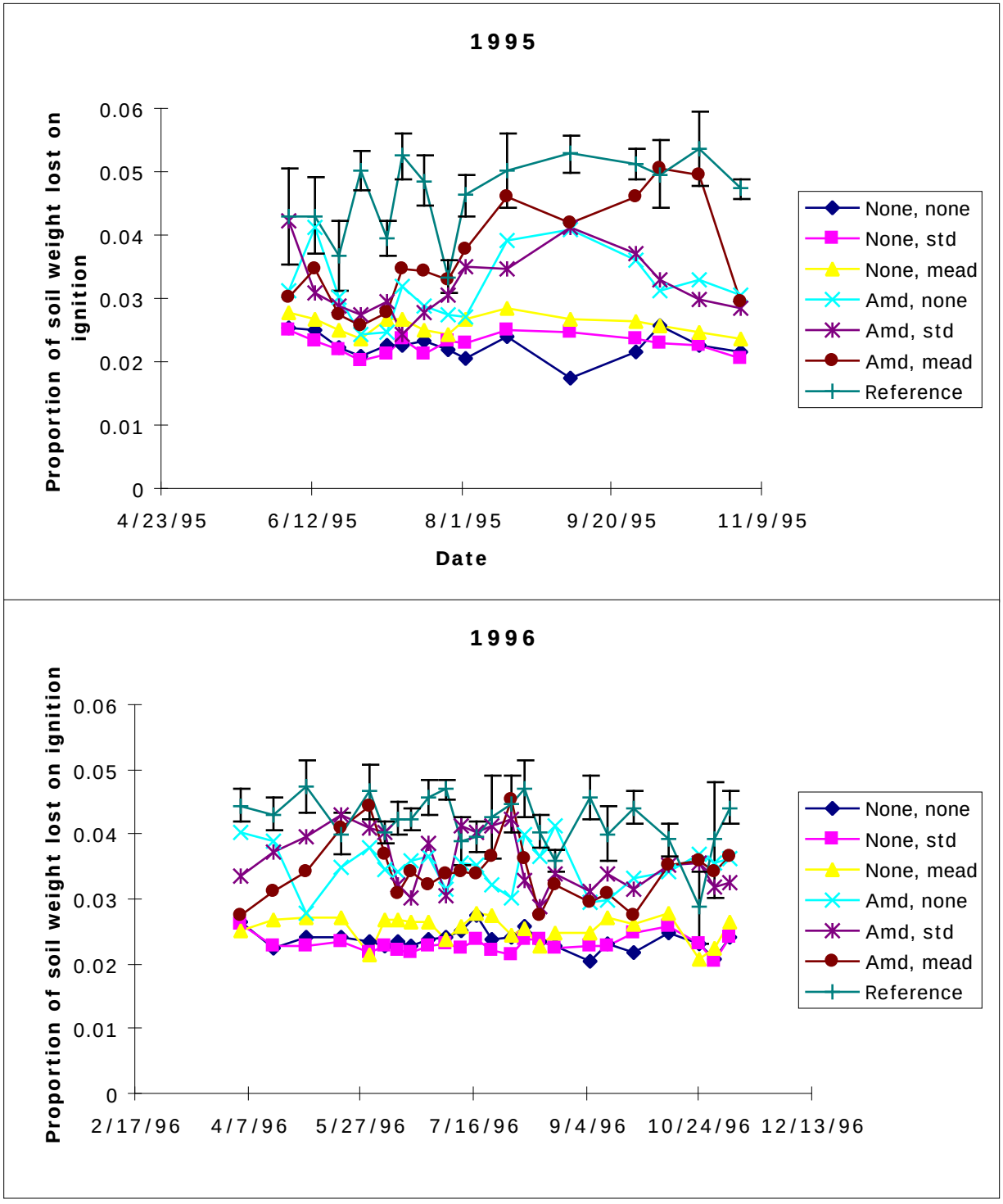

Figure 4.3 - Average soil organic matter for treatment combinations in 1995 and 1996. Error bars on the reference data series represent one standard error.

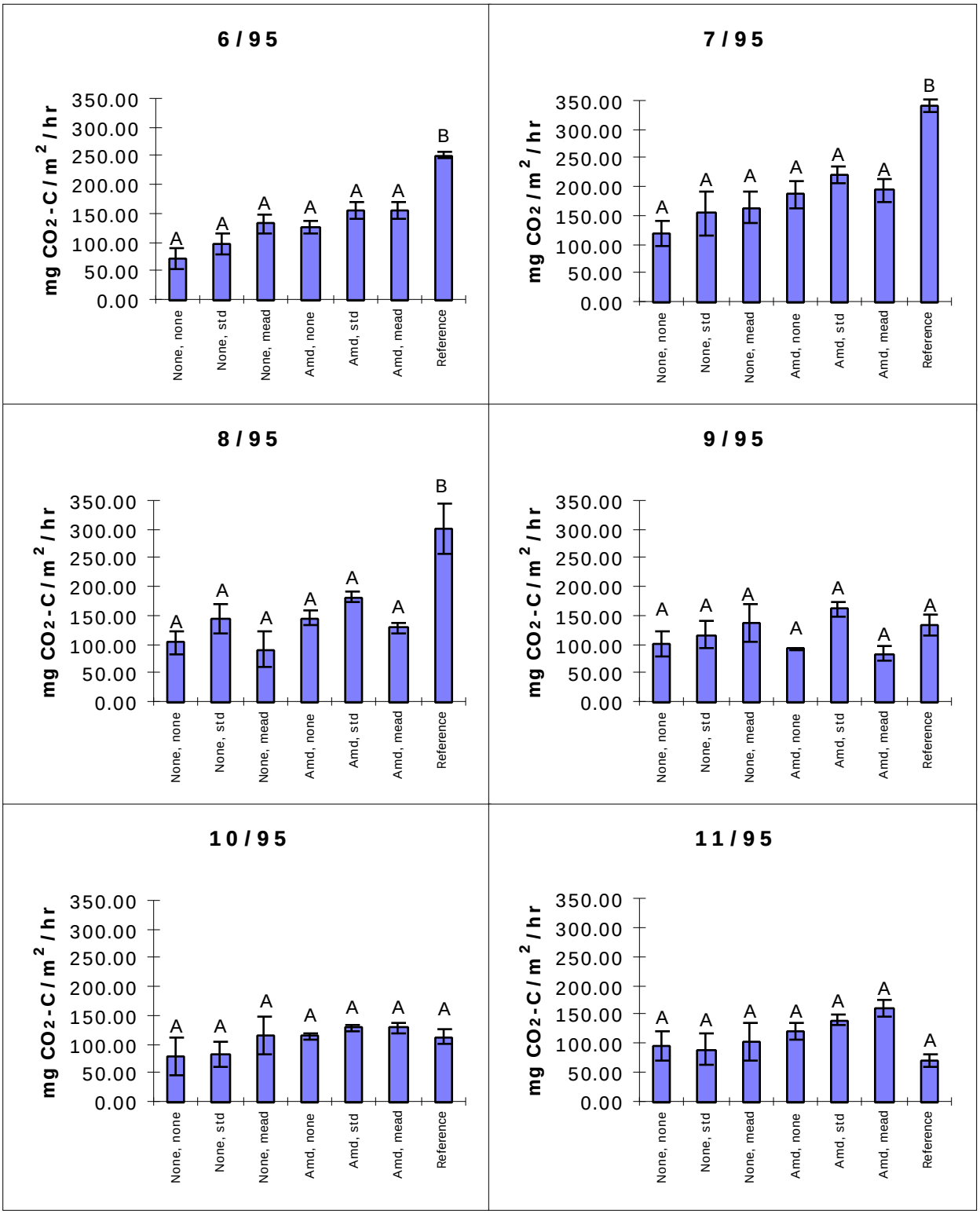

Figure 4.4 - Average monthly CO_2 flux by treatment combination in 1995. Error bars represent one standard error. Columns that do not share a common letter are considered significantly different using Tukey's HSD with a family error rate of 0.05 (individual error rate of 0.00381).

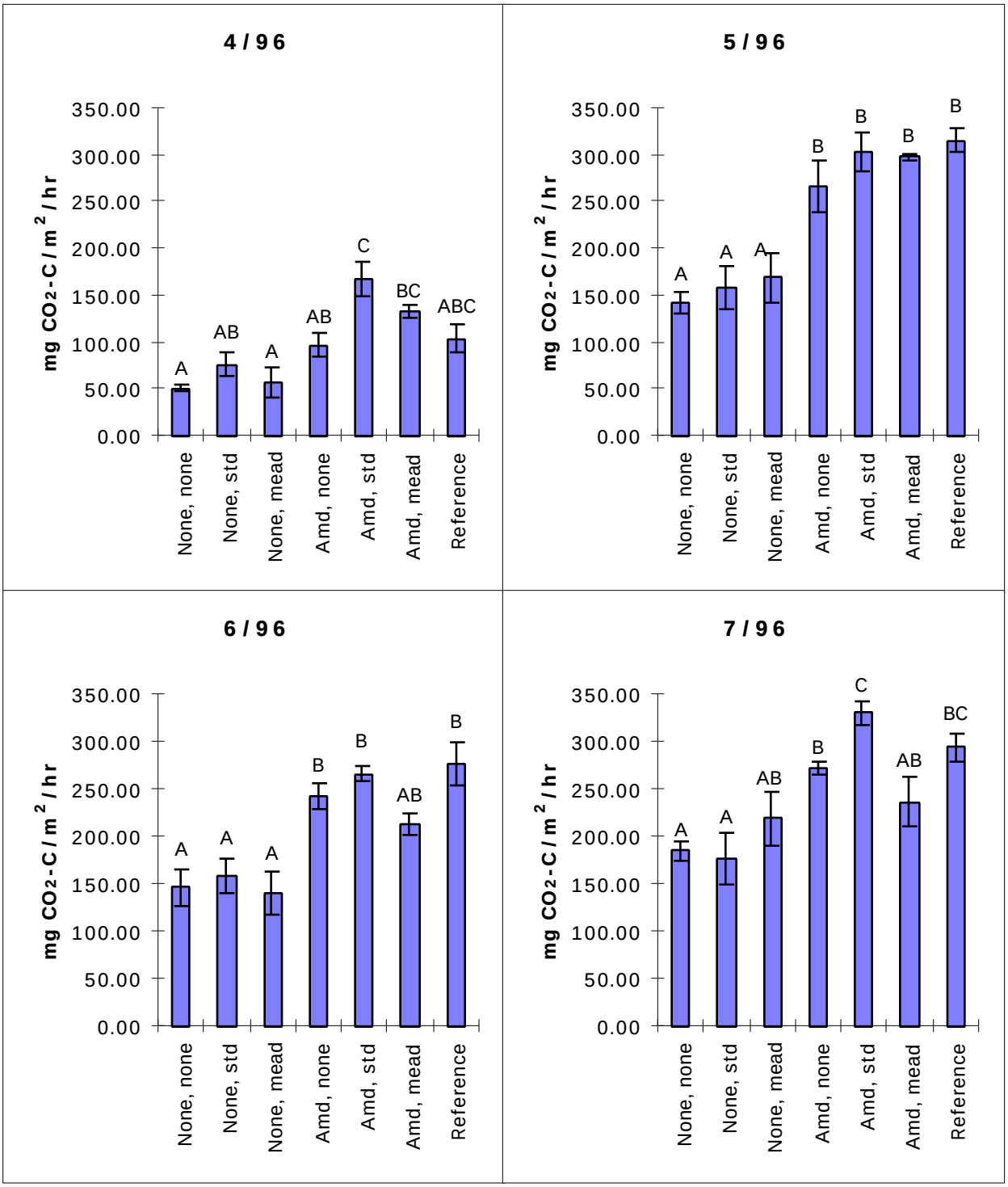

Figure 4.5a - Average monthly CO_2 flux by treatment combination in the first four sampled months of 1996. Error bars represent one standard error. Columns that do not share a common letter are considered significantly different using Tukey's HSD with a family error rate of 0.05 (individual error rate of 0.00381).

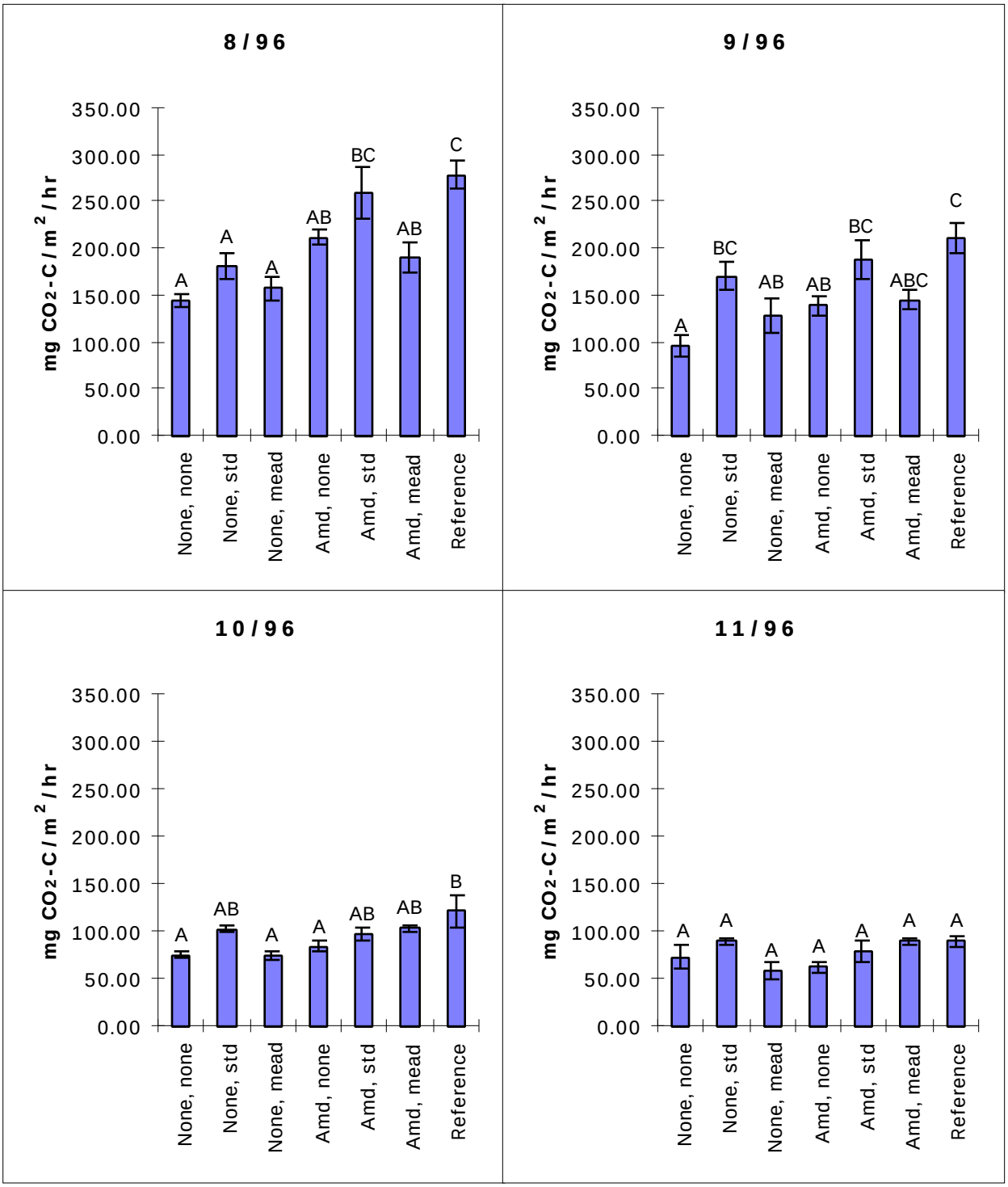

Figure 4.5b - Average monthly CO_2 flux by treatment combination in the last four sampled months of 1996. Error bars represent one standard error. Columns that do not share a common letter are considered significantly different using Tukey's HSD with a family error rate of 0.05 (individual error rate of 0.00381).

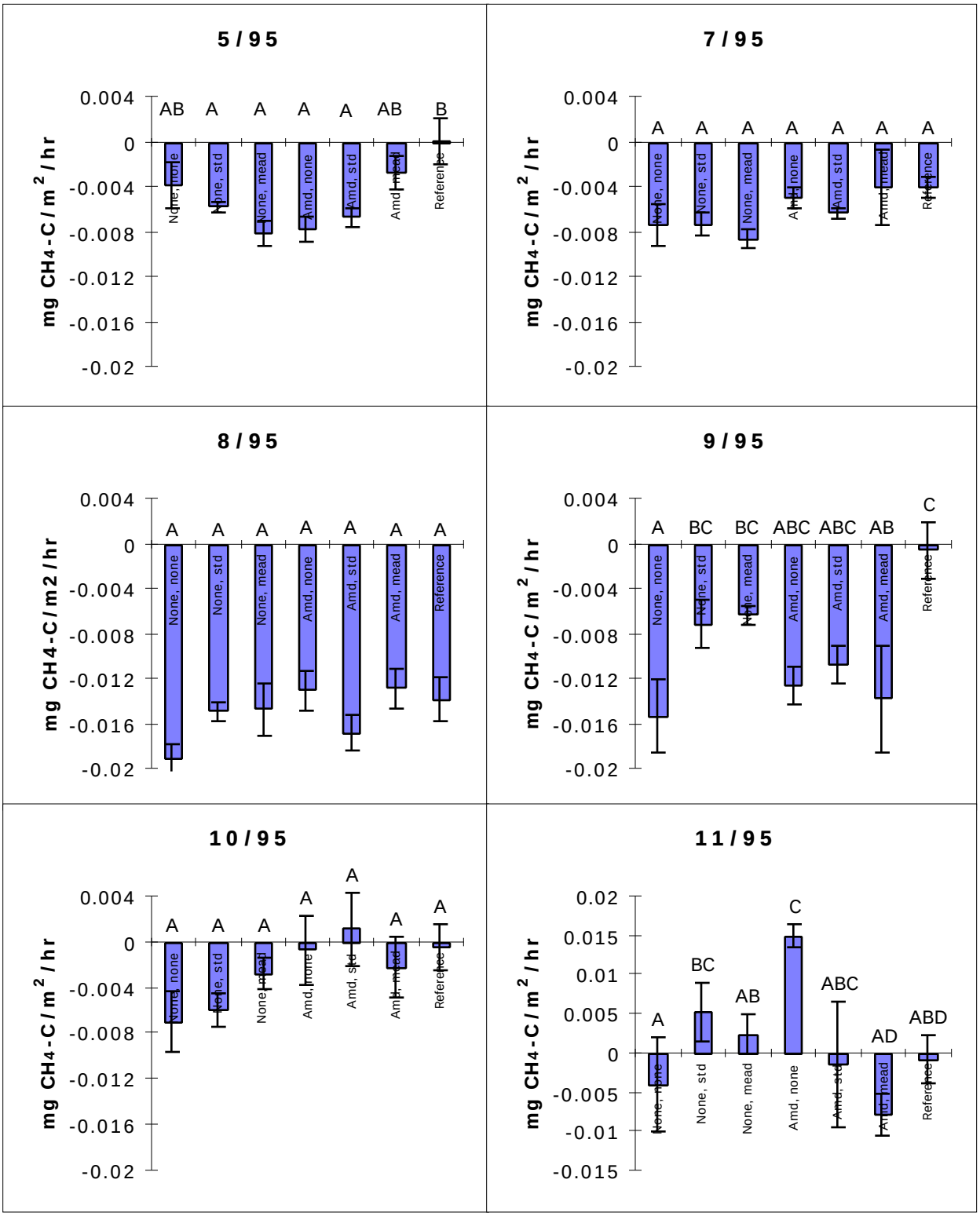

Figure 4.6 - Average monthly CH_4 flux by treatment combination in 1995. Error bars represent one standard error. Columns that do not share a common letter are considered significantly different using Tukey's HSD with a family error rate of 0.05 (individual error rate of 0.00381).

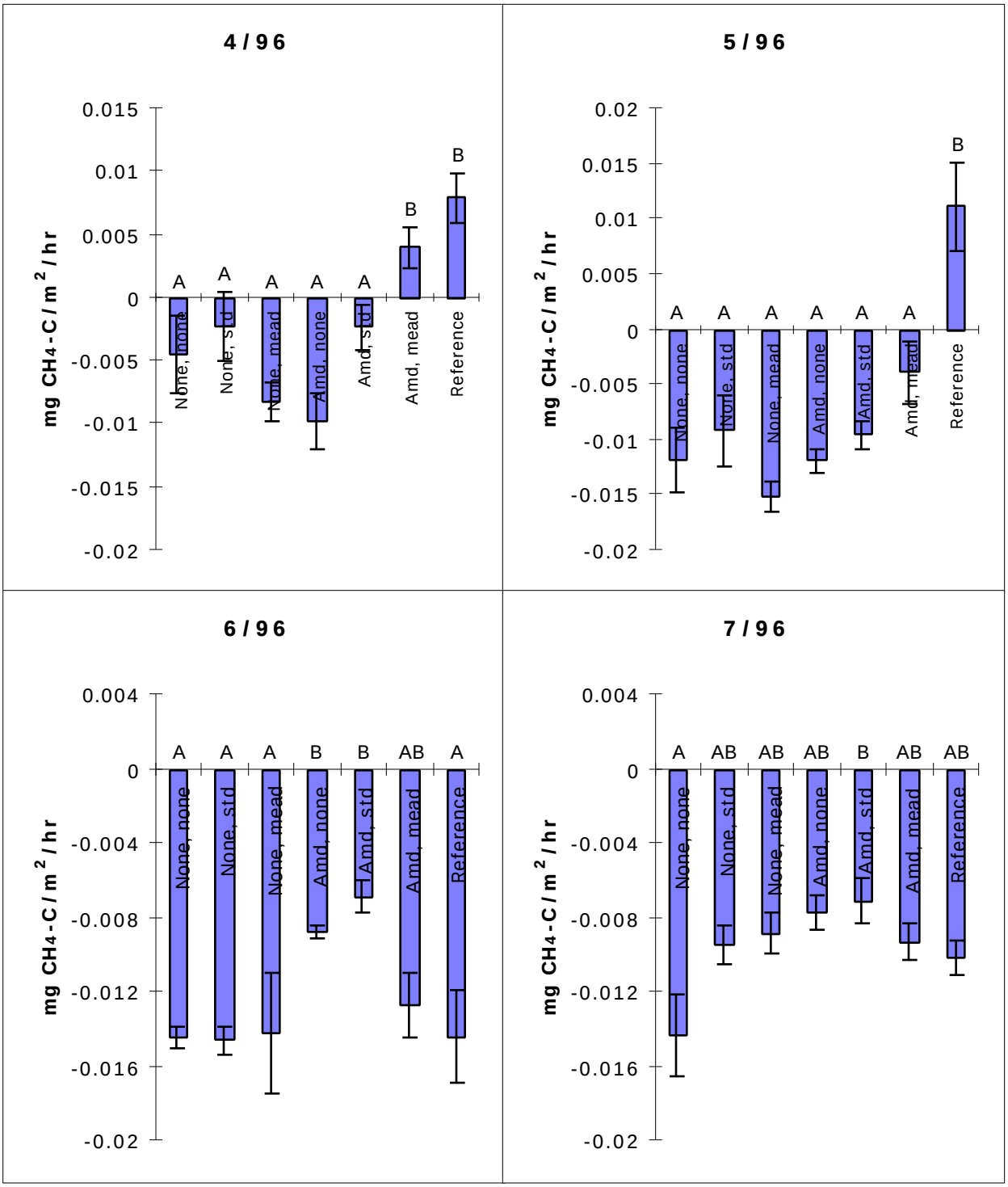

Figure 4.7a - Average monthly CH_4 flux by treatment combination in the first four sampled months of 1996. Error bars represent one standard error. Columns that do not share a common letter are considered significantly different using Tukey's HSD with a family error rate of 0.05 (individual error rate of 0.00381).

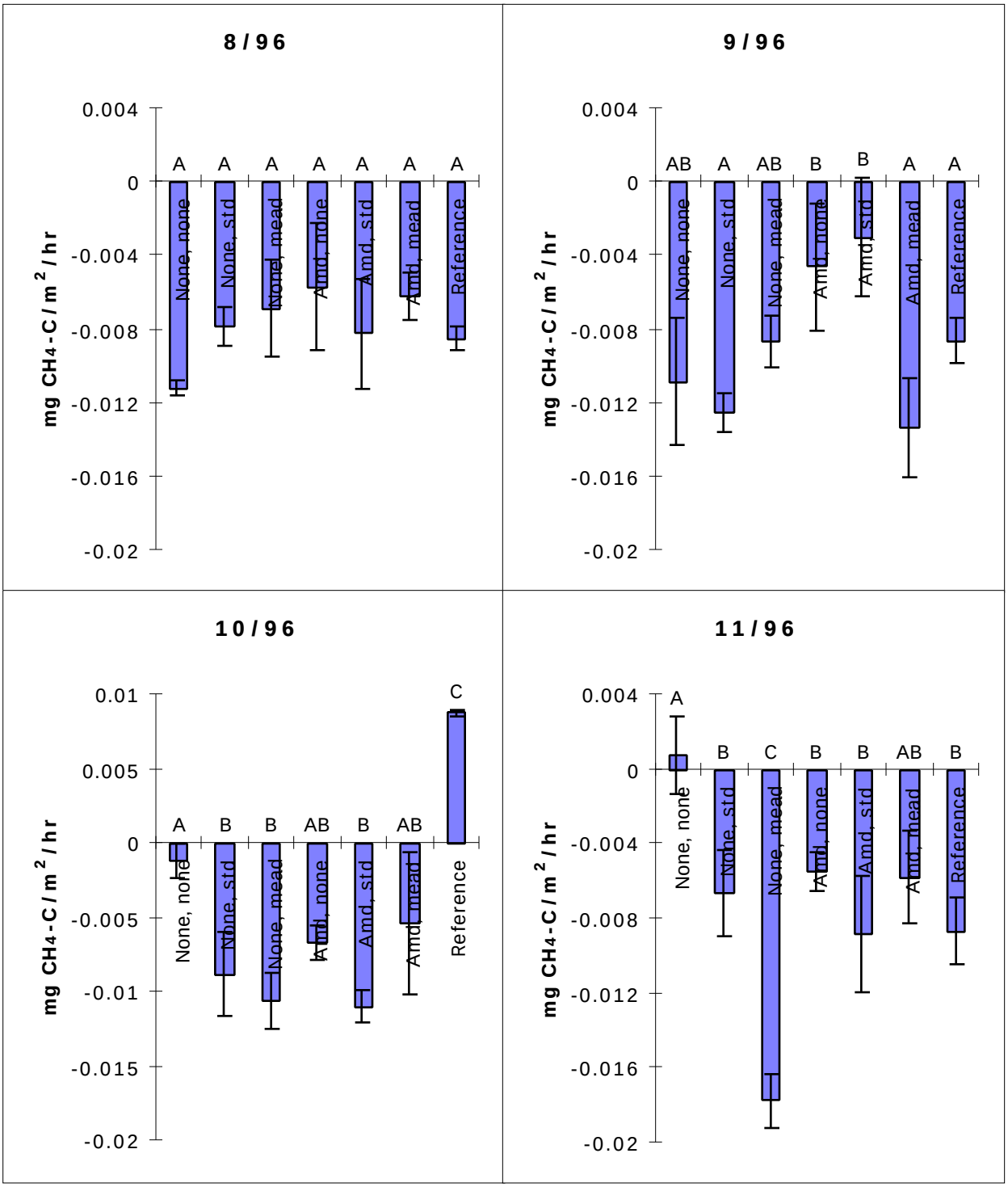

Figure 4.7b - Average monthly CH_4 flux by treatment combination in the last four sampled months of 1996. Error bars represent one standard error. Columns that do not share a common letter are considered significantly different using Tukey's HSD with a family error rate of 0.05 (individual error rate of 0.00381).

Chapter 5

A COMPARISON OF STRUCTURAL AND FUNCTIONAL MEASURES: QUANTIFICATION OF ECOLOGICAL RESTORATION EFFICACY

Integrated assessment approaches

The aim of restoration ecology is to gain a clearer understanding of complex, dynamic systems as they recover from a human-caused disturbance. To make reasonable judgments about the performance of such systems, it is necessary to observe a number of subsystems over time (Hobbs and Norton 1996, Cairns and Niederlehner 1993). This type of approach has been largely pioneered in the field of water resource quality assessment. Water quality was initially quantified mainly by physical and chemical parameters, but this approach was deemed insufficient as ecosystems were better understood (Meybeck and Helmer 1989). A modern, more integrative method for stream assessment is the index of biotic integrity (IBI), which incorporates physical and chemical parameters and community structure data such as species richness and composition, trophic composition, and organism abundance and condition (Karr 1981, 1991). This approach adds a substantial amount of information to the assessment process, allowing for more enlightened decisions to be made.

Integrative community assessment protocols such as the IBI provide good information on ecological condition at a specific point in time and space. They are less effective, however, for understanding the status of ecosystem processes that interact across regional and landscape boundaries. Ecosystem ecology has documented trends expected in stressed ecosystems over

time (Odum 1985, Rapportet al. 1985), and the application of these theories to the assessment of ecosystem condition has been grouped into the field of ecosystem health management (Costanza et al. 1992). These two approaches have underscored the importance of taking ecosystem function into account when judging the impacts of disturbance and subsequent recovery. Important changes can be occurring in ecosystems that are not immediately evident from their structural appearance. This is exacerbated by the biased temporal perspective displayed by humans when compared to the time scales of ecological processes. For example, Van Voris et al. (1980) documented functional differences between cores of old field communities that were structurally indistinguishable. In addition, this study showed that the functionally complex systems showed greater stability to a heavy metal stressor. No community metric could be found to explain the functional differences, yet these differences played a significant role in system stability. On a larger scale, Milchunas and Lauenroth (1995) did not find plant community changes caused by nutrient stress until 18 years after the stress ended. Clearly, ecosystem functioning had been altered, but was only evident in the community structure years later.

A good example of a terrestrial assessment system that integrates functional and structural observations is the vital ecosystem attributes (VEA) system proposed by Aronson et al. (1993a, b). This approach integrates soil physical, chemical, micro- and macro-biological parameters with plant community, energy cycling, and nutrient cycling measurements. Such a comprehensive strategy increases the monitoring demands for a restoration project, but it also

approaches the problem from a holistic viewpoint, similar to the use of multiple analyses for diagnosing a patient's medical condition. It also markedly increases the monitoring resolution, allowing for the detection and correction of unsatisfactory conditions earlier and the opportunity to deduce methods for facilitating key recovery processes.

The main goals of the current study were not to replicate the VEA approach (Table 5.1) but to document the structural and functional recovery of differently restored areas, to understand better the relationship between function and structure during the recovery process, and to determine which type measurements are best for assessing restoration success. In the previous chapters, an array of structural and functional measurements was used separately to compare the different experimental treatment combinations with the undisturbed reference plots. This broad array of measurement types allows for a multivariate analysis of system recovery. While information concerning the different functional and structural components within the recovering ecosystem is useful in its own right, integrative assessments should provide more information as a whole than their subunits do separately.

Table 5.1 - Comparison of the vital ecosystem attributes from Aronson et al. (1993b) and the measurements from the current study.

Vital ecosystem attributes	Measurements of the current study
Annual and perennial species richness	Species richness
Total plant cover	Total cover
Microbial biomass	Dehydrogenase, beta-glucosidase activity
Soil organic matter	Soil organic matter (loss on ignition method)
Microsymbiont effectiveness	Methane uptake rate
Cycling indices	Soil respiration, decomposition rate

Univariate vs. multivariate approaches towards assessment

Univariate approaches

Assessments of recovery based upon only one end-point show a wide variability of outcomes (Table 5.2). Figure 5.1 shows the trends over time of average plant cover and species richness. Depending upon the experimental treatment combination, the experimentally disturbed plots showed the potential to regain fully their vegetational cover within the two year study period. Amended plots had full coverage within one full growing season, and plots that were seeded and amended exhibited slightly faster recovery than all other treatments. No unamended plots regained 100% coverage during the study period. Species richness showed a much different response over time than average cover (Figure 5.1b). Meadow seeded plots exhibited an initial advantage over all other plots in species richness but this quickly faded until mid-1996 when

Table 5.2 - Overview of univariate measurements of recovery.

Assessment end-point	Recovery after two years?
Average cover	Yes, all amended sites
Species richness	Yes, all amended sites, earlier in “meadow” seeded plots
Community composition	No
Enzyme activity	No
Decomposition rate	Yes, amended and seeded sites
Soil respiration	Yes, amended and “standard” seeded sites
Methane flux	Too variable

"meadow" seeded plots were indistinguishable from "standard seeded" plots. None of the experimental plots recovered to levels similar to reference plots over the period of the study.

Soil dehydrogenase activity over the study period showed little or no trend towards recovering to the reference levels, and reference plots consistently exhibited higher activity levels (Figure 5.2a). Seeding mixture had no observable effect, as reported in Chapter 3. Any separation within the disturbed plots was due to amendment status, with no significant changes over time. A similar relationship between experimental and reference plots was exhibited in soil moisture levels over time, showing no real change over the study period (Figure 5.2b). This lack of change underscores the slow recovery times for soil systems.

Soil respiration, on the other hand, exhibited a reasonable degree of recovery during the second year of the study (Figure 5.3a). Reference plots had much greater respiration rates at the beginning of the study but were equalled or surpassed by amended sites during 1996, with amended and "standard" seeded sites exhibiting the highest rates of all plots. Therefore, with respect to soil respiration, these plots "recovered" to their predisturbance level. Unamended plots consistently showed lower respiration rates. Methane flux showed little or no response to experimental treatment, except for the overall increase in methane uptake exhibited by all disturbed plots (Figure 5.3b). No recovery of the experimental plots could be surmised from this information.

Multivariate approaches

While univariate approaches towards restoration assessment give widely variable information, multivariate weighted averaging procedures provide an avenue for assessing available information. Figures 5.1 - 5.3 document the community structural and functional measurements from this study that are directly comparable from 1995 to 1996. Beta-glucosidase could not be used because it was not measured in 1995. Dehydrogenase was very highly correlated to beta-glucosidase, however, so the amount of information lost was small. Similarly, decomposition rate could not be used because of the methodological differences between the two years (see Chapter 3). In this case, however, none of the other end-points are highly correlated, so a substantial amount of information was unavailable for the analyses.

Principal components analysis was used to explore the relationships between the experimental and reference plots when all measurements are taken into account. Table 5.3 shows the Pearson's correlation coefficients of the major end-points observed in the study. The PCA was done using all end-points in Table 5.3 except for those previously mentioned as excluded. Figures 5.4 and 5.5 show the experimental and reference plots distributed in PCA ordination space. It is interesting to compare this plot with the PCA plots generated from the vegetation data in Figures 2.7 and 2.8. The vegetation plots show similar separations between treatment combinations and references, which is analagous to the ecological differences between the plot types, although the primary axis in Figures 5.4 and 5.5 account for more than 70% of the variance. The primary axis explains, at most, 40% of the variance in the plant

Table 5.3 - Pearson's correlation coefficients for the major end-points of the current study.

	Decomp. rate	Total cover	Species richness	Organic matter	Soil moisture	Dehyd. activity	ß-gluc. activity	Soil respiration
Total cover	. 0.707							
Species richness	- 0.700	0.877						
Soil organic matter	- 0.653	0.898	0.836					
Soil moisture	- 0.653	0.853	0.805	0.896				
Dehydrogenase activity	- 0.483	0.734	0.730	0.734	0.755			
ß-glucosidase activity	- 0.436	0.884	0.838	0.884	0.822	0.900		
Soil respiration	- 0.629	0.912	0.770	0.865	0.834	0.721	0.857	
Methane flux	- 0.453	0.736	0.633	0.697	0.734	0.475	0.604	0.660

community plots. Of most interest, however, is the fact that similar separations across the primary axis are found using both plant community and environmental data. The greatest difference between the two ordinations is the position of the amended and "meadow" seeded plots. Using the community data, this treatment combination is maximally separated from the reference plots in 1995 and 1996. Using the environmental data, it is one of the most similar of the treatment combinations in comparison to the references.

Canonical correspondence analysis (CCA) was used to explore the relationships between the experimental plots using the entire data set (Jongman et al. 1995). This approach allows for further exploration of the apparently opposite results given by the two PCA ordinations because it provides direct gradient analysis of community structural dependence upon environmental variables. Figures 5.6 and 5.7 show the CCA biplots of the community structure data and the environmental variables. These biplots also include soil nutrient data in the environmental variables. In both 1995 and 1996, none of the experimentally disturbed plots show any

similarity to the reference plots. In both years, disturbed plots are mainly separated by seeding treatment; however, little of this separation is explained by the environmental variables. This separation suggests that it is largely controlled by the seeding treatment itself and does not interact substantially with the other measurements. The reference plots are highly correlated with soil organic matter, soil moisture, and soil dehydrogenase activity, which the independent tests showed to be lower in all disturbed plots. Overall, the CCA biplots support the other evidence that univariate assessment techniques are subject to a high degree of variability, which increases the possibility of an inaccurate judgment of system recovery. Multivariate tests all support the conclusion that none of the disturbed plots indicate a high degree of recovery within the study period.

The value of multivariate restoration assessment

This study has shown that it is possible to assess restoration success using an array of functional and structural end-points. However, the results have emphasized the subjectivity in making assessment decisions – average total cover and species richness showed a return to predisturbance condition within two years when multivariate approaches and all functional measurements showed little or no recovery. In any situation, outcomes of resource exploitation and conservation practices are uncertain (Ludwig et al. 1993); therefore, models for sustainable use and related strategies must be viewed cautiously. It seems highly probable that, if the present global rate of human population increase, natural resource exploitation, habitat

destruction, and loss of biodiversity continue beyond the year 2000, major initiatives will have to be undertaken to achieve anything close to "sustainable use" as it is presently understood.

A useful method for interpreting these changes in the environmental support system is to quantify structural and functional parameters in socially important terms such as ecosystem services. Ecosystem services may be defined as any ecological function perceived as beneficial to human society. The integration of social and ecological values into economically important units eases the discussion of inherent ecological value when comparisons are made with economic resource use. If the goal of restoring or enhancing delivery of ecosystem services is part of an ecological restoration strategy and if the public understands that these services are part of the ecological life support system upon which human society depends, society may be more supportive of large-scale ecological restoration.

There are problems with using the need for ecosystem services as the primary justification for ecological restoration. Biotic impoverishment, or loss of species richness, is well documented (Wilson 1988). As demonstrated by the current study, it is not yet clear what the relationship is between species richness or diversity and the delivery of ecosystem services, nor is it likely to become clear in the very near future. Since ecological restoration has focused on re-establishment of species far more than re-establishment of ecological function, it is not clear how such restoration will improve the delivery of those functions (i.e., services) once provided by the undamaged or relatively undamaged ecosystem. Also unclear is to what extent managed systems (e.g., agribusiness) deliver services qualitatively and quantitatively similar to those of natural

systems. It would be astonishing if agricultural systems could replace all ecosystem services lost when the natural system was initially replaced. For good management, however, robust evidence, rather than assumptions, is needed.

Conclusions

Restoration ecology is a relatively young field. As the success of many ecological restoration activities may not be known for many decades or even centuries, it is necessary to state very explicitly what is intended for each restoration project so that the degree of success or failure can be determined on a site-specific basis. This means that any restoration plan should be accompanied by an explicit statement of criteria for success and failure that will permit rigorous examination of the activity itself and, equally important, identify changes in strategy more likely to reach intended goals. Moreover, considering the rate of modification all natural systems are currently undergoing, it is necessary to develop wide-ranging restoration objectives with the aim to ameliorate past, present, and future damage.

This study has shown that single measurements of restoration success, especially gross structural measurements such as average cover and species richness which are commonly used in assessment protocols, can suggest recovery at a much earlier stage than multiple end-point methods would support. Additionally, in early successional systems, community composition can indicate a low degree of similarity between reference and disturbed areas even as those systems exhibit similar functional capacities. Ecological functions mediated in the soil system

begin to recover faster than community composition, but are slower to recover than the gross structural characteristics. It is important to take into account that this result may hold only for the ecological functions mediated in the soil and measured in this study. It is also important to note that the two year period of this study can only be used to indicate trends. The long period of time necessary for plant community development may actually be necessary before soil system functioning has fully recovered. Longer term, concurrent monitoring of vegetative and soil parameters is necessary in order to understand this relationship.

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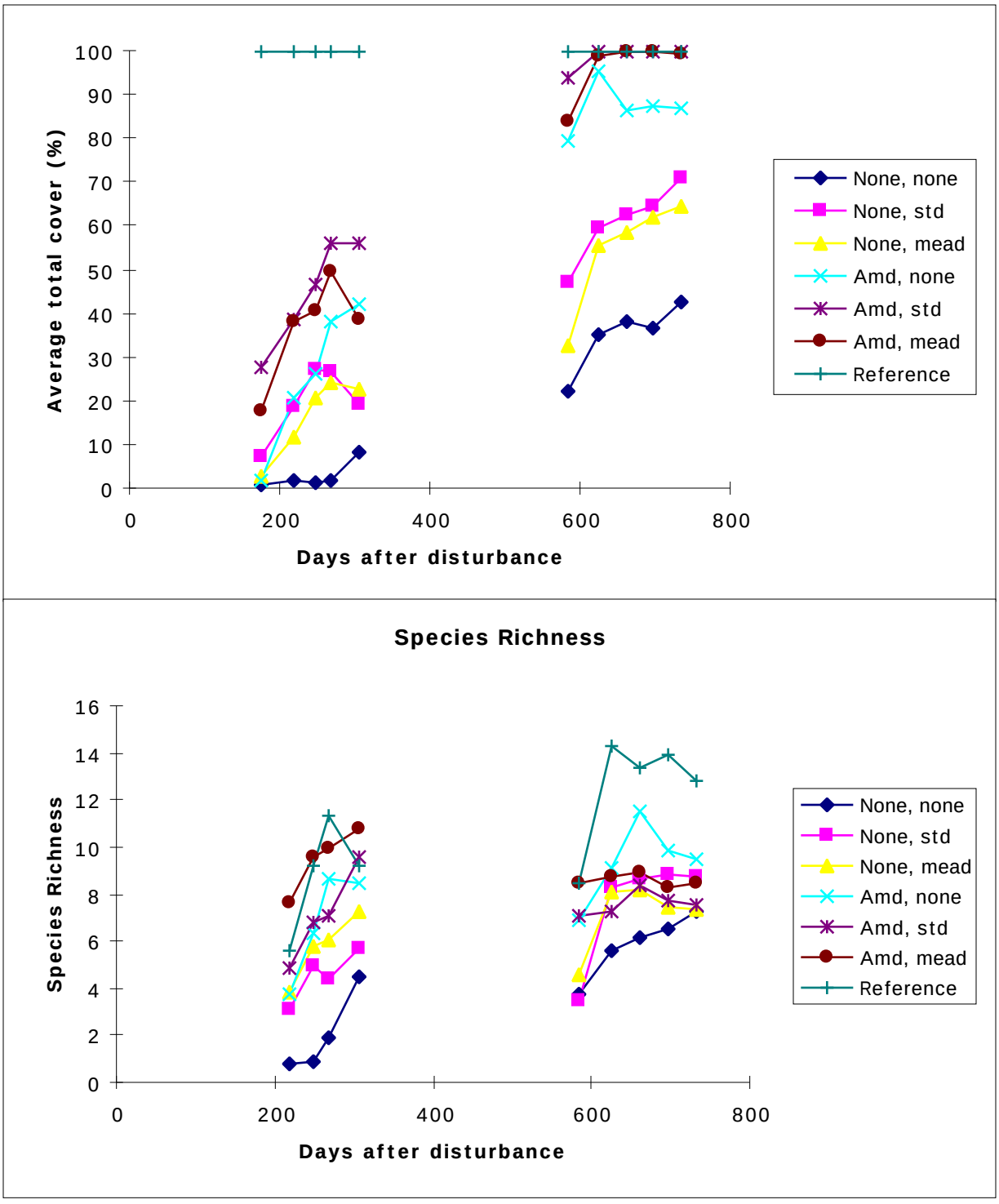

Figure 5.1 - Summary of (a) average vegetational cover and (b) species richness over the entire study period.

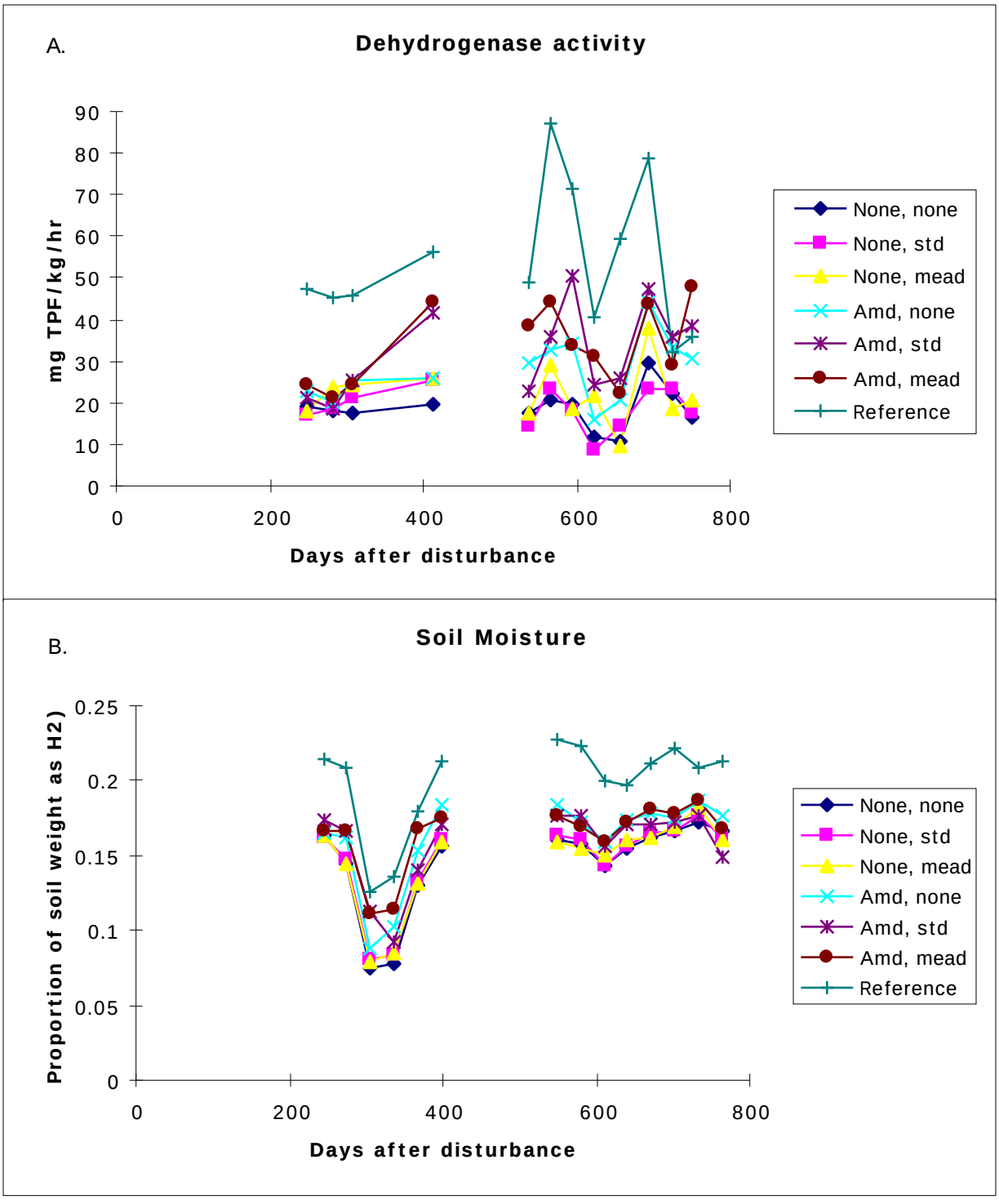

Figure 5.2 - Summary of (a) soil dehydrogenase activity and (b) soil moisture over the entire study period.

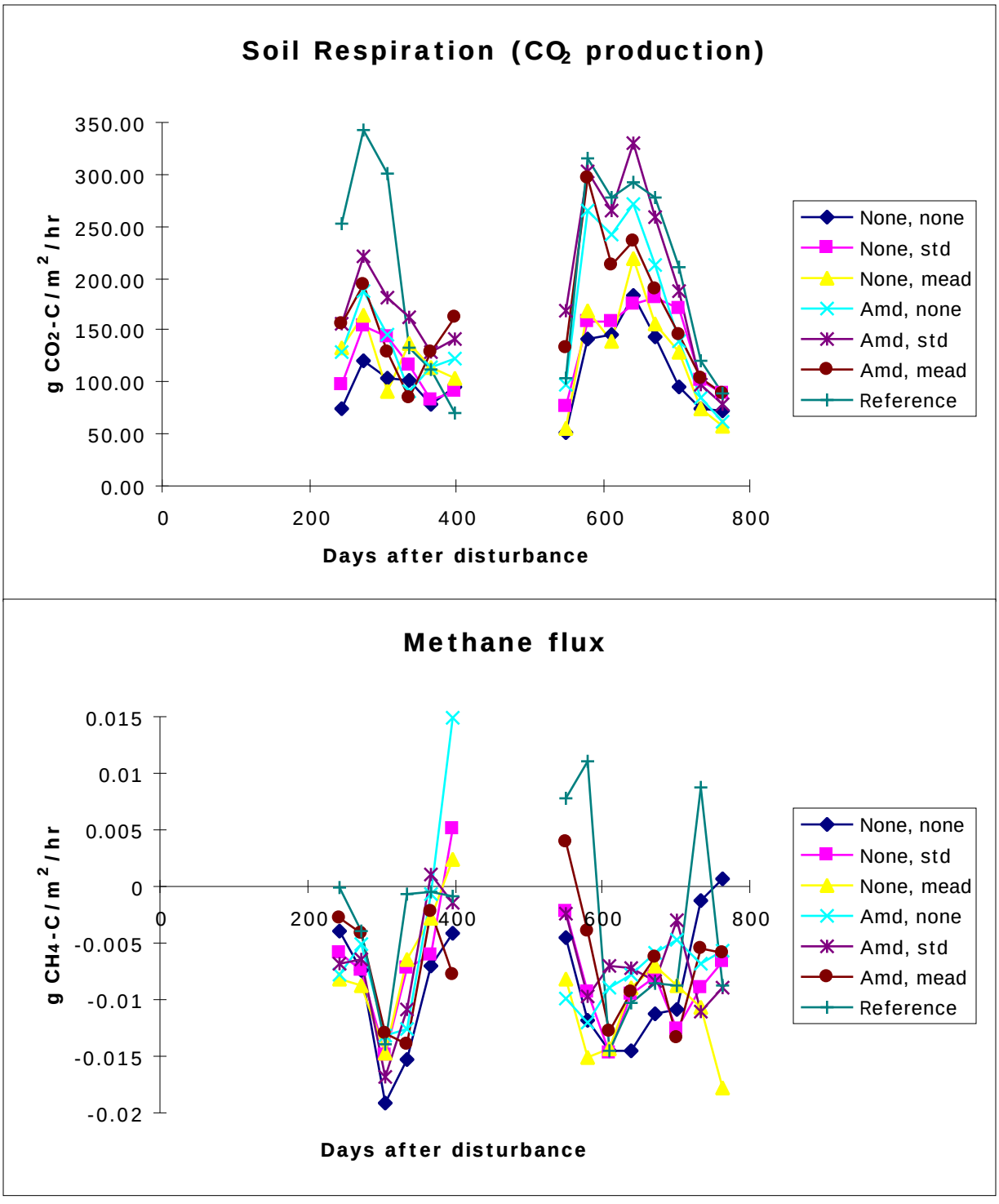

Figure 5.3 - Summary of (a) soil respiration and (b) soil/atmosphere methane flux over the entire study period.

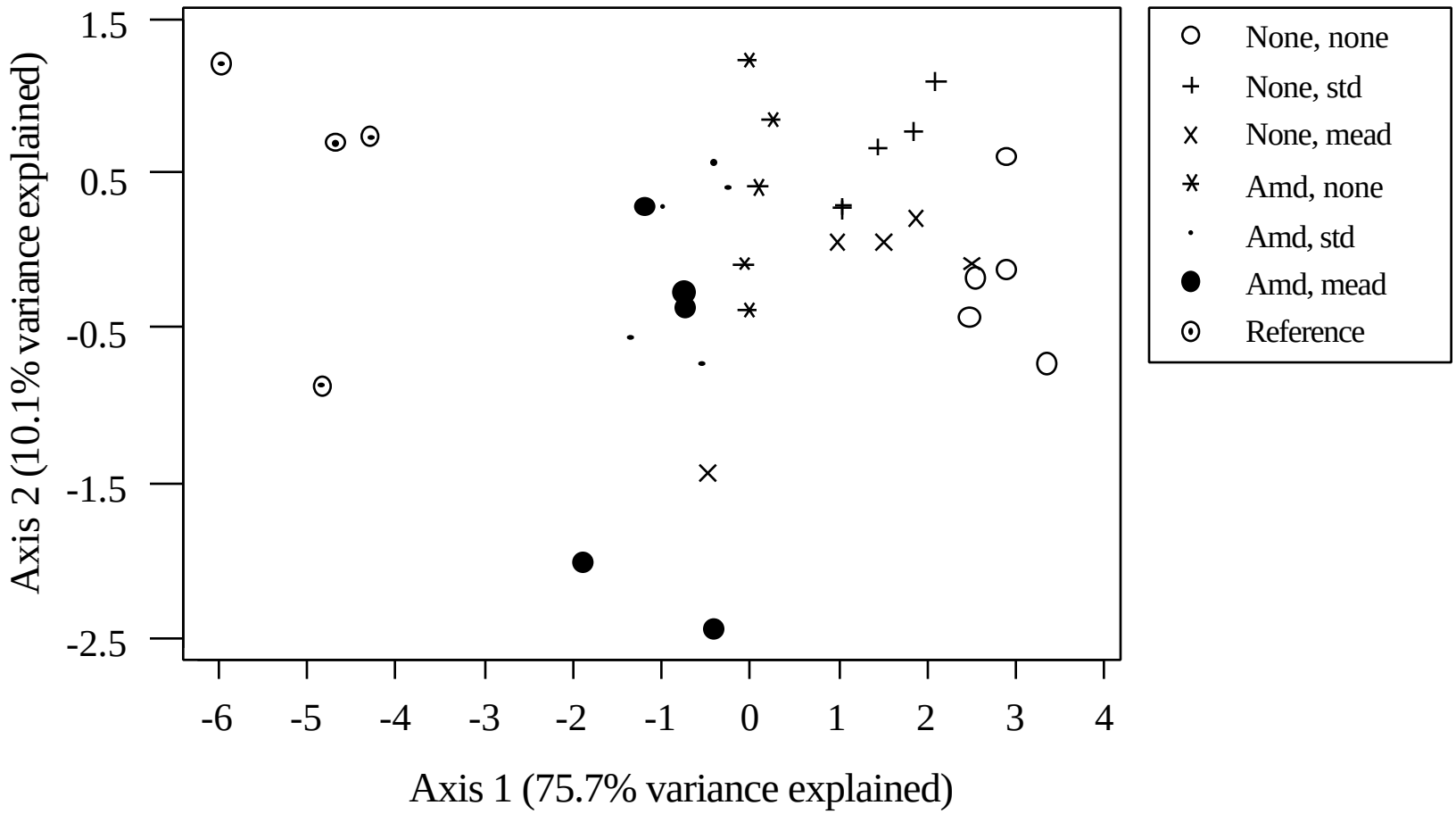

Figure 5.4 - Principal components analysis for 1995 incorporating average plant cover, species richness, dehydrogenase activity, soil respiration and methane oxidation rate.

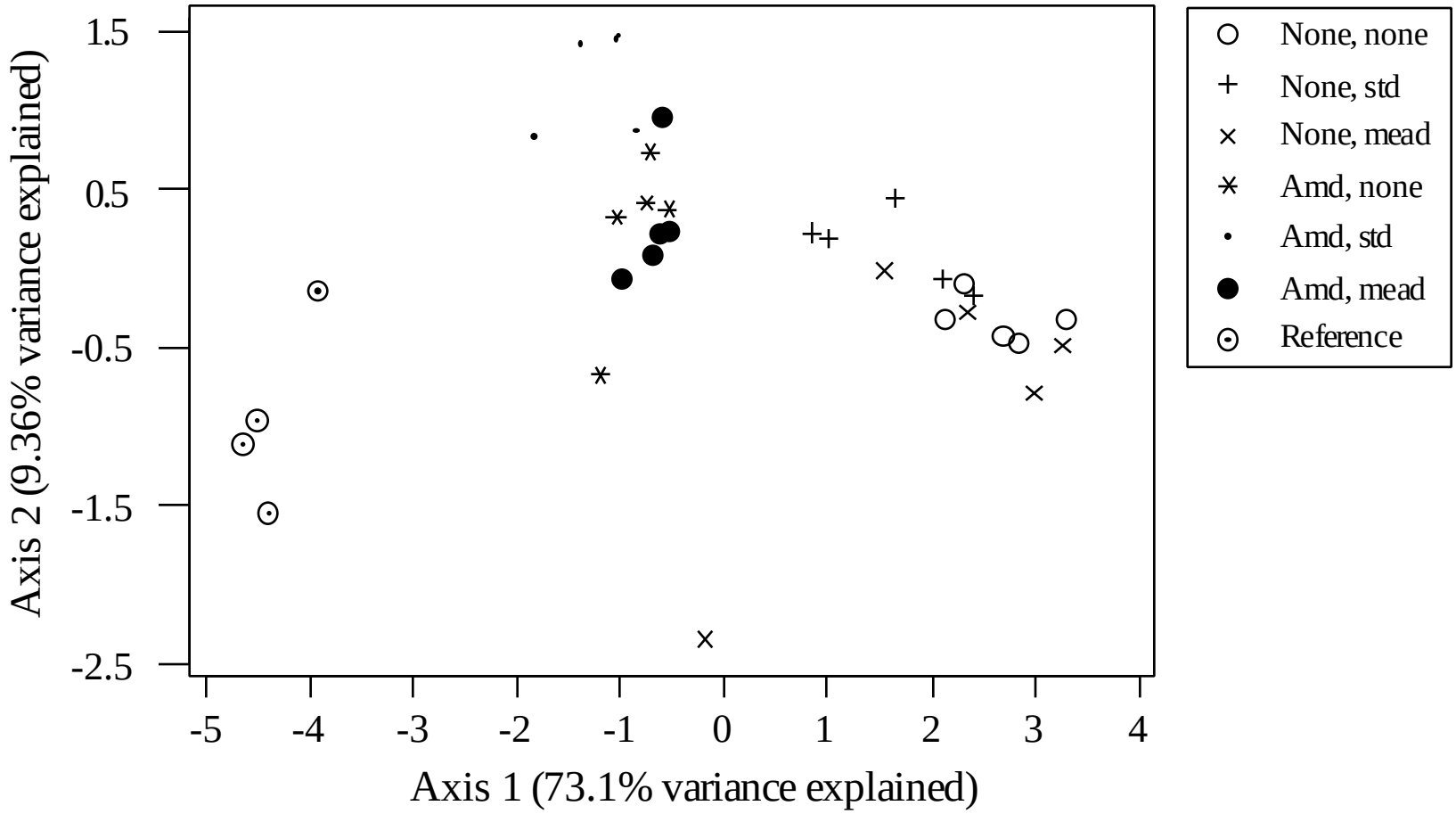

Figure 5.5 - Principal components analysis for 1996 incorporating average plant cover, species richness, dehydrogenase activity, soil respiration and methane oxidation rate.

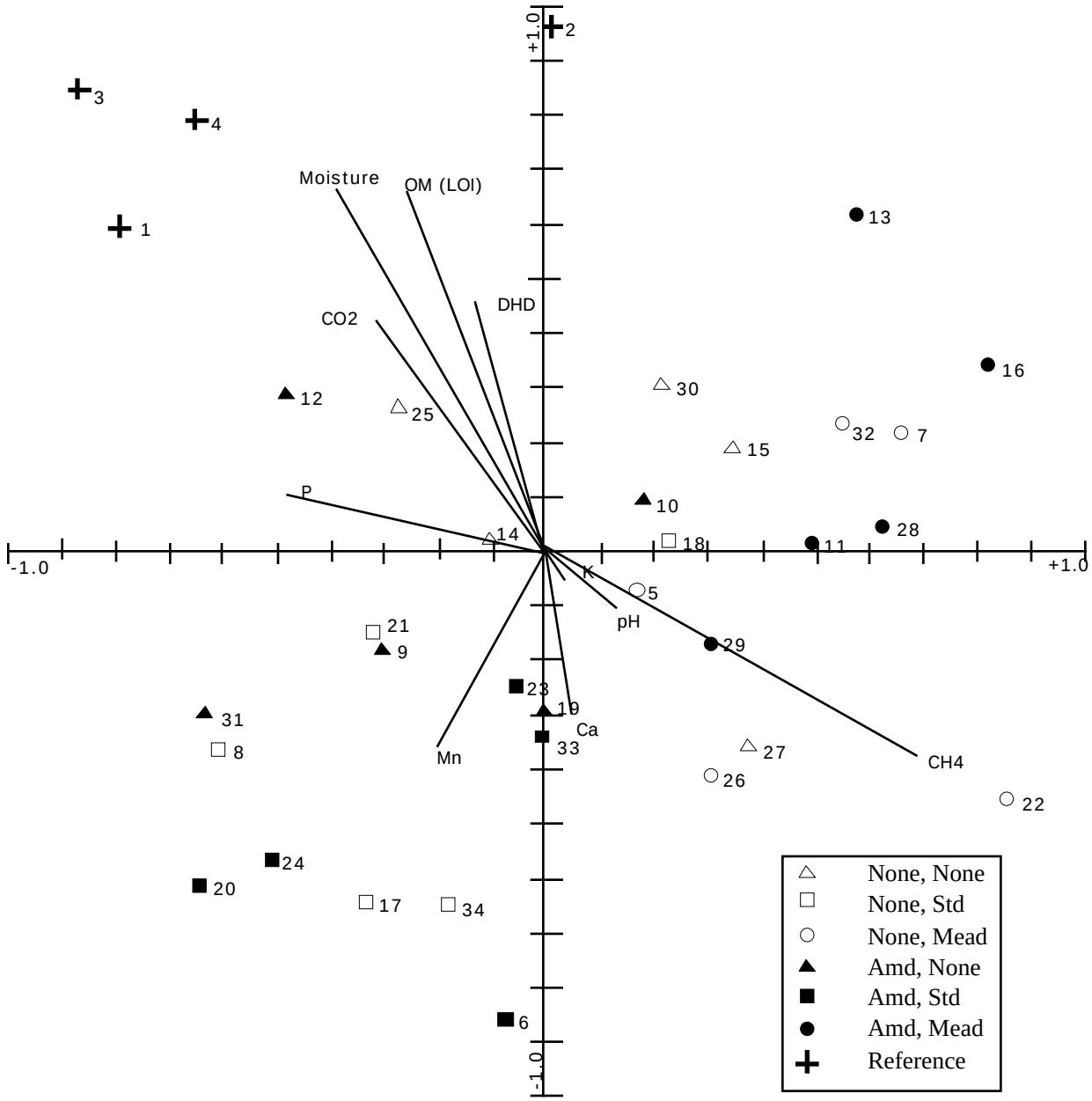

Figure 5.6 - Canonical correspondence biplot of plant community data and environmental variables for August 1995.

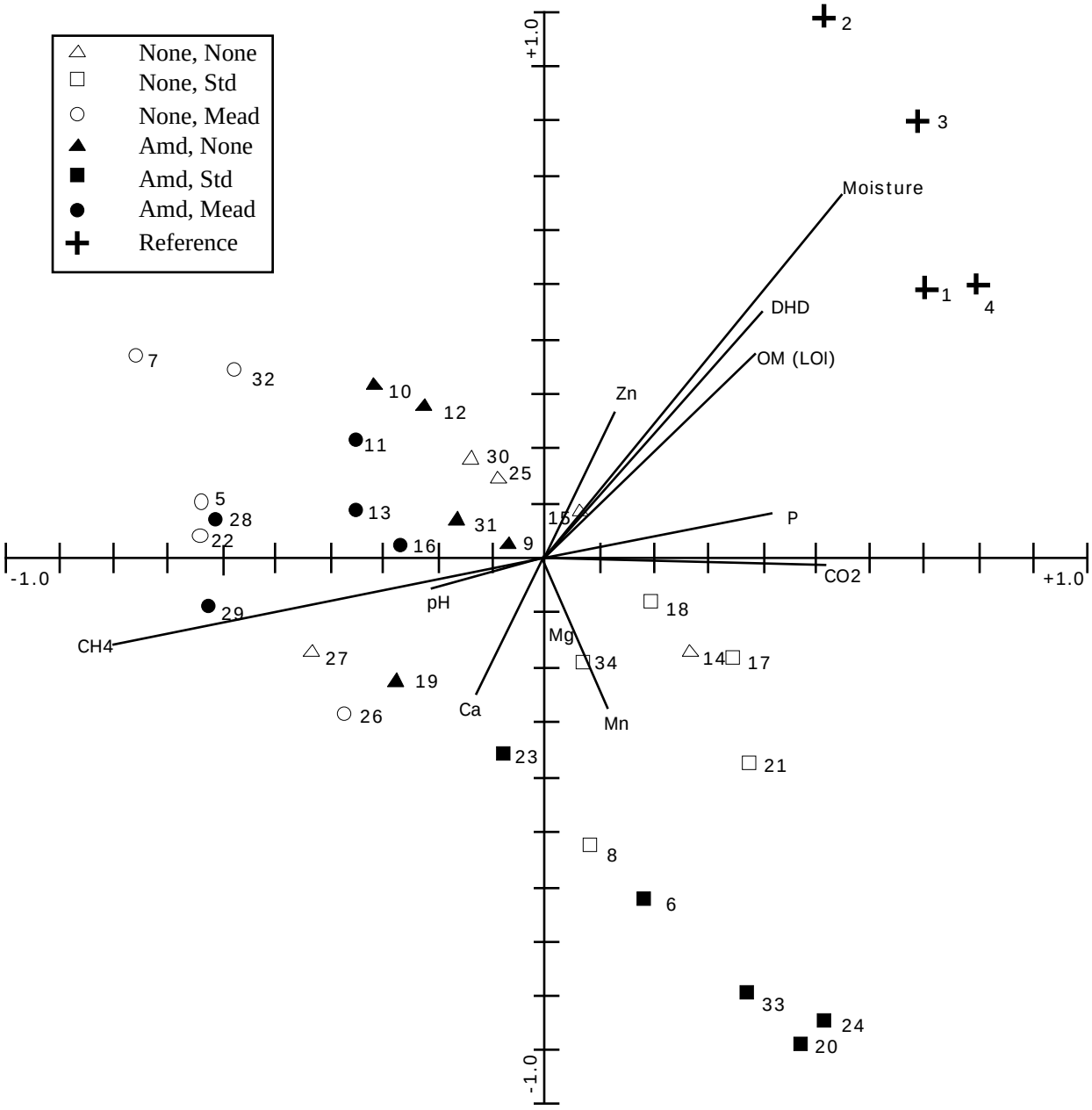

Figure 5.7 - Canonical correspondence biplot of plant community data and environmental variables for August 1996.

Appendix 1
PLANT SPECIES LIST

* average representation < 1%
** average representation 1 - 5%
*** average representation > 5%
P planted species
N species not originally native to the southeastern United States

Species Name	None, None	None, Rec	None, Mead	Comp, None	Comp, Rec	Comp, Mead	Ref
Agropyron repens[N]					*		*
Agrostis alba[PN]		*	*	*			***
Allium vineale[N]	***	*	*	*	*	*	**
Ambrosia artemisifolia	**	**	*	*	*	*	**
Anthoxanthum odoratum[N]		*	*		*	*	***
Aster pilosa	***	***	***	***	*	**	*
Barbarea vulgarus[N]	***	**	**	**	*	*	*
Bouteloua curtipendula		*		*			*
Bromus japonica[N]	*		*	*	*	*	
Carduus spp.[N]	**	*		*		*	
Centaurea cyanus[PN]			***			***	
C. maculosa[N]	**		*	*		*	
Chrysanthemum leucanthemum	*	*	***	*		*	*
Coreopsis lanceolata[P]			***			***	
C. tinctoria[PN]			**			**	
Coronilla varia[PN]		**			***		**
Dactylis glomerata[N]				*	*		*
Daucus carota[N]	**	**	**	**	**	**	***
Dianthus armeria[N]	*	*	*	*	*		*
Echinachea purpurea[P]			*			*	
Festuca arendinacaea[PN]		***			***		
F. ovina[N]	**	**		**	*		***
F. rubra	***	*	**	**	*	*	**
Fragaria virginiana	*			*			
Gnaphalium obtusifolium[N]	*	*	*	**	*		
Hedeoma pulegioides		*	**	**	**	**	**
Helianthus annuus[PN]			*			*	
Hesperis matronalis[PN]			**			***	
Hieracium venosum	*			*		*	*

Species Name	None, None	None, Rec	None, Mead	Comp, None	Comp, Rec	Comp, Mead	Ref
Hypericum perforatum[N]		*		*	*		*
Juncus tenuis	*	*	*	*			*
Lactuca spp.	*	*	*	***	*	**	
Lathyrus latifolius[N]			**				
Lepidium campestre[N]	*		*	*	*	*	
Lespedeza cuneata[PN]		**			*		*
Lobelia inflata	*	*					*
Lolium perenne[PN]		***	*		***	**	*
Lupinus perennis[P]			**			**	
Medicago lupulina[N]				*		*	
Meliolotus officianalis[N]		*		*	*	*	
Oenothera biennis					*		
Oxalis stricta	***	**	**	**	*	**	***
Paspalum spp.			*				
Phleum pratense[N]		*					*
Plantago lanceolata[N]	**	**	**	*	*	*	***
P. major	**	*		*		*	
Potentilla simplex		*		*			**
Ranunculus bulbosa[N]			*	*	*	*	*
Robinia pseudoacacia							**
Rubus allegheniensis	*		*				*
Rudbeckia hirta[P]			***			***	
Rumex acetosella[N]	**	*	*	**	*	*	*
Satureja vulgaris				*			**
Scutellaria nervosa		*	*	*		*	*
Secale cereale[PN]		***			***		
Setaria viridis[N]	**	**	*	***	*	*	***
Silene armeria[PN]	*		***			***	
Solanum carolinense	*	*	*	*	*	*	*
Solidago altissima	***	***	**	***	**	**	**
Stellaria graminea[N]	***	**	**	**	*	*	*
Taraxacum officianales[N]	**	**		**	*	*	*
Toxicodendron radicans	**	*					*
Trifolium agrarium[N]				*			
T. pratense[PN]	**	**	**	***	**	***	**
T. repens[PN]	**	**	**	***	**	***	*
Verbascum blattaria[N]	**		*		**		
Verbascum thapsus[N]			*	*		*	

Curriculum Vitae

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Current Research Interests: Functional responses to anthropogenic disturbances in terrestrial ecosystems, the incorporation of ecological system performance into human economies, the development of educational tools and models to facilitate the transition to an economically and environmentally mature society.

Education

Candidate for Ph.D. degree
Virginia Polytechnic Institute and State University
Expected Completion: Spring 1997
Major Professor: Dr. John Cairns, Jr.

Bachelor of Science with Highest Distinction
Nebraska Wesleyan University
May 1993
Major: Biology Minor: Physics

Professional Experience

1993 - 1997. Cunningham Doctoral Fellow, Virginia Polytechnic Institute and State University, Blacksburg, VA. Research addressed: (1) the effects of terrestrial restoration techniques on the return to the predisturbance structure and function, (2) integration of restoration management practices with industrial activities, (3) the use of active, research-based curricula for high school science education

1996 - 1997. Special Research Assistant, Virginia Polytechnic Institute and State University, Blacksburg, VA.. Developing an intra-net based communications network for facilitating asynchronous learning in General and Principles of Biology laboratories. Funded by the Sloan Foundation

1994 - 1996. Research Assistant, Virginia Polytechnic Institute and State University, Blacksburg, VA. Air Force Office of Scientific Research. Principal Investigators: B. R.

Niederlehner and John Cairns, Jr. "Chronic Toxicity of Complex Mixtures: Development of Efficient Test Design and Analyses of Predictive Errors"

1992 - 1993. Research Assistant, Rocky Mountain Biological Laboratory, Gothic, CO. Principal Investigator: R. J. Smith, "Effect of Small Mammal Herbivory in Sub-Alpine Meadows"

Teaching Experience

1996 - present. Laboratory coordinator, Virginia Polytechnic Institute and State University, Blacksburg, VA. Coordinate and teach Principles of Biology labs for majors. Developing inquiry based extensions to lab modules

1995 - present. Editor of the *Empiricist*, an on-line, peer-reviewed journal for high school science research. Accessible via the internet at http://biology.nebrwesleyan.edu

1995. Instructor, AWARE, Inc., Newport News, VA. Led training workshops for high school science teachers on incorporating the scientific method into the classroom

1994 - 1995. Honor's Colloquia Instructor, Virginia Polytechnic Institute and State University, Blacksburg, VA. Developed and co-taught Virginia Tech Honor's Colloquia in Restoration Ecology and Sustainable Issues

1993 - 1994. Lab Instructor, Virginia Polytechnic Institute and State University, Blacksburg, VA. Taught General and Principles of Biology laboratory courses

1992. Teaching Assistant, Nebraska Wesleyan University, Lincoln, NE. General Ecology

Advising Experience

1995 - present. Caroline Uhlik, Undergraduate Honors Research: Gene Flow between Remnant and Introduced Populations of Big Bluestem (*Andropogon gerardii*): Implications for Ecological Restoration

1994 - present. Andrew Heaton, Undergraduate Honors Research: Soil Enzyme Response to Land Degradation and Alternative Reclamation Techniques

1994 - present. Scott Cooney, Undergraduate Honors Research: Colonization of Soil Microarthropods as a Potential Index for Recovery of Degraded Ecosystems

1994 - 1995. Jennifer Sollenberger, Undergraduate Research: Soil Microbial Community Development on Degraded and Recovering Land

Publications

Cairns, John, Jr. and John R. Heckman. 1996. Restoration Ecology: The State of an Emerging Field. Annual Reviews of Energy and the Environment 21:167-189.

Heckman, John R., Karen D. Holl, Mara Sabre, and John Cairns, Jr. 1996. The potential for using wildflower species to increase natural habitat in contour surface mine reclamation. Proceedings of the American Society for Surface Mining and Reclamation 13th Annual Meeting: 453-461.

Publications in Press

Heckman, John R., and John Cairns, Jr. *In Press*. Ecosystem restoration: A new perspective for sustainable use of the planet *In:* B.C. Rana, ed., Ecosystem Restoration. Worldwide Scientific. Singapore.

Cairns, John Jr. and John R. Heckman. *In Press.* Book review: "Everglades: The Ecosystem and Its Restoration," ed. Steven M. Davies and John C. Ogden. 1994. 826 pages. Ecological Economics.

Cairns, John Jr. and John R. Heckman. *In Press*. Book review: "Land Restoration and Reclamation: Principles and Practice," Harris, J. A., P. Birch, and J. Palmer. 1996. 230 pages. Restoration and Management Notes.

Papers in Preparation

Heckman, John R. and John Cairns, Jr. Ecological Disturbance and Methane Oxidation Rates: Effects of Restoration Treatments. *Target journal:* Ecological Applications.

Heckman, John R. and John Cairns, Jr. Correlation of soil respiration with enzymatic activity and cellulose decomposition rate in differently restored grassland systems. *Target journal:* Soil Biology and Biochemistry.

Heckman, John R. and John Cairns, Jr. Structural vs. Functional end-points in restoration ecology: A direct comparison. *Target journal:* Restoration Ecology.

Heckman, John R., Andrew C. P. Heaton, and John Cairns, Jr. The Restoration of the Virginia Tech Debris Landfill: An Unexpected Lesson in the Value of Concurrent Restoration. *Target journal* : Restoration & Management Notes.

Selected Abstracts and Presentations

Heckman, John R. and John Cairns, Jr. 1996. Primary restoration of industrially degraded land: Preliminary tests for correlation between initiated community structure and return of functional capacity. Bulletin of the Ecological Society of America 81(supp.): 190.

Heckman, John R. and John Cairns, Jr. 1996. Preliminary Tests For Correlation Between Initiated Community Structure And Return Of Functional Capacity On Recovering Land. Proceedings, Society for Ecological Restoration 1996 International Conference: 60.

Heaton, Andrew C. P., John R. Heckman and John Cairns, Jr. 1996. Concurrent Restoration of Disturbed Sites. Proceedings, Society for Ecological Restoration 1996 International Conference: 60.

Heckman, John R., and John Cairns, Jr. 1995. Restoration of Degraded Land: Structural and Functional Comparisons between Differently Reclaimed Areas. Taking a Broader view: Proceedings of the 1995 Society for Ecological Restoration Conference: 113.

Heckman, John R., and John Cairns, Jr. 1995. A comparison of structural and functional measures of soil community dynamics in recovering terrestrial systems: preliminary results. Virginia Journal of Sciences.

Heckman, John R., and John Cairns, Jr., Structural and functional approaches for assessing the recovery of degraded land. Biology Seminar. April, 1995

Heckman, John R., and John Cairns, Jr., The development of a field and laboratory study to observe soil community dynamics on recovering land. Virginia Branch of the American Society of Microbiology. December 1994.

Heckman, J. R. and R. J. Smith, 1993. Effects of small mammal herbivory on sub-alpine meadow vegetation. Nebraska Journal of Sciences. April 1993.

Grants and Funded Projects

1997. Uhlik, Caroline and John R. Heckman. Gene Flow between Remnant and Introduced Populations of Big Bluestem (*Andropogon gerardii*): Implications for Ecological Restoration. Sigma Xi. $310.00 - *In Review*

1997. Heckman, John R., The *Empiricist*, an on-line, peer-reviewed journal for high school science research. *In collaboration with*: Duncan, Garry and Dale Benham, Science Outreach to Rural High Schools in Nebraska, Howard Hughes Medical Institute - Funded.

1996. Heckman, John R., Direct and indirect human impacts on soil microbial community dynamics: A potential indicator of ecological change. National Science Foundation Postdoctoral Fellowship. - *In Review*.

1996. Heckman, John R., Revegetation of the Virginia Tech Debris Landfill. Virginia Tech Physical Plant. $3,200.00 - Funded.

1996. Heckman, John R., Dissertation Research: Structural and functional responses to restoration of degraded land. Waste Policy Institute. $2,500.00 - Funded

1995. Heaton, Andrew and John R. Heckman, Re-establishment of Organic Cycling in Recovering Wildflower and Grassland Soils. Sigma XI Society, $280.00 - Funded.

1995. Heckman, John R. and John Cairns, Jr., Effect of Land Degradation and Subsequent Restoration on Methane Flux: Further investigation of initial results. Sigma Xi Society. $450.00 - Funded.

1995. Heckman, John R. and John Cairns, Jr., Early ecosystem recovery dynamics: A comparison of structural and functional endpoints. Virginia Tech Graduate Research Development Program. $400.00 - Funded

1994. Heaton, Andrew and John R. Heckman, Soil Enzyme Response to Land Degradation and Alternative Reclamation Techniques. Sigma XI Society, $630.00 - Rejected.

1994. Heckman, John R. and John Cairns, Jr., Effect of Land Degradation and Subsequent Restoration on Methane Flux. Sigma Xi Society. $1000.00 - Funded.

1994. Sollenberger, Jennifer E., John R. Heckman, and John Cairns, Jr., Soil Microbial Community Development on Degraded and Recovering Land. Sigma Xi Society. $548.00 - Rejected.

1994. Cooney, Scott R., John R. Heckman, and John Cairns, Jr., Colonization of soil microarthropods as a potential index for recovery of degraded ecosystems. Sigma Xi Society. $505.00 - Rejected.

1994. Heckman, John R., Restoration ecology and education: A practical approach. Cool-It/Jostens Foundation $2000 - Funded

1993. Heckman,. John R. and R. J. Smith, Habitat specificity and rodent herbivory: A quantification of perceived risk. Howard Hughes Medical Institute Summer Research Grant. $1000 - Funded

1993. Heckman, John R. and R. J. Smith, Habitat specificity and rodent herbivory: A quantification of perceived risk. Council for Undergraduate Research. $2500 - Funded

Professional and Honorary Societies

Society for Ecological Restoration
Sigma Xi Research Society
Virginia Academy of Sciences
Phi Kappa Phi Academic Honor Society

Beta Beta Beta Biological Society
Sigma Phi Physics Society

Awards

1997 - Phi Sigma Outstanding Dissertation Research Award
1996 - Graduate Participant: Annual Meeting of the National Center for Ecological Analysis and Synthesis

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