University of Alberta

Competition and community structure in a rough fescue grassland

by

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Abstract

In this thesis I examine some of the mechanisms structuring a rough fescue grassland plant community in the aspen parkland ecoregion of central Alberta, Canada. My first objective was to determine how environmental conditions, interactions with the soil microbiota, and plant biomass and productivity structured the species richness, evenness, and composition of this plant community. I monitored the responses of the plant and soil bacterial communities to a three year experimental manipulation of light, nitrogen, and water. Plant growth was limited by both nitrogen and water, and additional water strongly delayed plant senescence. Through structural equation modeling I show that litter accumulation was the primary mechanism influencing plant community structure. I found no evidence that interactions between plant roots and soil bacteria had any influence on community structure.

My second objective was to examine the role of competition for limiting resources in rough fescue grasslands. Individual plants were severely affected by root competition, and both water and nitrogen addition altered the intensity of competition. There was little evidence, however, to link competition to any aspect of plant community structure. Root competition intensity and root biomass were unrelated, and there were no links between variation in competition intensity and plant community species richness, evenness, or composition. Root competition likely was not linked to plant community structure because it is size-symmetric. Without the positive feedback mechanisms of size-asymmetric (shoot) competition, there are few mechanisms through which root competition could systematically exclude certain individuals or species from a community.

I present a conceptual model to integrate my findings that root competition and community structure are not linked with the well-understood relationships between shoot competition and plant community structure. If root competition can affect the outcome of shoot competition, then that root competition may indirectly structure a plant community. The total competition intensity experienced by a plant is a function of root competition, shoot competition, and root – shoot competition interactions. The separate influences of each of these elements of competition on plant community structure can be integrated by considering the effect of each component on the overall asymmetry of competition.

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1. General Introduction

Understanding the mechanisms that structure the diversity and composition of plant communities is a central goal of community ecology. Plant ecologists have assembled an enormous body of knowledge describing how a wide range of abiotic and biotic mechanisms contribute to the structure of plant communities. A primary challenge for contemporary plant ecologists is to develop an understanding of how multiple mechanisms interact to produce predictable assemblages of plant species.

In this thesis I examine some of the mechanisms structuring a rough fescue grassland plant community. My overall objective is to answer two general questions. First, how do environmental conditions, interactions with the soil microbiota, and plant community biomass and productivity structure the species richness, evenness, and composition of this plant community? Second, what role does competition for limiting resources play in the network of mechanisms that structure this plant community?

In this introductory chapter I review how interactions between multiple mechanisms play a role in structuring plant communities, and the specific roles of competition and plant – microbial feedbacks in structuring communities. I then describe my study site, including the community composition and species – environment relationships in rough fescue grasslands. Finally, I describe how rough fescue grasslands form an ideal model system for studying the role of competition in structuring plant communities, and I list my detailed research objectives.

Background

Interactions among multiple mechanisms structure plant communities

Plant community structure can be defined as the features such as species richness, species relative abundance, dominant life-forms, and spatial and temporal patterns that distinguish a particular plant community. Numerous factors ranging from soil and environmental conditions to competition, disturbance regimes, herbivory, productivity, and standing biomass have been identified as important controls on plant community structure (e.g. Al-Mufti et al. 1977; Di Tommaso and

Aarssen 1989; Carson and Pickett 1990; Facelli and Pickett 1991; Foster and Gross 1998; Grace 1999; Xiong and Nilsson 1999; Grime 2001; Keddy 2001; Mittelbach et al. 2001; Rajaniemi 2003; Aarssen 2004; Crawley et al. 2005; Balvanera et al. 2006; Gillman and Wright 2006; Stevens et al. 2006; Adler and Levine 2007). While much is known about the net effects that individual processes may have on plant communities, it is becoming clear that the structure of most plant communities is influenced by many factors linked through complex networks of correlation, causation, interaction, and feedback (Grace 1999). Thus the problem of explaining plant community structure is not one of identifying which of several competing explanations is most important in a particular community, but rather determining how multiple mechanisms both directly and indirectly affect the community.

The most common approach to examining how multiple mechanisms interact to affect community structure has been large multi-factor experiments. This approach has been very successful, but there are practical limits to the size of experiments. A more recent approach has been to apply multivariate methods such as structural equation modeling (SEM) to explicitly evaluate the networks of correlation, causation and interaction among mechanisms using sets of largely observational data (Shipley 2000; Grace 2006). A number of studies using this approach have examined the mechanisms controlling species richness in plant communities including coastal wetlands, grasslands, and shrublands (Grace and Pugesek 1997; Gough and Grace 1999; Grace and Guntenspergen 1999; Grace and Jutila 1999; Grace et al. 2000; Weiher et al. 2004; Mancera et al. 2005; Grace and Keeley 2006). Much of the value of this holistic approach comes from the capacity to place well known patterns and mechanisms into a comprehensive framework. Points where theory is insufficient to explain patterns are readily identified using these methods. Placing a wider array of patterns and mechanisms into such frameworks is likely to prove an effective strategy to advance the study of plant ecology.

Competition and Plant Community Structure

Competition is one of the key mechanisms structuring plant communities (Keddy 2001). Some form of competition between neighbouring plants for limited light, water, space, or mineral nutrients occurs in nearly every plant community

(Clements et al. 1929; Goldberg and Barton 1992; Gurevitch et al. 1992; Keddy 2001). Competition can have severe direct consequences for individual plants, reducing growth, survival and fecundity (Keddy 2001; Aarssen and Keogh 2002), but it is the consequences of competition for plant community structure that has generated the most interest among plant ecologists. Competition is a critical component of many influential theories (e.g. Newman 1973; Grime 1973; 2001; Tilman 1988), yet many fundamental aspects of the relationship between competition and the diversity and composition of plant communities remain poorly understood (Keddy 2001; Craine 2005). In this thesis I focus on one particular unanswered question: does root competition play an important role in structuring the diversity and composition of low-statured plant communities where shoot competition is, at most, very weak?

Distinguishing the intensity and importance of competition is critical to any evaluation of the role of competition in structuring plant communities (Welden and Slauson 1986; Brooker et al. 2005). Intensity is the degree to which competition for a limiting resource reduces plant performance from the physiological maximum achievable in a given environment, while importance is the relative impact of competition versus other environmental conditions (Welden and Slauson 1986). A great deal of confusion in the literature can be traced to failures to distinguish between intensity and importance (Grace 1991; Brooker et al. 2005). In this thesis I focus on the importance of competition, but I take a broader view than in the definition above. I consider competition to be important if variation in the intensity of competition can be identified as the cause of predictable variation in plant community structure.

Root competition is the dominant form of competition in plant communities including dry grasslands, arctic and alpine tundra, and deserts (Casper and Jackson 1997) where roots make up the majority of the plant biomass (Jackson et al. 1996; Mokany et al. 2006). Evidence for the predominance of root competition comes from a wide array of studies including surveys of rooting patterns and resource uptake (e.g. Brisson and Reynolds 1994; Hawkes and Casper 2002; Casper et al. 2003) and experiments using trenching or root exclusion tubes (e.g. Aarssen and Epp 1990;

Peltzer et al. 1998; Cahill 1999; 2002, 2003b). While the root competition experienced by individual plants in low-statured plant communities can clearly be intense, whether that competition is important in structuring community diversity and composition is less clear.

Many questions regarding the relationship between root competition and plant community structure arise because the links between root competition intensity and plant community characteristics such as productivity can be highly variable (e.g. Belcher et al. 1995; Peltzer et al. 1998; Cahill 1999; 2002). There is little question that the intensity of shoot competition is directly linked to community structure because shoot competition intensity and the amount of light intercepted by the vegetation are highly correlated (Grime 2001, Keddy 2001). A slight advantage in size allows a larger plant to capture a disproportionate fraction of the available light, leading to positive feedbacks where the larger plant grows faster and captures an even greater proportion of the resource pool (Weiner 1986; Keddy 2001). In contrast, root competition is size-symmetric and as a consequence larger plants cannot capture a disproportionate fraction of the resource pool (e.g. Weiner 1986; Casper and Jackson 1997; Schwinning and Weiner 1998; Cahill and Casper 2000; von Wettberg and Weiner 2003; Schenk 2006). Without a clear mechanism linking root competition intensity to plant size, it is likely that the widely recognized relationships between aboveground productivity, competition, and community structure do not hold belowground. In this thesis, I test whether any aspects of plant community structure vary along gradients of root competition intensity.

Plant – soil community interactions and plant community structure

Interactions between plant roots and the soil microbiota can influence some aspects of plant community structure. Soil microbes compete strongly with plants for limited soil nutrients (Hodge et al. 2000; Dell and Rice 2005), and mutualists such as mycorrhizae can determine the relative dominance of plant species in a community (e.g. van der Heijden et al. 1998; Hartnett and Wilson 1999). The relationships between the plant and soil microbial communities can be particularly challenging to study in natural systems because each community has the potential to influence the structure of the other. A change in plant community composition or species richness, for example, can affect the soil bacterial community by altering root exudate chemistry (Wardle et al. 1999, Hopkins and Gregorich 2005, Orwin et al. 2006), while mutualistic and pathogenic soil microbes can strongly enhance or inhibit, respectively, the performance of individual plants or species (e.g. van der Heijden et al. 1998; Bever 2003; Casper and Castelli 2007). Such interrelationships may be particularly complex when the direct effects of a change in environmental conditions on each community also have indirect effects resulting from feedbacks between the communities (Hooper et al. 2000, Bardgett et al. 2005).

The microbial community is an important component of a study of root competition, because belowground plant – plant interactions are likely to be mediated, at least in part, through plant – microbial relationships. In this thesis I examine whether changes in the plant – soil bacterial interactions along a soil resource gradient had any impact on the structures of either community.

Study Site

I conducted my research in the native rough fescue grasslands at the University of Alberta Kinsella Research Ranch (53°05 N, 111°33 W). In this section I describe the plant community composition and species – environment relationships at my study site. Rough fescue grasslands are a remnant native plant community in the Central Parkland subregion of Alberta, Canada characterized by high species richness and conservation values (Sims and Risser 2000; Natural Regions Committee 2006). The study site is a savanna-type habitat, containing a mixture of trembling aspen (*Populus tremuloides*) groves and rough fescue (*Festuca hallii*) prairie. My research focused exclusively on the rough fescue prairies. The study site historically has been lightly grazed by cattle in the fall, but grazing was halted two years prior to the beginning of this study. The majority of soils at the site are classified as thin Orthic Black Chernozems, or grassland soils with thin organic-matter enriched topsoil horizons, over glacial till (Howitt 1988; Soil Classification Working Group 1998).

Data Collection and Analysis

Plant community structure was measured at 149 sampling locations in mid-July 2004. These sampling locations were widely distributed across the study fields and included the control samples for the experiments described in both Chapters 4 and 5. At each location the percent cover of all vascular plant species was recorded by eye in a 0.5 m by 0.5 m quadrat. Cover of bare ground, bryophytes, lichens, and cattle dung were also estimated in each quadrat. Species richness and evenness (Pielou's J; Pielou 1969) were estimated from the percent cover data. Aboveground biomass (g m^{-2}) was measured by clipping all standing biomass in a 20 cm by 50 cm quadrat. Root biomass (g m^{-2}) was measured by washing the roots from a 5.3 cm diameter root core taken to a depth of 12 cm. Soil % total nitrogen was measured on soil sieved from the root biomass samples. The sieved soil was dried, ground, and a subsample analyzed using a Leco FP-428 N-Determinator (Leco, St. Joseph MI). Relative soil moisture was sampled at four points at each sample location using a Hydrosense moisture probe (Campbell Scientific, Logan UT). Light interception by the vegetation was measured using an Accu-Par light meter (Decagon, Pullman WA). Topographic position was estimated as the amount of incident radiation and calculated from slope and aspect following McCune and Keon (2002).

Non-metric Multidimensional Scaling (NMS) ordinations were used to describe species – environment relations in rough fescue grassland. Unconstrained ordinations were used because the goals of the analysis were to determine the overall patterns of variation in rough fescue grasslands, rather than to determine how a particular environmental variable explained the plant community. NMS is recommended as the method of choice for ordination of ecological data because, unlike other methods, it does not require assumptions such as multivariate normality of the data and linear relationships between variables (Clarke 1993; McCune and Grace 2002). All of the NMS analyses in this paper were carried out using Sorenson distance and the autopilot option in PC-ORD 4 (McCune and Mefford 1999).

Two major grassland communities, one dominated by *Poa pratensis* and *Galium boreale* and the other dominated by *Hesperostipa comata*, *Solidago missouriensis*, and *Artemisia frigida*, were found at the site. The plant species data were used to classify the samples into the *Poa* and *Hesperostipa* communities using PC-ORD 4 with Euclidian distance and Ward's method (McCune and Mefford 1999; McCune and Grace 2002). Plant species richness and evenness, and root and shoot biomass were compared between the two communities and the classifications were overlain on the ordination results.

Species – Environment Relationships in Rough Fescue Grassland

The rough fescue grasslands at the study site were species rich with few dominant species (Figure 1.1; Table 1.1). Species richness across all sample plots averaged 14.13 ± 2.63 (SD) and evenness (Pielou's J; Pielou 1969) averaged 0.83 ± 2.63 (SD). Average aboveground standing biomass was 259 g m^{-2} ± 78 (SD) and average belowground standing biomass was 983.5 g m^{-2} ± 396.4 (SD). The plant species in rough fescue grasslands represent a wide array of families, life forms, and ecological strategies. A list of the species including a description of some of these strategies is included in Appendix A. Ordination of the plant community data yielded a three-dimensional solution with a final stress of 18.53 (Fig. 1.2; 1.3). Species – axis correlations are listed in Table 1.2 and environment - axis correlations are listed in Table 1.3. The first axis accounted for 42.7% of the variation in the distance matrix, the second 21.8%, and the third 12.0% for a total r^2 of 0.765. The first two axes separated grassland dominated by *Poa pratensis* and *Galium boreale* from grassland dominated by *Hesperostipa comata*, *Solidago missouriensis*, and *Artemisia frigida*, while the third axis separated *Poa* dominated grasslands with high abundances of *Galium* from ones with high abundance of *Rosa arkansana* and *Artemisia ludoviciana*. Several important species including *Carex stenophylla, Festuca hallii,* and *Geum triflorum* were widely distributed through both grassland communities. The *Poa*-dominated grassland was associated with higher aboveground biomass and light interception, while lichen cover was higher in the *Hesperostipa* dominated grasslands. Both above- and below-ground biomass was higher in *Poa* dominated communities (Fig. 1.1). The *Hesperostipa* grasslands were found on drier locations on steeper south facing slopes than the *Poa* grasslands. There were few strong correlations between community summary statistics such as species richness and evenness and the ordination axes, nor were there any differences in average species richness or evenness between the two community types (Fig. 1.1).

Rough Fescue Grasslands as a Model System

I chose to use rough fescue grasslands as a model system for examining the mechanisms structuring plant communities for both practical and theoretical reasons. Practical and logistical reasons included the ease of carrying out experimental manipulations in a low-statured community with strong resource limitation, and the advantages of working in a well – studied system. A great deal is known about the impacts of herbivory, competition, drought, and plant characteristics on the structure of this system (Cahill 2003a, b; Coupe 2003; Brown 2004; Haag et al. 2004; Lamb and Cahill 2006). Insect herbivory, for example, is known to have few effects on overall plant community structure (Coupe 2003), even though insect herbivory can alter the importance of competition for some species in the community (Haag et al. 2004).

Rough fescue grasslands provide an ideal model system for examining the role of competition in structuring the community for several reasons. We know that competition is intense in this system, but diversity has no effects on the intensity of root competition in this system (Cahill 2003a, b). The lack of diversity effects on root competition suggests that the opposite is also likely to be true. This system is also very diverse relative to many other grassland systems. For example, Gross et al. (2000) found species richness ranged from 8.7 to 13.2 species m^{-2} across a long productivity gradient (45 - 600 g m^{-2} yr^{-1}) in North American grasslands, while average species richness in this system was ~14 species per 0.25 m^{-2} quadrat (Fig. 1.1). In addition evenness is very high, reaching ~0.8 of the theoretical maximum of 1.0 (Fig 1.1). Clearly plants are strongly competing for one or more resources in this system, yet that competition does not seem to be resulting in a species poor community dominated by one or a few very good competitors, as predicted by many theories of plant competition (Keddy 2001). Resolving this question of why such strong competition is apparently not leading to competitive exclusion is the primary aim of my thesis research. Competition, however, cannot be isolated from the characteristics of the system in which it occurs (Keddy 2001; Cahill and Lamb 2007).

For this reason, much of my thesis research was devoted to studies of the general mechanisms structuring fescue grassland communities.

Objectives

The goal of this thesis was to examine the mechanisms structuring plant species abundance and diversity patterns in a rough fescue grassland community. In this thesis I determine how environmental gradients, interactions with the soil microbiota, and plant biomass interact to affect the species richness, evenness, and composition of the plant community. In particular, I focus on the role played by competition for soil resources in structuring this community. My specific objectives were to:

1) Identify the resources limiting to plant growth in rough fescue grassland, and determine how the plant shoot community diversity and composition changes along gradients of those resources (Chapter 2).
2) Determine whether interactions between the plant and soil microbial communities have any influence on the plant community structure of a rough fescue grassland (Chapter 2).
3) Determine how the intensity of root and shoot competition varies along gradients of limiting resources in a rough fescue grassland and whether interactions between root and shoot competition occur in this community (Chapter 3).
4) Describe the relationships between competition intensity and plant community shoot and root biomass in a rough fescue grassland (Chapter 3).
5) Describe the networks of causation and interaction among environmental conditions, and plant community biomass that affect the diversity and composition of rough fescue grassland (Chapter 4, 5).
6) Test whether competition is an important mechanism structuring rough fescue grassland by determining if variation in the intensity of competition can be used to explain variation in plant community diversity or composition (Chapter 5).

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Table 1-1. Relative abundance (% cover over all quadrats and only across quadrats where the species was present), and relative frequency (% of quadrats found in) of vascular plant species in rough fescue grassland.

Species	Avg. Cover	Avg. Cover if Present	Frequency
Achillea millefolium	2.05	2.97	69.13
Agropyron spp.	1.37	2.52	54.36
Agrostis scabra	0.14	3.42	4.03
Amelanchier alnifolia	0.04	3.25	1.34
Androsace occidentalis	0.70	1.07	65.10
Antennaria microphylla	0.57	5.31	10.74
Antennaria neglecta	0.26	2.29	11.41
Artemisia frigida	0.79	3.28	24.16
Artemisia ludoviciana	3.73	8.06	46.31
Astragalus agrestis	0.76	2.52	30.20
Bouteloua gracilis	1.46	6.21	23.49
Bromus inermis	0.05	7.00	0.67
Campanula rotundifolia	0.21	1.09	19.46
Carex stenophylla	9.47	9.73	97.32
Cerastium arvense	0.82	1.79	45.64
Chenopodium album	0.17	1.04	16.78
Comandra umbellata	1.48	2.37	62.42
Descurainia pinnata	0.05	2.67	2.01
Elaeagnus commutata	0.02	1.75	1.34
Erigeron philadelphicus	0.47	1.86	25.5
Festuca hallii	3.28	4.69	69.8
Fragaria virginiana	0.48	6.55	7.38
Galium boreale	5.18	9.08	57.05
Geum triflorum	1.56	5.54	28.19
Hesperostipa comata	12.18	12.69	95.97
Heuchera richardsonii	0.11	2.43	4.70
Koeleria macrantha	2.15	3.73	57.72
Lactuca biennis	0.5	5.73	8.72
Lepidium densiflorum	0.01	0.67	2.01
Melilotus officinalis	0.01	2.00	0.67
Muhlenbergia richardsonis	0.03	0.90	3.36
Orthocarpus luteus	0.23	1.35	17.45
Oxytropis campestris	0.61	3.16	19.46
Penstemon procerus	0.31	1.98	15.44
Poa pratensis	7.65	13.10	58.39

Species	**Avg. Cover**	**Avg. Cover if Present**	**Frequency**
Polygonum spp	0.04	1.10	3.36
Populus tremuloides	0.03	4.00	0.67
Potentilla arguta	0.34	3.57	9.40
Potentilla concinna	0.04	1.10	3.36
Pulsatilla patens	0.39	3.66	10.74
Rosa arkansana	5.24	6.85	76.51
Silene spp	0.05	1.00	4.70
Solidago missouriensis	4.99	8.16	61.07
Stellaria spp	0	0.50	0.67
Symphoricarpos occidentalis	0.73	4.74	15.44
Symphyotrichum falcatum	1.43	4.95	28.86
Symphyotrichum laeve	0.97	5.58	17.45
Taraxacum officinale	0.14	1.43	10.07
Thalictrum venulosum	0	0.50	0.67
Thermopsis rhombifolia	1.02	3.32	30.87
Vicia americana	0.16	1.44	11.41

Table 1-2. Correlations (r) between species and ordination axes in rough fescue grassland.

Species	Axis 1	Axis 2	Axis 3
Achillea millefolium	-0.393	0.295	-0.015
Agropyron spp.	-0.437	-0.035	-0.031
Agrostis scabra	0.038	-0.294	0.058
Amelanchier alnifolia	-0.013	0.153	0.063
Androsace occidentalis	0.092	-0.422	0.072
Antennaria microphylla	0.099	0.043	0.147
Antennaria neglecta	0.119	0.106	0.243
Artemisia frigida	0.378	-0.566	-0.108
Artemisia ludoviciana	-0.453	0.015	-0.450
Astragalus agrestis	-0.097	0.431	0.099
Bouteloua gracilis	0.549	-0.468	-0.219
Bromus inermis	-0.142	0.120	-0.147
Campanula rotundifolia	-0.175	0.145	0.136
Carex stenophylla	0.291	-0.270	0.156
Cerastium arvense	0.173	-0.108	0.304
Chenopodium album	-0.093	-0.411	-0.164
Comandra umbellata	-0.072	0.232	0.044
Descurainia pinnata	-0.181	0.076	-0.029
Elaeagnus commutata	0.031	-0.178	-0.023
Erigeron philadelphicus	-0.005	0.057	0.190
Festuca hallii	-0.050	0.211	0.416
Fragaria virginiana	-0.406	0.400	-0.055
Galium boreale	-0.572	0.624	0.262
Geum triflorum	-0.018	0	-0.085
Hesperostipa comata	0.452	-0.495	0.348
Heuchera richardsonii	-0.244	0.163	-0.186
Koeleria macrantha	0.341	-0.509	0.268
Lactuca biennis	-0.355	0.083	0.004
Lepidium densiflorum	0.050	-0.168	-0.003
Melilotus officinalis	-0.062	0.075	0.031
Muhlenbergia richardsonis	-0.031	0.009	0.034
Orthocarpus luteus	0.234	-0.310	0.025
Oxytropis campestris	0.107	-0.011	0.225
Penstemon procerus	0.119	-0.179	0.166
Poa pratensis	-0.754	0.624	-0.273
Polygonum spp	-0.201	0.084	0.036
Populus tremuloides	-0.163	0.229	0.048
Potentilla arguta	0.083	0.082	0.077
Potentilla concinna	0.163	-0.068	0.003
Pulsatilla patens	0.305	-0.143	-0.083
Rosa arkansana	-0.065	0.044	-0.462
Silene spp	0.133	-0.021	0.153

Species	**Axis 1**	**Axis 2**	**Axis 3**
Solidago missouriensis	0.489	0.366	-0.041
Stellaria spp	0.043	0.027	0.178
Symphoricarpos occidentalis	-0.248	0.103	-0.291
Symphyotrichum falcatum	0.217	-0.243	-0.179
Symphyotrichum laeve	-0.275	0.438	0.061
Taraxacum officinale	-0.111	-0.015	-0.094
Thalictrum venulosum	-0.142	0.12	-0.147
Thermopsis rhombifolia	-0.246	0.105	-0.097
Vicia americana	-0.204	0.243	0.136
Unk Brassicaceae	0.216	-0.301	0.141
Unk Forb	0.009	0.017	-0.055
Unk Grass	-0.218	0.198	-0.013

Table 1-3. Correlations (r) between ordination axes and environmental and plant community variables in rough fescue grassland.

Environmental Variable	**Axis 1**	**Axis 2**	**Axis 3**
Aboveground biomass (g m^{-2})	-0.543	0.306	0.030
Belowground Biomass (g m^{-2})	-0.307	0.176	-0.132
Soil Moisture	-0.172	0.365	-0.013
Light Interception (%)	-0.509	0.331	-0.024
Topographic Position	0.382	-0.336	-0.022
Total Nitrogen (%)	-0.255	0.181	0.065
Species Richness	-0.135	0.158	0.049
Evenness	-0.016	0.016	-0.139
Bare ground cover (%)	-0.346	0.223	-0.283
Bryophyte cover (%)	-0.025	0.104	0.162
Lichen Cover (%)	0.614	-0.462	0.164
Cow Dung (%)	0.070	-0.041	-0.053

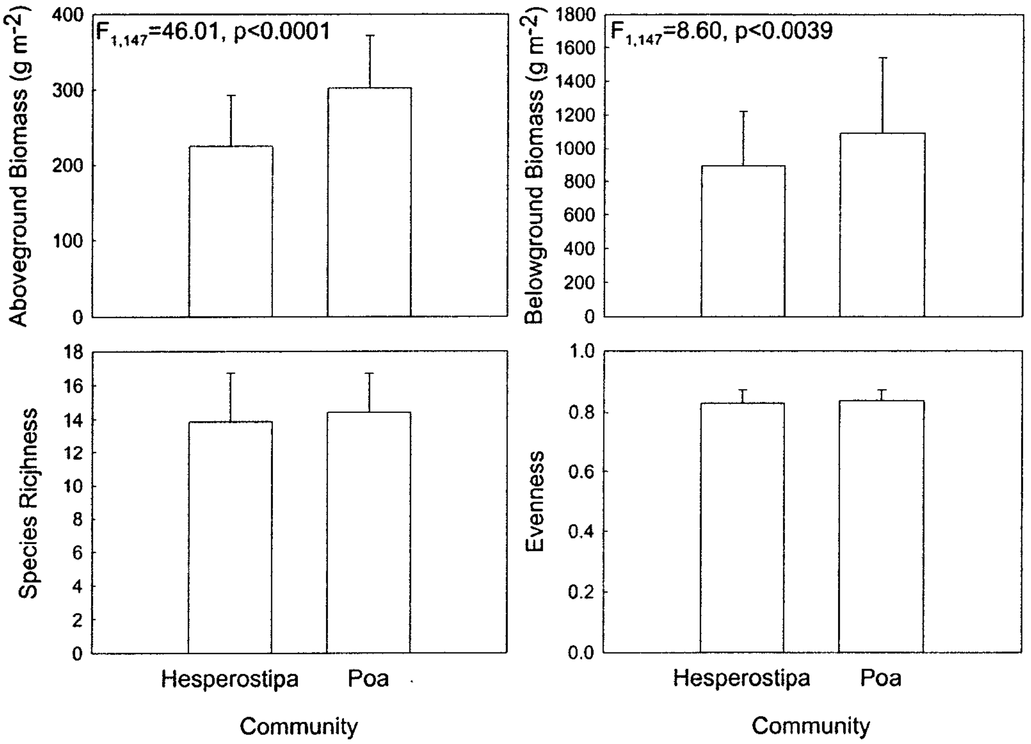

Figure 1-1. Figure comparing aboveground and belowground biomass, species richness, and evenness between *Hesperostipa comata* and *Poa pratensis* dominated grassland communities. Error bars are one standard deviation.

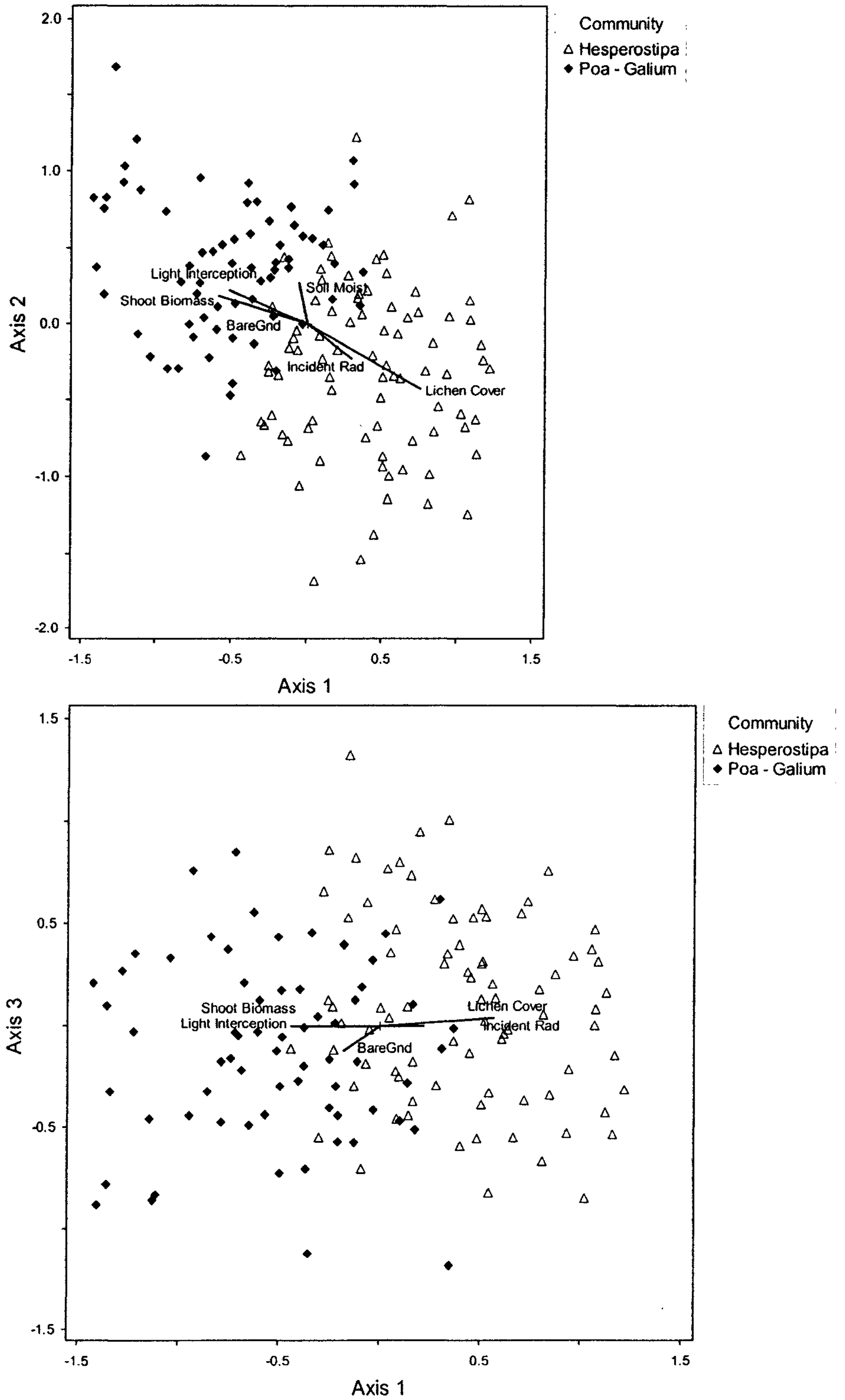

Figure 1-2. Ordinations showing the relationships between environmental conditions and Poa-Galium dominated grasslands and Hesperostipa-dominated grasslands. Environmental variables with an axis correlation r2>0.100 are shown.

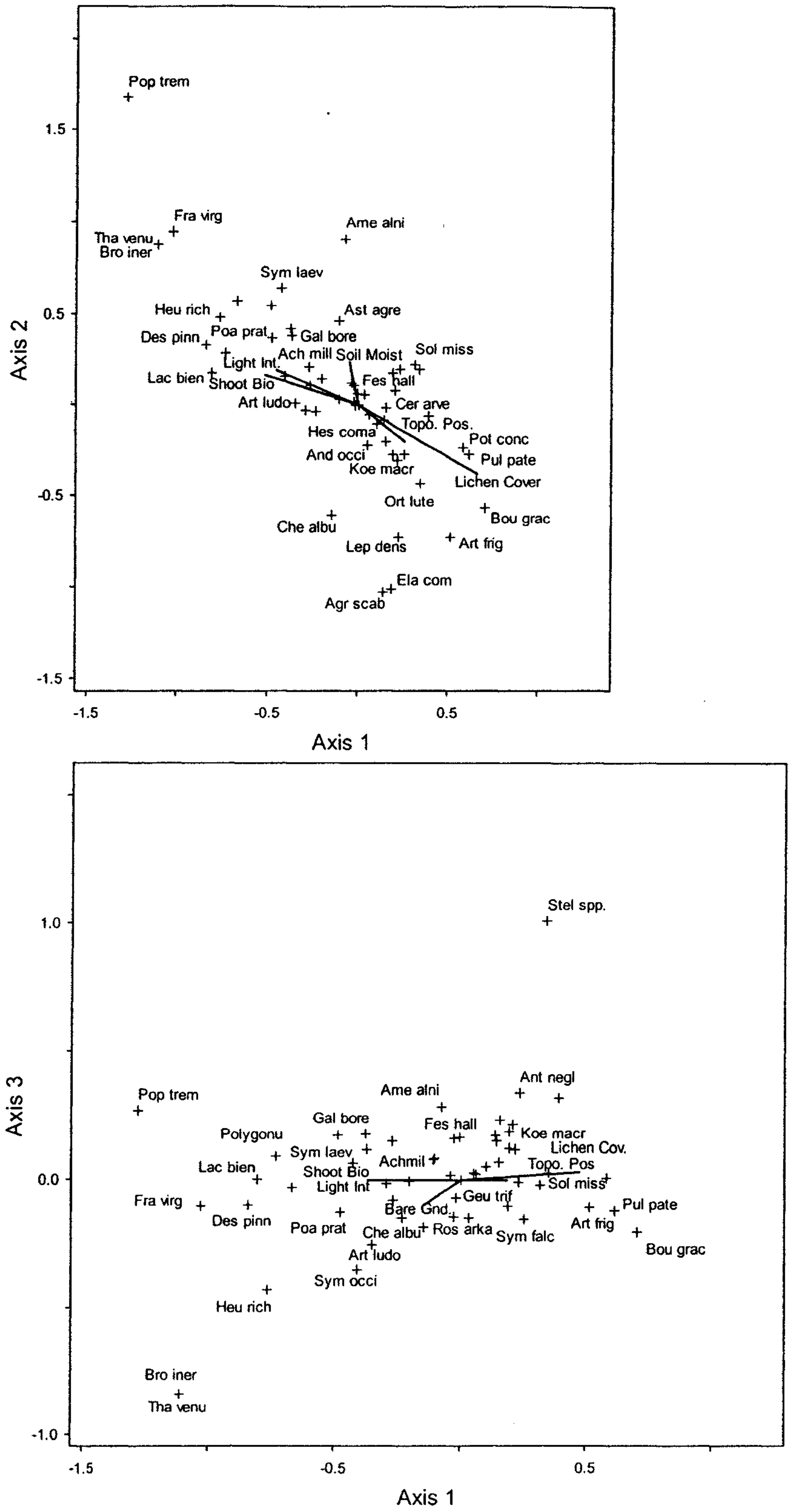

Figure 1-3. Ordinations showing the relationships between selected species and environmental conditions in rough fescue grasslands. Environmental variables with an axis correlation r2>0.100 are shown.

2. The effects of water, nitrogen, and plant-soil feedbacks on the plant and soil bacterial communities in a rough fescue grassland[1]

Introduction

The addition of resources such as water and soil nutrients can have dramatic effects on the structure and composition of both plant (e.g. DiTommaso and Aarssen 1989, Carson and Pickett 1990; Crawley et al. 2005, Stevens et al. 2006) and soil microbial communities (e.g. Wardle 2002, Kennedy et al. 2004, McCarthy et al. 2005). In addition to direct abiotic controls, interactions and feedbacks between plants and microbes are thought to be an important mechanism structuring the productivity and composition of both communities (Wardle 2002; Bever 2003). For example, a change in resource levels that directly alters plant community richness or composition may indirectly affect the microbial community by changing root exudate chemistry (Wardle et al. 1999, Hopkins and Gregorich 2005, Orwin et al. 2006). Similarly, the abundance of mutualistic and pathogenic soil microbes can strongly enhance or inhibit the performance of individual plants or species (e.g. van der Heijden et al. 1998; Bever 2003; Casper and Castelli 2007). Separating the direct and indirect effects of changing abiotic resource levels on plant and microbial community structure from indirect effects resulting from feedbacks between the communities is challenging, particularly in natural systems where direct manipulations of the microbial community are very difficult (Hooper et al. 2000, Bardgett et al. 2005).

Differences in scale between the plant and microbial communities also present a challenge to assessing the importance of plant – microbial feedbacks in a field setting. Interactions among microbes occur at scales of micro-meters to millimeters, while interactions among plants occur at scales of centimeters to meters (Casper et al. 2003; Watt et al. 2006). Individual plants strongly influence microbes only within their rhizosphere, the soil within ~1mm of the root surface (Watt et al. 2006). At the scale of plant root systems, the soil microbial community is a metacommunity (Leibold et al. 2004) including both the rhizosphere communities of

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[1] Raw data used in this chapter are available in Appendix E

individual plants and free-living microbial communities in soil not directly influenced by living plant roots. In plant monocultures there is likely great potential for direct plant – microbial feedbacks to influence both population dynamics and community composition. In natural plant communities, however, roots from numerous species can densely intermingle. Thus the influence of each plant species on the microbial meta-community is likely to be proportional to the dominance of the roots of that species. To understand the role of plant-microbial feedbacks in natural multispecies communities, the most important question is not how a particular plant species interacts with its rhizosphere community, but how the entire plant community interacts with its associated microbial meta-community.

At the scale of the plant community, important plant-microbial feedbacks should be detectable as an association between the structures of the plant and microbial communities (Wardle et al. 1999, Hooper et al. 2000). Strong and specific interactions should result in a 1:1 correspondence between the two communities such that for any given composition of the plant community there will be a corresponding structure in the microbial community. Weak or nonspecific interactions, in contrast, imply that a given plant community structure could be associated with one of many configurations in the microbial community. Sullivan et al. (2006) used this approach to assess the relative importance of abiotic controls and interactions, finding significant associations between microbial and plant community structure following a 12 year experimental sewage sludge application. A manipulative experiment that alters the composition of a plant or microbial community will also disrupt any pre-existing associations between the communities. The maintenance of a measure of association such as a multivariate correlation through the disruption of a manipulative experiment is a strong indication that interactions or feedbacks were important in structuring community composition.

In this study we test whether plant – bacterial interactions had structured the diversity and composition of the plant and soil bacterial communities in a native rough fescue grassland in central Alberta, Canada. We examine both the direct effects of increased levels of two limiting resources, water and nitrogen, on the biomass, diversity, and functional composition of each community, and use tests of association to determine whether feedbacks were an important mechanism structuring the two communities. Understanding the effects of changing levels of soil resources in this system is critical given that climatic conditions and soil nutrient levels are predicted to change substantially over the next century. Average precipitation on the Canadian prairies has varied substantially in the last century (Akinremi et al. 1999; Schindler and Donohue 2006). Climate models (assuming a doubling of atmospheric CO_2) predict a 7 to 29% rise in precipitation in the agricultural regions of Alberta by 2060 (Shepherd and McGinn 2003), and rising temperatures will alter potential evapotranspiration rates (Schindler and Donohue 2006). Deposition of anthropogenic nitrogen is also of concern because the aspen parkland region of eastern Alberta receives as much as 22 kg N ha^{-1} yr^{-1} (Köchy and Wilson 2001), a rate greater than that (17 kg N ha^{-1} yr^{-1}) causing a 23% decline in plant species richness in European *Agrostis-Festuca* grasslands (Stevens et al. 2004).

Methods

Field Site

The study area is in a 50 ha field at the University of Alberta Research Ranch near Kinsella, Alberta, Canada (53°05 N, 111°33 W) in the Aspen Parkland Ecoregion (Sims and Risser 2000). The study site is a savanna-type habitat, containing a mixture of trembling aspen (*Populus tremuloides*) groves and rough fescue (*Festuca hallii*) prairie. Plant biomass is limited by both nitrogen and water availability (Lamb et al. 2007). The site historically has been lightly grazed by cattle in the fall, but grazing was halted two years prior to the beginning of this experiment. The soils are dominantly classified as thin Orthic Black Chernozems, or grassland soils with thin organic-matter enriched topsoil horizons, over glacial till (Howitt 1988, Soil Classification Working Group 1998).

Experimental Design

Twenty-two blocks, each containing four 1.5m by 1.5m plots separated by 1m wide buffers, were established in May 2003. The 22 blocks encompassed both *Poa pratensis* dominated grasslands in wetter microsites and *Stipa comata* dominated grasslands in drier locations. Control, nitrogen, water, and nitrogen + water treatments were randomly assigned to plots in each block. The plant community was examined in all 22 blocks, while logistical constraints limited soil bacterial sampling to a subset of 10 blocks in *Stipa*-dominated grassland.

In the nitrogen treatments, 5.44 g m^{-2} y^{-2} granular ammonium nitrate fertilizer was applied in two 2.72 g m^{-2} doses in mid May and late June from 2003 through 2005. Water was added weekly from mid May through late September at rates equivalent to a 50% addition to long-term average rainfall. Rainfall varies through the growing season, so plots received the equivalent of 5 mm of rain per week in May, 10.5 mm in June, 9.5 mm in July, 7.5 mm in August, and 4.5 mm in September for a total of 139 mm each growing season. This represents a 54% increase over natural rainfall (256 mm) during the same period in 2003, 48% (290 mm) in 2004, and 52% (265 mm) in 2005. Precipitation was measured at the Viking, Alberta weather station (53°16 N, 111°46 W) (Environment Canada 2006). Watering significantly increased relative soil moisture levels ($F_{1,105}=37.68$, $p<0.001$) as measured using a Hydrosense soil moisture probe (Campbell Scientific, Logan UT).

Bacterial Community

The community-level substrate utilization profile (CLSU) of the bacterial community was sampled in 10 of the 22 blocks using Biolog Ecoplates (Biolog Inc., Hayward CA, USA). Logistical constraints precluded sampling the remaining blocks. A CLSU profile assesses the potential functional diversity of a bacterial community by measuring the ability of a sample from that community to metabolize 31 carbon sources in seven categories (Amines, Amino acids, Carbohydrates, Carboxylic acids, Esters, Phosphorylated compounds, and Polymers). The degree of substrate utilization is measured by the intensity of colour changes in a tetrazolium dye (Garland and Mills 1991). CLSU profiles need to be interpreted with caution as they capture only a subset of the bacterial community (Smalla et al. 1998, Preston-Mafham et al. 2002). Comparative studies, however, have shown that both CLSU profiling and alternative methods such as phospholipid-fatty acid profiling and DNA fingerprinting are effective for distinguishing the bacterial communities and detecting associations between plant species and the bacterial community (e.g. Widmer et al. 2001, Grayston et al. 2004, Ritz et al. 2004, Singh et al. 2006).

Five soil cores (1.9 cm diameter and 5 cm deep) were taken from each plot on July 27, 2005. The corer was washed in 95% ethanol between plots to avoid cross contamination. Samples were homogenized and refrigerated overnight. One gram of soil from each sample was added to 100 ml of sterile 0.85% NaCl solution, shaken for 3 hr and diluted (1:10). Each microplate well was inoculated with 120 μl of suspension. Plates were incubated in the dark at 25 °C. The first readings were taken after 48 hours using a Biolog Microstation Reader with subsequent readings at 24 hr intervals for five days.

Bacterial functional richness was measured as the number of carbon substrates per plate with colour development greater than that in the control (water) wells on each plate at the first reading (48 hrs). Bacterial activity in each well over the seven-day incubation was assessed as the area under the colour development curve (Hackett and Griffiths 1997, Preston-Mafham et al. 2002). All values reported in this study are the average of the three replicate wells for each substrate on each plate. The area under the curve for the control wells was subtracted from the values for each substrate, and any negative values were recorded as zeros. The values for all 31 substrates were summed across each plate as a proxy for the overall bacterial activity in each plot (Kersters et al. 1997, Preston-Mafham et al. 2002). Evenness was measured as Pielou's J (Pielou 1969).

Six randomly selected plots were re-sampled to confirm that the field sampling and inoculation protocol had yielded a consistent representation of the bacterial CLSU. All steps from soil sampling to plating were carried out separately for the duplicates. No significant differences between duplicates were found using a Blocked Multiple Response Permutation Procedure (MRBP; see below) with sampled plot as the blocking variable and repeated sample as the grouping variable (A=-0.05; p=0.722), demonstrating that the procedures were consistent.

Plant Community

Plant community composition (% cover of all vascular species) was measured in mid-July 2005 in permanently marked 0.5 by 0.5 m quadrats. Shoot biomass was measured by clipping all live biomass from a 0.1 by 1 m quadrat. Root biomass was measured by washing the roots from a single 5.3 cm diameter by 12 cm deep root core in each treatment plot. For some analyses, plant species cover was divided into five functional groups (annual forbs, perennial forbs (excluding legumes), legumes, woody shrubs, and graminoids). Evenness was measured as Pielou's J (Pielou 1969).

Observations in the first two years of the experiment indicated that a major effect of water was to delay plant senescence. To quantify senescence the relative greenness (the % of the current year's leaf area that had not yellowed or otherwise developed signs of senescence) of nine common forbs (*Achillea millefolium* L, *Artemisia frigida* Willd, *Artemisia ludoviciana* Nutt., *Symphyotrichum laeve* (L.) A.& D. Löve, *Cerastium arvense* L, *Galium boreale* L, *Geum triflorum* Pursh, *Lactuca tatarica* (L) C.A. Mey., and *Solidago missouriensis* Nutt.) and five graminoids (*Carex stenophylla* Wohl., *Festuca hallii* (Vasey) Piper., *Koeleria macrantha* (Ledeb.) J.A. Schultes, *Poa pratensis* L, and *Hesperostipa comata* (A.S. Hitchc.) Barkworth) was estimated weekly throughout the growing season. The fourteen species examined for greenness comprise ~74% of the total vascular cover in July (Chapter 1). The raw phenology data for all nine species are available in Appendix

Statistical Analysis

Plant species and carbon substrate-use richness and evenness, total bacterial activity, shoot and root biomass, and the activity of each of the seven carbon substrate classes and five plant functional groups were evaluated using mixed models with nitrogen and water treatments as fixed factors and block as a random factor. Richness was evaluated using a generalized linear mixed model with poisson errors in PROC GLIMMIX and the remaining response variables were evaluated using similar models in PROC MIXED (SAS 9.1; SAS Institute Inc., Cary NC). In cases where the covariance parameter for block was zero the results reported are for models without the blocking variable.

Relative allocation to root and shoot biomass was examined using a general linear model with shoot biomass as the response variable, root biomass as a covariate, and the nitrogen and water treatments as fixed factors in PROC MIXED (SAS 9.1; SAS Institute Inc., Cary NC). All interactions involving the covariate were included in an initial model but non-significant interactions were sequentially removed in subsequent models (Engqvist 2005). Significant covariate interactions remaining in the final model indicate shifts in biomass allocation.

The effects of water and nitrogen on the average greenness of forbs and graminoids from June 1, 2005 through September 21, 2005 were analyzed using repeated measures mixed models with PROC MIXED (SAS 9.1; SAS Institute Inc., Cary NC). Greenness was the response variable and nitrogen and water addition were fixed factors. Experimental block was a random factor and survey date the repeated factor. Graminoid and forb greenness were analyzed separately since combining these data and adding life form as a nested fixed factor resulted in models too complex to converge. To detect differences between graminoids and forbs, analyses of the combined data were conducted for the July 20, 2005 and August 17, 2005 surveys (at peak growth and three weeks after the general onset of senescence). In these analyses, random factors nesting life form, nitrogen, and water addition within each sampled quadrat were included. Significant life-form by treatment interactions indicated differences in senescence rate between graminoids and forbs.

Blocked Multiple Response Permutation Procedures (MRBP) were used to determine whether the treatments had caused significant differences in plant or bacterial community structure. MRBP is a multivariate test of the null hypothesis of no difference between a-priori groups of samples, analogous to a discriminant function analysis, but requiring no distributional assumptions (McCune and Grace 2002). An MRBP is carried out by comparing ecological distances within a group of samples (treatment) to the distribution of distances when those samples are randomly assigned to groups. MRBP is limited to only one blocking variable and one treatment variable, so a series of contrasts were used to test for treatment interactions. First, each treatment combination (nitrogen, water, nitrogen + water) was separately compared to the control. Second, each treatment that alone was significantly different from the control was compared to the nitrogen + water treatment to determine whether the effects of the first treatment alone had been altered by the second treatment. The MRBPs were carried out using Euclidian distance in PC-ORD 4 (McCune and Mefford 1999).

Mantel tests were used to test for associations between the plant and bacterial communities. An association between the structure of two communities results in a multivariate correlation if for a given composition of one community there is a corresponding structure in the second community. A multivariate correlation results when the ecological distance between samples taken from one community (i.e. differences in community composition between samples) is correlated with the ecological distance between samples of a second community from the same locations (McCune and Grace 2002). Associations between communities following an experimental manipulation that altered at least one of those communities indicates that the subsequent development of both communities was somehow linked (Wardle et al. 1999, Hooper et al. 2000, Sullivan et al. 2006). Mantel tests evaluate the correlation between two multivariate data sets using the Mantel statistic, analogous to a Pearson correlation, and a random permutation procedure to test for significance (McCune and Grace 2002). Mantel tests were carried out using Sorenson distance and 9999 random permutations using PC-ORD 4 (McCune and Mefford 1999).

Results

Plant – Bacterial Feedbacks

Plant and bacterial community structures were uncorrelated when the plant community was measured using both plant species (r=-0.008; p=0.49) and plant functional groups (r=0.010; p=0.43). There were no correlations between bacterial and plant community structures within individual resource treatment combinations (Control r=0.157, p=0.23; Nitrogen r=-0.049, p=0.423; Water r=-0.135, p=0.27; Nitrogen + Water r=-0.144, p=0.20). Similarly, there were no univariate correlations between bacterial and plant richness (r=-0.143, p=0.378) or evenness (r=-0.161, p=0.322). The only significant univariate correlations were between the abundance of perennial forbs and the activity of the carbohydrate (r=0.405, p=0.009), carboxylic acid (r=0.319, p=0.044), ester (r=0.468, p=0.002), and polymer (r=0.347, p=0.028) groups.

Bacterial Community

Both water and nitrogen addition significantly altered bacterial community structure, but these effects were driven primarily by water since there were no significant differences between the water and water by nitrogen treatments (Table 2-1). Rather than causing a shift in the relative abundance of the bacterial functional groups present, water appears to have primarily affected bacterial community structure by increasing the total abundance of all groups (Figure 2-1). There were no effects of either resource on bacterial functional richness, though both water and nitrogen addition decreased functional evenness. Total bacterial activity increased with water addition, but was unaffected by nitrogen. Water addition increased the activity of all bacterial functional groups while nitrogen increased the activity of the carboxylic acid, ester, and polymer groups (Figure 2-1). A water by nitrogen interaction increased the positive effects of water on the carbohydrate group. A second interaction indicated that the phosphorylated group was negatively affected by nitrogen alone, but positively affected when nitrogen was added with water.

Plant Community

Overall plant community structure was significantly altered by an interaction between nitrogen and water addition (Table 2-1). The interaction was driven by a decline in both annual and perennial forbs in plots receiving both nitrogen and water and a concurrent increase in graminoids. Nitrogen addition reduced plant species richness, but evenness was unaffected by either water or nitrogen (Figure 2-2). Both nitrogen and water addition increased shoot biomass, water decreased root biomass, and nitrogen interacted with water to increase the negative effect of water on root biomass (Figure 2-2). Even though the water treatment had a positive net effect on shoot biomass and a negative effect on root biomass, there were no significant root biomass (as a covariate) by treatment interactions, indicating that resource addition did not significantly alter relative allocation to shoot and root biomass. Nitrogen addition increased graminoid cover and decreased annual forb and legume cover while water led to an increase in perennial forb cover (Figure 2-2). There were no nitrogen by water interactions affecting the abundance of individual plant functional groups.

Some forbs, particularly *Cerastium arvense*, began to senesce in the first week of July, but senescence for the majority of graminoids and forbs began at the end of July (Figure 2-3). Forbs were greener with nitrogen addition, and water addition delayed the senescence of both graminoids and forbs. There was no significant water by life-form interaction on July 20th ($F_{1,84}$=0.20, p=658), but the interaction was significant on August 17th ($F_{1,83.9}$=7.95, p=0.006), indicating that late in the growing season water delayed forb senescence more than graminoids.

Discussion

Plant-Bacterial Feedbacks

Both the plant and bacterial communities in rough fescue grassland were extremely diverse. The high plant community diversity may have contributed to the high bacterial functional diversity even though few correlations were found between plant and soil diversity. Significant plant – microbe diversity correlations have been observed along a plant diversity gradient ranging from 1 through 32 species (Bartelt-Ryser et al. 2005), while the resource treatment – induced changes in plant diversity in this study were very small relative to unmanipulated diversity levels. Also, microbial diversity in this study ranged between 20 and 30 functional groups (average = 26.72 ±2.31 (std. dev.) out of a possible 31 groups. Correlations should likely not be expected with such a small range of diversity. A second explanation for the lack of diversity correlations may be that the aboveground plant diversity measures in this study are an underestimate of belowground plant diversity. Above- and belowground plant diversity may be poorly correlated because of the extensive lateral root systems of many grassland plant species (Coupland and Johnson 1965).

Both the plant and bacterial communities were altered by nitrogen and water addition, but there was little evidence that plant-microbial feedbacks had any effect on the structure of either community. The lack of association between the plant and microbial communities does not indicate that feedbacks at the level of individual plant species or bacterial functional types were absent; rather it indicates that any interactions that did occur were unimportant for the overall community structure. Neither does the lack of interactions indicate that we had only sampled free-living soil microbes from soil unaffected by plant roots because the majority of the soil bacterial meta-community was within a plant rhizosphere. The mean root length density in twelve 5.3cm diameter root cores taken to a depth of 10 cm was 31.36 cm cm^{-3} ±13.76 (std. dev.) and mean root diameter was 0.20mm ±0.03 (std. dev.) (McNickle and Clark, personal communication). At that root length density, assuming a rhizosphere extending ~1mm from the root surface (Watt et al. 2006) and an even distribution of roots, the entire surface soil volume was influenced by plant roots.

Given the extent of the rhizosphere in this community, why then were there so few effects of the plant community on the composition of the soil bacterial community? Numerous studies have demonstrated strong effects of plant monocultures on the composition of soil microbial communities (e.g. Grayston et al. 1998; Wardle 2006). However, a plant species can only strongly influence the soil bacterial meta-community if the species contributes a large proportion of the total community root biomass. Individual plant species may be involved in strong interactions with their rhizosphere communities, but the net effects of multiple interactions will likely be very weak when no single species dominates the plant community. With mean evenness greater than 0.8 in all treatments (Figure 2.2) it should then be no surprise that there were no significant plant-bacterial community relationships in this rough fescue grassland. We suggest that there may be a general relationship between the influence that the plant community has over the composition of the microbial meta-community and plant community diversity (Figure 2-4). Diverse plant communities are unlikely to have strong plant – microbial relationships, but depending on the biology of the dominant plant species, low diversity plant communities may have both strong and weak influences on the microbial community. There is some empirical evidence for the proposed pattern because Sullivan et al. (2006) found significant plant – microbial community coupling in a system where plant species richness averaged between 11 and 19 species per $5m^2$ sampled. In contrast a species-area curve at this site indicates that an average of 42.22 ±2.40 (std. dev) species will be encountered per $5m^2$. The strength of plant – microbial feedbacks may also vary depending on the degree of segregation among plant root systems. In systems where each plant dominates a distinct "zone of influence" (Casper et al.

2003), individual plants are likely to have a strong influence on the soil community. However in systems where the roots of multiple species extensively intermingle, strong feedbacks are unlikely to be found at any scale.

Two caveats must be placed on the finding that plant – bacterial interactions may not be important in structuring this diverse native grassland. First, the three-year span of this experiment may have been insufficient for plant-bacterial associations to develop following experimental manipulations. Sullivan (2006) found significant plant microbe associations following a 12-year experiment, but did not report interim measures leaving it unclear how quickly the associations observed developed. Similarly, many of the field studies that have found important microbial – plant community coupling used sites with long histories of similar vegetation or management regimes (e.g. Bardgett et al. 2001, Grayston et al. 2004). Second, interactions may have occurred in this system, but only affecting the microbial community at a finer taxonomic resolution than permitted by CLSU profiling or involving aspects of the community such as fungi that were not measured (Wardle 2006). It is unlikely, however, that such interactions could have occurred without at least minor interactions at the level of resolution of this study being found. Comparative studies using both CLSU profiles and other techniques have generally reached similar conclusions and several previous studies have found strong links between plant species composition and CLSU profiles (e.g. Widmer et al. 2001, Grayston et al. 2004, Ritz et al. 2004, Singh et al. 2006). We expect that if important interactions were occurring, at a minimum, weak associations would have been detected. The correlation coefficients in this study were essentially zero, so the lack of response was not an artifact of weak relationships obscured by noisy data.

Bacterial Community

Water was the primary resource limiting bacterial activity. Water can limit bacterial populations because it determines the space available in the aqueous films around soil particles (Wardle 2002). Low water levels can also limit the availability of dissolved organic carbon, a key energy source (Marschner and Kalbitz 2003). The importance of water as a limiting resource, and the increases in bacterial community evenness with both water and nitrogen addition may indicate strong resource competition within the bacterial community. In the absence of severe abiotic stresses or increased predation in particular treatments, an increase in evenness can indicate that the intensity of competition for a limited resource was relaxed (Cotgreave and Harvey 1994, Keddy 2001). Competition is thought to be unimportant relative to predation in structuring bacterial communities (Wardle and Yeates 1993, Wardle 2002), however several studies have observed increased microbial evenness with increasing resource availability, suggesting that strong resource competition within microbial communities may be common (Derry et al. 1999, Degens et al. 2000, Zhou et al. 2002).

Plant Community

Plant community responses to the addition of limiting nitrogen and water were similar to those in many other studies. Nitrogen addition led to a decline in species richness and legume and annual forb abundance, but an increase in grass and sedge abundance (DiTommaso and Aarssen 1989; Pennings et al. 2005; Suding et al. 2005). Declines in annual forb abundance were likely due to physical interference from litter accumulation over the course of the experiment (Facelli and Pickett 1991; Lamb, Chapter 4). Both nitrogen and water addition increased aboveground productivity, however only nitrogen affected species richness. Goldberg and Miller (1990) found a similar pattern in an annual plant community, and suggested that resources such as nitrogen that were limiting early in the growing season may have stronger effects on mortality resources such as water that limit growth later. The importance of water in this system late in the growing season is consistent with Goldberg and Miller's (1990) hypothesis. The effects of nitrogen and water on root competition intensity may offer an alternative explanation, since nitrogen addition increased root competition intensity in this system, but water had few effects (Lamb et al. 2007).

It is not clear why the forbs in this system responded so much more strongly to water than the graminoids, particularly since the forbs are generally more deeply rooted (Coupland and Johnson 1965). Increases in forb productivity in C_4-grass dominated systems occur following irrigation because the major competitive advantage of the C_4 strategy (high water-use efficiency) is reduced under higher moisture conditions (Knapp et al. 2001). In fescue grassland, however, only one C_4 species (*Bouteloua gracilis*) is present at low abundance. Forbs generally have more plastic root foraging responses to soil nutrient heterogeneity (Kembel and Cahill 2005); the patterns in this study could be explained by a similar plasticity in response to variation in soil moisture.

The observed declines in species richness with nitrogen addition confirms that increased nitrogen deposition should be of conservation concern in this system (Köchy and Wilson 2001; Stevens et al. 2004; Lamb Chapter 4). The potential consequences of changes in precipitation patterns are less clear. In the absence of temperature-driven changes in evapotranspiration, increased soil moisture will likely increase productivity and may encourage a forb dominated plant community. Given the importance of soil moisture for plant senescence, changes in late summer precipitation may be more important than changes in other seasons or in total rainfall. The relationships between soil bacterial activity and soil moisture may also have important implications for soil carbon dynamics. A more extensive study to examine the interactions between temperature and precipitation on both the plant and soil communities in this system is underway.

Summary

Both the plant and soil microbial communities in rough fescue grassland were under strong abiotic control, but were largely unaffected by feedbacks from the other community. While plant-microbial relationships were unimportant in the short term, the potential for important feedbacks in the longer term remains unclear. Long-term interactions could be particularly important if increased nitrogen led to a greater dominance of grasses in the community or increased soil moisture altered microbe-driven processes such as litter decomposition and nutrient cycling. Separating the roles of abiotic factors and plant – microbe interactions in structuring communities is key to fully understanding aboveground – belowground interactions in natural communities (Bardgett et al. 2005).

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Table 2-1 MRBP results comparing the plant and bacterial communities between resource treatments.*

	Bacterial Community		*Plant Community*	
Contrast	A	p	A	P
Control vs. Water	0.188	**0.004**	-0.002	0.539
Control vs. Nitrogen	0.019	0.232	0.011	0.061
Control vs. Nitrogen + Water	0.275	**0.001**	0.027	**<0.001**
Water vs. Nitrogen + Water	0.077	0.040	n/a	
Nitrogen vs. Nitrogen + Water	n/a		n/a	

*A-values measure within group heterogeneity, with A=1 indicating that all samples within a group are identical and A=0 indicating that the within-group heterogeneity is equal to that expected by chance (McCune and Grace 2002). Ten samples from each treatment were included in the bacterial analyses and 21 samples in the plant analyses. To protect experiment-wise error rates only p-values less than 0.012 should be considered significant for the bacterial community tests and less than 0.017 for the plant community. Note that since the control vs. nitrogen contrast was insignificant for both the bacterial and plant communities, and the control vs. water contrast for the plant community was insignificant, those treatments were not contrasted against the nitrogen plus water treatment.

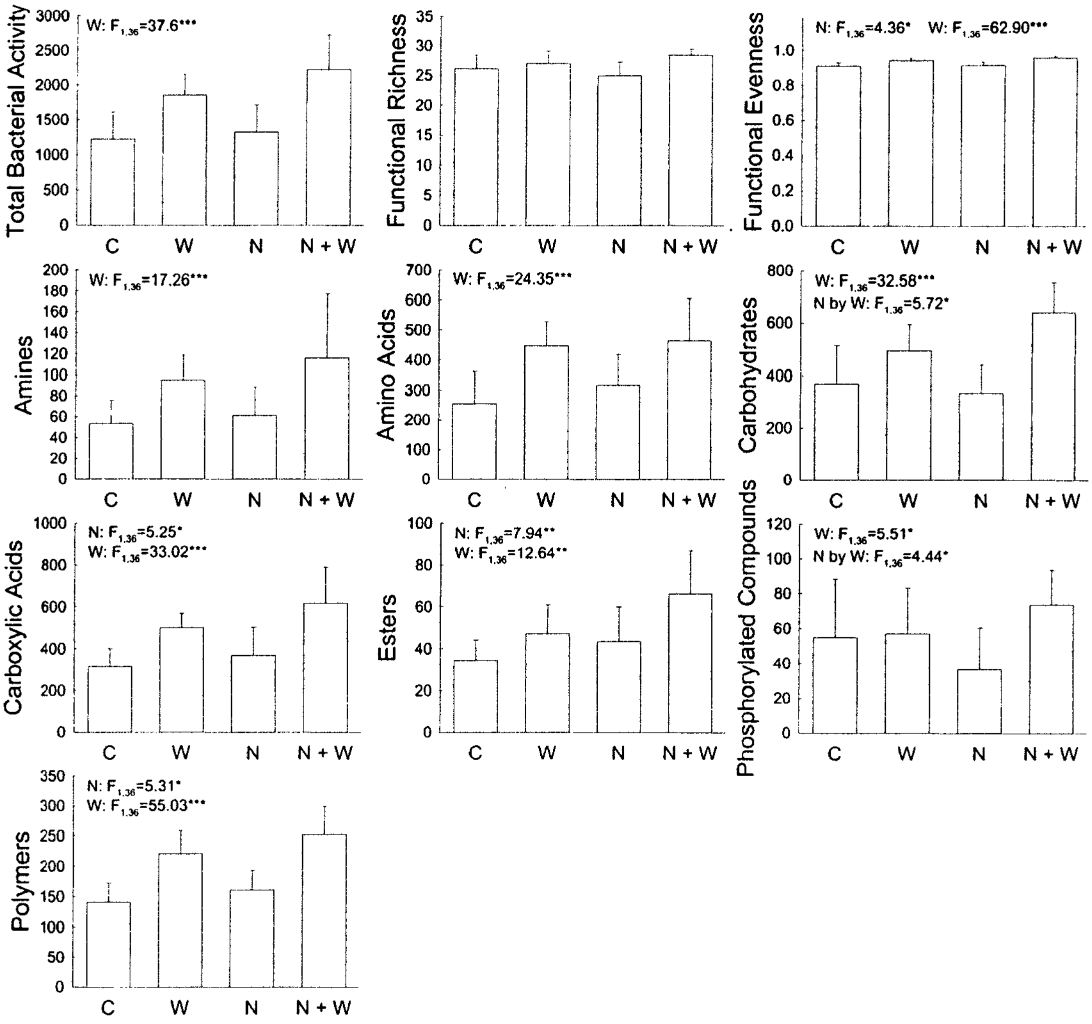

Figure 2-1 Bacterial richness, evenness, total activity, and the activity of seven categories of carbon substrate in the four treatments. Bacterial activity is measured as the area under the color development curve (light absorption versus incubation time). Error bars are one standard deviation. Significant terms from mixed models comparing between treatments are indicated on each panel (* $p<0.05$; **$p<0.01$; ***$p<0.001$).

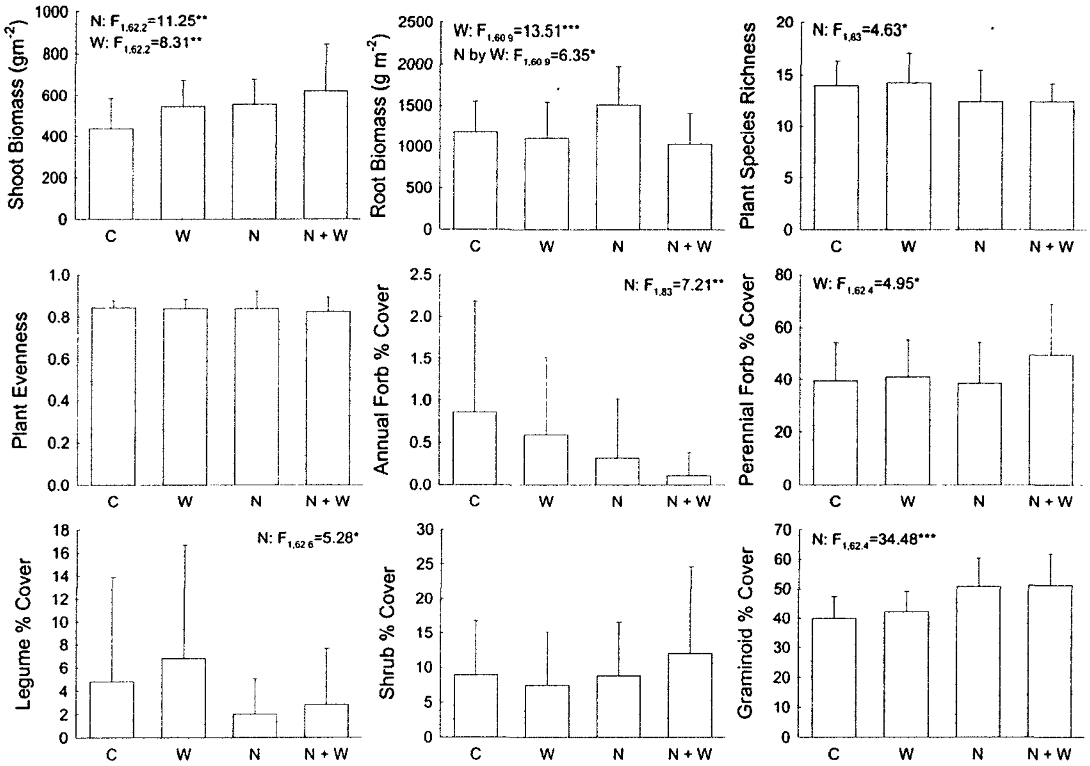

Figure 2-2 Plant species richness, evenness, shoot and root biomass, and the cover of five functional groups in the four treatments. Error bars are one standard deviation. Significant terms from mixed models comparing between treatments are indicated on each panel (* $p<0.05$; ** $p<0.01$; *** $p<0.001$).

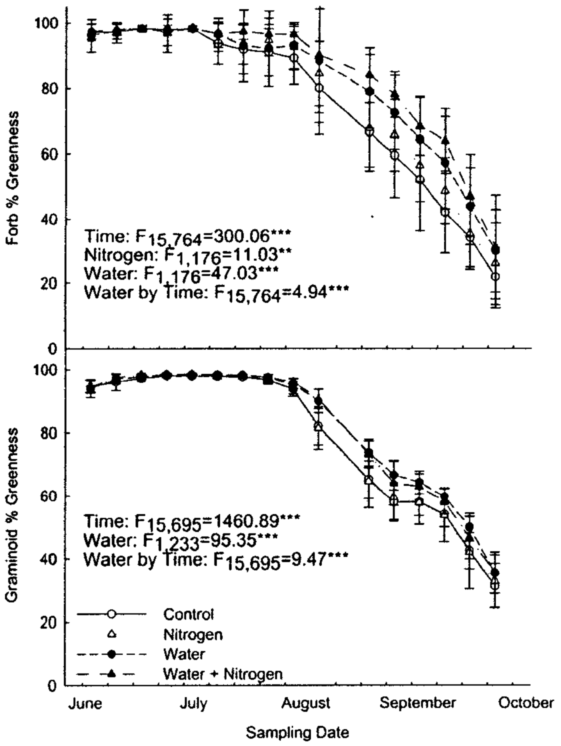

Figure 2-3 Percent greenness through the growing season of fourteen common forb and graminoid species in the four resource addition treatments. Error bars are one standard deviation. Significant terms from mixed models comparing greenness over time and between treatments are indicated on each panel (* $p<0.05$; ** $p<0.01$; *** $p<0.001$).

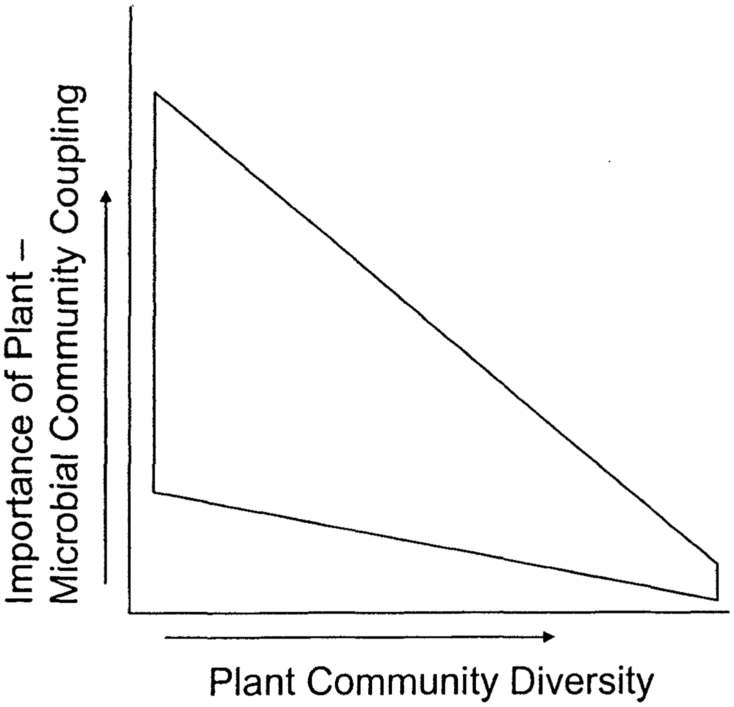

Figure 2-4 Conceptual model showing how the importance of plant – microbial community coupling (the degree to which the composition of one community influences the composition of the other) may relate to plant community diversity. Most communities should fall within the grey zone, with a wide range of possible outcomes at low diversity depending on the identity of the plant species. Only weak coupling is expected at high diversity because the influence of each plant species on the microbial community is diluted by the number and biomass of other species also present.

3. Water and nitrogen addition differentially impact plant competition in a native rough fescue grassland[1]

Introduction

The predicted patterns of root, shoot, and total competition intensity along gradients of resource availability and productivity (Grime 1973, 2001, Newman 1973, Tilman 1988) have prompted numerous experimental studies with conflicting results and no resolution (reviewed by Goldberg and Barton 1992, Keddy 2001, Craine 2005, Schenk 2006). Understanding why and if root and shoot competition intensity varies with productivity and resource availability remains key to linking the mechanisms of resource competition to the consequences of competition for community structure (Keddy 2001). It is generally agreed that the intensity of shoot competition increases with increasing productivity since shading is closely correlated with neighbour size (Tilman 1988, Grime 2001, Keddy 2001). In contrast, the relationships between root competition intensity and productivity vary widely between studies (e.g. Goldberg and Barton 1992, Belcher et al. 1995, Twolan-Strutt and Keddy 1996, Peltzer et al. 1998, Cahill 1999, Keddy 2001, Sammul et al. 2006). Additionally, root and shoot competition are interdependent with the relative strength of one competitive form dependent upon the level of the alternative form (Cahill 1999, 2002a).

Belowground, plants compete for multiple resources with differing physical properties (Casper and Jackson 1997). The addition of a limiting soil resource should reduce the intensity of root competition by reducing the degree of deficiency for the limiting resource relative to other resources (Taylor et al. 1990, Casper and Jackson 1997, Davis et al. 1998), but experimental studies have found that the outcome can depend on the resource involved. Root competition intensity typically declines as

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[1] A version of this chapter has been published.

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nitrogen levels increase (Wilson and Tilman 1991, 1993, 1995, Peltzer et al. 1998, Cahill 1999), though Cahill (2002a) observed no change in intensity and Brewer (2003) an increase following fertilization. Competition for phosphate may be similar to nitrogen since Santos et al. (2004) found that when root competition was severe phosphate addition reduced belowground competition intensity. In contrast to the studies of mineral nutrients, several studies have shown that water addition can increase productivity without significant effects on the strength of root competition (Burger and Louda 1995, Haugland and Froud-Williams 1999, Semere and Froud-Williams 2001, Weigelt et al. 2005). Minimal effects of both water and mineral resources on total competition intensity have been found (Wetzel and van der Valk 1998, Fynn et al. 2005), but no study has examined root competition for both water and mineral resources in a single experiment. Without such an experiment it is difficult to determine whether these differences in outcome result from differences in the mechanisms of competition for water and mineral resources or are due to factors such as the concentration of studies of competition for water in more arid systems.

Equally important to differences in mechanisms of competition for belowground resources may be interactions between resources such as the close links between soil moisture, the nitrogen cycle, and plant nitrogen uptake (Fitter and Hay 2002, Booth et al. 2005, James and Richards 2005). If for example, available nitrogen or nitrogen-use efficiency increase with water addition, then water addition could cause increased nitrogen supply and reduced competition. Such interactions may be important in natural systems where productivity gradients often follow multiple covarying resource gradients (Keddy 2001). Interactions between resources have been largely ignored in studies of competition except in arid and semi-arid systems where the frequency and intensity of pulses of the nitrogen and water that follow rainfall are important (Goldberg and Novoplansky 1997, Novoplansky and Goldberg 2001).

In this study we used a field experiment in native rough fescue grassland to examine the intensity of root and shoot competition along productivity gradients created by water and nitrogen addition. The rough fescue grasslands in the aspen parkland region of western Canada represent a unique opportunity to study the interactions of water and nitrogen as both resources can be limiting to plant growth in this community (Chapter 2). This is the first study to compare the effects of both nitrogen and water addition on the intensity of competition and the relationships between competition and productivity. Specific questions examined in this study include: 1) whether water and nitrogen addition have similar effects on the intensity of root and shoot competition, 2) if the relationships between competition and productivity are a function of the resource used to create the productivity gradient, and 3) whether interactions between nitrogen and water have important consequences for the outcome of competition.

Methodology

Experimental Design

This experiment was conducted in native rough fescue grassland on the University of Alberta Research Ranch near Kinsella, Alberta, Canada (53°05 N, 111°33 W). The study site is a savanna-type habitat in the aspen parkland ecoregion (Sims and Risser 2000), containing a mixture of aspen (*Populus tremuloides* Michx.) stands and rough fescue (*Festuca hallii* (Vasey) Piper) prairie. The soils are thin, moderately well drained, black grassland soils over glacial till (Howitt 1988). Root competition in this community is strong (Cahill 2003a, 2003b), and both nitrogen and water availability can limit plant growth (Chapter 2).

One hundred and twenty 1m by 1m plots were established in a 20m by 24m grid on a south-facing slope in the spring of 2003. The two nitrogen treatments (control and 5.44 g m^{-2} $year^{-1}$ ammonium-nitrate applied in two 2.72g m^{-2} doses in mid May and late June) and water (control and 7.5 l $week^{-1}$) were applied to the plots in a factorial design. There were 30 replicates of each nitrogen by water treatment combination. Each of these replicates contained four subplots with the following competition treatments: all neighbours (AN), shoot neighbours (SN), root neighbours (RN), no neighbours (NN). Root exclusion tubes (10.2 cm diameter and 10 cm deep) made of PVC pipe were used to separate focal plants from root neighbours in the SN and NN treatments. Plastic netting was used to hold neighbouring shoots back from focal plants in the RN and NN treatments. Root and rhizome connections in the treatments without root exclusion tubes were cut to ensure a similar soil environment to that in the root exclusion tubes. The existing plants within each tube/trenched area were sprayed with herbicide (Roundup$^{©}$). The nitrogen treatment was applied in both 2003 and 2004 while the watering treatment was begun in 2004. Cattle grazed the site in September 2003, but were not present during the experiment.

The experiment was begun in 2004, providing a year delay between the setup and the beginning of the experiment to allow the neighbouring plants to re-establish around the root exclusion tubes. In May 2004 the germination of *Artemisia frigida* Willd. (a perennial forb) and *Chenopodium leptophyllum* (Nutt ex Moq.) S. Wats (an annual forb) from the soil seedbank was encouraged by watering all plots weekly for three weeks. If more than one seedling was in a plot, one was randomly selected for study and the rest removed. Once the initial watering ceased, plots in the watered treatments continued to receive water at a rate of 7.5l per week, or the equivalent of an extra 7.5mm wk^{-1}of rain for a total of 97.5mm, a 60% increase over natural rainfall (160.5 mm) measured at the Viking, Alberta station (53°16 N, 111°46 W) during the same period (Environment Canada National Climate Archive; http://climate.weatheroffice.ec.gc.ca).

Focal plants were harvested in the third week of August 2004, after 14 weeks of growth. At harvest many of the *Chenopodium* had finished flowering, but none of the *Artemisia* had flowered. Shoot biomass was harvested, dried, and weighed. Root biomass was not harvested due to the difficulty in accurately extracting the root systems of the focal plants from the AN and RN treatments, as the roots in those treatments would be intertwined with those of the neighbouring plants (Cahill 2002b).

Soil moisture content, photosynthetically active radiation (PAR) transmission through the vegetation, and root and shoot neighbour biomass were measured in each plot immediately following the harvest of the focal plants. PAR was measured above and below the canopy using a handheld light meter (AccuPAR model PAR-80; Decagon Devices, WA). Shoot biomass was measured by clipping the live vegetation from a 20cm by 50cm quadrat. Root biomass was measured by washing the roots from 5.3cm diameter root cores taken to a depth of 12cm. Gravimetric soil moisture content was measured by collecting and weighing the wet and dry masses of a small soil sample (~35g) sieved from the root biomass core. Soil moisture was measured five days after a water application. As the intervening weather had been hot and dry, the differences in moisture content between treatments likely represent minimum differences.

Statistical Analysis

The effects of the nitrogen and water treatments on environmental conditions and the neighbouring plant community were analyzed using general linear models with the nitrogen and water treatments as fixed factors. The response variables were arcsine-transformed % soil moisture, arcsine-transformed % light transmission, and ln-transformed root and shoot biomass. The effects of the nitrogen and water treatments on relative allocation to root and shoot biomass were analyzed using a general linear model with aboveground biomass as the response variable, root biomass as a covariate, and nitrogen and water treatments as fixed factors. All interactions including the covariate were included in an initial model but non-significant interactions were removed (Engqvist 2005) leaving a significant root biomass – water interaction in the final model. Since the root biomass – water interaction indicated that the effects of water on shoot biomass were dependent on root biomass levels, these data were divided into four groups (root biomass <500, 500-800, 800-1100, and >1100 gm^{-2}) and the effect size (least-squares means) of the water treatment was estimated for each group. All analyses were conducted using proc GLM in SAS 8.02.

Focal plant survival rates were analyzed using a log-linear model (G-test) with species, nitrogen addition, water addition, root, and shoot competition as fixed factors. A log-linear model is a generalized linear model with the number of surviving plants per treatment combination as the response variable and a poisson error distribution (SAS Institute 2004). The initial number of plants (between 8 and 20 depending on the treatment) was used as an offset variable to standardize for the different numbers of starting plants between treatment combinations. A saturated model including all possible main effects and interactions was fit to these data using proc GENMOD in SAS 8.02.

Focal plant biomass was analysed using a mixed model with species, nitrogen addition, water addition, root competition, and shoot competition as fixed factors and plot as a random factor. Models were fit using proc MIXED in SAS 8.02. Satterthwaite approximate degrees of freedom were used since these data were unbalanced. Changes in the intensity of root and shoot competition caused by the resource addition treatments are indicated by significant competition – resource interactions.

Competition intensity, or the relative difference in performance between plants with and without neighbours, was directly examined using log response ratios (lnRR) (Hedges et al. 1999). The lnRR was chosen because, among the competition indices in common use, it has statistical properties that are best suited for linear analysis (Hedges et al. 1999, Weigelt and Jolliffe 2003). These indices were calculated for shoot (ln[SN/NN]), root (ln[RN/NN]), and total (ln[AN/NN]) competition following Cahill (1999). Positive values of the lnRR indicate facilitation while increasingly negative values indicate increasing intensity of competition. These indices are intended for pairs of focal plants, but in this study the biomass of each focal plant from an SN, RN, or AN treatment was divided by the mean biomass of NN plants from the same species by water by nitrogen treatment combination. This procedure was used because the use of focal plants germinated from the seedbank and mortality during the experiment left very few plots with plants of the same species in competition treatments appropriate for pairing. Indices of competition are problematic because they require the assumption that competitive ability does not vary with plant size, however without pairing plants this assumption could not be tested nor could statistically more rigorous alternatives such as ANCOVA be used (Lamb et al. 2006). Since we were interested in the relationships between competition, productivity, and the resource addition treatments, we standardized the response ratios to eliminate differences in competitive ability between the species using z-scores. The z-scores were analysed using general linear models with nitrogen and water addition as fixed factors and neighbouring plant biomass as a covariate using PROC GLM in SAS 8.02. Separate analyses were run for each combination of competition intensity (root, shoot, and total) and productivity (root, shoot, and total).

In each GLM all possible interactions including the covariates were included in the initial models but non-significant interactions were removed from the final models (Engqvist 2005).

Results

Soil moisture content was higher with water addition ($F_{1,109}$=12.18, p<0.001), but was not affected by nitrogen addition ($F_{1,109}$=0.37, p=0.546) (Figure 3-1a). Light transmission through the plant canopy was reduced by both nitrogen ($F_{1,115}$=49.34, p<0.001) and water addition ($F_{1,115}$=12.42, p=0.001) (Figure 3-1b). Shoot biomass increased with both nitrogen ($F_{1,115}$=26.03, p<0.001) and water addition ($F_{1,115}$=6.09, p=0.015) (Figure 3-1c). In contrast, root biomass increased with water addition ($F_{1,104}$=6.40, p=0.013) but not nitrogen addition ($F_{1,104}$=0.17, p=0.677) (Figure 3-1d). Nitrogen addition increased relative allocation to shoot biomass, however water addition increased relative allocation to shoot biomass only when root biomass was <500 gm^{-2} (p=0.09) and 500 to 800 gm^{-2} (p=0.02), but not when root biomass was 800 to 1100 gm^{-2} (p=0.85), or >1100 gm^{-2} (p=0.44) (Table 3-1, Figure 3-2). There were no significant water by nitrogen interactions, indicating that nitrogen and water did not interact to affect productivity in this community.

Artemisia seedling survival (90%) was higher than *Chenopodium* (71%) (χ^2_1=6.98, p=0.008), and nitrogen increased *Chenopodium* survival (79% vs. 57%; χ^2_1=5.96, p=0.015; nitrogen by species interaction χ^2_1=10.43, p=0.001). No other main effects or interactions were significant (p>>0.1), indicating that neither water nor competition altered survival.

Nitrogen increased focal plant biomass, with *Chenopodium* experiencing larger benefits than *Artemisia* (Table 3-2, Figure 3-3). Both species were larger when released from root but not shoot competition. Root competition intensity increased with nitrogen addition (significant root competition by nitrogen interaction). *Chenopodium* was a poorer belowground competitor than *Artemisia* (significant species by root competition interaction). The only significant effect of water addition was a four way species by nitrogen by water by shoot competition interaction (p=0.049). This complex interaction appears to indicate that when shoot competition was removed *Artemisia* increased slightly in biomass under all combinations of the nitrogen and water treatments, while *Chenopodium* only increased in biomass when one of the resources was added but not when neither or both were added. There were no root by shoot competition interactions indicating that the two modes of competition were independent.

Both root and total competition intensity increased with nitrogen addition, but the only significant effect involving water addition was a decline in total competition intensity with shoot biomass as a covariate (Table 3-3, Figure 3-4). There were no significant competition – productivity relationships or nitrogen by water interactions for any measure of competition intensity (Table 3-3; Figure 3-5).

Discussion

Both nitrogen and water were limiting to shoot biomass, though only water addition increased root biomass. Allocation to shoot biomass increased with nitrogen addition, consistent with observations that plants allocate relatively less biomass to roots following fertilization (Reynolds and D'Antonio 1996, Poorter and Nagel 2000). Such a change in allocation could also result from resource-driven changes in community composition but this is unlikely given the short duration of this experiment and that most species are long-lived perennials. Water addition increased relative allocation to shoot biomass at low levels of standing root biomass, but did not affect allocation at high root biomass. Most studies have found that, similar to nitrogen, water addition leads to decreased allocation to roots (Poorter and Nagel 2000), though increased root allocation has been observed in sandy soils with minimal water holding capacity (e.g. Pregitzer et al. 1993, Weigelt et al. 2000, 2005). The switch in biomass allocation with water addition could be explained if the plots with high root biomass were on poorer soils with lower water holding capacity than plots with lower root biomass.

The lack of water effects on survival is surprising since many studies have found that both water and nitrogen addition can increase seedling survival (e.g. Bertiller et al. 1996, Davis et al. 1998, 1999, Liancourt et al. 2005). Mortality from water stress is most prevalent among very young seedlings (Bertiller et al. 1996), suggesting that the three weeks of watering used to induce germination may have supported seedlings past the stage where they were most vulnerable to water stress.

The lack of significant competition or competition-resource interaction effects on survival suggests that competition-induced mortality is likely only important in this system when resources are extremely limited (Cahill 2003a, 2003b).

There were no significant competition – productivity relationships in this study, even though both water and nitrogen directly affected both productivity and competition intensity. The minor role of shoot competition in this system likely explains the lack of shoot competition – productivity relationships, but the reasons for the lack of strong root competition – productivity relationships are less clear. The simple patterns of change in the intensity of root and total competition along resource and productivity gradients predicted by many theories (Newman 1973, Grime 1973, 2001, Tilman 1988) are inadequate to explain these data. These results also differ from recent studies that found patterns of competition intensity and productivity at variance with the prevailing theories (Twolan-Strutt and Keddy 1996, Peltzer et al. 1998, Cahill 1999, Fynn et al. 2005, Sammul et al. 2006). The patterns observed in this study could arise if the competition – productivity relationship is nonlinear (Belcher et al. 1995, Arii and Turkington 2001), however given the wide range of patterns found in previous studies, broadly applicable root competition – productivity relationships may not occur. In particular, clear relationships may not occur in communities with very high levels of root biomass, such as the present study. Cahill and Casper (2000) found that root competition intensity saturated at root biomass levels of approximately 300g m^{-2} in a productive old field, well below the 400 – 1400g m^{-2} observed in this study. Saturation of root competition at similar levels in rough fescue grassland could explain why resource addition-induced changes in root biomass have minimal effects on root competition intensity, but leaves open the question of why plants still alter root biomass allocation in response to resource addition. The relationship between competition intensity and fine root biomass may be obscured since 25% or more of the belowground biomass in grasslands can be in organs such as thick roots and rhizomes dedicated to functions other than resource capture (Pucheta et al. 2004), or because it is necessary for plants to overproduce roots to prevent neighbours from gaining advantage in a "Tragedy of the Commons" (Gersani et al. 2001).

Shoot competition was much weaker than root competition, indicating that shoot competition is unlikely to be an important process structuring this plant community. The intensity of shoot competition generally increases with increasing productivity since the degree of shading a plant experiences is closely correlated with the relative size of its neighbours (Tilman 1988, Grime 2001, Keddy 2001). Similar studies in low-statured plant communities have found aboveground competition to be unimportant at shoot biomass levels much in excess of those in this study (e.g. Belcher et al. 1995, Peltzer et al. 1998). Peltzer et al. (1998) suggested that the light penetration to the soil surface in these systems may be sufficient, even at the highest standing biomass levels, to preclude significant shoot competition. In this experiment transmission of photosynthetically active radiation (PAR) was 42% ±2.25 SD in plots receiving both nitrogen and water. At full sunlight (1200-1800 μmol $m^{-1}s^{-1}$) leaves at the bottom of the canopy in these plots would receive 500-750 μmol $m^{-1}s^{-1}$, well above the photosynthetic compensation point for most plants (Fitter and Hay 2002). The lack of shoot competition and root - shoot competition interactions also supports the prediction that such interactions should not be expected without significant shoot competition (Cahill 1999)

The increase in root competition intensity with nitrogen addition is in direct contradiction to a large body of experimental evidence (Wilson and Tilman 1991, 1993, 1995, Casper and Jackson 1997, Peltzer et al. 1998, Cahill 1999; Schenk 2006). While we do not doubt that in general root competition intensity declines following fertilization, a great deal of variation is masked within the general pattern. For example, figure 4 in Wilson and Tilman (1995) shows that of eight species studied, two experienced an increase in root competition intensity with fertilization. In addition, other studies have observed either no change (Cahill 2002a) or an increase in root competition intensity following fertilization (Brewer 2003). This variation could be explained if, similar to the nonlinear relationships proposed between competition intensity and productivity (Belcher et al. 1995, Arii and Turkington 2001), the relationship between root competition intensity and resource availability is non-linear. This variation could also be explained through an interaction between root competition and the timing of nitrogen availability. Experimental nitrogen applications can produce pulses of available nitrogen that last for only a few days (e.g. Jackson et al 1989; Dell and Rice 2005). Given that root competition is size-symmetric (Casper and Jackson 1997; Cahill and Casper 2000; Schenk 2006), nitrogen capture from an ephemeral pulse should be proportional to a plants root system size. Since plant size is likely a function of the degree of root competition it previously experienced (Cahill and Casper 2000), a plant with low root competition should benefit proportionally more from a nitrogen addition than a plant experiencing severe competition. This combination could cause an increase in competition intensity following nitrogen addition by increasing the size differences between plants with and without competition.

Several studies have shown that water addition can increase productivity without significant effects on the strength of root competition (Burger and Louda 1995, Haugland and Froud-Williams 1999, Semere and Froud-Williams 2001, Weigelt et al. 2005). As with nitrogen there are exceptions, for example the significant declines in intensity with watering in two of nine species combinations found by Weigelt et al. (2005), but the general pattern of invariant root competition intensity along moisture gradients is well supported. In contrast to the clear patterns of root competition, total competition intensity can be highly variable along moisture gradients. This study found a decline in total competition intensity with increasing moisture while other studies have found either increases (e.g. Kadmon 1995, Briones et al. 1998, Corcket et al. 2003) or few effects (e.g. Wetzel and van der Valk 1998, Haugland and Froud-Williams 1999, Novoplansky and Goldberg 2001, Fynn et al. 2005, Liancourt et al. 2005, Weigelt et al 2005). If root competition is invariant, changes in total competition intensity should be correlated with changes in shoot competition intensity, however, the only study to isolate both root and shoot competition along a moisture gradient in the presence of strong shoot competition found no changes in either root or total competition even though shoot competition intensity increased with increasing moisture (Haugland and Froud-Williams 1999). Without more studies in water-limited systems with significant shoot competition, generalizations on shoot and total competition patterns along moisture gradients are difficult to make.

The very different effects of water and nitrogen on root competition intensity suggest that the mechanisms of competition differ between the two resources. The lack of water effects on root competition intensity is contrary to the theory that the addition of a limiting resource will reduce the intensity of competition for that resource by reducing the degree of deficiency (Taylor et al. 1990, Casper and Jackson 1997, Davis et al. 1998). Competition for water remains poorly understood (Casper and Jackson 1997, Schwinning and Weiner 1998), but given that the transpirational demands of competing plants can reduce water availability (e.g. Burger and Louda 1995, Davis et al. 1999) why should plants not compete more strongly when water is limiting? A potential explanation may lie in the different mechanisms of uptake between water and mineral resources. Plants can expend energy to enhance mineral resource uptake through a variety of mechanisms including interception by root growth, increasing bulk flows of water by increasing transpiration, producing more ion uptake enzymes, and by encouraging mycorrhizal associations (Casper and Jackson 1997, Fitter and Hay 2002). In contrast, plants can enhance water uptake only through root growth and by lowering leaf water potential to increase transpiration rates (Fitter and Hay 2002). Constraints on the ability of plants to actively compete for water could explain why competition intensity does not increase as moisture levels fall.

Finally, even though nitrogen and water had independent significant effects on neighbour plant biomass and the intensity of competition, there were few interactions between the two resources. The only significant interaction involving water and nitrogen was a four-way species by nitrogen by water by shoot interaction affecting focal plant biomass. This complex interaction appears to indicate that the two species differed in their responses to shoot competition depending on the resource treatment combination such that removing shoot competition increased *Artemisia* performance under all combinations of nitrogen and water treatment, while *Chenopodium* only increased when one of the resources was added but not when neither or both were added. The lack of interactions affecting root competition is surprising given the close links between soil moisture, nitrogen cycling, and plant uptake rates (Fitter and Hay 2002, Booth et al. 2005, James and Richards 2005). The lack of interactions suggests that factors other than soil moisture regulate the availability of nitrogen in this system, and that increased soil moisture promoted growth through mechanisms independent of nitrogen. A wide range of mechanisms could be responsible since water stress can impact plants independently of nutrient availability through mechanisms ranging from reduced CO_2 capture to disruptions in xylem and phloem transport and reduced protein synthesis (Fitter and Hay 2002). While this study suggests that water – nitrogen interactions may only be important in systems with close links between nitrogen availability and water, interactions between other belowground resources remain to be evaluated.

Conclusion

This study demonstrates that nitrogen and water addition can have very different effects on root competition intensity, even though both resources limit productivity. The increase in root competition intensity following nitrogen addition suggests that competition for mineral resources is more complex than currently thought and that monotonic declines in competition intensity with increasing resources predicted by theory should not always be expected. The lack of change in root competition intensity following water addition suggests that the mechanisms of competition for water and mineral resources are very different, and that plants may not compete strongly for water even when it is limiting. The lack of significant relationships between competition and productivity in this study likely occurred because shoot biomass levels were too low to cause significant shoot competition and root biomass levels were far above the level at which root competition saturates. Finally, the lack of nitrogen – water interactions suggests that in rough fescue grassland the availability of the two resources are not closely linked.

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Table 3-1 Results from the general linear model testing the effects of nitrogen and water addition on shoot biomass with root biomass as a covariate. The initial model included all covariate-fixed factor interactions, but non-significant interactions were removed from the final model.

Source	**DF**	**MS**	**F**	**P**
Root Biomass	1	0.002	0.03	0.873
Nitrogen	1	1.915	23.21	**<0.001**
Water	1	0.533	6.47	**0.012**
Nitrogen by Water	1	0.002	0.03	0.863
Root Biomass by Water	1	0.485	5.87	**0.017**

Table 3-2 Results from the mixed model testing the effects of species, nitrogen and water addition, and root and shoot competition on focal plant biomass.

Effect	**DF_{num}**	**DF_{den}**	**F Value**	**P**
Species	1	289	5.70	**0.018**
Nitrogen	1	131	15.12	**<0.001**
Water	1	131	0.02	0.885
Shoot Competition	1	250	3.22	0.074
Root Competition	1	261	32.08	**<0.001**
Nitrogen x Water	1	131	0.55	0.459
Nitrogen x Shoot	1	250	1.91	0.168
Water x Shoot	1	250	0.76	0.385
Nitrogen x Root	1	261	12.28	**<0.001**
Water x Root	1	261	0.04	0.844
Species x Water	1	289	0.02	0.891
Species x Nitrogen	1	289	4.13	**0.043**
Species x Shoot	1	284	0.10	0.750
Species x Root	1	291	3.93	**0.048**
Nitrogen x Water x Shoot	1	250	1.71	0.192
Nitrogen x Water x Root	1	261	0.64	0.426
Shoot x Root	1	245	2.34	0.127
Water x Shoot x Root	1	245	0.48	0.487
Nitrogen x Shoot x Root	1	245	1.43	0.233
Species x Nitrogen x Water	1	289	0.04	0.840
Species x Water x Shoot	1	284	1.50	0.221
Species x Nitrogen x Shoot	1	284	0.50	0.479
Species x Water x Root	1	291	0.06	0.804
Species x Nitrogen x Root	1	291	3.25	0.072
Species x Shoot x Root	1	280	0.17	0.679
Nitrogen x Water x Shoot x Root	1	245	0.80	0.370
Species x Nitrogen x Water x Shoot	1	284	3.90	**0.049**
Species x Nitrogen x Water x Root	1	291	0.01	0.934
Species x Nitrogen x Shoot x Root	1	280	0.84	0.359
Species x Water x Shoot x Root	1	280	1.67	0.197
Species x Nitrogen x Water x Shoot x Root	1	280	2.60	0.108

Table 3-3. Summary of the competition – productivity relationships in this study. F-values are reported for each term in general linear models with z-scores of shoot (SCI), root (RCI), and total (TCI) competition intensity as the response variables, nitrogen and water treatment as fixed factors, and productivity (shoot, root, and total biomass) as covariates. A significant covariate would indicate a significant competition – productivity relationship. The initial models included all covariate-fixed factor interactions, but since these interactions were non-significant they were removed from the final models.

Productivity Measure	**Model Terms**	**SCI**	**RCI**	**TCI**
Shoot Biomass	Water	$F_{1,71}=0.36$	$F_{1,73}=0.28$	**$F_{1,80}=5.71*$**
	Nitrogen	$F_{1,71}=2.10$	**$F_{1,73}=6.86*$**	**$F_{1,80}=5.91*$**
	Water by Nitrogen	$F_{1,71}=1.40$	$F_{1,73}=1.48$	$F_{1,80}=0.03$
	Shoot Biomass	$F_{1,71}=0.02$	$F_{1,73}=0.00$	$F_{1,80}=1.50$
Root Biomass	Water	$F_{1,63}=0.18$	$F_{1,64}=0.06$	$F_{1,72}=3.09$
	Nitrogen	$F_{1,63}=2.35$	**$F_{1,64}=7.20**$**	**$F_{1,72}=8.08**$**
	Water by Nitrogen	$F_{1,63}=1.93$	$F_{1,64}=0.63$	$F_{1,72}=0.00$
	Root Biomass	$F_{1,63}=0.02$	$F_{1,64}=0.29$	$F_{1,72}=0.11$
Total Biomass	Water	$F_{1,63}=0.13$	$F_{1,66}=0.01$	$F_{1,72}=3.24$
	Nitrogen	$F_{1,63}=2.41$	**$F_{1,66}=8.52**$**	**$F_{1,72}=7.91**$**
	Water by Nitrogen	$F_{1,63}=1.98$	$F_{1,66}=0.66$	$F_{1,72}=0.00$
	Total Biomass	$F_{1,63}=0.08$	$F_{1,66}=1.60$	$F_{1,72}=0.25$

* $p<0.05$, **$p<0.01$

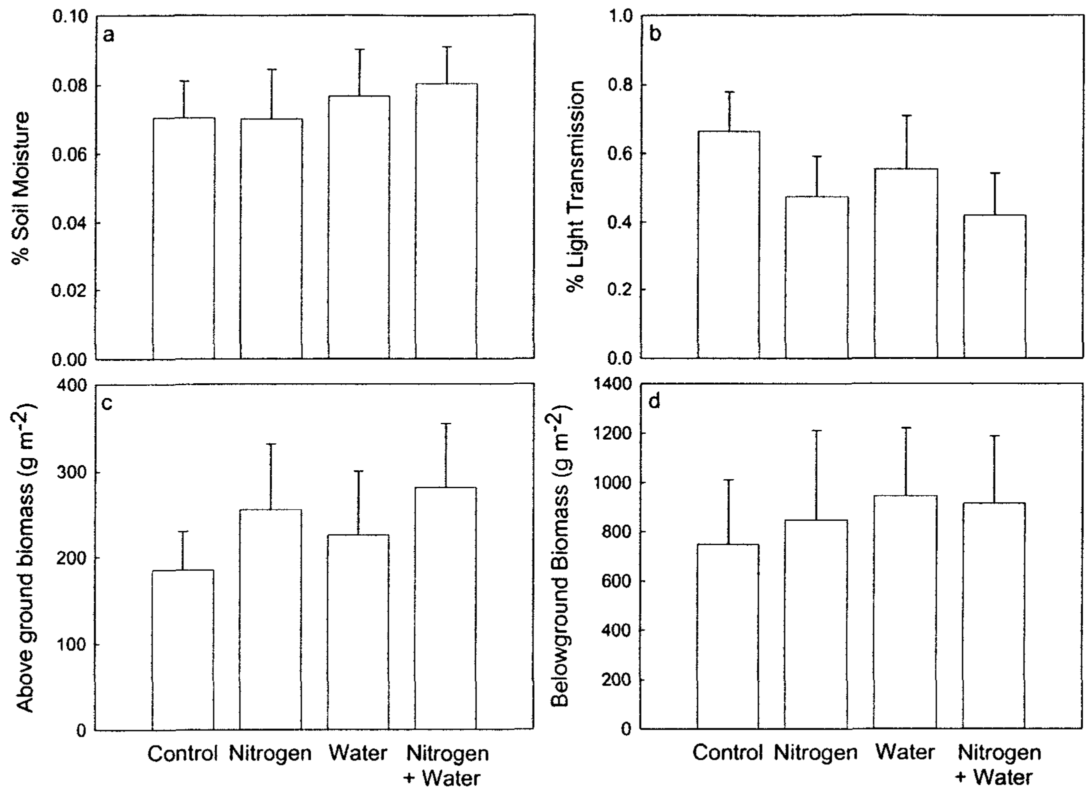

Figure 3-1 Percent soil moisture (A), light transmission through the canopy (B), shoot (C), and root (D) standing biomass (g m-2) in the four resource addition treatments. Error bars are one standard deviation.

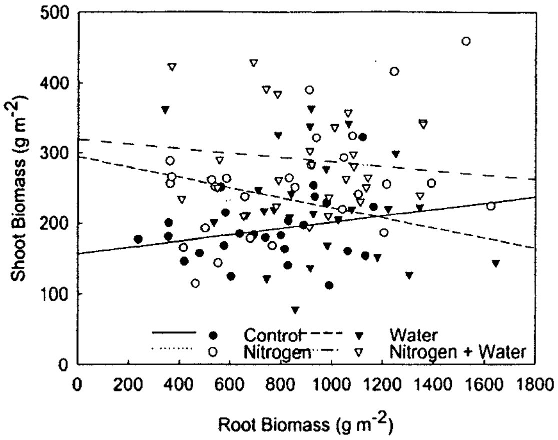

Figure 3-2 Relationships between root and shoot biomass allocation in the four resource addition treatments.

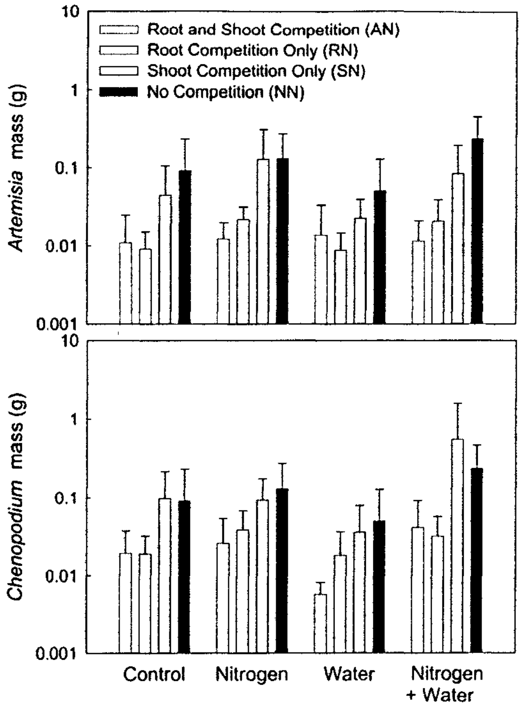

Figure 3-3 Focal plant aboveground biomass (g) in all combinations of resource and competition treatments. Error bars are one standard deviation. Note the logarithmic scale on the y-axis.

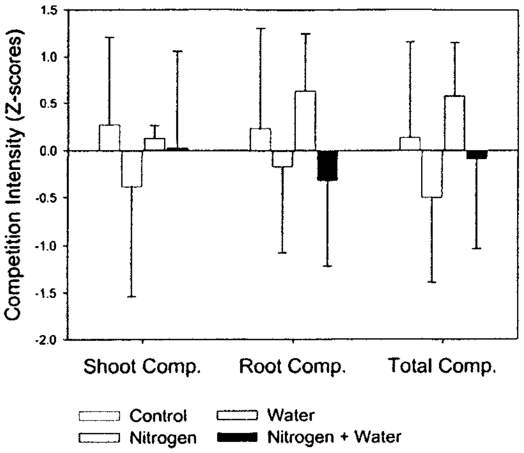

Figure 3-4 Competition intensity measured as z-scores of log-response ratios in the four resource addition treatments. More negative values of the z-scores indicate increasing intensity of competition. Error bars are one standard deviation.

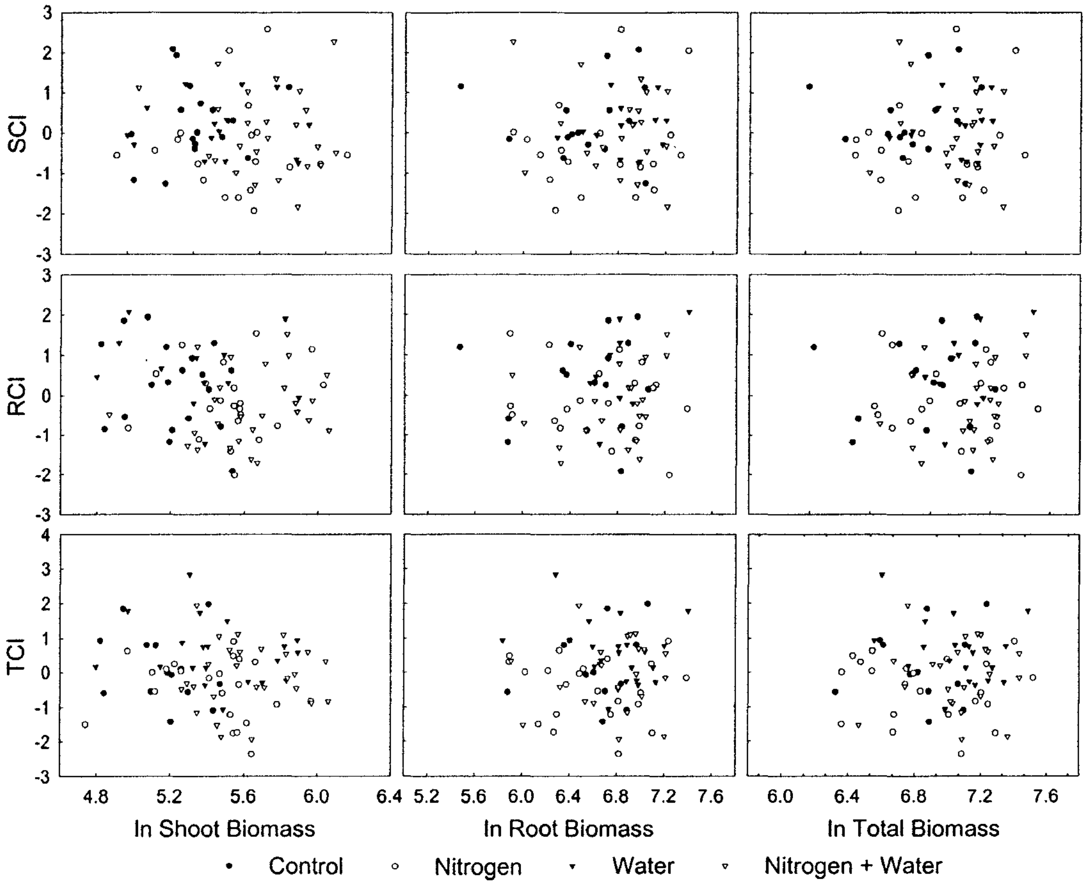

Figure 3-5 Competition – productivity relationships for total (TCI), root (RCI), and shoot (SCI) competition intensity measured as z-scores of log-response ratios and root, shoot, and total neighbour biomass. More negative values of the z-scores indicate increasing intensity of competition

4. Direct and indirect control of species richness and evenness by litter, resources, and biomass in a native grassland[1] [2]

Introduction

Understanding the mechanisms that control plant diversity is a central goal of community ecology. Numerous studies have identified important influences on diversity ranging from soil and environmental conditions to disturbance regimes, herbivory, productivity, and standing biomass (e.g. Al-Mufti et al. 1977; Facelli and Pickett 1991; Foster and Gross 1998; Grace 1999; Xiong and Nilsson 1999; Gross et al. 2000; Grime 2001; Keddy 2001; Mittelbach et al. 2001; Rajaniemi 2003; Aarssen 2004; Crawley et al. 2005; Balvanera et al. 2006; Gillman and Wright 2006; Adler and Levine 2007). While much is known about the net effects that individual factors have on diversity, it is becoming clear that in most plant communities diversity is actually controlled by multiple factors linked through complex networks of interactions (Grace 1999). Thus the problem of explaining diversity is not one of identifying which of several competing explanations is most important in a particular community, but rather determining how each mechanism affects diversity both directly and indirectly. This problem is challenging because the interactions among mechanisms mean that most of the important variables measured in a field study will be intercorrelated. Some factors may be a part of causal relationships influencing diversity, while others can be without any importance beyond a correlation with a third factor that does have a causal influence on diversity (Grace 1999; 2006). There can even be hidden interactions where a factor with no net impact on diversity can be involved in multiple mechanisms with opposite effects on diversity (e.g. Grace and Jutila 1999).

A number of recent studies have taken a holistic approach to examine the controls on plant diversity in a range of communities including coastal wetlands,

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[1] A version of this chapter has been published:

Lamb, E.G. *In Press*. Direct and indirect control of species richness and evenness by litter, resources, and biomass in a native grassland. *Ecology*.

[2] The raw data used in this study are available in Appendix F.

grasslands, and shrublands (Grace and Pugesek 1997; Gough and Grace 1999; Grace and Guntenspergen 1999; Grace and Jutila 1999; Grace et al. 2000; Weiher et al. 2004; Mancera et al. 2005; Grace and Keeley 2006). These studies used Structural Equation Modeling (SEM) to explicitly evaluate the causal relationships among multiple interacting variables that together affect diversity (Shipley 2000; Grace 2006). A number of important generalities emerge from these studies. 1) Species richness was directly affected by either aboveground standing biomass or a variable highly correlated with biomass such as light interception by vegetation. Similar to the well known hump-shaped species richness – biomass relationship (e.g. Al-Mufti et al. 1977; Gross et al. 2000; Grime 2001; Keddy 2001; Mittelbach et al. 2001; Rajaniemi 2003; Gillman and Wright 2006), in the SEM studies species richness was often found to peak at intermediate levels of shoot biomass. 2) Environmental conditions indirectly influence diversity through the effects of those conditions on standing biomass and directly through "species pool" effects (Gough at al. 1994; Grace and Pugesek 1997). Species pools become an important control of diversity along environmental gradients such as salinity where fewer species have evolved the traits necessary to establish on certain parts of the gradient. 3) Recent disturbances (e.g. herbivory, wave damage, fire) have few direct effects on species richness; rather disturbance influences diversity indirectly through the effects of disturbance on variables such as aboveground biomass.

The studies cited above provide a very firm foundation for understanding the mechanisms controlling plant diversity, but several key questions remain unanswered. Aboveground standing biomass is clearly an important influence on diversity, but in the SEM studies the effects of live shoot biomass were not separated from those of litter. This may be an important distinction because, in addition to shading, litter accumulation can have strong negative effects on diversity through mechanisms such as alteration of germination cues, direct physical interference, sheltering invertebrate seed predators, and encouraging pathogens (Carson and Peterson 1990; Facelli and Pickett 1991; Facelli 1994; Foster and Gross 1998; Xiong and Nilsson 1999). In addition, it is important to separate the direct effects of live biomass and litter from indirect effects due to shading. For example, Grace and

Pugesek (1997) and Grace et al. (2000) found that the majority of the effects of biomass on diversity could be explained indirectly through the effects of biomass on light, providing strong evidence that competition for light was an important mechanism in those communities.

The roles of root biomass and root competition in driving diversity have not been addressed in a holistic framework. This gap is critical because in many plant communities, roots make up the majority of the plant biomass (Jackson et al. 1996; Mokany et al. 2006), the dominant form of competition is often belowground (Casper and Jackson 1997), and root competition intensity can be correlated with neighbour root biomass (Cahill and Casper 2000). A positive bivariate relationship between diversity and root biomass has often been found in studies where diversity was experimentally manipulated (Balvanera et al. 2006), but the shape of the relationship between diversity and root biomass can be similar to the aboveground biomass – diversity relationship found in the same system (Liira and Zobel 2000). Since root and shoot biomass are closely linked in most systems (Cairns et al. 1997; Mokany et al. 2006), it is difficult to separate a causal relationship between root biomass and diversity from a simple correlation between root and shoot biomass.

Finally, structural equation modeling studies of the controls on diversity have focused entirely on species richness. Evenness is an equally important component of diversity that can be affected by changes in environmental conditions independent of species richness (Wilsey et al. 2005). The observed relationships between productivity or biomass and evenness can be quite variable (e.g. Wilsey and Potvin 2000; Mulder et al. 2004; Wilsey and Polley 2004), suggesting that much remains to be learned about this component of diversity. Plant community evenness is linked to a wide range of ecological functions including competition, productivity, and species richness. For example, low evenness indicates the dominance of a small number of species and, in the absence of severe herbivory or abiotic stress, can imply intense interspecific competition (Cotgreave and Harvey 1994; Keddy 2001). Low evenness also can indicate that there are species with very small population sizes in the community that may be at risk of local extinction (Wilsey and Polley 2004).

In this study I examine how factors including soil resource availability, root biomass, shoot biomass, litter, and light availability control species richness and evenness in a grassland plant community. I quantify the effects of these factors and examine the networks of interaction among them using Structural Equation Modeling (SEM).

Methods

Field Site.

The study area is in a 50 ha field at the University of Alberta Research Ranch near Kinsella, Alberta, Canada (53°05 N, 111°33 W) in the Aspen Parkland Ecoregion (Sims and Risser 2000). The study site is a savanna-type habitat, containing a mixture of trembling aspen (*Populus tremuloides*) groves and rough fescue (*Festuca hallii*) prairie. Plant biomass at the field site can be limited by both nitrogen and water availability, and root competition is much more intense than shoot competition (Lamb et al. 2007). The study site included more productive *Poa pratensis* dominated grasslands in wetter microsites and less productive *Hesperostipa comata* dominated grasslands in drier locations. The study site has an average of 14.1 ±2.6 (std. dev) species per 0.25 m^{-2} plot and mean aboveground standing biomass of 259.5 ±78.0 g m^{-2} (Chapter 1). This site is very diverse relative to the range of species richness (8.7 - 13.2 species m^{-2}) across a long productivity gradient (45 - 600 g m^{-2} yr^{-1}) in North American grasslands (Gross et al. 2000). The study site historically has been lightly grazed by cattle in the fall, but grazing was halted two years prior to the beginning of this experiment. The majority of soils at the site are classified as thin Orthic Black Chernozems, or grassland soils with thin organic-matter enriched topsoil horizons, over glacial till (Howitt 1988; Soil Classification Working Group 1998).

Experimental Design.

I manipulated three essential resources (nitrogen, water, and light) in this study to establish strong gradients of community biomass and diversity. Natural diversity gradients occur at the site, but measuring the community biomass and diversity responses to resource manipulations provides much more specific information on the mechanisms controlling diversity than simply observing the unmanipulated relationships (Keddy 2001; Grace 2006). Twenty-two blocks distributed through both the *Poa pratensis* and *Hesperostipa comata* dominated grasslands, each containing six 1.5m by 1.5m plots separated by 1m wide buffers were established in May 2003. Control, nitrogen, water, nitrogen + water, shade, and nitrogen + shade treatments were randomly assigned to plots in each block. Logistical constraints limited the water and shade treatments to only two plots each per block, and so no plots including both shade and water treatments were applied. Nitrogen and water were manipulated because both resources can be limiting to plant growth in this system (Lamb et al. 2007), and they have contrasting effects on species richness in other systems (Stevens et al. 2006). Reducing light using shade cloth does not alter the red: far-red ratio, and thus is not entirely equivalent to shading by neighboring plants, but other researchers have successfully used it to simulate the effects of shading without also manipulating soil nutrients (Rajaniemi 2002). In low-statured plant communities where shading by plants is limited even at high productivity, shade treatments are a practical method to impose light limitation without also influencing root competition.

In the nitrogen treatments granular ammonium nitrate fertilizer was applied in May and late June from 2003 through 2005. Each fertilizer application delivered 2.72g m^{-2} nitrogen for a total nitrogen application of 5.44 g m^{-2} y^{-1}. Water was added weekly from mid May through late September at rates equivalent to a 50% addition to long-term average rainfall. Rainfall varies through the growing season, so plots received the equivalent of 5 mm of rain per week in May, 10.5 mm in June, 9.5 mm in July, 7.5 mm in August, and 4.5 mm in September for a total of 139 mm each growing season. This represented a 54% increase over natural rainfall (256 mm) during the same period in 2003, 48% (290 mm) in 2004, and 52% (265 mm) in 2005. Precipitation was measured at the Viking, Alberta weather station (53°16 N, 111°46 W) (Environment Canada 2006). Light levels were reduced using shadecloth stretched over 1.8m by 1.8m wooden frames ~30cm above the ground. The shadecloth reduced light reaching the top of the vegetation by 73% ±4% (std. dev.).

Relative soil moisture levels were significantly higher ($F_{1,105}$=37.68, p<0.001) in the watered plots, but the shade treatments had no effect on relative soil moisture ($F_{1,105}$=0.46, p=0.499).

Plant community composition (% cover of all vascular species) was visually estimated at the beginning of the experiment in May 2003 and in mid-July from 2003 to 2005 in permanently marked 0.5 by 0.5 m quadrats in each plot. Biomass was measured in mid-July in 2003 and 2005. Live shoot biomass (g m^{-2}) and litter biomass (g m^{-2}) were measured by removing all live and dead biomass from a 0.1 by 1 m quadrat in each plot. Live and dead materials were later sorted in the lab. Root biomass (g m^{-2}) was estimated by washing the roots from 5.3 cm diameter root cores taken to a depth of 12 cm in each plot. Light interception (percentage of ambient light intercepted by both vegetation and the shade cloth, if present) was measured using an Accu-Par light meter (Decagon, Pullman WA). Species richness was measured as the density of species in each permanent quadrat. Evenness was calculated from the cover data using the "odds measure of evenness" (Simpson's D`-1)/(Species richness -1) (Kvålseth 1991).

Statistical Analysis.

Examining the bivariate relationships between variables is an important precursor to structural equation modeling (SEM) because it allows potentially non-linear relationships to be identified (Grace 2006). The bivariate relationships between species richness and evenness and shoot, root, and litter biomass were explored using generalized linear mixed models with experimental block as the random term. In each analysis the fit of a model with a linear relationship was compared to the fit of a model with a quadratic relationship. The lmer function in the R Package (Bates 2005; R Development Core Team 2006) was used for these analyses. Species richness was modeled using a Poisson distribution, while a normal distribution was used for evenness.

Structural Equation Modelling (SEM) using observed variables (Path modelling) was used to examine the relationships between species richness and biomass (Shipley 2000; Grace 2006). SEM is most often applied to survey data, but is equally appropriate for experiments (Grace 2006). Univariate analyses such as

ANOVA can only quantify the net effects of an experimental treatment on a response variable, while SEM allows the net effects of an experimental treatment to be partitioned into direct effects and indirect effects that occur through other aspects of the system under study. The primary drawback of SEM is that the results are dependent on correctly specifying the theoretical causal relationships between variables prior to analysis (Shipley 2000; Grace 2006). I chose to model the observed variables directly, rather than using the observed variables as indicators of latent variables because the latter model would have had only a single indicator per latent variable. SEM can be used in either a confirmatory or exploratory mode (Grace 2006). In a confirmatory application the model is specified based on prior theoretical knowledge and then tested to determine whether the model adequately fits the data. In an exploratory application, such as used in this paper, the initial theoretical model is altered based on modification indices to improve the fit between model and data.

Path models were developed to relate both species richness and evenness to neighbourhood biomass, litter, and light conditions. The continuous variables included in the models are described in Table 4-1, and the initial model setup in Figure 4-1. The experimental nitrogen, water, and shade treatments were entered as dummy variables (0,1). Since quadratic relationships better described the relationships between biomass and richness and biomass and evenness than linear models (Figure 4-2), shoot, root, and litter biomass were ln-transformed to improve the fit of the linear relationships. Following transformation, quadratic relationships still better described the relationships between shoot and root biomass and species richness (Shoot: χ^2_1=5.48, p=0.019; Root: χ^2_1=8.45, p=0.004), but not between evenness and litter biomass (χ^2_1=3.55, p=0.059). While the relationships between shoot and root biomass remained non-linear, inspection of the transformed relationships (Figure 4-3) shows that in each case the dominant pattern was for a linear increase across the range of biomass sampled in this study. For this reason, I chose to model the non-linear relationships as if they were linear.

The initial species richness model (Figure 4-1) included direct paths from shoot and root biomass, litter biomass, and light interception to richness. A direct path from pre-treatment richness measured in May 2003 was included to control for the initial conditions in each plot. Light interception received direct paths from shoot biomass, litter biomass and shade. Shoot, root, and litter biomass and species richness all received direct paths from the three experimental treatments. Litter biomass received both a direct path from shoot biomass and a path from initial ground cover in May 2003. Initial ground cover (bare ground and litter) was included to account for pre-treatment differences in litter accumulation. The only experimental treatment with a direct path to light interception was shading, since it was assumed that the effects of water and nitrogen on light interception could be accounted for by their effects on aboveground biomass and litter. I chose not to include direct paths from species richness to above and belowground biomass even though diversity is not necessarily only a consequence of environmental and community characteristics but can also be a cause of those community characteristics (Aarssen 1997; Weiher et al 2004). Initial analyses indicated that including the reciprocal relationships between plant biomass and species richness could interfere with fully solving the structural equation model. I chose to focus on the paths from biomass to species richness in this study because those paths represented the effects of root and shoot competition on species richness.

The models were fit using M-plus 4.1 (Muthén and Muthén 2006). Experimental blocks were included as a random factor using the "TYPE=COMPLEX" option. The χ^2 test of model fit was used to determine whether the fit between model and data was adequate ($p>0.05$). Of the numerous tests of model fit available, the χ^2 is recommended since a non-significant result is a strong indication of an adequate fit between model and data (Grace 2006, p.130). Each path coefficient was divided by its standard error to assess significance. The resulting value follows a t-distribution, allowing p-values to be calculated. Given the exploratory nature of these analyses, coefficients with $p<0.100$ were considered significant. Non-significant paths were retained in the final model (Grace 2006).

The initial species richness model did not have an adequate fit ($\chi^2_{12}=32.48$, $p=0.001$). The modification indices indicated that paths from nitrogen and water to light interception should be added. The path from water to light interception can be justified because regularly pouring water onto the plots could have altered the physical arrangement of shoots and litter, increasing light interception. The justification for the path from nitrogen to light is less clear, but clearly the net effects of the experimental nitrogen treatment on light interception were not completely accounted for by shoot biomass and litter. The fit of the modified model was adequate (χ^2_{10}=14.98, p=0.133).

The initial evenness model included all of the paths added to the final richness model. I retained the additional paths involving light interception since that part of the model was unchanged by the substitution of evenness for richness. The fit of this model was not adequate (χ^2_{10}=18.35, p=0.049). Modification indices suggested the addition of a path from initial litter cover to light interception. The fit of this modified model was adequate (χ^2_9=12.75, p=0.174), however there is little theoretical justification for the path from initial litter to light interception. Given that there were no changes in the significance and extremely small changes in magnitude of the path coefficients involving evenness between the initial and modified models, I chose to accept the initial model.

An important caveat for these analyses is that the number of parameters in the models exceeds the number of blocks in the experiment. This situation can lead to unreliable estimates for the standard errors of model parameters (Muthén and Muthén 2006). To ensure that these potentially unreliable estimates did not affect my interpretation, I re-ran the final models in this study without the blocking variable. Variation in the standard errors between the blocked and non-blocked models resulted in no changes in the paths that were deemed significant. Since this issue did not affect my overall interpretation of the models, I chose to ignore it. The standard errors reported in this paper are from the blocked models.

Results

Species Richness – Biomass Relationships.

Quadratic models better described the relationships between species richness and shoot and root biomass than linear models (Shoot: χ^2_1=6.02, p=0.014; Root: χ^2_1=6.28, p=0.012) (Figure 4-2). When the outlying point with root biomass of 3223 g m^{-2} was removed the quadratic model was not significantly better (χ^2_1=1.02, p=0.312). The species richness – biomass relationships in rough fescue grasslands are likely hump shaped, though the dominant pattern over the range of biomass values sampled in this study is for a linear increase in richness with increasing biomass. There was a negative linear relationship between species richness and litter biomass, since the quadratic model was not significantly better than the linear model (χ^2_1=0.87 p=0.352) (Figure 4-2). While all of these relationships were significantly better than a null model with only an intercept (Shoot: χ^2_2=575.67, p<0.001; Root: χ^2_2=570.83, p<0.001; Litter: χ^2_1=578.04, p<0.001), the R^2 values were low, ranging from 0.09 for root biomass to 0.16 for litter biomass.

Evenness – Biomass Relationships.

There were no significant relationships between evenness and shoot or root biomass as quadratic models were no better than null models including only an intercept (Shoot: χ^2_2=0.00, p=1.000; Root χ^2_2=2.16, p=0.340). A quadratic model better described the relationship between evenness and litter biomass than a linear model (Litter: χ^2_1=13.50, p<0.001) (Figure 4-2). The significant quadratic model between litter biomass and evenness does not appear to represent a hump-shaped relationship. Instead, the underlying pattern appears to be no relationship below ~300 g m^{-2} litter biomass, but a negative linear relationship above 300 g m^{-2}. The quadratic relationship between evenness and litter was significantly better than a null model including only an intercept (χ^2_2=7.45, p=0.024).

Structural Equation Models.

The fit between the modified structural equation models and data were adequate for species richness (χ^2_{10}=14.98, p=0.133) but not for evenness (χ^2_{10}=18.35, p=0.049) (Figure 4-4). I chose accept this model, however, because the modifications required to achieve adequate fit were not plausible, and there were only very minor differences in the magnitude of the path coefficients involving evenness between the initial and modified models. 42.2% of the variation in species richness and 16.6% in evenness were explained by these models. Un-standardized path coefficients, t-test results, and total direct and indirect effects are summarized in Appendix B. Increased litter biomass was strongly associated with declines in both species richness and evenness in this system (Figure 4-4). Even though there were significant bivariate relationships between biomass and species richness, shoot biomass had only an indirect negative effect on richness (-0.069) through the effects of shoot biomass on litter. Shoot biomass had a slightly stronger indirect effect (-0.095) on evenness through litter (Appendix B). All three experimental treatments had indirect negative effects on both species richness and evenness, primarily through the effects of the resource manipulations on litter biomass. The direct negative effects of both nitrogen and shade on species richness were compounded by these indirect negative effects Nitrogen had direct positive effects on evenness that were largely counterbalanced by negative indirect effects through litter.

Discussion

Litter was clearly the primary factor controlling species richness and evenness in rough fescue grassland; the resource treatments affected diversity largely through their effects on litter biomass. Litter can have strong negative effects on species richness in grasslands through many mechanisms including shading, alteration of germination cues, direct physical interference, sheltering invertebrate seed predators, and encouraging pathogens (Carson and Peterson 1990; Facelli and Pickett 1991; Facelli 1994; Foster and Gross 1998; Xiong and Nilsson 1999). The lack of an indirect pathway from litter to species richness through light interception suggests that the effects of litter were largely due to mechanisms other than shading.

The only major effects of the resource manipulations that could not be accounted for by litter were direct negative effects of nitrogen addition and shading on species richness and a positive effect of nitrogen on evenness. Environmental conditions can influence diversity directly by altering the "species pool", or the number of species that have evolved the traits necessary to establish on certain parts of the gradient (Gough at al. 1994; Grace and Pugesek 1997). The small number of grassland species likely able to tolerate the low light levels under the shade cloth may explain some of the direct effects of shading on species richness. Nitrogen addition can increase the intensity of root competition in rough fescue grassland independent of the effects of nitrogen on root biomass (Lamb et al. 2007), but how a change in the intensity of size-symmetric root competition could lead to competitive exclusion is not clear. The lack of direct nitrogen effects on above and belowground biomass were also surprising given that rough fescue grasslands can be strongly nitrogen limited (Lamb et al. 2007). Nitrogen increased shoot biomass in the first year of the experiment ($F_{1,99}$=15.98, p<0.001), but in 2005 a nitrogen by shade interaction ($F_{1,104}$=22.32, p<0.001) indicated that, while nitrogen addition increased shoot biomass in the unshaded plots, it reduced biomass in the shade treatments. The very large litter biomass that accumulated under the shade covers likely explains the nitrogen by shade interaction.

In contrast to the abundant evidence that litter and shoot biomass are important drivers of species richness, the relationship between biomass and evenness can be much more variable (e.g. Wilsey and Potvin 2000; Mulder et al. 2004; Wilsey and Polley 2004). Negative productivity – evenness relationships may arise because large, competitively dominant, species can both reduce evenness and increase overall community productivity (Cotgreave and Harvey 1994; Nijs and Roy 2000). The weak negative indirect effects of shoot biomass on evenness in this study occurred through litter biomass and light interception. The reductions in evenness associated with increased litter biomass and light interception suggest that a shift from symmetric root competition to asymmetric competition for light may have occurred at high levels of aboveground biomass and litter in this community (Cahill 1999; 2002). When shoot biomass is <300 g m^{-2} shoot competition is negligible in this community (Lamb et al. 2007), however I observed 80% ±0.1 (std. dev.) light interception in unshaded plots with biomass >600 g m^{-2}. In those plots low-statured plants would receive only 240-360 μmol m^{-2} s^{-1} in full sunlight (1200-1800 μmol m^{-2} s^{-1}), well below the photosynthetic saturation point of most plants (Fitter and Hay 2002). The 73% reduction in light by the shade cloth would have had similar effects on light availability. It is also of note that the peak of the quadratic regressions relating both species richness and evenness to shoot biomass were at approximately 700 g m^{-2}. Even if competition for light is occurring at some locations in this community, with only 20% of plots having biomass >700 g m^{-2} (Figure 4-2) and all but one of those plots having received either water or nitrogen addition, it is likely that light competition is of minor importance in this community under natural conditions. The decline in evenness with increasing litter could also be interpreted as a consequence of competition. Plants can use litter as a competitive tool to suppress neighbours through a number of mechanisms. For example, the litter of a dominant species can discourage the establishment of competitors by altering nutrient cycling (Clark et al. 2005). Similarly, if a species is able to avoid mechanical interference from its own litter it may be at a competitive advantage (Facelli and Pickett 1991). The second explanation may be important in this system since *Poa pratensis*, the species with the largest increases in cover under conditions of high biomass, high litter, and low light, was also responsible for much of the litter production (Lamb, pers. observ). *Poa* is able to push leaves through a dense mat of litter since it has much more plasticity in leaf traits such as leaf size and specific leaf area than other species at the study site (S. Kembel, pers comm.).

There were few strong links between biomass and species richness or evenness in the structural equation models. The univariate relationships between richness and biomass are in agreement with numerous studies showing strong relationships between biomass and species richness (e.g. Mittelbach et al. 2001; Balvanera et al. 2006; Gillman and Wright 2006), so why should there be such weak relationships in the structural equation models? The weak relationships between shoot biomass and species richness and evenness can be explained by the minor role of shoot competition in rough fescue grasslands. However, given the intense root competition (Lamb et al. 2007), the lack of relationship between root biomass and species richness and evenness is surprising. Such a strong belowground process should have consequences for plant community diversity (e.g. Grime 2001; Rajaniemi 2002; 2003; Schenk 2006), though Cahill (2003) showed that the strength of root competition was not affected by neighborhood diversity. I am aware of no similar structural equation-based studies that have explicitly included root biomass in their analysis. Thus this study provides some of the only comprehensive evidence from a natural community for a lack of relationship between root biomass and species richness and evenness.

Studies where diversity has been experimentally manipulated generally have found positive bivariate relationships between diversity and root biomass (Balvanera et al. 2006), but it is not clear whether root biomass actually influences diversity or if it is simply a spurious correlation. Community root and shoot biomass are positively correlated for allometric reasons (e.g. Cairns et al. 1997; Liira and Zobel 2000; Mokany et al. 2006), and thus a significant shoot biomass – diversity relationship could be accompanied by a similar root biomass – diversity relationship in the absence of any important belowground processes. The hypothesis that any root biomass – diversity relationships are simply a result of this correlation is supported by the similarity of the shapes of the root and shoot biomass – diversity relationships in both this study and Liira and Zobel (2000). The evidence from studies of experimental plant communities with varying diversity is less clear. Some studies have found significantly different shoot and root biomass – diversity relationships (e.g. Spehn et al. 2000; He et al. 2002) while others have found matching above and belowground patterns (e.g. He et al. 2005; Lanta and Lepš 2006).

Several explanations could account for the lack of relationship between belowground biomass and species richness and evenness. 1) There may be no relationship between root biomass and shoot diversity because plant rooting systems generally cover much larger areas than canopies (Jackson et al. 1996). Thus the scale at which root biomass affects diversity may be very different from the scale at which aboveground diversity is generally measured. 2) There may be a relationship between root biomass and *root* community richness or evenness, but until advances in molecular methods make the direct measurement of root diversity practical (e.g. Moore and Field 2005) this possibility is likely to remain unresolved. 3) There may be important root productivity – species richness or evenness relationships that are obscured because standing root biomass samples include both live and dead roots and can be a poor indicator of actual rates of root productivity and turnover (Dahlman and Kucera 1965; Steinaker and Wilson 2005). 4) The belowground biomass – species richness or evenness relationships may be obscured by the large proportion of belowground biomass in grasslands that is allocated to organs such as thick roots and rhizomes dedicated to functions other than resource capture (Pucheta et al. 2004).

There is some evidence that this may be the case, as Spehn et al. (2000) found no relationship between diversity and total root biomass in an experimental plant community, but fine root biomass was positively correlated with diversity. 5) There may simply be no ecological mechanism through which root biomass can structure species richness or diversity. Root competition is frequently cited as an important mechanism structuring diversity (Rajaniemi et al. 2003; Schenk 2006), but root competition intensity may be saturated at all levels of root biomass found in this system (Cahill 2003; Lamb et al. 2007). Cahill and Casper (2000) found that root competition saturated at ~300 g m^{-2} in a productive old field; root biomass in the present study ranged between 308 and 3222 g m^{-2}. Competitive exclusion by root competition cannot occur along gradients of root biomass without variation in competition intensity along the same gradient. Given the extreme variability in the relationships between root biomass and root competition intensity (e.g. Belcher et al. 1995; Peltzer et al. 1998; Cahill 1999; 2002; Lamb et al. 2007), perhaps it should not be surprising that there are so few links between diversity and root biomass.

The lack of biomass effects in this study contrasts with other SEM analyses that found significant relationships between standing aboveground biomass or cover and species richness (Grace and Pugesek 1997; Gough and Grace 1999; Grace and Guntenspergen 1999; Grace and Jutila 1999; Grace et al. 2000; Weiher et al. 2004; Mancera et al. 2005; Grace and Keeley 2006), but in those studies live shoot biomass and litter were not considered separately. Finally, I found that initial species richness and evenness remained important, indicating that, similar to other studies (Grace and Guntenspergen 1999), plot history is an important determinant of current community structure. SEMs of species richness generally have much more explanatory power than univariate relationships (Grace 2006).

Conclusion

In summary, litter dynamics appear to be the primary mechanism structuring species richness and evenness in rough fescue grasslands. The lack of strong relationships between aboveground biomass and light interception and richness and evenness reflects the importance of litter in this system. More importantly, the lack of relationship between root biomass and species richness and evenness suggests that, even though root competition in grasslands is intense, belowground interactions may not play an important role in structuring grassland plant communities.

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Table 4-1 Description of the variables included in the structural equation model.

Variable	**Description**
Species Richness	Number of vascular plant species in 0.5 m by 0.5m permanent quadrats in July 2005. Square-root transformed.
Initial Species Richness	Number of vascular plant species in 0.5 m by 0.5m permanent quadrats in May 2003. Square-root transformed.
Evenness	Evenness calculated from the cover data collected in 0.5 m by 0.5m permanent quadrats in July 2005.using the "odds measure of evenness" (Simpson's D'-1)/(Species richness -1) (Kvålseth 1991). Not transformed.
Initial Evenness	Evenness calculated from the cover data collected in 0.5 m by 0.5m permanent quadrats in May 2003 using the "odds measure of evenness" (Simpson's D'-1)/(Species richness -1) (Kvålseth 1991). Not transformed.
Shoot Biomass	Aboveground live biomass (g m^{-2}) clipped from a 0.1 by 1m quadrat in July 2005. Ln transformed.
Root Biomass	Belowground biomass (g m^{-2}) washed from a 5.3cm diameter by 12 cm deep core taken in July 2005. Ln transformed.
Litter Biomass	Aboveground dead biomass (g m^{-2}) collected from the 0.1 by 1m quadrat used for shoot biomass in July 2005. Ln transformed.
Initial Ground Cover	Proportion of the ground surface in May 2003 covered by litter plus bare soil. The amount of bare soil without cover by lichens or bryophytes in this system is very small relative to the cover or litter, so this value is a reasonable proxy for pre-treatment litter levels. Arcsine transformed.
Light Interception	Light interception is the percentage of the total photosynthetically active radiation intercepted by the shade covers, aboveground biomass, and litter. Arcsine transformed.

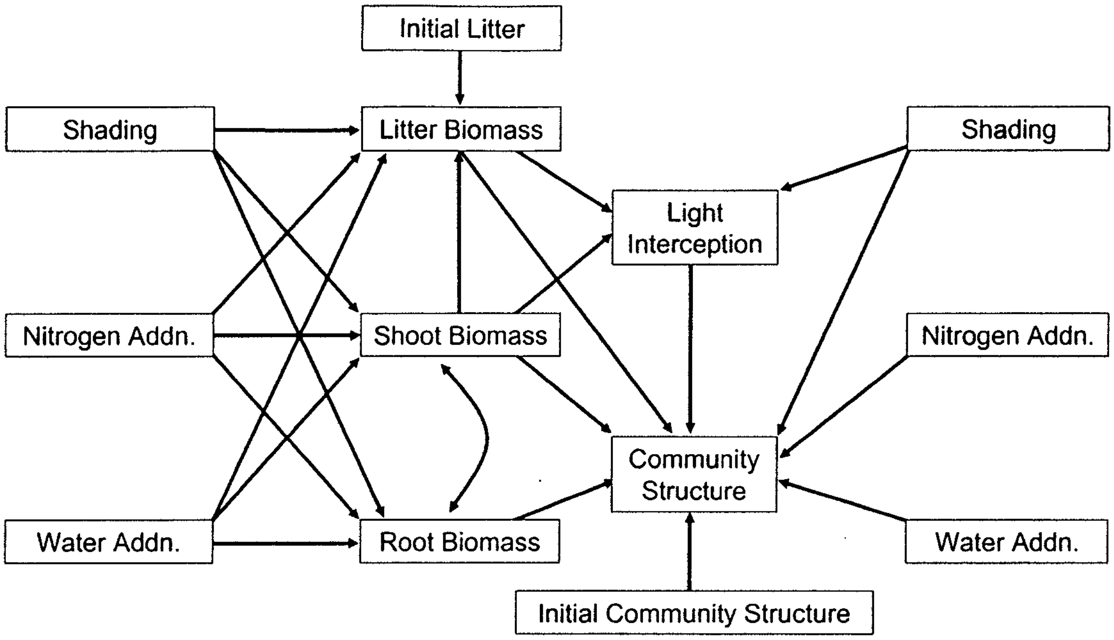

Figure 4-1 The initial structural equation models

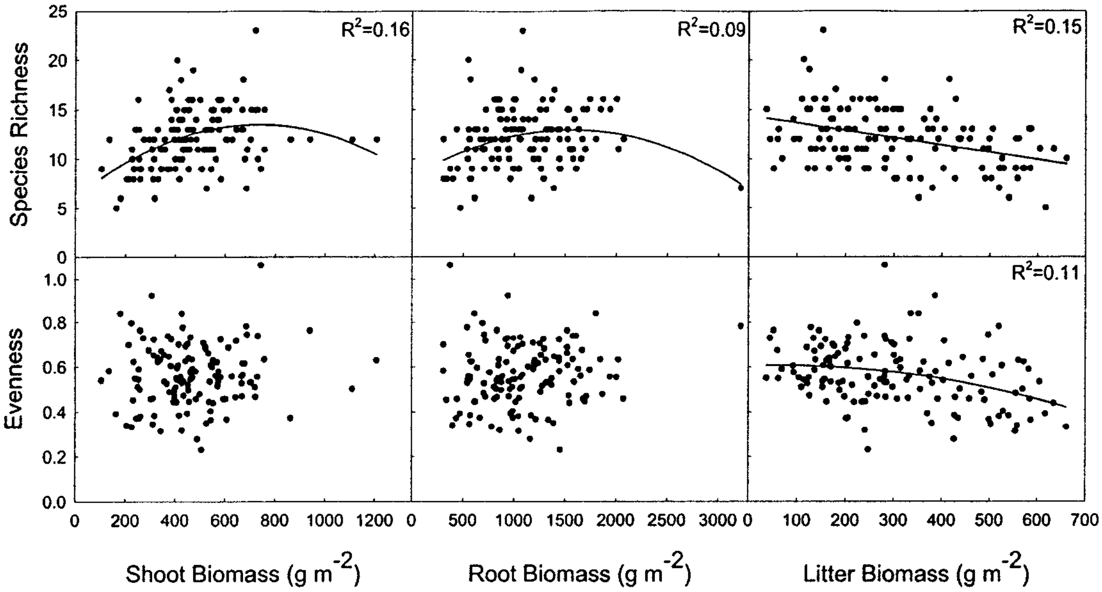

Figure 4-2 Bivariate relationships between shoot, root, and litter biomass and species richness and evenness.

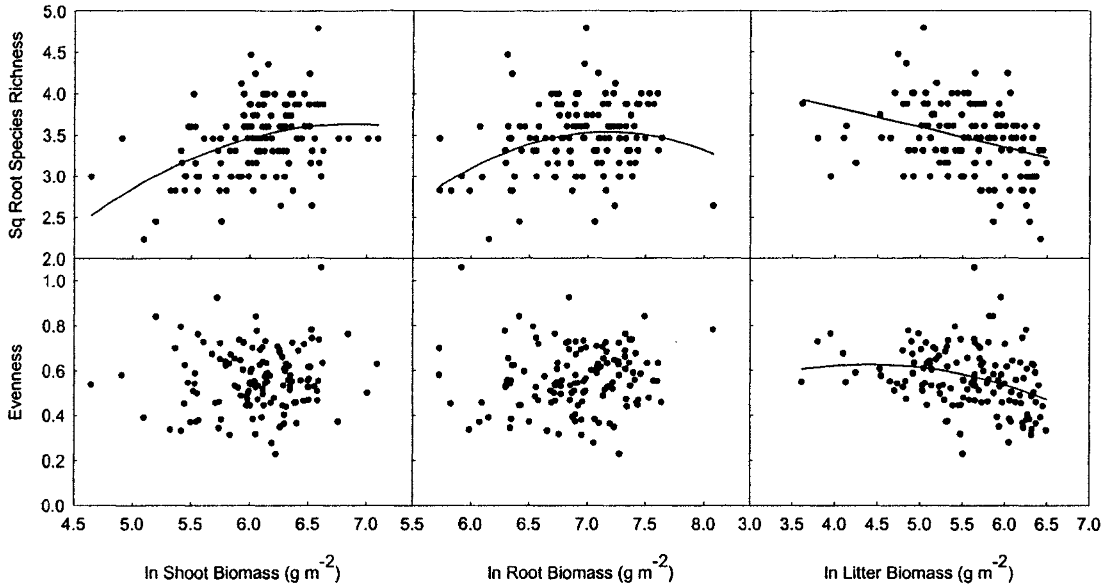

Figure 4-3 Bivariate relationships between ln-transformed shoot, root, and litter biomass and square root transformed species richness and untransformed evenness.

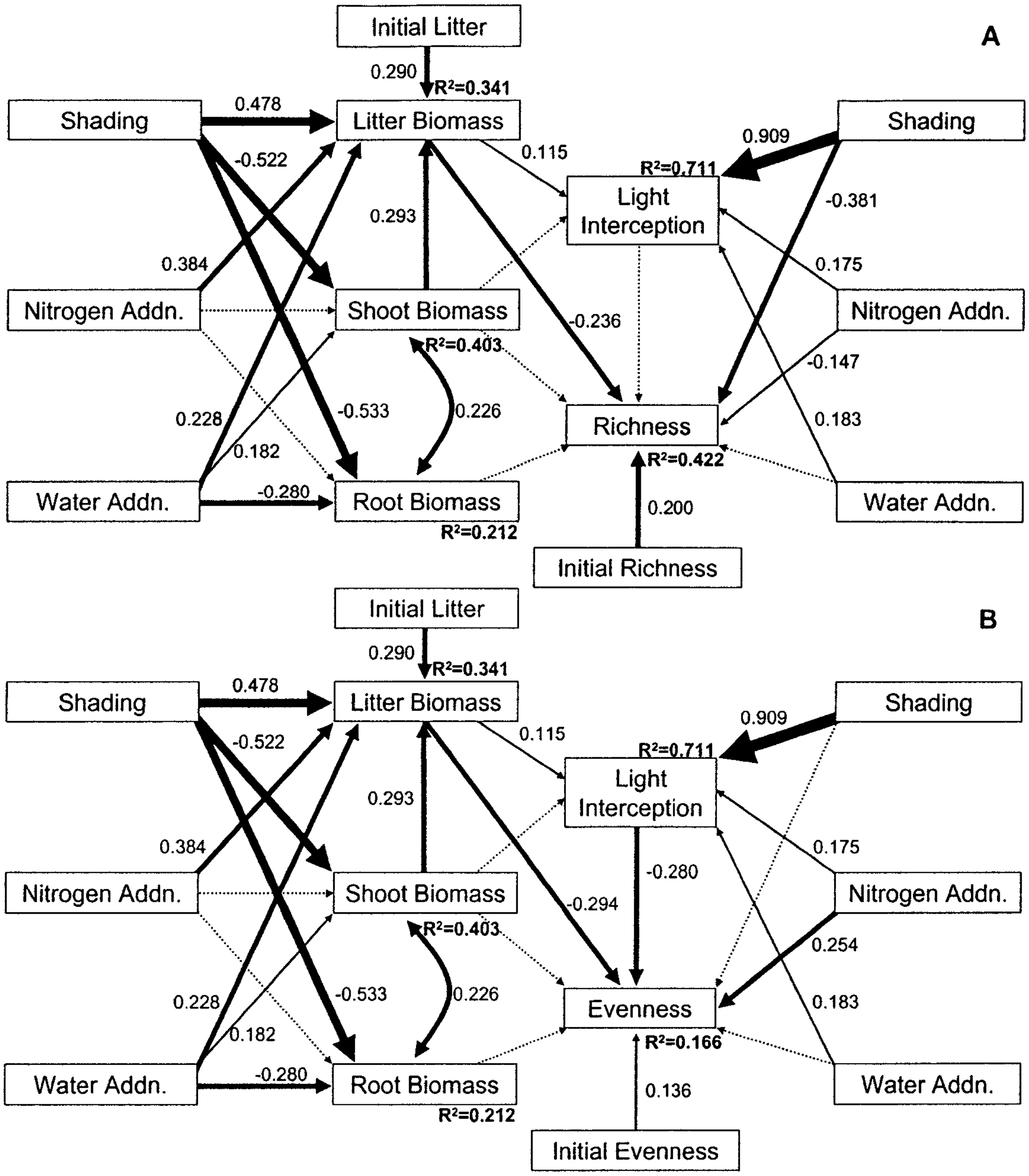

Figure 4-4 Final structural equation models for a) species richness and b) evenness. Non-significant paths are indicated by dashed arrows. Standardized coefficients are listed beside each significant path.

5. When Competition Doesn't Matter: Grassland Diversity and Community Composition[1]

Introduction

Competition for resources in limited supply is one of the key processes determining the growth, survival, and fecundity of individual plants, yet the role of competition in structuring the diversity and composition of plant communities remains poorly understood (e.g. Clements et al. 1929; Goldberg and Barton 1992; Gurevitch et al. 1992; Grime 2001; Keddy 2001; Aarssen and Keogh 2002; Schenk 2006). Size-asymmetric competition for light plays an obvious role in structuring plant communities because larger plants can shade and competitively exclude smaller neighbors (Weiner 1986; Schwinning and Weiner 1998; Keddy 2001). In many communities, however, roots make up the majority of the plant biomass (Jackson et al. 1996; Mokany et al. 2006), and the dominant form of competition is belowground (Casper and Jackson 1997). Many studies have documented variation in root competition intensity along environmental and community gradients, but whether that variation is *important* in structuring plant community diversity or composition has rarely been examined (Welden and Slauson 1986; Cahill 2003; Rajaniemi et al. 2003; Schenk 2006).

The intensity of competition is defined as the degree to which competition for a limiting resource reduces plant performance below the physiological maximum in a given environment, while importance is the impact of competition on fitness relative to other environmental conditions (Welden and Slauson 1986). More broadly, competition can be considered important if variation in the intensity of competition is the cause of predictable variation in plant community structure. Even though Welden and Slauson (1986) were clear that the two measures of competition are not necessarily related, the assumption that intensity and importance are highly correlated (Figure 5-1) pervades the literature (Grace 1991; Brooker et al. 2005).

The positive relationship between the intensity and importance of shoot competition is well established (e.g. Grime 2001; Keddy 2001). Though root

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[1] The raw data used in this study are available in Appendix G.

competition has been found to affect diversity in unproductive old fields (Rajaniemi 2002; Rajaniemi et al. 2003), a wide range of evidence suggests that root competition and community structure are generally unlinked. There are few consistent relationships between the intensity of root competition and plant root biomass (e.g. Belcher et al. 1995; Peltzer et al. 1998; Cahill 1999; Cahill and Casper 2000; Lamb et al. 2007). Similarly, in rough fescue grasslands there are few links between root biomass or competition intensity and plant shoot diversity (Cahill 2003; Lamb Chapter 4). Root competition may play only a small role in structuring plant community diversity and composition in many communities, but this hypothesis has never been comprehensively tested.

The importance of competition for community structure is measured relative to the importance of other environmental conditions (Welden and Slauson 1986). Plant community structure is generally under the control of complex networks of interaction among factors ranging from soil and environmental conditions to disturbance regimes, herbivory, productivity, litter, and standing shoot biomass (e.g. Grace and Pugasek 1997; Grace 1999; Grace and Jutila 1999; Aarssen 2004; Weiher et al. 2004; Lamb Chapter 4). Some studies of the networks influencing community structure have made inferences about the role of shoot competition in structuring plant communities, but none have measured competition intensity directly. Grace and Jutila (1999), for example, found that aboveground biomass had negative effects on species richness in ungrazed but not in grazed plots, suggesting that grazing had reduced the intensity of shoot competition. Explicitly incorporating competition into these networks of environmental and community factors is crucial for a full evaluation of the importance of competition in structuring plant communities.

In this study we test whether competition is an important factor controlling plant community diversity and composition in a rough fescue grassland by including competition intensity in a Structural Equation Model (Shipley 2000; Grace 2006) relating diversity and composition to environmental conditions and plant community biomass. This community is an ideal one to test these hypotheses because root competition is the dominant form of competition and plant community structure changes along gradients of nitrogen and water availability, the two key limiting soil resources (Lamb Chapter 2, 4; Lamb et al. 2007). We place the results of this study into a general framework in a new model describing how interactions between root and shoot competition can structure the diversity and composition of plant communities.

Methods

Field Site

The study area is in a 50 ha field at the University of Alberta Research Ranch near Kinsella, Alberta, Canada (53°05 N, 111°33 W) in the Aspen Parkland Ecoregion (Sims and Risser 2000). The study site is a savanna-type habitat, containing a mixture of trembling aspen (*Populus tremuloides*) groves and rough fescue (*Festuca hallii*) prairie. Plant biomass at the field site is limited by both nitrogen and water availability, and belowground competition is intense (Lamb Chapter 3, 4; Lamb et al. 2007). The site historically has been lightly grazed by cattle in the fall, but grazing was halted three years prior to the beginning of this experiment. Soils at the site are dominantly classified as thin Orthic Black Chernozems, or grassland soils with thin organic-matter enriched topsoil horizons, over glacial till (Howitt 1988; Soil Classification Working Group 1998).

Experimental Design

Total competition intensity, plant community biomass, diversity, species composition, and environmental variables were measured at 192 locations in the study field. Competition intensity was measured as the total effect of neighbors on the performance of an individual plant (Keddy 2001). Pairs of established plants of each of twelve species (*Achillea millefolium* L, *Artemisia frigida* Willd, *Artemisia ludoviciana* Nutt., *Carex stenophylla* Wohl., *Cerastium arvense* L, *Festuca hallii* (Vasey) Piper., *Galium boreale* L, *Geum triflorum* Pursh, *Hesperostipa comata* (A.S.) Hitchc., *Poa pratensis* L., *Rosa arkansana* Porter, and *Solidago missouriensis* Nutt.) were used to measure competition intensity. These species collectively account for more than 75% of total plant cover in these grasslands (Chapter 1). The use of established plants from multiple species differs from studies where competition intensity is measured by planting seedlings of a phytometer species (Keddy 2001). We chose this approach because the competition experienced by transplanted seedlings is a very poor indicator of the competition experienced by established perennial plants (Lamb and Cahill 2006).

Twenty pairs of established plants of each species were identified between 1-7 May 2004, for a total of 240 pairs. Plants in each pair were of similar size and separated by ~1m. One plant in each pair was randomly selected for neighbor removal. Neighboring shoots were clipped in a 12-15cm radius and the remnants brushed with glyphosate herbicide (Roundup®) to prevent regrowth. Root and rhizome connections around both focal plants in each pair were severed at a 15 cm distance to a depth of 15 cm. Regrowth within the clipped zone was re-clipped at two week intervals throughout the experiment. Half of the pairs from each species were randomly selected for a fertilization treatment applied to both the focal plants and the surrounding vegetation (5.4g m^{-2} NH_4-NO_3, half applied on May 15, and half on June 30).

The aboveground biomass of each focal plant was harvested when other plants of the same species in the fields had begun to senesce. *Cerastium* was harvested on July 9th (58 growing days), *Carex, Festuca,* and *Galium* were harvested on August 12th (92 days), *Achillea, Hesperostipa,* and *Poa* were harvested on August 13th (93 days), *Artemisia ludoviciana, Solidago, Rosa*, and *Geum* were harvested on August 31 (121 days) and *Artemisia frigida* was harvested on Sept 8 (129 days). Pairs where one of the focal plants had died or experienced severe herbivory (estimated loss of more than 10% of total leaf area) were excluded leaving 192 pairs (100 control and 92 +nitrogen).

Environmental and community variables were measured at each sampling location in mid-July. The percent cover of all vascular plant species was recorded by eye in a 0.5 m by 0.5 m quadrat. Aboveground standing biomass (g m^{-2}) was measured by clipping all standing biomass in a 20 cm by 50 cm quadrat. Root biomass (g m^{-2}) was measured by washing the roots from a 5.3 cm diameter root core taken to a depth of 12 cm. Soil % total nitrogen was measured on soil sieved from the root biomass samples. The sieved soil was dried, ground, and a subsample analyzed using a Leco FP-428 N-Determinator (Leco, St. Joseph MI). Relative soil moisture was sampled at four locations around the focal plants using a Hydrosense moisture probe (Campbell Scientific, Logan UT). Light interception by vegetation was measured using an Accu-Par light meter (Decagon, Pullman WA).

Statistical Analysis

The bivariate relationships between competition intensity, species richness, evenness, and community composition were directly examined using mixed effects models. In each analysis the fit of a model with a linear relationship was compared to the fit of a null model with only an intercept and a quadratic model using the lmer function in the R Package (R Development Core Team 2006). Species was included as a random term in each of these models.

Structural Equation Modelling (SEM) using observed variables (Path modelling) was used to examine the relationships between environmental conditions, competition intensity, and community structure (Shipley 2000; Grace 2006). SEM was chosen for this analysis because the network of direct and indirect theoretical causal relationships between variables can be specified, as can reciprocal effects where two variables each exert a causal influence on the other (Shipley 2000; Grace 2006). The primary goals of these analyses were to 1) evaluate the effects of competition intensity on measures of community structure including species richness, evenness, and community composition (defined as an ordination axis), and 2) to describe the overall network of interactions controlling community structure in rough fescue grassland. SEM can be used in either a confirmatory or exploratory mode (Grace 2006). In a confirmatory application the model is specified based on prior theoretical knowledge and tested to determine whether the model adequately fits the data. In an exploratory application, as in this paper, the initial theoretical model may be altered to improve the fit between model and data.

Path models were developed to relate species richness, evenness, and community composition to competition intensity, neighbourhood biomass, and environmental conditions. The initial path model structure is shown in Figure 5-2 and the variables included are described in Table 5-1. We chose to model the observed variables directly, rather than using the observed variables as indicators for latent variables because the resulting model would have had only a single indicator variable per latent. Two environmental variables (Topographic position and soil total nitrogen) served as indicators for a composite variable summarizing site conditions. This composite variable was included to simplify the model structure (Grace 2006). In the initial model site conditions were assumed to affect shoot and root biomass directly, soil moisture, and community structure. The nitrogen treatment was assumed to directly affect root and shoot biomass and community structure. Shoot biomass directly influenced light interception, while both root and shoot biomass affected soil moisture. Competition intensity was a function of focal species competitive ability, soil moisture, light interception, and root biomass. Species competitive ability was included to control for differences in competitive ability between the twelve species used in this study. The path from light interception to competition intensity represented competition for light. The paths from soil moisture to competition intensity represented competition for water, while the path from root biomass to competition intensity represented competition for nitrogen. Since available nitrogen was not measured directly, we included the path from root biomass to competition is a surrogate. Finally, paths from community structure to above- and belowground biomass were included because those variables can be a function of the species present in the community (Aarssen 2004).

This initial model configuration differs from most other structural equation models that have related environmental conditions to community biomass and diversity. Those models included direct paths from biomass, light interception, and soil resources to diversity. The strength of these paths was generally interpreted as representing the effects of competition on community structure. Those paths are not necessary in the present model, however, because competition intensity is directly included.

Each bivariate relationship represented by an arrow in the initial path model was examined using generalized linear models to identify potentially non-linear relationships. In each analysis, the fit of a model with a linear relationship was compared to the fit of a model with a quadratic relationship using the glm function in the R Package (R Development Core Team 2006). No potentially non-linear relationships were found.

The structural equation models were fit using M-plus 4.1 (Muthén and Muthén 2006). Competition intensity was nested within species using the "TYPE=TWOLEVEL" option with a species-level covariate (average competitive ability) affecting only competition intensity. The χ^2 test of model fit was used to determine whether the fit between model and data was adequate ($p>0.05$). The χ^2 test of model fit is recommended since a non-significant result is an unambiguous indication of adequate fit (Grace 2006).

The fit between the initial species richness model and data was not adequate ($\chi^2_{16}=86.111$, $p<0.001$). Modification indices suggested the inclusion of a direct path from topographic position to light interception, a path from nitrogen treatment to soil moisture, and a path from soil moisture to species richness. The fit of the modified model was adequate ($\chi^2_{12}=14.402$, $p=0.276$). The initial evenness and composition models were based on the modified species richness model. Both of these models failed to converge. Error messages indicated that the problem was due to the starting values for the path from total nitrogen to the site composite variable. Fixing this parameter to the value of that path in the species richness model allowed convergence. The fit of the evenness model was adequate ($\chi^2_{13}=9.406$, $p=0.742$), but the fit of the composition model was not adequate ($\chi^2_{13}=28.237$, $p<0.008$). The addition of a path from community composition to light interception resulted in a model with adequate fit ($\chi^2_{12}=16.266$, $p=0.179$). Path coefficient significance was evaluated by dividing each coefficient by its standard error. The resulting value follows a t-distribution, allowing p-values to be calculated. Given the exploratory nature of these analyses, coefficients with $p<0.100$ were considered significant. Non-significant paths were retained in the final model (Grace 2006).

An important caveat on these analyses is that the number of parameters in the models exceeded the number of species on which competitive ability was measured. This situation can lead to unreliable estimates for the standard errors of model parameters (Muthén and Muthén 2006). To ensure that these potentially unreliable estimates did not affect our interpretation, we re-ran the final models without the species-level covariate of competitive ability. The fit of all three reduced models was adequate, and variation in the standard errors between models resulted in only one change in the paths deemed significant. The path from competition intensity to evenness was significant in the full model (t_{192}=1.962, p=0.051), but not in the reduced model (t_{192}=1.642, p=0.102). Since the p-value for the path in the reduced model was very close to the cutoff value for significance (p=0.100), we chose to accept the significant result of the full model. The standard errors reported in this paper are from the full models.

Results

There were no significant bivariate relationships between competition intensity and either species richness (χ^2_1=0.000, p=1.000), evenness (χ^2_1=0.569, p=0.451), or community composition (χ^2_1=0.769, p=0.380) (Figure 5-3). The final structural equation models for species richness (χ^2_{13}=14.402, p=0.276), evenness (χ^2_{13}=9.406, p=0.742), and community composition (χ^2_{12}=16.266, p=0.179) adequately fit these data (Figure 5-4). The full model results are included in Appendix D. Competition intensity was strongly influenced by phytometer species identity and declined with increased soil moisture, but was not dependent on any other variables. Competition intensity did not affect species richness or community composition, but an increase in competition intensity was weakly associated with a decline in evenness. Environmental conditions strongly controlled shoot and to a lesser extent root biomass, and a combination of environmental conditions and plant biomass exerted strong control on light interception and soil moisture. Both species richness and evenness were positively influenced by the nitrogen addition treatment and higher soil moisture, but were otherwise not significantly related to other parameters. Plant community composition, however, was tightly linked to both environmental conditions and plant biomass. The R^2 values for the dependent variables (Figure 5-4) were very low, indicating that the most important factors controlling community structure in this system were missing from these models.

Discussion

Root Competition and Plant Community Structure

The intensity of competition in rough fescue grassland was unrelated to species richness and composition, but more intense competition was weakly associated with reduced evenness. Competition in this community is primarily belowground (Lamb et al. 2007), so these results raise serious questions about the role of competition in structuring low statured plant communities such as dry grasslands, deserts, and alpine and arctic tundra. There is no doubt that root competition is intense in such communities (e.g. Casper and Jackson 1997; Peltzer et al. 1998; Keddy 2001; Cahill 2003; Mitchell 2006; Lamb et al. 2007), but if that competition has no consequences for plant community structure then it is not *important* (Welden and Slauson 1986). Our findings that root competition was largely unimportant for plant community structure is consistent with the lack of consistent relationships between root biomass and root competition intensity (e.g. Belcher et al. 1995; Peltzer et al. 1998; Cahill 1999; 2002; Lamb et al. 2007). Our findings are also consistent with the lack of relationships between diversity and both root competition intensity (Cahill 2003) and root biomass (Lamb Chapter 4).

The only significant effect of competition on community structure was for a slight decline in evenness associated with increased competition intensity. This pattern is consistent with the view that, in the absence of severe abiotic stresses or increased predation, an increase in evenness indicates a reduction in the intensity of competition for a limiting resource (Cotgreave and Harvey 1994, Keddy 2001). A long-term increase in the dominance of certain species with more intense competition could lead to changes in species richness and community composition. However, given the extremely small magnitude of the competition – evenness path (0.078) and the low overall variance in evenness explained in this model (r^2=0.070), it is unlikely that this mechanism is of great importance in structuring rough fescue grasslands.

Why should intense root competition, capable of reducing individual plant performance by an order of magnitude or more (Lamb et al. 2007), have so little impact on plant community structure? Root competition is generally size-symmetric (e.g. Weiner 1986; Schwinning and Weiner 1998; Cahill and Casper 2000; von

Wettberg and Weiner 2003). In size-asymmetric competition, such as for light, competitive exclusion occurs because a slight advantage in size allows the larger plant to capture a disproportionate fraction of the available light. This advantage leads to positive feedbacks where the larger plant can grow faster and gain an even greater proportion of the resource pool (Weiner 1986; Keddy 2001). In contrast, there are no feedback mechanisms in size-symmetric root competition that can magnify small initial differences. Without a feedback mechanism all of the plants competing symmetrically for a limiting resource experience proportionally similar reductions in performance, rather than the selective exclusion of certain species or individuals.

This study has shown that size-symmetric root competition among established adult plants is unlikely to strongly affect plant community structure. This study does not, however, provide any information on the effects that root competition from established plants may have on seedling germination and establishment. The regeneration niche can be a strong filter determining which species can establish in a community (Grubb 1977) and seedling and adult plants can have very different competitive abilities (Lamb and Cahill 2006). Root competition may prevent some species from entering the community, even if, as adults, they are strong competitors. Finally, small-scale variation in the spatial distribution of competition intensity may leave refuges of low competition intensity that allow poor competitors to establish (Hölscher et al. 2002; Cahill and Casper 2002). The effects of root competition from established plants on the regeneration niche and whether those effects on establishment success are important for plant community structure needs further evaluation.

The Asymmetry of Competition Structures Plant Communities

Both this study and Cahill (2003) have shown that intense root competition can have little impact on community structure, but instances where root competition is important have been observed (Rajaniemi et al. 2003). We propose a general conceptual model to describe how root and shoot competition may act together to structure plant communities (Figure 5-5). Key to this model is the fact that, while root competition alone may be generally unimportant for plant community structure, root and shoot competition are not independent (Cahill 1999; 2002).

The model describes how both shoot competition and root – shoot competition interactions can contribute to the overall importance of competition in plant communities. Only size-asymmetric interactions can lead to the positive feedbacks that directly structure a plant community, but process affecting the outcome of asymmetric competition may indirectly structure a community. Key to this model is the recognition that each plant is a single integrated organism, and the interactions between root and shoot competition can determine whether a plant is able to reach the canopy and succeed in shoot competition (Cahill 1999). There are five central elements to the model. 1) Increasing intensity of shoot competition will result in an increase in the overall asymmetry of the competition a plant experiences, but 2) root competition intensity and asymmetry should be unrelated (Figure 5-5). 3) Mechanisms such as interactions between root and shoot competition or morphological plasticity in response to the shifting competitive environment will cause a great deal of variation in the asymmetry of total competition. 4) There should be a direct relationship between the overall asymmetry and importance of competition (Figure 5-5). 5) The shape of the relationship between asymmetry and importance should be a function of both the intensity of shoot competition and the importance of root – shoot competition interactions.

Integrating root and shoot competition into a single axis of asymmetry can explain why root competition can be intense but unimportant while relatively less intense shoot competition can have strong effects on community structure. There is empirical evidence for many of the relationships proposed in this conceptual model. The positive relationship between the intensity and importance of asymmetric shoot competition is well established (e.g. Grime 2001; Keddy 2001). Our prediction that the overall importance of competition should increase along gradients of competitive asymmetry is clearly related to Grime's (1973; 2001) prediction that competition should be most important in structuring plant communities at high productivity. Both this study and Cahill (2003) demonstrate that there are few relationships between competition and community structure in low-statured communities with intense root competition but little or no shoot competition. Finally, Rajaniemi et al. (2003) found that root competition had no effect on diversity in unfertilized artificial communities but had a negative effect in fertilized treatments. Productivity, light interception by vegetation, and presumably shoot competition intensity increased with fertilization in that study, consistent with our prediction that root competition is only important for plant community structure when there is the potential for root: shoot competition interactions.

The shape of the relationship between asymmetry and importance remains speculative. We predict that importance should saturate at high levels of asymmetry because the increasing importance of shoot competition with greater asymmetry should be counterbalanced by a decline in the importance of interactions as root competition becomes weaker relative to shoot competition. A peak in the strength of root – shoot competition interactions when root and shoot competition are similar in intensity was predicted by Cahill (1999), but has not been directly tested. Further research is necessary, particularly to confirm the shape of the root – shoot competition interaction – importance relationship.

Mechanisms Controlling Plant Community Structure in Rough Fescue Grasslands

The structural equation models in this study leave the mechanisms structuring rough fescue grasslands unexplained. Structural equation models routinely return R^2-values between 0.24 and 0.60 for species richness and evenness (e.g. Grace and Pugasek 1997; Grace 1999; Grace and Jutila 1999; Weiher et al. 2004; Lamb Chapter 4). This study is a conspicuous exception (R^2 for species richness =0.040, evenness =0.070, and community composition =0.197), indicating that important explanatory variables were missing from the model. The R^2 for community composition was higher largely because site conditions determined the extent of the two major grassland communities at the site. *Poa pratensis* dominated grasslands were found on flatter sites and north-facing slopes while *Hesperostipa comata* dominated grasslands were common on south-facing slopes.

Factors not included in the models that could be important in structuring this community include site history, herbivory, seed limitation, and random (neutral) patterns. Site history is likely important because there was a strong positive effect of initial species richness on final species richness following a three-year nitrogen, water, and shade manipulation experiment (Lamb Chapter 4). There may be significant stochastic or neutral elements to the structure of this community at the small scale (0.5m by 0.5m plots) measured in this study (Adler et al. 2007). Insect herbivores are likely unimportant since a long-term insect suppression experiment resulted in few changes in plant community structure (Coupe 2003); a long-term study examining the influence of native and introduced vertebrate herbivores in this community is currently underway. Other potentially important processes that were unmeasured or imperfectly measured include the role of litter, disturbance, and seed limitation (Facelli and Pickett 1990; Turnbull et al. 2000; Lamb Chapter 4).

Conclusion

In summary, this study demonstrates that root competition does not play an important role in structuring plant community diversity or composition in rough fescue grassland. It is surprising that an ecological process that has such a severe impact on individual plants should have so little effect on overall community structure. We propose that by integrating root and shoot competition intensity into the overall symmetry of competition, we can predict when competition is likely to be important in structuring plant communities. Root competition may not be directly important structuring plant communities, but root competition can be indirectly important if interactions between root and shoot competition determine which plants can succeed in shoot competition.

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Table 5-1 Observed variables included in the structural equation model

Variable	**Description**
Competition Intensity	Log response ratio: lnRR = ln(RGR_{AN} /RGR_{NN})* (Cahill 1999; Hedges et al. 1999). Positive values indicate facilitation while increasingly negative values indicate increasing competition intensity. The lnRR assumes that competitive ability does not vary with plant size (Lamb et al. 2006), but the assumption was met since the relationships between RGR_{AN} and RGR_{NN} for each species were linear.
Species Competitive Ability	The slope of a linear regression between RGR_{AN} and RGR_{NN}* (Lamb et al. 2006). Increasing slopes indicate increasing competitive ability, or species that achieved an increasing proportion of their potential growth (RGR_{NN}) when competing with neighbours. Negative slopes indicate facilitation.
Species Richness	Number of vascular plant species in 0.5 m by 0.5m quadrats in July 2004. Square-root transformed.
Species Evenness	Pielou's J (Pielou 1969). Calculated from percent cover data. Not transformed.
Community Composition	A single NMS ordination axis (McCune and Grace 2002) using percent cover data. PC-Ord 4 (McCune and Mefford 1999) was used to calculate a single axis ordination. The axis represents a gradient from *Poa pratensis* and *Galium boreal* dominated grassland to *Hesperostipa comata* dominated grassland. See Appendix C for details of the analysis setup and output.
Shoot Biomass	Aboveground live biomass (g m^{-2}) clipped from a 0.2 by 0.5m quadrat in July 2004. Ln transformed.
Root Biomass	Root biomass (g m^{-2}) washed from a 5.3cm diameter by 12 cm deep core taken in July 2004. Ln transformed.
Light Interception	Percentage of the total photosynthetically active radiation intercepted aboveground live biomass and litter. Arcsine transformed.
Soil Moisture	Relative soil moisture % (average of 4 readings at each plot). Arcsine transformed.
Topo. Position	Topographic position indicated by incident radiation calculated from slope and aspect following McCune and Keon (2002). Not transformed.
Total Nitrogen	Total surface soil nitrogen (%). Arcsine transformed.
Nitrogen Tmt.	0/1 indicating whether a plot received the nitrogen addition treatment

* RGR_{AN} = Relative growth rate with competition from neighbours
RGR_{NN} = Relative growth rate without competition from neighbours

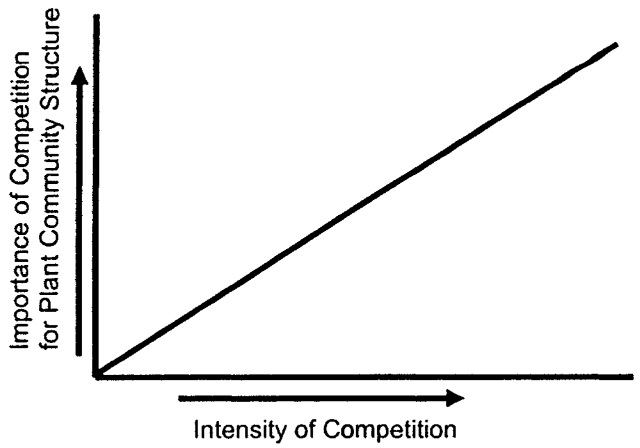

Figure 5-1 The generally assumed relationship between the intensity and importance of competition. This relationship is only true for shoot competition.

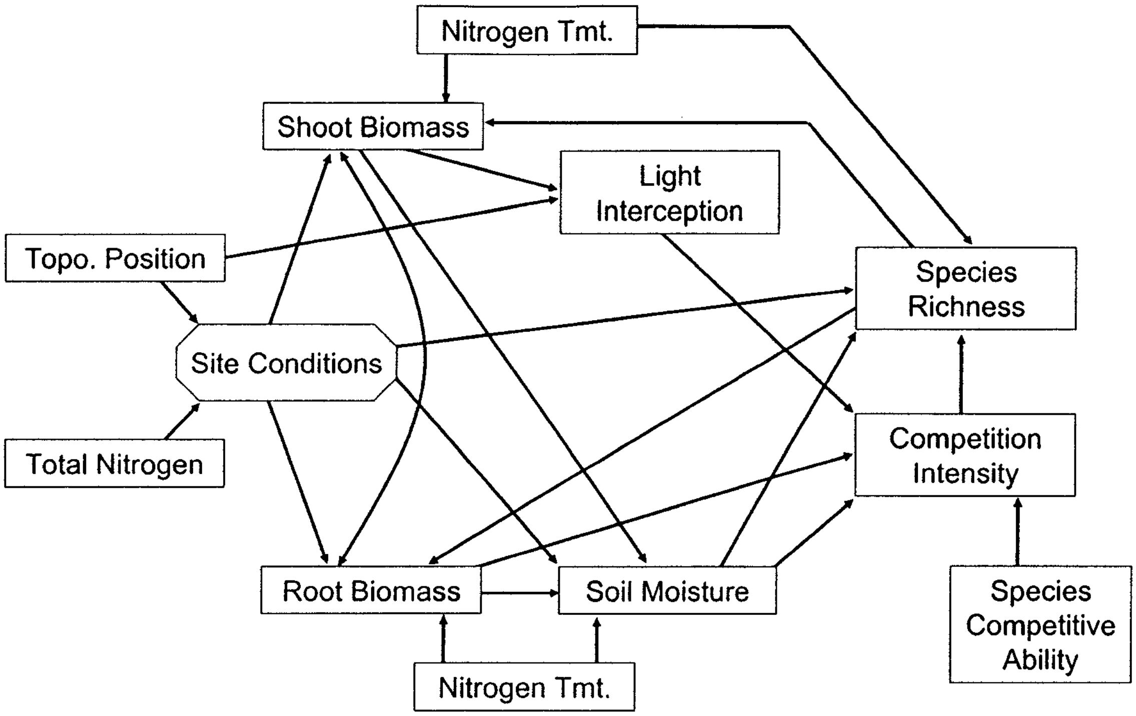

Figure 5-2 The initial structural equation model.

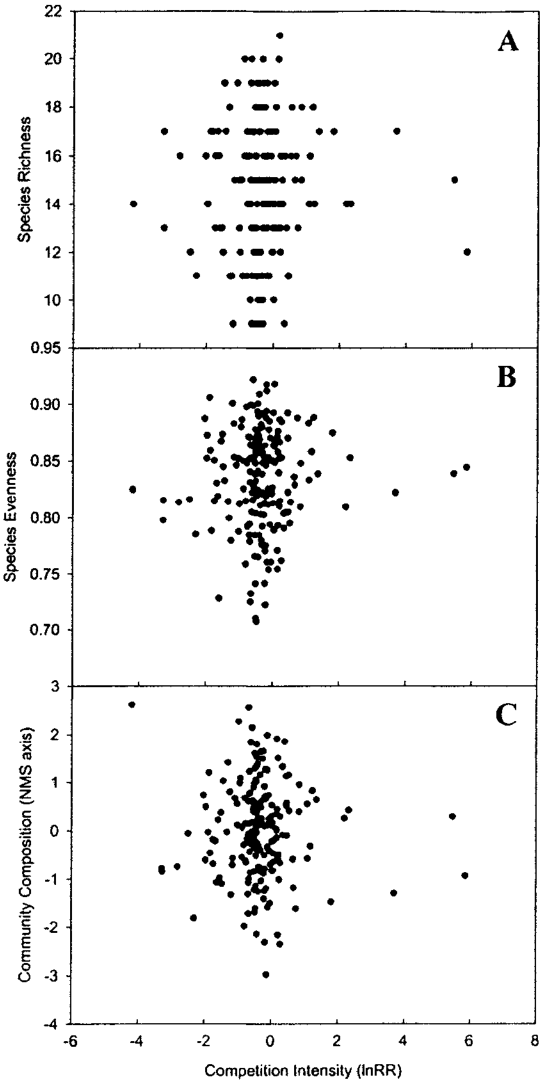

Figure 5-3 Bivariate relationships between competition intensity and A) species richness, B) evenness, and C) community composition.

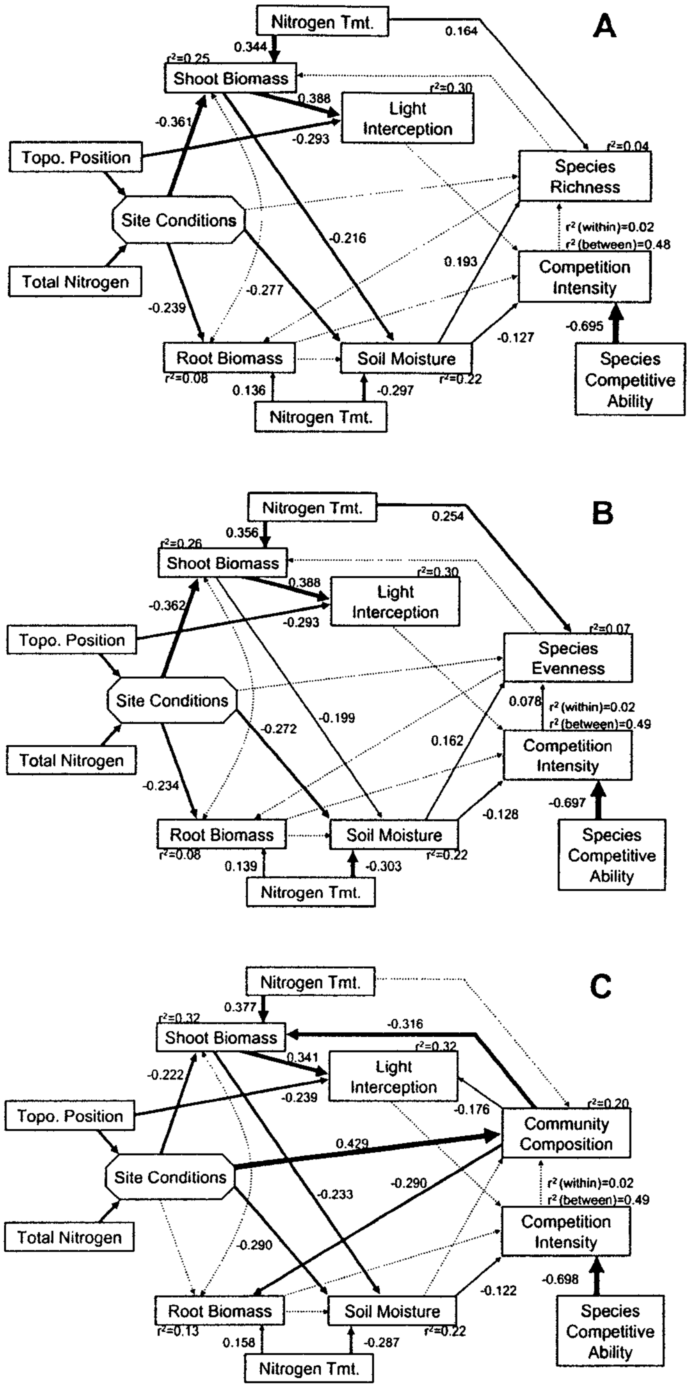

Figure 5-4 Structural equation model results for A) species richness, B) species evenness, and C) plant community composition. Standardized path coefficients are shown on the figure and r^2 values are listed for each dependent variable. The variance explained for competition intensity is separated into that due to species competitive ability (between) and that due to the other variables in the model (within). Paths that were not significant ($p \geq 0.10$) are indicated by dotted arrows.

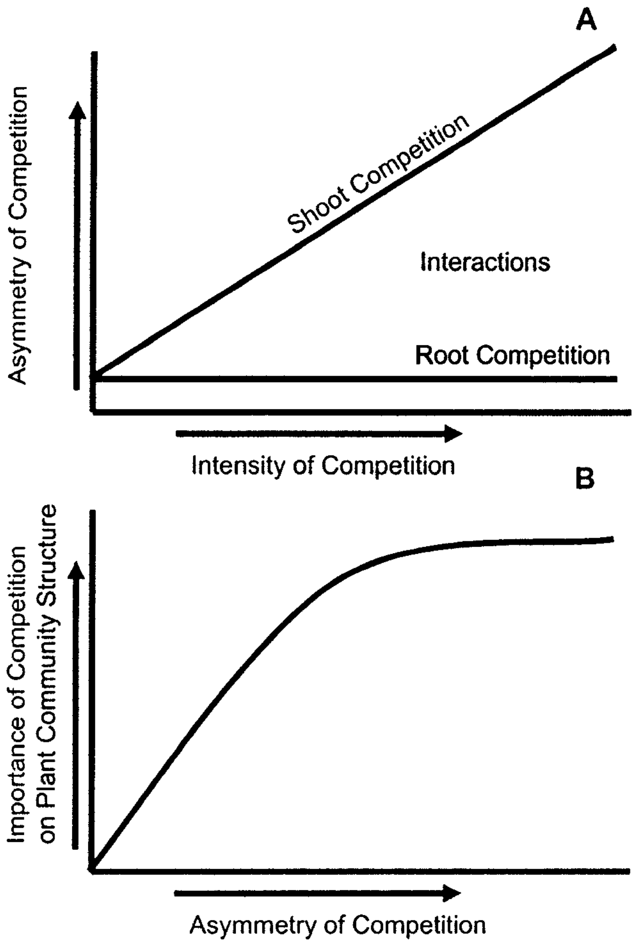

Figure 5-5 Conceptual model describing the relationships between competition intensity, asymmetry, and importance. A) Relationships between the intensity and asymmetry of root and shoot competition. Total competition asymmetry will often fall in the shaded region due to interactions between root and shoot competition. B) Relationship between the overall asymmetry and importance of competition. A balance between the increasing importance of shoot competition and declining importance of root – shoot competition interactions at high levels of asymmetry should produce the saturating relationship.

6. Discussion and Conclusions

The primary objective of this thesis was to examine the mechanisms structuring a rough fescue grassland plant community, particularly how competition for soil resources structures the diversity and composition of this community. A wide array of evidence, including the direct tests in Chapter 5, demonstrates that, while very strong, competition was unimportant in structuring rough fescue grassland. In this general discussion, I summarize some of the most important findings of this thesis.

General Discussion

Rough fescue grassland diversity and composition was influenced by numerous factors, particularly the availability of limiting soil resources, and the effect of those resources on litter accumulation. Experimental manipulations of nitrogen and water altered the intensity of competition (Chapter 3), and along with light manipulations affected many aspects of plant community structure (Chapter 4, 5). Litter accumulation appeared to be the primary mechanism through which these limiting resources affected the plant community. Site conditions, particularly topographic position, were an important overriding factor, determining the extent of the two major grassland communities at the site. *Poa pratensis*-dominated grasslands were found on less steeply sloping sites and north-facing slopes while *Hesperostipa comata*-dominated grasslands were common on south-facing slopes. The most interesting findings in this thesis involve the factors that were not linked to community structure: the soil bacterial community, live plant community biomass, and the intensity of competition. In the remainder of this discussion I will focus on these three factors and what can be learned from these negative responses.

Plant and soil bacterial community structures were unlinked

The direct control of plant species over rhizosphere chemistry (Wardle et al. 1999, Hopkins and Gregorich 2005, Orwin et al. 2006) suggests that there should be links between the structure and composition of the plant and soil microbial communities. I found, however, that there were no correlations between plant and microbial diversity, and that the plant and microbial communities responded independently to gradients of water and nitrogen availability (Chapter 2). These results are surprising given that nearly the entire surface soil volume was within a rhizosphere, and that similar studies have found significant plant – bacterial relationships (e.g. Bartelt-Ryser et al. 2005; Sullivan et al. 2006). Few correlations between plant and soil diversity were likely found in this study because the resource treatment – induced changes in diversity in this study were very small relative to unmanipulated diversity levels. In contrast Bartelt-Ryser (2005) found significant plant – microbial diversity correlations using artificial plant communities with 1 to 32 species. The potential lack of relationship between aboveground and belowground plant diversity described in the previous section may also have contributed to the lack of plant – microbial diversity correlations in this study.

The lack of associations between the composition of the plant and microbial communities may have been a function of the high plant community diversity in rough fescue grasslands (Figure 1-1). Plant monocultures are known to have very strong effects on the composition of soil microbial communities (e.g. Grayston et al. 1998; Wardle 2006), however in a plant community with very high evenness no individual plant species dominates the rhizosphere. Individual plant species are likely to still involved in strong interactions with their respective rhizosphere communities, but the net effects of the entire plant community on the microbial meta-community is likely to be relatively weak (Figure 2-4).

Plant community biomass and diversity were unlinked.

Numerous studies have identified strong relationships between aboveground biomass and diversity (e.g. Mittelbach et al. 2001; Balvanera et al. 2006; Gillman and Wright 2006). Significant hump-shaped relationships between both above- and belowground biomass and species richness were identified in Chapter 4 using univariate analyses. The shape of the root biomass – species richness relationships were very similar to the aboveground relationship, suggesting that relationships between root and shoot biomass or productivity and diversity will generally be similar simply due to the allometric links between root and shoot biomass (Cairns et al. 1997; Liira and Zobel 2000; Mokany et al. 2006). After finding such univariate relationships, it was a surprise to find no significant relationships between biomass and diversity in the structural equation models. In the structural equation models in Chapter 4, the overriding importance of litter accumulation on diversity led to the disappearance of the univariate diversity-biomass relationships, since litter biomass was correlated with both root and shoot biomass. While we can easily explain the lack of shoot biomass – diversity relationships in a system where competition is primarily belowground (Chapter 3), it is more difficult to explain the lack of root biomass – diversity relationships.

There are several possible explanations for the lack of relationship between belowground biomass and diversity. First, root biomass and the diversity of plant species in the root community may be linked, but not root biomass and plant shoot diversity. Second. the scale at which root biomass affects diversity may be very different from the scale at which aboveground diversity is measured since the root systems of many grassland plant species extend over much larger areas than the canopies (Coupland and Johnson 1965; Jackson et al. 1996; Casper et al. 2003). Practical molecular methods allowing direct measurement of root diversity (e.g. Moore and Field 2005) are necessary to fully evaluate how root biomass and root diversity may be linked. Third, inaccuracies in the measurement of belowground biomass and productivity may explain the lack of root biomass – diversity relationships. Important root productivity – diversity relationships may be obscured simply because standing root biomass samples include both live and dead roots and poorly reflect actual rates of root productivity and turnover (Dahlman and Kucera 1965; Steinaker and Wilson 2005). Similarly, root biomass – diversity relationships may be obscured by the high allocation of belowground biomass in grasslands to thick roots and rhizomes, organs with functions other than resource capture (Pucheta et al. 2004). It is revealing in light of these issues that Spehn et al. (2000) found no relationship between the diversity of experimental plant communities and total root biomass, but a significant relationship with fine root biomass. Finally there may simply be no direct ecological mechanism linking root biomass and diversity. If there were a link between root biomass and diversity, competition is a likely mechanism driving the relationship. Thus, the studies in Chapter 3 and 4 provide circumstantial evidence that root competition and plant community structure are mechanistically unlinked. I explicitly tested this link between competition and community structure in Chapter 5, and discuss the results in the next section.

Competition did not structure plant community diversity or composition

Individual plants in rough fescue grassland were strongly affected by root competition (Chapter 3), but I found little evidence to link competition to any aspect of plant community structure (Chapter 4, 5). If competition were important, significant relationships between root competition intensity and root biomass should have occurred, and there should have been links between variation in competition intensity and aspects of plant community structure. The lack of such relationships raise serious questions about the role of competition in structuring low statured plant communities such as dry grasslands, deserts, and alpine and arctic tundra. There is no doubt that root competition is intense in such communities (e.g. Casper and Jackson 1997; Peltzer et al. 1998; Keddy 2001; Cahill 2003; Mitchell 2006; Chapter 3), but if that competition has no consequences for plant community structure then it is not *important* (Welden and Slauson 1986). The distinction between intensity and importance is critical, but too many ecologists simply assume that intense competition is important (Figure 5-1; Welden and Slauson 1986; Keddy 2001; Brooker et al. 2005).

I found no significant relationships between root competition intensity and belowground biomass (Chapter 3, 5). This result is consistent with the wide range of root biomass – root competition relationships across studies (e.g. Belcher et al. 1995; Peltzer et al. 1998; Cahill 1999; 2002). I interpret the lack of consistency as an indication that meaningful ecological mechanisms do not connect the total root biomass and competition intensity. There are several means through which root biomass and competition could be unlinked. First, as discussed above in regard to the lack of links between root biomass and diversity, a lack of correlation between standing root biomass and the fine root biomass or productivity may explain the lack of biomass-competition relationships (Dahlman and Kucera 1965; Pucheta et al. 2004; Steinaker and Wilson 2005). A second possibility is that root biomass - root competition intensity relationships may be found at low levels of root biomass, but that the contribution of root biomass to competition intensity is saturated across the full range of root biomass found in many natural communities (Cahill and Casper 2000). Though this possibility can explain why variation in root competition intensity and biomass were uncorrelated in this study, it does not explain why plants may alter root biomass allocation in response to resource gradients (Chapter 3). If it is the case that root competition is saturated at all levels of biomass, the observed variation in root competition intensity may simply be too narrow to have any meaningful impact on plant community structure. Studies to measure the intensity of root competition over long gradients combined with very detailed assessment of fine root biomass and productivity are necessary to fully evaluate these hypotheses.

Theoretical arguments can be made that, even if root biomass and productivity were measured as described above, there would be no relationships between root competition and plant community structure. The size – symmetry of root competition provides a clear mechanism to explain why root competition and plant community structure should be unlinked. There is general agreement that root competition is generally size-symmetric (e.g. Weiner 1986; Casper and Jackson 1997; Schwinning and Weiner 1998; Cahill and Casper 2000; von Wettberg and Weiner 2003; Schenk 2006). In size-asymmetric competition, such as for light, competitive exclusion occurs because a slight advantage in size allows the larger plant to capture a disproportionate fraction of the available light. This advantage leads to positive feedbacks where the larger plant can grow faster and gain an even greater proportion of the resource pool (Weiner 1986; Keddy 2001). In contrast, in size-symmetric root competition a larger plant cannot capture a disproportionate fraction of the available resource pool. Without positive feedbacks where a larger plant has a disproportionate advantage in resource capture, grows faster, and eventually gains an even greater proportion of the resources, there are few mechanisms through which competition could systematically exclude certain individuals or species from a community (Weiner 1986; Keddy 2001). Root competition could structure aspects of a plant community by affecting mortality or the regeneration niche (Grubb 1977; Rosenzweig and Abramsky 1993; Hölscher et al. 2002; Cahill and Casper 2002; Suding et al. 2005; Lamb and Cahill 2006), but, symmetric root competition among adult plants likely has little direct impact on the structure of plant communities.

In Chapter 5 I detail a new conceptual model that describes how both shoot competition and root – shoot competition interactions can contribute to the overall importance of competition in plant communities (Figure 5-5). I assume that only size-asymmetric competition can generate the positive feedbacks necessary to directly structure a plant community, and that the importance of asymmetric shoot competition will increase in proportion to shoot competition intensity. Largely symmetric competition, regardless of the intensity, should be unimportant for plant community structure since only positive feedbacks driven by size-asymmetric interactions can directly structure a plant community. Any process, however, that affects the outcome of asymmetric competition may indirectly structure a plant community. Each plant is an integrated organism, and interactions between root and shoot competition can determine whether a plant is able to reach the canopy and succeed in shoot competition (Cahill 1999; 2002).

The most important element of the model is the selection of an aspect of competition that integrates the both symmetric and asymmetric forms of competition with the importance of competition. Total competition intensity is insufficient because it is a function of root competition, shoot competition, and root – shoot competition interactions. I propose that the overall asymmetry of competition may provide a good measure to integrate root and shoot competition, and root – shoot competition interactions (Figure 5-5). Asymmetry may integrate well with importance because root competition only contributes to total asymmetry when it is involved in interactions with shoot competition. Drawing on predictions that the importance of root – shoot competition interactions are most likely to be strong when forms of competition are of similar intensity (Cahill 1999), I suggest that the indirect effects of root competition on community structure should similarly peak when both forms of competition are of similar intensity. With this model we should be able to predict based on total asymmetry when and where competition is likely to be an important mechanism structuring communities. Experimental testing is required to validate the generality of this relationship and to establish the shape of the relationship, as the curvilinear relationship in Figure 5.5 is entirely hypothetical.

My proposed model moves past the dichotomy between root and shoot competition embedded in most theories of plant competition. The model integrates three key empirical facts: 1) Intense root competition can be unlinked to plant community structure (Cahill 2003; Chapter 5). 2) Shoot competition intensity and importance are closely linked (e.g. Grime 2001; Keddy 2001). 3) Root competition can have no effect on plant community structure at low productivity, but an effect at higher productivity, presumably because of root – shoot competition interactions (Rajaniemi et al. 2003). Only the second of these facts is fully accounted for in present theories. Some parts of my model remain speculative, particularly the shape of the relationship between asymmetry and importance. Further research is necessary, particularly to confirm that root – shoot competition interactions should peak in importance when root and shoot competition are of equal intensity.

Conclusions

Plant community structure is the product of complex interactions among a wide range of mechanisms. Plant ecologists have always considered competition to be a key mechanism structuring communities in their theories of plant community structure. The reasons for affording such a central role to competition are numerous, but are due, at least in part, to the enormous impact that competition can be observed to have on individual plants (Keddy 2001). In this thesis I directly address the central question of whether competition, even though it may be intense, is necessarily important for the structure of communities (Welden and Slauson 1986). Having shown that symmetric root competition is unimportant among the numerous mechanisms structuring a rough fescue grassland, I present a new model of competition that makes predictions on the conditions under which both root and shoot competition are likely to be important for plant community structure. With experimental testing and refinement, this integrated view of plant competition has the potential to significantly advance the study of plant ecology.

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7. Appendix A. Selected ecological traits of common rough fescue grassland species.

Table 7-1. Selected ecological traits of common rough fescue grassland species. Trait data are from Gerling H.S., M.G. Willoughby, and A. Schoepf. 1996. A guide to using native plants on disturbed lands. Alberta Agriculture, Food, and Rural Development. Steve Kembel kindly provided the transcription of these data.

Species	Life Form	Life History	Height (Avg m)	Growth Form	Reproduction	Ecology - Physiology	Grazing Response
Achillea millefolium L. (Asteraceae)	Forb	Perennial	0.55	erect solitary mat	rhizome seed aggressive	early cool	increaser
Agropyron spp. (Poaceae)	Gram.	Perennial		erect bunch sod	rhizome seed tiller	early late cool	increaser decreaser
Agrostis scabra Willd. (Poaceae)	Gram.	Perennial	0.5	erect bunch	seed tiller	early cool	increaser decreaser invader
Amelanchier alnifolia (Nutt.) Nutt. ex M. Roemer (Rosaceae)	Gram.	Perennial	0.5	erect bunch	seed tiller	early cool	increaser decreaser invader
Androsace occidentalis Pursh (Primulaceae)	Shrub	Perennial	3.5	erect solitary thicket	rhizome stolons seed	early cool	decreaser
Antennaria microphylla Rydb. (Asteraceae)	Forb	Perennial		trailing mat	stolons seed		
Antennaria neglecta Greene (Asteraceae)	Forb	Perennial		trailing mat	stolons seed		
Artemisia frigida Willd. (Asteraceae)	Forb	Perennial	0.25	erect mat	rhizome seed aggressive	early cool	increaser

Species	Life Form	Life History	Height (Avg m)	Growth Form	Reproduction	Ecology - Physiology	Grazing Response
Artemisia ludoviciana Nutt. (Asteraceae)	Forb	Perennial	0.45	erect bunch mat	rhizome seed aggressive	early warm	increaser
Astragalus agrestis Dougl. ex G. Don (Fabaceae)	Forb	Perennial		erect mat	rhizome seed	early N fixation	
Bouteloua gracilis (Willd. ex Kunth) Lag. ex Griffiths (Poaceae)	Gram.	Perennial	0.25	erect bunch sod	tiller seed rhizome	late warm	increaser
Bromus inermis Leyss. (Poaceae)	Gram.	Perennial	0.85	erect bunch sod	seed tiller rhizome	early cool	increaser decreaser
Campanula rotundifolia L. (Campanulaceae)	Forb	Perennial	0.3	erect solitary bunch	rhizome seed	early warm	increaser
Carex stenophylla Wohl. (Cyperaceae)	Gram.	Perennial	0.115	erect bunch solitary	rhizome seed	early late	increaser
Cerastium arvense L. (Caryophyllaceae)	Forb	Perennial	0.2	erect mat	seed aggressive	early cool	increaser decreaser
Chenopodium album L. (Chenopodiaceae)	Forb	Annual	0.8	erect solitary	seed	early	invader
Comandra umbellata (L.) Nutt. (Santalaceae)	Forb	Perennial	0.2	erect solitary bunch	rhizome seed	early cool parasitic	
Descurainia pinnata (Walt.) Britt. (Brassicaceae)	Forb	Annual	0.425	erect solitary	seed	cool	
Elaeagnus commutata Bernh. ex Rydb. (Elaeagnaceae)	Shrub	Perennial	4	erect solitary thicket	rhizome seed	early cool N fixation	increaser

Species	Life Form	Life History	Height (Avg m)	Growth Form	Reproduction	Ecology - Physiology	Grazing Response
Erigeron philadelphicus L. (Asteraceae)	Forb	Perennial	0.45	erect solitary	seed	early	increaser
Festuca hallii (Vasey) Piper (Poaceae)	Gram.	Perennial	0.4	erect bunch	rhizome seed	early late cool	decreaser
Fragaria virginiana Duchesne (Rosaceae)	Forb	Perennial	0.1	erect solitary mat	stolons seed aggressive	early cool	increaser
Galium boreale L. (Rubiaceae)	Forb	Perennial	0.45	erect solitary bunch	rhizome seed aggressive	early cool	increaser
Geum triflorum Pursh (Rosaceae)	Forb	Perennial	0.3	erect solitary	rhizome seed	early cool	increaser decreaser
Hesperostipa comata (Trin. & Rupr.) Barkworth (Poaceae)	Gram.	Perennial	0.5	erect bunch	seed tiller	late cool	increaser decreaser
Heuchera richardsonii R. Br. (Saxifragaceae)	Forb	Perennial	0.35	erect solitary	rhizome seed	early late cool	increaser
Koeleria macrantha (Ledeb.) J.A. Schultes (Poaceae)	Gram.	Perennial	0.35	erect bunch	seed tiller	early late cool	increaser
Lactuca biennis (Moench) Fern. (Asteraceae)	Forb	Perennial	0.45	erect bunch	rhizome seed aggressive	early warm	
Lepidium densiflorum Schrad. (Brassicaceae)	Forb	Annual		erect solitary	seed		
Melilotus officinalis (L.) Lam. (Fabaceae)	Forb	Annual Biennial	erect solitary	seed	early allelopathic		
Muhlenbergia richardsonis (Trin.) Rydb. (Poaceae)	Gram.	Perennial		erect bunch	rhizome seed		

Species	Life Form	Life History	Height (Avg m)	Growth Form	Reproduction	Ecology - Physiology	Grazing Response
Orthocarpus luteus Nutt. (Scrophulariaceae)	Forb	Annual	0.25	erect solitary	seed		
Oxytropis campestris (L.) DC. (Fabaceae)	Forb	Perennial	0.35	erect bunch	seed	cool N fixation	increaser
Penstemon procerus Dougl. ex Graham (Scrophulariaceae)	Forb	Perennial	0.275	erect bunch	seed aggressive	early cool	increaser
Poa pratensis L. (Poaceae)	Gram.	Perennial	0.55	erect sod	rhizome seed tiller	early cool	invader
Polygonum spp.	Forb	Annual	0.2	trailing solitary	seed		
Populus tremuloides Michx. (Salicaceae)	Tree	Perennial	18	erect solitary	rhizome tiller seed	late cool	decreaser invader
Potentilla arguta Pursh (Rosaceae)	Forb	Perennial	0.7	erect solitary	seed	early	increaser
Potentilla concinna Richards. (Rosaceae)	Forb	Perennial	0.1	trailing solitary	rhizome seed	early cool	increaser
Pulsatilla patens (L.) P. Mill. (Ranunculaceae)	Forb	Perennial	0.25	erect solitary bunch	seed	early late cool	increaser
Rosa arkansana Porter (Rosaceae)	Shrub	Perennial	0.3	erect solitary thicket	rhizome seed	early warm allelopathic	increaser decreaser
Silene spp.	Forb	Annual	0.045	t mat	seed	early	
Solidago missouriensis Nutt. (Asteraceae)	Forb	Perennial	0.35	erect solitary bunch	rhizome seed aggressive	early warm	increaser

Species	Life Form	Life History	Height (Avg m)	Growth Form	Reproduction	Ecology - Physiology	Grazing Response
Stellaria spp.	Forb	Perennial		erect solitary	rhizome seed		
Symphoricarpos occidentalis Hook. (Caprifoliaceae)	Shrub	Perennial	0.75	erect thicket	rhizome seed	early warm	increaser
Symphyotrichum falcatum Lindl. (Asteraceae)	Forb	Perennial	0.55	erect bunch mat	rhizome seed	early late warm	decreaser
Symphyotrichum laeve (L.) A.& D. Löve (Asteraceae)	Forb	Perennial	0.7	erect solitary bunch	rhizome seed	early late warm	increaser decreaser
Taraxacum officinale G.H. Weber ex Wiggers (Asteraceae)	Forb	Perennial		erect solitary	seed		
Thalictrum venulosum Trel. (Ranunculaceae)	Forb	Perennial	0.55	erect solitary	rhizome seed aggressive	early cool	increaser
Thermopsis rhombifolia (Nutt. ex Pursh) Nutt. ex Richards. (Fabaceae)	Forb	Perennial	0.25	erect bunch	rhizome seed aggressive	early cool N fixation	increaser
Vicia americana Muhl. ex Willd. (Fabaceae)	Forb	Perennial	0.65	climbing solitary bunch	seed	early late cool N fixation	decreaser

8. Appendix B: Detailed structural equation model results-Chapter 4

Table 8-1 Un-standardized and standardized path coefficients, the standard error of the unstandardized coefficients and t-test results from the structural equation model of species richness. The paths described in each section of the table were from the variables in lower case to the variable at the top in upper case.

	Unstand. path coefficients	**Std Error**	**t-value**	**p-value**	**Standard. coefficients**
Litter					
Initial Litter	1.187	0.338	3.507	<0.001	0.29
Nitrogen	0.467	0.072	6.514	0	0.384
Water	0.293	0.061	4.827	0	0.228
Shade	0.615	0.089	6.949	0	0.478
Shoot Biomass	0.441	0.18	2.453	0.015	0.293
Shoot Biomass					
Nitrogen	0.03	0.057	0.528	0.598	0.037
Water	0.156	0.043	3.618	<0.001	0.182
Shade	-0.446	0.051	-8.745	<0.001	-0.522
Root Biomass					
Nitrogen	0.014	0.068	0.2	0.842	0.016
Water	-0.255	0.073	-3.511	0.001	-0.28
Shade	-0.486	0.084	-5.798	<0.001	-0.533
Light Interception					
Shoot Biomass	0.064	0.049	1.301	0.196	0.093
Litter Biomass	0.053	0.027	1.946	0.054	0.115
Shade	0.533	0.042	12.792	<0.001	0.909
Water	0.108	0.035	3.098	0.002	0.183
Nitrogen	0.097	0.024	4.126	<0.001	0.175
Species Richness					
Shoot Biomass	0.148	0.1	1.478	0.142	0.139
Root Biomass	0.02	0.114	0.173	0.863	0.02
Litter	-0.166	0.067	-2.489	0.014	-0.236
Initial Species Richness	0.255	0.097	2.636	0.009	0.2
Light Interception	0.032	0.223	0.142	0.887	0.021
Nitrogen	-0.125	0.053	-2.356	0.020	-0.147
Water	0.043	0.071	0.601	0.549	0.047
Shade	-0.345	0.165	-2.09	0.039	-0.381
Shoot Biomass- Root Biomass Covariance	0.039	0.011	3.442	<0.001	0.226

Table 8-2 Total direct and indirect effects in the species richness model. These effects were calculated using standardized path coefficients. Non-significant effects are indicated by "ns", while a dash indicates a path that was not included in the model.

Litter Cover	**Direct**	**Indirect**	**Total**
Initial Litter Cover	0.290	-	0.290
Nitrogen	0.384	ns	0.384
Water	0.228	0.053	0.281
Shade	0.478	-0.153	0.325
Shoot Biomass	0.293	-	0.293

Shoot Biomass	**Direct**	**Indirect**	**Total**
Nitrogen	ns	-	ns
Water	0.182	-	0.182
Shade	-0.522	-	-0.522

Root Biomass	**Direct**	**Indirect**	**Total**
Nitrogen	ns	-	ns
Water	-0.280	-	-0.280
Shade	-0.533	-	-0.533

Light Interception	**Direct**	**Indirect**	**Total**
Shoot Biomass	ns	0.034	0.034
Litter Cover	0.115	-	0.115
Shade	0.909	0.037	0.946
Water	0.183	0.032	0.215
Nitrogen	0.175	0.044	0.219

Species Richness	**Direct**	**Indirect**	**Total**
Shoot Biomass	ns	-0.069	-0.069
Root Biomass	ns	-	ns
Litter Cover	-0.236	ns	-0.236
Initial Richness	0.200	-	0.200
Light Interception	ns	-	ns
Nitrogen	-0.147	-0.091	-0.238
Water	ns	-0.054	-0.054
Shade	-0.381	-0.113	-0.494
Initial Litter	-	-0.068	-0.068

Table 8-3 Un-standardized and standardized path coefficients, the standard error of the unstandardized coefficients and t-test results from the structural equation model of species richness. The paths described in each section of the table were from the variables in lower case to the variable at the top in upper case.

	Unstand. path coefficients	**Std Error**	**t-value**	**p-value**	**Standard. coefficients**
Litter					
Initial Litter	1.187	0.338	3.507	<0.001	0.29
Nitrogen	0.467	0.072	6.514	<0.001	0.384
Water	0.293	0.061	4.827	<0.001	0.228
Shade	0.615	0.089	6.949	<0.001	0.478
Shoot Biomass	0.441	0.18	2.453	0.015	0.293
Shoot Biomass					
Nitrogen	0.03	0.057	0.528	0.598	0.037
Water	0.156	0.043	3.618	<0.001	0.182
Shade	-0.446	0.051	-8.745	<0.001	-0.522
Root Biomass					
Nitrogen	0.014	0.068	0.2	0.842	0.016
Water	-0.255	0.073	-3.511	<0.001	-0.28
Shade	-0.486	0.084	-5.798	<0.001	-0.533
Light Interception					
Shoot Biomass	0.064	0.049	1.301	0.196	0.093
Litter Biomass	0.053	0.027	1.946	0.054	0.115
Shade	0.533	0.042	12.792	<0.001	0.909
Water	0.108	0.035	3.098	0.002	0.183
Nitrogen	0.097	0.024	4.126	<0.001	0.175
Species Evenness					
Shoot Biomass	0.028	0.048	0.582	0.562	0.083
Root Biomass	-0.008	0.026	-0.311	0.756	-0.025
Litter	-0.066	0.016	-4.079	<0.001	-0.294
Initial Species Evenness	0.151	0.059	2.58	0.011	0.136
Light Interception	-0.137	0.079	-1.73	0.086	-0.28
Nitrogen	0.069	0.026	2.649	0.009	0.254
Water	0.004	0.025	0.175	0.861	0.015
Shade	0.039	0.066	0.59	0.556	0.135
Shoot Biomass- Root Biomass Covariance	0.039	0.011	3.442	<0.001	0.226

Table 8-4 Total direct and indirect effects in the evenness model. These effects were calculated using standardized path coefficients. Non-significant effects are indicated by "ns", while a dash indicates a path that was not included in the model.

Litter Cover	**Direct**	**Indirect**	**Total**
Initial Litter Cover	0.290	-	0.290
Nitrogen	0.384	ns	0.384
Water	0.228	0.053	0.281
Shade	0.478	-0.153	0.325
Shoot Biomass	0.293	-	0.293

Shoot Biomass	**Direct**	**Indirect**	**Total**
Nitrogen	ns	-	ns
Water	0.182	-	0.182
Shade	-0.522	-	-0.522

Root Biomass	**Direct**	**Indirect**	**Total**
Nitrogen	ns	-	ns
Water	-0.280	-	-0.280
Shade	-0.533	-	-0.533

Light Interception	**Direct**	**Indirect**	**Total**
Shoot Biomass	ns	0.034	0.034
Litter Cover	0.115	-	0.115
Shade	0.909	0.037	0.946
Water	0.183	0.032	0.215
Nitrogen	0.175	0.044	0.219

Species Evenness	**Direct**	**Indirect**	**Total**
Shoot Biomass	ns	-0.095	-0.095
Root Biomass	ns	-	ns
Litter Cover	-0.294	-0.032	-0.326
Initial Evenness	0.136	-	0.136
Light Interception	-0.28	-	-0.28
Nitrogen	0.254	-0.162	0.092
Water	ns	-0.134	-0.134
Shade	ns	-0.350	-0.350
Initial Litter	-	-0.085	-0.085

9. Appendix C: Results of the NMS analysis of cover data (Chapter 5)

A single NMS ordination axis (McCune and Grace 2002) using percent cover data was used to summarize plant community structure. PC-Ord 4 (McCune and Mefford 1999) was used to calculate a single axis ordination using the Sorenson distance measure and 1000 randomized runs. The resulting solution had a final stress of 38.475 and explained 53.8% of the variation in the species data.

The axis represents a gradient from *Poa pratensis* and *Galium boreal* dominated grassland to *Hesperostipa comata, Bouteloua gracilis,* and *Artemisia frigida* dominated grassland. Species with a correlation coefficient of at least 0.200 between species abundance and the ordination axis are listed in table B1.

Table 9-1 Correlation coefficients and R^2-values between species abundances and position on the ordination axis.

Species	r	R^2
Poa pratensis	-0.675	0.456
Bouteloua gracilis	0.604	0.365
Galium boreale	-0.549	0.301
Artemisia frigida	0.423	0.179
Hesperostipa comata	0.407	0.165
Orthocarpus luteus	0.381	0.145
Symphyotrichum falcatum	0.362	0.131
Koeleria macrantha	0.333	0.111
Fragaria virginiana	-0.309	0.095
Agropyron spp.	-0.277	0.077
Anemone patens	0.277	0.077
Symphyotrichum laeve	-0.274	0.075
Achillea millefolium	-0.26	0.068
Artemisia ludoviciana	-0.221	0.049
Vicia americana	-0.218	0.048
Androsace septentrionalis	0.215	0.046
Populus tremuloides	-0.215	0.046
Symphoricarpos occidentalis	-0.208	0.043

10. Appendix D: Detailed structural equation model results (Chapter 5)

Table 10-1 Un-standardized and standardized path coefficients, the standard error of the unstandardized coefficients and t-test results from the structural equation model of species richness. The paths described in each section of the table were from the variables in lower case to the variable at the top in bold.

	Unstand. path coefficients	Std Error	t-value	p-value	Standard. coefficients
Shoot Biomass					
Nitrogen Treatment	0.197	0.028	7.077	<0.001	0.344
Species Richness	0.040	0.066	0.604	0.547	0.050
Site Conditions	-2.787	0.441	-6.318	<0.001	-0.361
Root Biomass					
Nitrogen Treatment	0.115	0.047	2.433	0.016	0.136
Species Richness	-0.052	0.072	-0.726	0.469	-0.045
Site Conditions	-2.725	1.169	-2.330	0.021	-0.239
Soil Moisture					
Root Biomass	-0.005	0.004	-1.107	0.270	-0.071
Shoot Biomass	-0.022	0.009	-2.526	0.012	-0.216
Nitrogen Treatment	-0.017	0.004	-3.789	<0.001	-0.297
Site Conditions	-0.214	0.042	-5.025	<0.001	-0.277
Light Interception					
Shoot Biomass	0.289	0.044	6.639	<0.001	0.388
Topographic Position	-2.641	0.405	-6.524	<0.001	-0.293
Competition Intensity					
Soil Moisture	-4.654	1.981	-2.349	0.020	-0.127
Light Intensity	-0.335	0.318	-1.053	0.294	-0.068
Root Biomass	-0.062	0.162	-0.383	0.702	-0.025
Species Competitive Ability	-0.836	0.470	-1.778	0.077	-0.695
Species Richness					
Soil Moisture	2.448	1.356	1.805	0.073	0.193
Nitrogen Treatment	0.119	0.053	2.24	0.026	0.164
Competition Intensity	0.000	0.016	-0.016	0.987	-0.001
Site Conditions	-0.279	0.483	-0.578	0.564	-0.029
Shoot Biomass with Root Biomass	0.012	0.010	1.171	0.243	0.101

Table 10-2 Un-standardized and standardized path coefficients, the standard error of the unstandardized coefficients and t-test results from the structural equation model of species evenness. The paths described in each section of the table were from the variables in lower case to the variable at the top in bold.

	Unstand. path coefficients	**Std Error**	**t-value**	**p-value**	**Standard. coefficients**
Shoot Biomass					
Nitrogen Treatment	0.204	0.025	8.294	<0.001	0.356
Species Evenness	-0.255	0.537	-0.475	0.635	-0.039
	-2.804	0.346	-8.105	<0.001	-0.362
Root Biomass					
Nitrogen Treatment	0.118	0.048	2.464	0.015	0.139
Species Evenness	-0.374	0.398	-0.94	0.348	-0.039
Site Conditions	-2.676	1.039	-2.576	0.011	-0.234
Soil Moisture					
Root Biomass	-0.005	0.004	-1.257	0.21	-0.075
Shoot Biomass	-0.020	0.008	-2.461	0.015	-0.199
Nitrogen Treatment	-0.017	0.004	-3.982	<0.001	-0.303
Site Conditions	-0.210	0.03	-6.944	<0.001	-0.272
Light Interception					
Shoot Biomass	0.289	0.044	6.639	<0.001	0.388
Topographic Position	-2.641	0.404	-6.532	<0.001	-0.293
Competition Intensity					
Soil Moisture	-4.688	1.969	-2.38	0.018	-0.128
Light Intensity	-0.329	0.308	-1.067	0.287	-0.067
Root Biomass	-0.050	0.161	-0.309	0.758	-0.020
Species Competitive Ability	-0.849	0.455	-1.864	0.064	-0.697
Species Evenness					
Soil Moisture	0.250	0.102	2.441	0.016	0.162
Nitrogen Treatment	0.022	0.007	3.020	0.003	0.254
Competition Intensity	0.003	0.002	1.962	0.051	0.078
Site Conditions	0.105	0.096	1.091	0.277	0.088
Shoot Biomass with Root Biomass	0.012	0.010	1.134	0.258	0.096

Table 10-3 Un-standardized and standardized path coefficients, the standard error of the unstandardized coefficients and t-test results from the structural equation model of community composition. The paths described in each section of the table were from the variables in lower case to the variable at the top in bold.

	Unstand. path coefficients	Std Error	t-value	p-value	Standard. coefficients
Shoot Biomass					
Nitrogen Treatment	0.216	0.024	9.028	<0.001	0.377
Community Composition	-0.091	0.019	-4.726	<0.001	-0.316
Site Conditions	-1.722	0.381	-4.522	<0.001	-0.222
Root Biomass					
Nitrogen Treatment	0.133	0.051	2.591	0.01	0.158
Community Composition	-0.123	0.029	-4.292	<0.001	-0.290
Site Conditions	-1.214	1.026	-1.184	0.238	-0.106
Soil Moisture					
Root Biomass	-0.007	0.004	-1.601	0.111	-0.100
Shoot Biomass	-0.023	0.009	-2.666	0.008	-0.233
Nitrogen Treatment	-0.016	0.004	-3.703	<0.001	-0.287
Site Conditions	-0.224	0.035	-6.334	<0.001	-0.290
Light Interception					
Shoot Biomass	0.254	0.043	5.87	<0.001	0.341
Topographic Position	-2.149	0.431	-4.989	<0.001	-0.239
Community Composition	-0.037	0.011	-3.269	0.001	-0.176
Competition Intensity					
Soil Moisture	-4.472	2.004	-2.232	0.027	-0.122
Topographic Position	-0.400	0.336	-1.192	0.235	-0.081
Root Biomass	-0.100	0.162	-0.619	0.537	-0.040
Species Competitive Ability	-0.809	0.468	-1.728	0.086	-0.698
Community Composition					
Soil Moisture	-3.662	3.698	-0.99	0.323	-0.105
Nitrogen Treatment	0.100	0.118	0.845	0.399	0.050
Competition Intensity	-0.068	0.043	-1.578	0.116	-0.071
Site Conditions	11.574	1.574	7.354	<0.001	0.429
Shoot Biomass with Root Biomass	0.004	0.008	0.497	0.620	0.034

11. Appendix E. Raw Phenology Data (Chapter 2)

Table 11-1. Raw phenology data for *Achillea millefolium* (AchMil), *Artemisia frigida* (ArtFrig), *Artemesia ludoviciana* (ArtLud), *Symphyotrichum laeve* (SympLae), and *Cerastium arvense* (CeraArv). Average indicates the average % greenness (% leaf area that was not yell owed or otherwise showing signs of senescence), standard deviation of the greenness, and the number of observations (out of a possible 22) made. "C" indicates control plots, "N" nitrogen addition, "W" water addition, and "NW" nitrogen and water (see Chapter 2 for details). Surveys were made weekly from June 1, 2005 through September 21, 2005, with the exception of August 10th.

Tmt	Date	AchMil			ArtFrig			ArtLud			SympLae			CeraArv		
		Avg	SD	N	Avg	SD	N	Avg	SD	N	Avg	SD	N	Avg	SD	N
C	01-Jun-05	98.2	2.1	19	68	n/a	1	98.9	0.4	8	95.7	7	7	95.4	3.8	14
C	08-Jun-05	98.3	0.8	19	80	n/a	1	98.9	0.4	8	88	25.7	7	95.6	2.3	15
C	15-Jun-05	98.6	0.5	19	88	n/a	1	99	0.5	8	98.5	0.8	6	96.4	2.6	15
C	22-Jun-05	98.4	1	16	87	n/a	1	98.9	0.4	8	98.8	0.4	6	93.9	3.3	11
C	29-Jun-05	98.4	0.8	19	96	n/a	1	98.3	0.5	8	99	0	6	95.4	2.7	13
C	06-Jul-05	97.9	0.8	18	97	n/a	1	97.9	0.8	8	98.7	0.8	6	61.7	29.7	13
C	13-Jul-05	98.1	0.8	18	98	n/a	1	98.3	0.7	8	98.8	0.4	6	51.7	30.3	13
C	20-Jul-05	96.5	2.5	19	98	n/a	1	98.1	0.6	8	99	0	6	59.1	26	15
C	27-Jul-05	94.4	3.6	17	97	n/a	1	97.3	1.4	8	97.7	0.5	6	47.8	23.8	13
C	03-Aug-05	90.9	9.6	19	94	n/a	1	94.7	3.7	9	97.8	0.4	5	31.7	22.8	14
C	10-Aug-05															
C	17-Aug-05	72.9	11	19	78	n/a	1	84.9	5.2	8	90.2	2.9	6	20.5	13.1	12
C	24-Aug-05	61.6	18	17	70	n/a	1	73.1	7.5	8	86.4	5.6	7	18.2	15.2	12
C	31-Aug-05	45.4	17.9	18	70	n/a	1	72.1	8.2	8	82.6	8.7	7	12.7	8.8	12
C	07-Sep-05	36.3	18.3	18	40	n/a	1	56	17.3	8	69.3	15.7	7	9	7.1	12
C	14-Sep-05	28.4	17	18	40	n/a	1	40.1	20.3	8	56.4	15.7	7	10.1	9.1	13
C	21-Sep-05	21.6	13.8	18	50	n/a	1	12.5	15.5	5	37.1	19.5	7	8.5	7.9	13

Tmt	Date	AchMil			ArtFrig			ArtLud			SympLae			CeraArv		
		Avg	SD	N	Avg	SD	N	Avg	SD	N	Avg	SD	N	Avg	SD	N
N	01-Jun-05	98.9	0.3	17	81	1.8	4	99.4	0.5	5	99.3	0.5	4	97.4	1.2	11
N	08-Jun-05	98.8	0.4	18	86.3	2.6	4	99.4	0.5	5	98.8	1.3	4	97	1.2	10
N	15-Jun-05	98.7	0.6	17	93.8	2.5	4	99.2	0.4	5	99	0	4	97.9	0.4	8
N	22-Jun-05	98.8	0.6	18	95.3	1	4	98.8	0.5	4	99.3	0.6	3	95.4	2.3	10
N	29-Jun-05	98.4	0.7	17	97.8	1.5	4	98.8	0.4	5	98.8	0.5	4	95.8	3.4	8
N	06-Jul-05	98.1	1.1	16	98.5	0.6	4	98.7	0.5	6	99	0	3	81	12.9	9
N	13-Jul-05	97.8	1.3	16	99	0	4	98.3	0.8	6	99	0	3	58	31.7	11
N	20-Jul-05	96.9	2.1	18	99	0	4	98.2	0.8	6	99	0	3	69.1	21.5	10
N	27-Jul-05	92.5	5.4	16	98.5	0.6	4	97.8	0.4	6	98.3	0.6	3	59.6	28.2	8
N	03-Aug-05	90.3	5.4	17	97.3	0.5	4	96.3	2.2	6	96.7	1.5	3	35.6	21	10
N	10-Aug-05															
N	17-Aug-05	73.4	13.8	16	89.5	4.8	4	79.3	12.5	6	75.7	9.8	3	26.9	16.5	7
N	24-Aug-05	65.7	16.1	18	78.3	7.2	4	73.7	6.7	6	80.7	9.3	3	24.6	11.6	7
N	31-Aug-05	58.7	16.5	19	79	4.5	4	79.2	6.6	6	66.7	5.8	3	14	8	9
N	07-Sep-05	50.5	14.5	19	63.3	7.6	3	72.5	7.6	6	66.7	5.8	3	15.3	11.8	9
N	14-Sep-05	28.3	19	18	57.5	13.2	4	45	16.6	5	56.7	10.4	3	20.2	15.1	10
N	21-Sep-05	23.7	18.1	17	55	7.1	4	26	31.1	4	38.3	2.9	3	12.5	13.2	8
W	01-Jun-05	98.8	0.4	16	50	n/a	1	98.9	0.4	7	98.8	0.4	5	87.9	18.8	13
W	08-Jun-05	98.5	1	17	83	n/a	1	99	0	7	98.8	0.8	6	95.2	3.3	10
W	15-Jun-05	98.7	0.5	16	88	n/a	1	99.1	0.4	8	97.8	2.9	6	96.8	2.6	11
W	22-Jun-05	98.3	0.6	14	90	n/a	1	98.8	0.5	8	80.2	42	5	95.5	2.3	11
W	29-Jun-05	98.6	0.8	17	96	n/a	1	98.9	0.4	8	97.2	4	5	96.9	1.6	12
W	06-Jul-05	98.2	1	17	98	n/a	1	98.8	0.5	8	99	0	6	84.9	14.3	9
W	13-Jul-05	98.2	0.9	16	98	n/a	1	98.8	0.5	8	98.7	0.5	6	64.9	23.7	10
W	20-Jul-05	97.6	1.6	16	98	n/a	1	98.4	0.7	8	98.7	0.5	6	57.2	33.6	8
W	27-Jul-05	95.4	3.4	17	97	n/a	1	97.9	1.2	8	97.8	1.9	6	69.2	29.9	9

Tmt	Date	AchMil			ArtFrig			ArtLud			SympLae			CeraArv		
		Avg	SD	N	Avg	SD	N	Avg	SD	N	Avg	SD	N	Avg	SD	N
W	03-Aug-05	93.8	3.3	17	97	n/a	1	96.9	2.3	7	97.8	0.4	6	52.6	28.7	9
W	10-Aug-05															
W	17-Aug-05	81.4	9.5	16	90	n/a	1	86.8	7.4	8	92	4.3	5	41.1	25.8	8
W	24-Aug-05	78.5	15.6	17	80	n/a	1	79.4	7.7	8	90.7	7.1	6	31.9	24.4	8
W	31-Aug-05	67.4	13.5	16	70	n/a	1	73.4	9.3	7	84.2	9.6	6	14.4	15.5	5
W	07-Sep-05	60.9	17.8	17	71	n/a	1	66.1	12.2	7	78.3	11.7	6	14.1	16.7	6
W	14-Sep-05	45.5	17.8	16	60	n/a	1	46.4	22.7	8	67	14.8	5	18	16	9
W	21-Sep-05	31.5	20.4	15	40	n/a	1	31.8	20.2	8	50.8	17.2	6	9.9	14.6	7
NW	01-Jun-05	98.9	0.3	19	80	4.1	4	98.7	0.5	7	99	0	4	95.1	3.5	9
NW	08-Jun-05	98.8	0.5	19	86.5	3.7	4	99	0.6	7	99.3	0.5	4	97.3	1.2	6
NW	15-Jun-05	98.8	0.6	19	94.8	0.5	4	98.9	0.4	7	98.8	0.5	4	97.4	1.3	9
NW	22-Jun-05	98.8	0.4	18	96.3	1.5	4	98.9	0.4	7	67	55.4	3	89.8	12.4	6
NW	29-Jun-05	98.4	1	19	98.5	1	4	98.4	0.8	7	98.3	0.5	4	97.7	0.5	7
NW	06-Jul-05	98.3	1	19	98.3	0.5	4	98.1	0.7	7	98.3	0.6	3	73.7	34.6	6
NW	13-Jul-05	98.4	0.8	17	99	0	4	98.1	0.4	7	98.3	1	4	81.7	7.7	7
NW	20-Jul-05	97.8	1.2	19	99	0	4	98.3	0.5	7	98.8	0.5	4	70.2	37.5	5
NW	27-Jul-05	96.3	2.5	19	98.8	0.5	4	98	0.6	7	98.5	0.6	4	81.3	9	7
NW	03-Aug-05	94.4	3.6	18	98.3	1	4	96.6	1.7	7	97.8	0.5	4	57.3	30	5
NW	10-Aug-05															
NW	17-Aug-05	84.5	7.1	19	91.8	3.3	4	87.9	4.2	7	93.3	2.9	3	51.1	28.6	7
NW	24-Aug-05	77.2	11.6	18	82.4	5.7	5	82.8	2.2	6	86.5	11.4	4	44.6	20	5
NW	31-Aug-05	69.9	11.2	20	79.5	7.1	4	76.6	3.9	7	84.5	6.4	4	27.9	22.9	6
NW	07-Sep-05	65.7	10.1	21	70	10	3	59.4	24.7	7	75	5.8	4	29.2	22.1	6
NW	14-Sep-05	44.1	21.3	19	64.5	5.3	4	40.4	25.8	6	62.5	10.4	4	30.5	16.7	6
NW	21-Sep-05	29.6	21.7	19	56.3	11.1	4	25.4	23.7	6	50.8	18.3	4	14.1	10.9	7

Table 11-2. Raw phenology data for *Galium boreale* (GalBor), *Geum triflorum* (GeuTri), *Lactuca biennis* (LactBie), *Rosa arkansana* (RosArk), and *Solidago missouriensis* (SolMis). Average indicates the average % greenness (% leaf area that was not yellowed or otherwise showing signs of senescence), standard deviation of the greenness, and the number of observations (out of a possible 22) made. "C" indicates control plots, "N" nitrogen addition, "W" water addition, and "NW" nitrogen and water (see Chapter 2 for details). Surveys were made weekly from June 1, 2005 through September 21, 2005, with the exception of August 10th.

Tmt	Date	GalBor			GeuTri			LactBie			RosArk			SolMis		
		Avg	SD	N	Avg	SD	N	Avg	SD	N	Avg	SD	N	Avg	SD	N
C	01-Jun-05	98.4	1.9	14	94.9	2.4	10	99	0	4	74.8	16	13	98.4	2.1	15
C	08-Jun-05	98.8	0.6	14	96.5	1.6	10	98.6	0.5	5	86.6	7	14	98.9	0.4	14
C	15-Jun-05	98.9	0.4	14	97.1	1.1	10	99	0	5	91.9	3.5	14	98.9	0.3	14
C	22-Jun-05	98.5	0.7	14	96.9	1.2	9	98.8	0.5	4	95.4	1.4	12	98.8	0.4	12
C	29-Jun-05	98.4	0.6	14	97.6	0.5	10	99	0	4	96.1	2.1	14	98.7	0.7	12
C	06-Jul-05	97.9	0.8	14	97.3	0.7	10	99	0	4	97.1	1.2	14	98.7	0.5	12
C	13-Jul-05	97.9	0.8	14	97.6	0.5	10	98.8	0.5	4	97.6	1.2	14	98.6	0.5	12
C	20-Jul-05	97.4	1	14	97.1	1.2	10	98.8	0.5	4	97.6	1.1	14	98.8	0.5	12
C	27-Jul-05	95.7	2	15	96.7	1.6	9	98.5	0.6	4	94.4	2.8	14	97.7	1.3	13
C	03-Aug-05	85.2	7.3	14	85.9	7.7	10	97	0.8	4	87.4	6	14	97.4	1.3	13
C	10-Aug-05															
C	17-Aug-05	59.9	10.1	14	61.3	12.9	10	71	8.4	4	67.8	9.1	14	87.2	7.1	12
C	24-Aug-05	57.3	11.5	14	63.2	14.1	10	64.3	10.4	4	60	14.9	14	78.7	10.4	13
C	31-Aug-05	48.1	16.3	14	60.5	10.3	10	57.5	5	4	50.5	7.4	14	77.1	11.3	13
C	07-Sep-05	33.9	20	14	53.4	8.8	10	45.8	10.9	4	42.9	12.5	14	67.5	12.8	13
C	14-Sep-05	14.1	11.7	13	53.5	4.7	10	45	10	4	37.4	17.1	14	56.2	17.1	13
C	21-Sep-05	2.2	4	7	42.1	10.6	10	0	0	0	16.6	11.4	14	43.8	17.4	14
N	01-Jun-05	98.7	0.6	13	96.1	1.4	11	99	0	4	76.8	11.7	16	98.3	1.6	14
N	08-Jun-05	98.5	0.7	13	97.7	0.9	11	99	0	4	86.3	6.9	16	98.5	1.2	14
N	15-Jun-05	98.8	0.4	13	97.8	0.6	11	98.8	0.5	4	94.4	3.2	16	98.3	2.5	13
N	22-Jun-05	98.8	0.6	14	97.9	0.5	11	98.5	0.6	4	95.1	2.2	14	98.8	0.4	9

Tmt	Date	GalBor			GeuTri			LactBie			RosArk			SolMis		
		Avg	SD	N	Avg	SD	N	Avg	SD	N	Avg	SD	N	Avg	SD	N
N	29-Jun-05	98.2	1.2	14	98.2	0.8	11	98.8	0.5	4	97.2	1.1	17	98.7	0.6	11
N	06-Jul-05	98.1	1.1	14	98.1	0.6	10	99	0	3	97.7	1.6	15	98.6	0.7	10
N	13-Jul-05	98.1	1	14	98.2	0.6	10	98.5	0.6	4	98.1	0.6	16	98.3	1.1	10
N	20-Jul-05	97.1	2.3	14	97.5	1.6	11	98.5	1	4	97.5	1.3	15	98.6	0.7	11
N	27-Jul-05	96.4	3.3	14	94.7	4.8	11	98.5	0.6	4	95.3	2.5	16	98.2	1.5	11
N	03-Aug-05	89.1	9	14	83.5	13.6	11	96.3	1.3	4	89.6	9.3	16	96.7	2.4	11
N	10-Aug-05															
N	17-Aug-05	63.1	20.5	14	65.8	9.2	11	63.8	7.5	4	68.6	14.6	16	78.4	10.5	10
N	24-Aug-05	60.1	14.3	13	72.8	12.3	10	56.3	11.1	4	65	9.3	16	77.8	9.1	9
N	31-Aug-05	46.3	19.1	13	61.7	12.4	11	47.5	22.5	4	56.3	9.1	16	71.8	7.7	9
N	07-Sep-05	32.2	22.3	13	60.1	11.5	11	28.3	22.5	4	46.9	16.4	16	61.1	12.2	9
N	14-Sep-05	19.1	16.7	13	49.5	12.3	11	20	14.1	4	38	17.2	14	52.5	17.3	11
N	21-Sep-05	4.4	9.2	6	46.8	13.8	11	0	0	0	21.3	16.9	15	41.6	24.1	11
W	01-Jun-05	98.9	0.5	15	94.9	3.2	7	99	0	6	70.5	19.7	13	98.7	0.7	12
W	08-Jun-05	98.7	0.5	15	97.1	1.2	7	97.5	3.7	6	84.8	6.3	13	98.8	0.7	12
W	15-Jun-05	99	0	15	97.1	1.2	7	98.8	0.4	6	90.5	4.7	13	98.8	0.5	12
W	22-Jun-05	98.9	0.4	14	97.8	0.4	6	98.8	0.4	6	93.9	2.1	12	98.7	0.5	11
W	29-Jun-05	98.7	0.5	15	97.9	0.7	7	99	0	6	96.7	1.4	13	98.3	0.9	11
W	06-Jul-05	98.7	0.6	15	97.4	0.8	7	99	0	6	96.8	2.6	13	98	0.8	11
W	13-Jul-05	98.3	0.8	15	97.7	0.5	7	99	0	6	98	1.2	13	98.4	0.5	11
W	20-Jul-05	98.4	0.6	15	97.9	0.7	7	98.7	0.5	6	97.2	1.4	13	98.5	0.5	11
W	27-Jul-05	98	0.5	15	94.9	4.6	7	98	0.9	6	95.5	2.8	13	97.9	0.8	11
W	03-Aug-05	95.7	2.9	15	93.9	4.5	7	97.8	0.4	6	87.7	11.7	13	97.4	0.7	11
W	10-Aug-05															
W	17-Aug-05	86.5	6.9	14	78	8.3	7	80.5	11.9	6	80.4	12.1	13	90.8	2.6	11
W	24-Aug-05	79.5	5.8	15	75.3	5.8	7	73.5	5.9	6	69.3	12.8	12	80.3	6.6	11

Tmt	Date	GalBor			GeuTri			LactBie			RosArk			SolMis		
		Avg	SD	N	Avg	SD	N	Avg	SD	N	Avg	SD	N	Avg	SD	N
W	31-Aug-05	72	9.7	15	64.6	6.4	7	68.8	6.6	6	50.2	20.1	11	76.4	9	11
W	07-Sep-05	58.7	13	15	64.4	8.6	7	56.5	7.2	6	47.5	16.4	13	69.3	6.1	11
W	14-Sep-05	42.5	19.3	15	57	6.8	7	40	16.7	6	44.3	13	12	59.5	7.7	11
W	21-Sep-05	14	16.9	14	52.3	9.6	7	0.3	0.8	1	21.3	15.8	13	47.7	13.3	11
NW	01-Jun-05	98.9	0.4	15	96	1.4	5	98.5	0.5	6	72.9	21.2	16	98.5	1	11
NW	08-Jun-05	98.3	2.2	16	97.6	1.5	5	99	0	6	83.4	19.2	16	99.1	0.6	9
NW	15-Jun-05	98.7	0.8	17	98.3	0.5	4	98.8	0.4	6	91.7	5.8	16	97.5	2.9	10
NW	22-Jun-05	98.8	0.4	14	98.4	0.5	5	99	0	6	95.4	2.1	14	98.4	1.2	8
NW	29-Jun-05	98.8	0.4	17	98.6	0.5	5	98.3	1.6	6	97.2	2.1	16	98.9	0.3	9
NW	06-Jul-05	98.8	0.4	16	98.6	0.5	5	98.8	0.4	6	98.1	1	16	98.5	1	10
NW	13-Jul-05	98.5	0.5	16	98.7	0.8	6	98.9	0.4	7	98.3	1	16	98.8	0.4	9
NW	20-Jul-05	98.1	1.4	16	98	1	5	98.9	0.4	7	97.9	0.6	15	98.8	0.7	9
NW	27-Jul-05	97.9	1	15	97.2	0.8	5	98.4	0.5	7	91.3	23.8	16	98.3	0.9	9
NW	03-Aug-05	95.4	3.2	14	94.2	5.3	5	96.9	1.5	7	91.8	4.2	16	97.4	1	9
NW	10-Aug-05															
NW	17-Aug-05	85	6.7	13	87	8	5	83.3	11.3	7	80.1	10.8	16	92.7	2.3	9
NW	24-Aug-05	76.4	7.9	15	81.4	7.4	5	74.3	9.8	7	67.7	10.7	16	90.6	3.2	9
NW	31-Aug-05	69.4	9.8	15	77.4	5.1	5	64.3	10.6	7	61.3	9.2	16	77.4	9.9	9
NW	07-Sep-05	56.9	17.8	14	73.4	6.1	5	63.4	17.1	7	54.8	8.9	16	72.6	9.2	9
NW	14-Sep-05	42.5	23	16	59.8	18.6	5	46.4	18.4	7	44.9	15.3	16	61.9	12.2	9
NW	21-Sep-05	20.9	19.8	14	56.6	7.4	5	2.4	5.6	3	27.3	17.6	16	48.4	21.7	9

Table 11-3. Raw phenology data for *Carex stenophylla* (CareSte), *Festuca hallii* (FesHal), *Koeleria macrantha* (KoelMac), *Poa pratensis* (PoaPra), and *Hesperostipa comata* (HespCom). Average indicates the average % greenness (% leaf area that was not yellowed or otherwise showing signs of senescence), standard deviation of the greenness, and the number of observations (out of a possible 22) made. "C" indicates control plots, "N" nitrogen addition, "W" water addition, and "NW" nitrogen and water (see Chapter 2 for details). Surveys were made weekly from June 1, 2005 through September 21, 2005, with the exception of August 10th. Note that *Koeleria macrantha* was not surveyed following August 3, 2005.

Tmt	Date	CareSte			FesHal			KoelMac			PoaPra			HespCom		
		Avg	SD	N	Avg	SD	N	Avg	SD	N	Avg	SD	N	Avg	SD	N
C	01-Jun-05	96.7	1.6	21	96.6	1.7	20	94.8	2.9	10	95.9	2.3	18	88.4	5.3	17
C	08-Jun-05	97.4	1.7	21	97.5	1.3	20	96.5	1.9	11	96.8	1.2	18	91.6	11.1	17
C	15-Jun-05	98.7	0.5	21	98.2	0.4	18	98.1	1	11	97.2	1.1	18	93.5	2.2	17
C	22-Jun-05	98.3	0.7	19	98.1	0.5	17	98.1	0.6	10	97.6	1.3	16	97.4	1.1	14
C	29-Jun-05	98	1	21	97.9	0.5	19	98.5	0.5	12	97.4	0.6	17	97.9	0.8	17
C	06-Jul-05	97.6	0.9	21	98	0.5	21	98.2	0.4	11	97.8	0.4	17	97.9	0.3	17
C	13-Jul-05	97.6	1.1	21	97.6	0.7	21	98.2	0.8	11	97.1	0.9	17	97.8	0.6	17
C	20-Jul-05	95.4	2.7	21	97.5	1.1	21	97.2	2.3	12	96.6	0.7	16	97.6	0.5	17
C	27-Jul-05	93.9	2.1	21	94.7	2.5	20	93.1	3.3	12	93.5	2.1	16	94.1	2.3	18
C	03-Aug-05	83.1	4.9	21	89.3	5	21	63.2	14.4	11	81.1	10.6	16	83.9	7.7	17
C	10-Aug-05															
C	17-Aug-05	62.4	9.4	21	69.3	9.7	21	n/a	n/a	0	57.5	8.1	16	68.1	4.8	16
C	24-Aug-05	55.6	7.3	21	61	8.8	20	n/a	n/a	0	55.3	9	16	60.9	7.9	17
C	31-Aug-05	56.3	7	21	59.2	5.2	21	n/a	n/a	0	57.6	7.1	16	60.2	5	17
C	07-Sep-05	50.8	5.9	21	55.7	9.2	21	n/a	n/a	0	53.5	8.5	16	57.2	5.7	17
C	14-Sep-05	37.1	10.4	21	43.1	10.8	21	n/a	n/a	0	44.1	9.5	16	47.9	5.8	17
C	21-Sep-05	24	7.4	21	33.1	13	21	n/a	n/a	0	35.6	11.5	16	34.7	6.7	17
N	01-Jun-05	96.3	2.1	20	96.9	1.9	17	94.7	3.8	13	96.6	2.3	14	88.4	5.6	16
N	08-Jun-05	97.9	1.3	20	98.1	2.1	18	96.4	1.5	13	98.2	0.9	13	95.4	3.2	14
N	15-Jun-05	98.5	0.6	20	98.7	0.5	19	98.8	0.6	14	97.9	2.3	15	96.1	2.2	15

Tmt	Date	CareSte			FesHal			KoelMac			PoaPra			HespCom		
		Avg	SD	N	Avg	SD	N	Avg	SD	N	Avg	SD	N	Avg	SD	N
N	22-Jun-05	97.9	0.5	18	98.6	0.5	17	98.8	0.5	12	98.2	0.7	13	97.7	1.1	11
N	29-Jun-05	98.2	0.7	20	98.7	0.5	18	98.8	0.4	13	98.1	0.6	14	98.4	0.6	17
N	06-Jul-05	97.5	1.9	19	98.2	0.6	18	98.4	0.5	13	98.1	0.6	13	98.3	0.5	16
N	13-Jul-05	97.2	1.5	20	98	0.7	18	98.4	0.7	13	97.8	0.8	13	98.2	0.6	19
N	20-Jul-05	93.6	3.3	20	97.2	1.9	19	98.2	0.9	12	97.3	0.7	14	97.6	0.5	19
N	27-Jul-05	91.4	3.6	20	95.2	2.8	19	94.8	3.6	12	94.5	2.4	14	95.2	2.3	19
N	03-Aug-05	79.8	10.4	20	88.6	4.4	19	69.5	11.6	11	80	9.4	14	82.3	9.9	18
N	10-Aug-05															
N	17-Aug-05	62.5	11.5	20	67.9	9.1	19	n/a	n/a	0	58.3	9.7	12	68.1	11.3	19
N	24-Aug-05	57.4	9.5	20	60.8	11.5	19	n/a	n/a	0	61.6	6.6	11	61.3	7.8	19
N	31-Aug-05	54.6	8.4	20	56.1	9.8	19	n/a	n/a	0	61.4	8.8	14	61	8	19
N	07-Sep-05	51.1	10.3	20	52.5	11.4	18	n/a	n/a	0	56.7	10.9	14	56.5	11.9	19
N	14-Sep-05	36.8	13.7	20	42.1	9	17	n/a	n/a	0	45.4	13.6	14	43.7	12.8	19
N	21-Sep-05	25.9	9.1	20	31.2	7	17	n/a	n/a	0	38.2	9.9	14	36.8	5.9	18
W	01-Jun-05	96.3	1.7	21	96.8	1.1	21	88.7	9.1	6	96.1	2.3	16	86.5	4.5	17
W	08-Jun-05	98	0.8	21	98	0.8	21	94.9	3.4	7	97.7	0.8	16	93.5	3.1	15
W	15-Jun-05	98.5	0.5	21	98.7	0.5	21	98.2	0.8	9	98.1	0.8	16	93.8	2.5	16
W	22-Jun-05	98.5	0.6	20	98.6	0.5	20	98.1	0.6	9	98.5	0.5	15	97.9	0.8	14
W	29-Jun-05	98.3	0.6	21	98.5	0.6	21	98.4	0.5	9	98.1	0.5	16	98.4	0.6	17
W	06-Jul-05	98.3	0.8	21	98.1	0.5	21	98.3	0.5	10	98.3	0.5	16	98.4	0.5	19
W	13-Jul-05	98.1	0.9	21	98.2	0.7	20	98.4	0.5	7	98.2	0.5	16	98.4	0.6	20
W	20-Jul-05	96.5	1.7	21	97.8	0.7	21	97.3	2.6	10	97.4	1	16	97.9	0.9	20
W	27-Jul-05	94.4	2.4	21	96.1	2.5	21	93.2	3.5	10	95.6	1.7	16	96.3	1.9	20
W	03-Aug-05	87.8	4.7	21	93.6	4.5	21	79.7	8.7	9	92.1	3	16	91.5	2.8	20
W	10-Aug-05															
W	17-Aug-05	66.9	8.1	21	78	6.5	21	n/a	n/a	0	73.7	6.8	16	75.9	5.8	20

Tmt	Date	CareSte			FesHal			KoelMac			PoaPra			HespCom		
		Avg	SD	N	Avg	SD	N	Avg	SD	N	Avg	SD	N	Avg	SD	N
W	24-Aug-05	62.9	8	21	69.4	8.5	21	n/a	n/a	0	67.9	4.9	16	67.7	4.9	20
W	31-Aug-05	60	5.5	21	63.1	7.3	21	n/a	n/a	0	68.9	4.5	16	66.4	4.2	20
W	07-Sep-05	54.9	4.9	21	57.2	8.2	21	n/a	n/a	0	64.1	4.4	16	64.6	2.9	20
W	14-Sep-05	41	7	20	49.4	9.3	20	n/a	n/a	0	56.1	7.3	16	55.1	5.8	20
W	21-Sep-05	24.2	6.2	21	36.1	9.7	21	n/a	n/a	0	46.6	9.4	16	38.8	9.7	19
NW	01-Jun-05	96.6	2.3	19	97.9	0.9	19	94	4.1	6	96.3	2.3	20	85.4	6.6	14
NW	08-Jun-05	98.2	0.8	20	98.6	0.8	21	96.8	1.5	6	98	2	20	94.1	2.5	14
NW	15-Jun-05	98.5	1.2	19	99	0.5	21	98.9	0.4	7	98.8	0.4	20	96.1	2	14
NW	22-Jun-05	98.4	0.6	19	98.9	0.4	20	98.8	0.5	8	98.6	0.6	19	97.9	1	12
NW	29-Jun-05	98.4	0.6	20	98.6	0.5	21	99	0	8	98.7	0.5	20	98.6	0.6	14
NW	06-Jul-05	98.3	0.6	20	98.2	0.5	21	98.7	0.5	9	98.2	0.4	19	98.6	0.5	15
NW	13-Jul-05	98.2	0.8	20	98.4	0.6	21	98.7	0.5	7	98	0.7	20	98.4	0.5	17
NW	20-Jul-05	96.1	2.1	20	97.8	0.6	21	98.3	0.5	9	97.8	0.9	20	98.4	0.6	17
NW	27-Jul-05	94.3	2.2	20	97.4	0.8	20	96	1.9	8	95.9	1.3	19	97	1.7	17
NW	03-Aug-05	86.7	6.4	20	93.2	2.4	21	88	3.6	8	91.3	3.7	19	92.6	3.1	17
NW	10-Aug-05															
NW	17-Aug-05	66.4	8.8	20	79.6	6.2	21	n/a	n/a	0	70.6	9.7	18	75.4	3.3	17
NW	24-Aug-05	55.7	7.6	19	63.6	19.5	18	n/a	n/a	0	68.8	6.9	17	67.6	4.3	16
NW	31-Aug-05	58.4	7	20	61.5	6.7	21	n/a	n/a	0	66.9	4.7	19	66.4	4.8	17
NW	07-Sep-05	52.9	9.9	20	59	5.7	21	n/a	n/a	0	60.4	8.9	18	61.9	5.2	17
NW	14-Sep-05	37.1	9.6	20	47	10.4	19	n/a	n/a	0	52.5	10.7	18	51.4	8.7	17
NW	21-Sep-05	24.5	7.7	20	39	9.7	21	n/a	n/a	0	41.2	11.1	18	40.3	9.6	17

12. Appendix F: Raw Resource Manipulation Community Data (Chapters 2, 4)

Table 12-1 Raw plant community data used in both Chapter 2 and the SEM analysis in Chapter 4. See table 4-1 for an explanation of the variable descriptions.

Block	Nitrogen	Water	Shade	Initial Ground Cover	Shoot Biomass	Root Biomass	Litter Biomass	Final Species Richness	Initial Species Richness	Light Intercept.	Initial Even	Final Even
1	No	No	No	0.35	6.8453	7.3284	4.985	3.4641	3.1623	0.804	0.549	0.7633
1	Yes	No	No	0.35	6.1459	7.462	4.9229	4	3.6056	0.7505	0.3169	0.5863
1	No	No	Yes	0.2	5.8427	6.9004	4.9171	3	3.3166	1.3826	0.4589	0.672
1	Yes	No	Yes	0.3	5.987	6.8537	5.2898	3.1623	3.873	1.3439	0.544	0.468
1	No	Yes	No	0.4	6.579	6.9836	5.0344	4.7958	3.7417	1.2976	0.4538	0.5102
1	Yes	Yes	No	0.35	6.5911	7.5704	5.9269	3.873	3.6056	1.3162	0.6205	0.5554
2	No	No	No	0.25	5.4769	7.2217	4.132	3.6056	2.8284	0.6161	0.5942	0.549
2	Yes	No	No	0.2	5.8319	7.6116	4.9338	3.3166	3.7417	0.421	0.3529	0.6325
2	No	No	Yes	0.35	5.5373	7.0835	4.2471	3.1623	3.7417	1.2539	0.5084	0.5901
2	Yes	No	Yes	0.2	5.546	6.8958	5.3254	3	3.1623	1.3605	0.5316	0.373
2	No	Yes	No	0.3	5.5219	6.6875	4.7005	4	4	0.5029	0.4935	0.5105
2	Yes	Yes	No	0.08	6.2582	7.1673	5.2998	3.3166	3.873	0.8708	0.5283	0.6821
3	No	No	No	0.3	6.2559	6.945	5.0133	3.6056	3.1623	0.8481	0.5057	0.6933
3	Yes	No	No	0.15	6.0266	6.9878	5.1585	3.7417	3.7417	0.9362	0.6024	0.7019
3	No	No	Yes	0.35	5.9506	6.9004	4.9031	4	3.7417	1.2148	0.7754	0.7286
3	Yes	No	Yes	0.1	6.0584	6.7583	5.4836	3.7417	4.4721	1.3346	0.754	0.3181
3	No	Yes	No	0.2	5.9488	7.091	4.5294	3.7417	3.873	0.5974	0.5788	0.6052
3	Yes	Yes	No	0.2	6.5576	6.774	5.6384	3.873	3.873	1.1771	0.5779	0.5311
4	No	No	No	0.15	5.6073	6.8392	3.8	3.4641	3.3166	0.8343	0.7003	0.729
4	Yes	No	No	0.1	6.315	7.1777	5.0839	3.873	3.873	1.0511	0.6105	0.631

Block	Nitrogen	Water	Shade	Initial Ground Cover	Shoot Biomass	Root Biomass	Litter Biomass	Final Species Richness	Initial Species Richness	Light Intercept.	Initial Even	Final Even
4	No	No	Yes	0.2	5.5607	6.7208	3.9512	3	3.3166	1.1967	0.6234	0.7636
4	Yes	No	Yes	0.1	5.9143	7.3834	5.4794	3	3	1.3207	0.5661	0.7383
4	No	Yes	No	0.35	6.1366	6.6353	4.5454	3.4641	3.4641	0.7991	0.7015	0.5757
4	Yes	Yes	No	0.2	6.3521	7.3721	5.1376	3.7417	4.1231	1.0286	0.5032	0.5331
5	No	No	No	0.35	6.2995	7.3314	5.0441	3.873	3.873	0.6323	0.5554	0.6074
5	Yes	No	No	0.05	6.4208	7.3284	4.7958	3.873	3.7417	0.9069	0.5926	0.6881
5	No	No	Yes	0.25	5.8018	6.3555	5.7226	2.8284	3.4641	1.4901	0.7119	0.6233
5	Yes	No	Yes	0.15	5.9514	6.8196	5.0708	3.6056	4	1.289	0.5039	0.7234
5	No	Yes	No	0.3	6.0486	6.774	4.6492	3.4641	3.3166	0.9607	0.6046	0.552
5	Yes	Yes	No	0.08	6.4437	6.7843	5.5114	3.4641	4.1231	0.9307	0.6868	0.5577
6	No	No	No	0.2	6.0068	6.7371	3.6136	3.873	3.873	0.6281	0.5044	0.5499
6	Yes	No	No	0.05	6.119	7.2734	5.1144	3	3.4641	0.5375	0.3411	0.6404
6	No	No	Yes	0.1	5.9045	6.5612	4.8048	3	3.1623	1.3398	0.6567	0.5263
6	Yes	No	Yes	0.25	5.4157	6.5352	5.4125	3.3166	3.3166	1.1152	0.5283	0.7962
6	No	Yes	No	0.25	6.3694	7.6026	5.5126	4	3.6056	0.7166	0.3788	0.5537
6	Yes	Yes	No	0.1	6.1382	6.9666	5.3303	3.6056	4.1231	0.9416	0.4826	0.7329
7	No	No	No	0.3	6.0064	6.3071	4.7327	4.4721	4.1231	0.5627	0.5379	0.5432
7	Yes	No	No	0.25	6.2418	7.0797	5.6897	3.3166	3.6056	1.1449	0.7003	0.7087
7	No	No	Yes	0.1	6.0565	6.2988	5.2274	3.1623	3.1623	1.2419	0.5447	0.5281
7	Yes	No	Yes	0.4	4.9097	5.7308	5.8713	3.4641	3.3166	1.361	0.6456	0.5824
7	No	Yes	No	0.3	6.0922	6.844	5.1807	3.3166	3.7417	0.8543	0.4444	0.6935
7	Yes	Yes	No	0.25	6.0122	6.4601	5.7513	3.6056	4.2426	1.0208	0.4814	0.5961
8	No	No	No	0.35	6.0445	6.3476	5.6384	4.2426	4	0.7783	0.6225	0.556
8	Yes	No	No	0.04	6.1159	7.2217	5.3664	4	3.7417	1.0927	0.3099	0.5196
8	No	No	Yes	0.3	5.4984	6.0757	5.3088	3.6056	3.6056	1.3856	0.5051	0.3712
8	Yes	No	Yes	0.4	5.4528	6.3711	6.3484	3	3.7417	1.4149	0.5797	0.6234
8	No	Yes	No	0.1	6.1549	6.9709	4.8307	4.3589	3.6056	0.6689	0.5957	0.5528
8	Yes	Yes	No	0.15	5.797	7.2607	6.0965	3.6056	4.1231	1.0141	0.5008	0.643

Block	Nitrogen	Water	Shade	Initial Ground Cover	Shoot Biomass	Root Biomass	Litter Biomass	Final Species Richness	Initial Species Richness	Light Intercept.	Initial Even	Final Even
9	No	No	No	0.35	5.5342	6.8958	5.6065	3.6056	3.4641	0.7574	0.347	0.544
9	Yes	No	No	0.5	6.6284	7.5201	5.7491	3.873	3.6056	0.8492	0.5135	0.6332
9	No	No	Yes	0.45	5.4459	5.8288	6.1946	2.8284	3.873	1.4129	0.6389	0.4534
9	Yes	No	Yes	0.25	5.3259	5.9887	6.3251	2.8284	4.2426	1.425	0.5432	0.3388
9	No	Yes	No	0.15	6.3063	7.0368	5.1352	3.7417	4	0.9206	0.5035	0.601
9	Yes	Yes	No	0.15	6.0208	6.3396	5.7918	3.4641	3.7417	1.0829	0.4665	0.5421
10	No	No	No	0.7	6.1808	6.9004	5.9605	3.7417	3.4641	0.7919	0.7009	0.5801
10	Yes	No	No	0.45	6.1844	6.6931	5.9723	3.4641	3.873	1.2882	0.5615	0.4573
10	No	No	Yes	0.4	5.9314	7.1389	6.1819	3	3.4641	1.4919	0.5516	0.4887
10	Yes	No	Yes	0.55	4.6473	6.7208	5.9994	3	3	1.4116	0.8639	0.54
10	No	Yes	No	0.25	6.5344	6.5612	6.2094	3.3166	2.8284	1.0224	0.4381	0.7452
10	Yes	Yes	No	0.4	5.8786	6.7263	6.4056	3.3166	3.3166	0.9365	0.5974	0.5345
11	No	No	No	0.25	5.9972	6.8912	5.6978	3.873	3.873	1.0081	0.3871	0.5102
11	Yes	No	No	0.25	6.5101	7.0873	6.0292	4.2426	3.873	0.9878	0.3914	0.616
11	No	No	Yes	0.3	5.5672	6.9494	6.255	3	3	1.2281	0.6631	0.3798
11	Yes	No	Yes	0.25	5.3655	5.7308	5.7081	2.8284	3.873	1.3976	0.4971	0.6999
11	No	Yes	No	0.25	6.5098	6.9878	6.2271	3.6056	3.7417	1.0234	0.6609	0.565
11	Yes	Yes	No	0.25	5.9802	6.5547	6.32	3.4641	3.1623	1.228	0.461	0.4846
12	No	No	No	0.55	6.0737	7.3373	4.841	3.873	3.873	0.8433	0.4638	0.473
12	Yes	No	No	0.35	6.2279	7.2796	5.5114	3	3.3166	1.0099	0.551	0.231
12	No	No	Yes	0.5	6.1258	7.4356	5.4877	3.3166	3.1623	1.4056	0.5556	0.4462
12	Yes	No	Yes	0.35	6.023	6.7424	6.2653	3.1623	3.3166	1.5314	0.3321	0.6068
12	No	Yes	No	0.5	6.0654	6.2904	4.8621	3.3166	4	0.97	0.5848	0.777
12	Yes	Yes	No	0.35	6.7586	6.5018	6.0747	3.4641	3.3166	0.8307	0.4225	0.3727
13	No	No	No	0.45	6.2142	7.5323	5.5162	4	3.7417	0.8492	0.5677	0.4796
13	Yes	No	No	0.3	6.3327	7.4112	5.8069	3.1623	3.7417	0.9759	0.5145	0.5595
13	No	No	Yes	0.25	6.0314	6.3476	6.0568	2.8284	3.7417	1.3774	0.4909	0.3836
13	Yes	No	Yes	0.5	5.0999	6.1557	6.4254	2.2361	3.7417	1.4408	0.4297	0.3912

Block	Nitrogen	Water	Shade	Initial Ground Cover	Shoot Biomass	Root Biomass	Litter Biomass	Final Species Richness	Initial Species Richness	Light Intercept.	Initial Even	Final Even
13	No	Yes	No	0.3	6.5038	7.1777	5.9417	3.6056	3.3166	0.9631	0.4864	0.5274
13	Yes	Yes	No	0.45	6.2977	6.8958	6.2716	3	3.873	1.1506	0.362	0.4036
14	Yes	No	No	0.05	6.5208	7.1208	5.323	3.1623	3.7417	0.9212	0.532	0.6156
14	No	No	Yes	0.05	6.0568	7.4953	5.815	3.4641	3.7417	1.2601	0.3891	0.841
14	Yes	No	Yes	0.05	5.7268	6.844	5.9548	3.3166	3.7417	1.2605	0.6819	0.9251
14	No	Yes	No	0.25	6.5023	6.3153	6.136	3.6056	3.4641	0.6548	0.3833	0.5582
14	Yes	Yes	No	0.2	6.6104	5.918	5.6387	3	3.7417	0.8256	0.6139	1.0611
15	No	No	No	0.4	6.1379	6.9185	5.062	4	3.6056	0.6597	0.3869	0.5451
15	Yes	No	No	0.6	6.3687	7.1603	5.8078	2.8284	4	0.6969	0.4203	0.7252
15	No	No	Yes	0.3	5.7605	7.0643	6.2927	2.4495	4.1231	1.2167	0.3823	0.3835
15	Yes	No	Yes	0.35	5.8374	6.9537	6.3182	3	3.3166	1.468	0.4407	0.3146
15	No	Yes	No	0.5	6.5047	7.4436	5.5835	3.873	4.2426	0.8168	0.6039	0.4699
15	Yes	Yes	No	0.55	6.4696	6.5802	6.0046	3.6056	3.6056	0.9167	0.6893	0.7178
16	No	No	No	0.05	6.0929	7.2734	5.118	3.4641	3.4641	0.5917	0.4383	0.6265
16	Yes	No	No	0.15	6.6292	7.3635	6.1868	3.3166	3.3166	0.608	0.5249	0.6345
16	No	No	Yes	0.15	6.076	6.7317	5.0324	3.3166	3.873	1.3655	0.7334	0.5362
16	Yes	No	Yes	0.1	6.1944	7.0565	6.0544	3.3166	3.7417	1.2636	0.5372	0.2798
16	No	Yes	No	0.1	6.5812	6.5802	5.6479	3.873	3.7417	0.8438	0.6993	0.4669
16	Yes	Yes	No	0.05	7.0972	7.0948	6.3294	3.4641	3.1623	0.885	0.5449	0.63
17	No	No	No	0.05	6.2908	6.8537	5.2725	3.3166	3.4641	0.7222	0.6114	0.535
17	Yes	No	No	0.05	6.5936	7.3635	5.6391	3.1623	3.7417	0.8367	0.6259	0.7388
17	No	No	Yes	0.05	6.1079	6.8726	5.9138	3.6056	3.4641	1.286	0.3771	0.3927
17	Yes	No	Yes	0.05	5.7497	7.1425	5.7074	3.4641	4.1231	1.3293	0.4619	0.6531
17	No	Yes	No	0.25	6.286	6.4313	5.4562	3.3166	3.873	1.1163	0.5938	0.445
17	Yes	Yes	No	0.25	6.5532	7.1846	5.6567	3.4641	3.4641	1.1538	0.5884	0.5307
18	No	No	No	0.46	6.1578	7.3974	6.3665	3.6056	3.4641	0.7809	0.3487	0.5906
18	Yes	No	No	0.25	6.2997	7.1983	6.3743	3.6056	3.7417	0.7991	0.2342	0.3637
18	No	No	Yes	0.2	5.743	6.9581	5.7991	3.4641	4.2426	1.3808	0.327	0.4612

Block	Nitrogen	Water	Shade	Initial Ground Cover	Shoot Biomass	Root Biomass	Litter Biomass	Final Species Richness	Initial Species Richness	Light Intercept.	Initial Even	Final Even
18	Yes	No	Yes	0.2	5.7127	6.0963	6.3709	3	3.6056	1.3655	0.3438	0.4575
18	No	Yes	No	0.1	6.4016	7.636	6.1269	3.4641	3	0.97	0.3562	0.4582
18	Yes	Yes	No	0.25	6.3135	7.3432	6.4525	3.3166	3.7417	0.9696	0.2412	0.4403
19	No	No	No	0.2	6.0078	6.923	5.3863	3.6056	3.873	0.6678	0.5287	0.4447
19	Yes	No	No	0.5	6.5303	8.078	6.2525	2.6458	3.4641	1.0258	0.4435	0.7817
19	No	No	Yes	0.1	6.2649	7.2349	5.9402	2.6458	3.3166	1.3013	0.4505	0.3493
19	Yes	No	Yes	0.35	5.421	6.6588	6.4936	3.1623	3.7417	1.3547	0.648	0.3334
19	No	Yes	No	0.1	6.3476	7.1532	5.5626	4	3.873	0.9212	0.5157	0.5148
19	Yes	Yes	No	0.05	6.4094	7.1023	6.2124	3.4641	3.7417	1.2717	0.5498	0.3664
20	No	No	No	0	5.6846	7.4194	4.1026	3.4641	3.3166	0.6392	0.5283	0.6754
20	Yes	No	No	0.05	6.354	7.2765	5.6447	3.6056	3.4641	0.8826	0.5728	0.5807
20	No	No	Yes	0.1	5.9753	6.4166	5.0864	3.6056	3.1623	1.1931	0.3319	0.4449
20	Yes	No	Yes	0.05	5.8761	6.3235	5.5638	3.4641	3.7417	1.2702	0.6695	0.655
20	No	Yes	No	0.05	6.3862	7.4248	5.7288	3.873	3	0.6956	0.817	0.4576
20	Yes	Yes	No	0.05	6.4661	6.7263	6.0594	4	3.3166	0.7955	0.4318	0.4659
21	No	No	No	0.3	6.1192	6.774	5.2396	3.873	4	0.6251	0.59	0.4971
21	Yes	No	No	0.25	6.28	7.3284	5.222	3.6056	3.873	1.0892	0.5461	0.6619
21	No	No	Yes	0.4	5.7417	6.3396	6.2208	2.8284	3.3166	1.2175	0.367	0.3454
21	Yes	No	Yes	0.16	5.5541	6.8679	5.8732	2.8284	3.6056	1.1932	0.6435	0.5006
21	No	Yes	No	0.4	6.1493	6.7478	5.4376	4	4.1231	0.8786	0.5333	0.6343
21	Yes	Yes	No	0.25	6.3416	6.8294	5.8922	3.7417	4.1231	1.1857	0.7678	0.6213
22	No	No	No	0.3	5.7513	7.2734	5.6483	3.1623	3.6056	0.3864	0.5735	0.7234
22	Yes	No	No	0.05	5.9259	7.2382	5.1879	4.1231	3.4641	0.642	0.7665	0.647
22	No	No	Yes	0.35	5.9887	6.7153	6.3448	3	3.1623	1.1704	0.5229	0.5016
22	Yes	No	Yes	0.05	5.2002	6.4166	5.8619	2.4495	3.3166	1.2808	0.4638	0.841
22	No	Yes	No	0.05	6.1119	7.1317	5.3196	3.873	4	0.5656	0.5621	0.7051
22	Yes	Yes	No	0.35	7.0117	6.9666	6.0836	3.4641	3.6056	0.8776	0.3372	0.5023

13. Appendix G: Raw data (Chapter 5)

Table 13-1 Raw data used in the SEM in Chapter 5. See table 5-1 for a description of the variables. Species names are as follows: Achil = *Achillea millefolium,* Artfr = *Artemisia frigida,* Artlud = *Artemisia ludoviciana,* Carex = *Carex stenophylla*, Cera = *Cerastium arvense,* Festu = *Festuca hallii*, Galiu = *Galium boreale,* Geum = *Geum triflorum,* Hespe = *Hesperostipa comata*, Poa = *Poa pratensis, Rosa* = *Rosa arkansana*, and Solid = *Solidago missouriensis.*

#	Species	Ntmt	Comp. Intensity	Shoot Biomass	Root Biomass	Sp Rich	Even	Soil Moist	Light Intercept	Topog. Pos.	Total Nitrogen	Community Composition
1	Rosa	No	-0.0602	5.535	7.1254	4.1231	0.87	0.2167	0.8007	0.684	0.379	0.233
2	Rosa	No	-1.8791	4.906	6.92	4.1231	0.9059	0.2553	0.6237	0.6551	0.4115	-0.0325
3	Rosa	No	-0.7878	6.082	7.2296	3.3166	0.7587	0.1708	1.2743	0.6665	0.3047	-1.974
4	Geum	Yes	-0.5022	5.4756	6.4246	4.3589	0.8558	0.2218	0.8366	0.6603	0.4334	-1.2228
5	Achil	Yes	1.8062	5.546	6.8626	4.1231	0.8743	0.2372	0.9845	0.6457	0.5352	-1.4753
7	Achil	Yes	-0.5708	5.4099	6.6911	3.873	0.8284	0.1784	0.9476	0.6532	0.3363	0.1702
8	Cera	Yes	-0.8767	5.8284	6.6734	4.4721	0.8499	0.2218	0.9197	0.6397	0.478	-0.5419
9	Carex	No	0.8508	5.1422	6.7752	3.873	0.8475	0.2116	0.964	0.6364	0.5469	0.9453
10	Rosa	Yes	-3.2804	5.5831	6.8917	4.1231	0.7977	0.181	1.2512	0.678	0.3469	-0.7713
11	Rosa	No	-0.1469	5.5102	7.0946	4	0.7605	0.2039	0.7051	0.6332	0.5007	-1.1998
12	Achil	Yes	-0.3229	5.9035	7.1441	4.4721	0.8583	0.2039	0.9522	0.6315	0.478	-0.3979
13	Carex	No	0.2734	5.6567	7.2124	3.873	0.8525	0.1912	0.915	0.6982	0.478	0.2885
14	Geum	No	-0.7924	5.6856	7.2598	4.1231	0.8148	0.1937	1.0911	0.6827	0.4556	0.6746
17	Solid	No	-0.4794	5.1711	7.0788	3.3166	0.71	0.2014	0.7037	0.6406	0.3898	-1.6912
18	Solid	No	-0.5154	5.229	6.1241	3.3166	0.7657	0.2167	0.6417	0.6563	0.5944	0.8995
19	Achil	No	0.2154	5.6316	7.286	3.6056	0.8661	0.2218	0.8996	0.6461	0.5586	-0.5248
21	Rosa	Yes	-0.5813	5.3945	7.1216	3	0.8156	0.1784	0.4351	0.6743	0.4225	2.142
22	Carex	Yes	0.2102	5.4004	6.8855	4	0.8517	0.181	0.4644	0.7026	0.4668	1.5066
24	Solid	No	-0.4826	4.7613	7.0507	3.7417	0.8231	0.2014	0.3084	0.7072	0.4115	1.2951

#	Species	Ntmt	Comp. Intensity	Shoot Biomass	Root Biomass	Sp Rich	Even	Soil Moist	Light Intercept	Topog. Pos.	Total Nitrogen	Community Composition
25	Rosa	Yes	-0.4002	5.1773	7.3506	4.2426	0.8671	0.148	0.45	0.6747	0.4556	1.3736
31	Rosa	Yes	-0.6823	5.6437	7.1523	3.873	0.8705	0.1632	0.86	0.7023	0.5704	-0.0694
38	Achil	Yes	-0.1192	5.633	7.0433	3.7417	0.853	0.1759	0.8315	0.6791	0.4668	1.2545
41	Rosa	No	1.3601	5.6781	6.7312	4.1231	0.8384	0.2039	0.893	0.6749	0.4556	0.6369
47	Festu	Yes	-0.649	5.6265	7.2445	3.6056	0.8997	0.1759	0.5192	0.6486	0.4668	1.2284
49	Artfr	Yes	-0.6819	5.3808	7.0217	3.1623	0.7942	0.181	0.4005	0.7443	0.4225	2.5631
50	Artfr	Yes	-0.425	5.3725	6.7943	3.873	0.8407	0.1379	0.7506	0.7087	0.478	1.7941
51	Achil	No	-0.1919	5.1168	6.8121	3.6056	0.8878	0.2116	0.6084	0.7004	0.3576	0.0925
52	Carex	No	-1.9534	5.2144	6.687	3.7417	0.8722	0.209	0.7083	0.71	0.4334	0.4902
54	Cera	No	0.5236	5.2068	6.5171	4	0.7948	0.1531	0.6346	0.7128	0.4006	1.153
55	Cera	No	2.2041	5.4935	6.4694	3.7417	0.8092	0.1658	0.8531	0.7043	0.6687	0.2516
56	Festu	No	-1.3001	5.2533	7.1004	3.3166	0.7999	0.1658	0.7521	0.6854	0.4445	1.4152
57	Achil	No	-0.3073	5.4085	7.1291	3.6056	0.8917	0.1937	0.7343	0.6956	0.3257	-0.3894
58	Artfr	No	-0.307	5.0505	6.9831	3.1623	0.8792	0.1759	0.4487	0.7211	0.3469	1.6443
59	Festu	Yes	-0.499	5.5247	7.302	4.2426	0.8669	0.2346	1.0307	0.6818	0.5236	0.9721
61	Festu	No	-1.4386	5.2988	6.7312	4.1231	0.8327	0.2682	0.7756	0.6648	0.379	1.0344
62	Geum	No	-1.8568	4.9185	6.9107	4.1231	0.8588	0.2838	0.4329	0.6781	0.379	1.2051
63	Geum	Yes	-4.1908	5.2617	6.4839	3.7417	0.8251	0.2218	0.9074	0.6603	0.4334	2.6149
64	Hespe	Yes	-0.9888	5.0389	6.5993	3.4641	0.8124	0.1886	0.78	0.6687	0.4556	2.2735
65	Artfr	Yes	-0.432	5.2796	7.4327	4.1231	0.9004	0.2269	0.4449	0.6581	0.5352	1.5234
66	Geum	Yes	-0.921	5.5235	6.9566	3.3166	0.8863	0.1607	0.9197	0.6774	0.4334	1.0946
67	Carex	Yes	-0.2106	5.2709	6.8224	4	0.7414	0.1531	0.7099	0.6547	0.3469	-1.4131
68	Festu	Yes	0.2129	5.6479	7.3177	3.7417	0.8101	0.1683	1.0993	0.6639	0.3363	-0.5567
69	Hespe	No	0.1674	5.5154	7.177	3.6056	0.7542	0.1937	0.8011	0.665	0.4445	0.3431
70	Geum	No	-1.6308	5.6832	7.1552	4	0.8192	0.1683	0.7647	0.6571	0.4115	-1.071
73	Rosa	Yes	0.4615	5.8499	6.9655	3.3166	0.8697	0.1708	1.0356	0.6383	0.5469	0.5087
74	Poa	Yes	-0.1873	5.6699	7.4974	4.3589	0.8189	0.1632	0.9682	0.6536	0.5469	-0.7866
75	Gali	Yes	-0.5109	5.8853	7.0867	4	0.8773	0.1658	1.0251	0.6312	0.5469	-0.2281
76	Poa	Yes	0.0622	5.4192	6.4621	4.1231	0.918	0.1835	1.053	0.6521	0.5352	-0.6472

#	Species	Ntmt	Comp. Intensity	Shoot Biomass	Root Biomass	Sp Rich	Even	Soil Moist	Light Intercept	Topog. Pos.	Total Nitrogen	Community Composition
77	Solid	Yes	-0.392	5.4894	5.213	3.873	0.9088	0.1759	0.7744	0.6378	0.3152	0.5032
78	Geum	No	-0.6822	5.3254	6.7643	3.873	0.852	0.2269	0.8384	0.6421	0.5007	0.6038
79	Festu	No	-1.7333	5.6774	5.5567	3.6056	0.8148	0.209	0.8573	0.6617	0.5469	-0.6793
80	Hespe	No	-0.2806	5.803	5.5567	3.7417	0.8211	0.2269	0.6716	0.6571	0.5469	0.2474
81	Gali	Yes	-1.6621	5.9932	7.0301	4.1231	0.8303	0.1607	1.1343	0.6402	0.4893	-0.2093
83	Geum	Yes	-0.6729	5.6974	7.009	4.3589	0.831	0.1886	0.5508	0.6506	0.6065	-1.0756
84	Gali	No	-0.6733	5.6326	6.7534	3.7417	0.7787	0.2578	0.9843	0.6467	0.5352	-1.7197
85	Poa	No	0.2146	5.8908	7.2532	3.4641	0.8864	0.2372	0.7959	0.6265	1.3705	-2.1594
86	Rosa	No	0.6594	6.1833	7.6936	3.873	0.8356	0.2116	0.763	0.6663	0.5586	-0.5864
87	Festu	No	-0.2915	5.1716	7.5729	4	0.8479	0.2167	0.5126	0.6774	0.3898	0.4805
89	Poa	Yes	0.6762	5.9932	7.3784	4	0.8289	0.181	0.8903	0.6377	0.7342	-1.1844
90	Hespe	No	-0.4453	5.3162	6.6246	4.1231	0.8199	0.2321	0.5837	0.6604	0.7615	0.055
91	Festu	Yes	-0.5236	5.8236	7.1698	4	0.7846	0.2116	0.8288	0.6581	0.3257	0.5777
92	Poa	No	-0.6365	5.7918	7.0132	3.3166	0.863	0.2141	1.1498	0.6547	0.4006	-0.4294
95	Carex	No	-0.2968	5.3904	7.1949	3	0.7922	0.1988	0.7951	0.666	0.5236	0.5948
96	Hespe	Yes	0.0174	6.0234	6.9385	3.1623	0.8127	0.1683	1.103	0.6575	0.4556	0.2978
97	Achil	Yes	-0.0167	5.6472	7.1178	3.4641	0.8214	0.1556	0.8303	0.6547	0.2942	-0.6921
98	Geum	No	-1.5824	5.3822	7.1878	3.6056	0.7281	0.2193	0.6993	0.683	0.3257	0.2191
99	Rosa	No	-0.5302	5.3868	6.8017	3.4641	0.8386	0.2218	0.7502	0.6619	0.5121	0.4555
100	Hespe	Yes	-0.2854	5.4381	6.8917	3.6056	0.8577	0.1835	0.8094	0.6389	0.3257	0.1881
101	Poa	Yes	-0.5006	5.9493	6.9611	3.6056	0.804	0.1861	0.7208	0.6505	0.5469	-0.8392
103	Carex	No	-0.6456	5.718	6.4169	3	0.7251	0.2167	0.5773	0.6606	0.4893	0.7685
110	Geum	Yes	1.1032	5.9229	6.8577	4	0.8331	0.2269	0.6933	0.6664	0.7342	-0.5702
112	Cera	No	-0.5435	5.8263	7.1216	4	0.8523	0.2424	0.6282	0.6575	0.7208	-0.2876
113	Geum	No	-0.8165	5.687	6.6057	4	0.8492	0.2604	1.2032	0.6573	0.6065	-0.2821
114	Rosa	Yes	-0.4237	5.9322	7.2431	3.1623	0.8728	0.1912	1.1557	0.6722	0.4893	0.3666
115	Cera	Yes	0.7483	5.8354	6.5864	3.6056	0.8876	0.2553	1.3777	0.6531	0.5352	-1.6211
116	Geum	No	-0.5004	5.2933	6.7912	4.3589	0.8586	0.2424	0.7403	0.6547	0.4445	0.5858
117	Cera	Yes	0.4668	5.4664	6.1033	3.3166	0.8226	0.2218	0.5994	0.6594	0.5704	0.5669

#	Species	Ntmt	Comp. Intensity	Shoot Biomass	Root Biomass	Sp Rich	Even	Soil Moist	Light Intercept	Topog. Pos.	Total Nitrogen	Community Composition
118	Poa	Yes	-0.306	5.9715	6.6793	3.7417	0.7757	0.2167	0.6552	0.6632	0.4668	-0.8485
120	Gali	No	-0.1233	5.4298	6.943	3.3166	0.8116	0.2942	0.7395	0.6605	0.6065	-2.9738
121	Achil	Yes	-0.5039	5.8072	7.1441	3.873	0.8476	0.1988	1.1817	0.6603	0.6065	-0.1412
122	Hespe	Yes	-0.3416	5.9597	7.1842	4.2426	0.8031	0.1861	0.7096	0.6834	0.5007	0.5347
123	Carex	Yes	0.0025	5.491	6.8069	3.7417	0.8263	0.2218	1.0282	0.6663	0.4556	0.1066
124	Solid	No	-1.013	5.665	7.2193	3.6056	0.7879	0.2065	0.9328	0.678	0.5236	0.1163
125	Rosa	No	-0.519	5.7018	6.4694	4.2426	0.8485	0.1835	1.0056	0.6952	0.6561	0.3856
127	Achil	No	-1.7397	5.9682	6.7368	4	0.8502	0.2116	1.0523	0.676	0.4006	-0.1819
128	Festu	Yes	-0.2915	5.4972	7.3515	3.873	0.8224	0.1886	0.4775	0.6785	0.7342	-1.0384
129	Gali	No	-0.8651	5.8556	6.5466	4	0.8256	0.181	0.512	0.6589	0.5352	0.0707
130	Achil	Yes	-0.414	5.6931	6.92	4.2426	0.8895	0.2065	0.8802	0.6543	0.4893	-0.2466
131	Hespe	No	0.0508	5.7884	7.1024	3.7417	0.7889	0.2218	0.9887	0.6644	0.5824	0.1622
132	Festu	No	-0.2506	5.7411	6.9831	3.7417	0.8027	0.2578	0.5161	0.6642	0.8038	-0.8028
133	Poa	Yes	-1.2053	6.0157	7.5027	3	0.9009	0.2014	1.1926	0.6636	0.5007	-1.3267
134	Festu	No	-2.3007	5.7608	7.393	3.3166	0.7852	0.2475	0.9409	0.6881	0.5704	-1.8118
135	Gali	No	-0.3687	5.7436	7.3871	3.4641	0.8685	0.2527	1.0128	0.6761	0.6561	-0.7402
137	Solid	Yes	-0.3311	5.5759	6.9961	3.3166	0.882	0.1988	1.1601	0.6818	0.5586	0.128
138	Artlud	No	-0.6191	5.3827	7.1441	4.1231	0.8524	0.2424	0.7555	0.6572	0.6816	-0.2655
139	Rosa	Yes	-2.4813	5.895	6.9699	3.4641	0.8164	0.1734	0.899	0.6592	0.7342	-0.0577
140	Artlud	No	-1.1501	5.7897	6.4839	3.873	0.853	0.1886	1.1393	0.6592	0.6311	-0.5603
141	Poa	No	-0.4939	5.7621	7.1178	3.4641	0.8321	0.2372	0.9716	0.6544	0.4334	-0.3376
142	Solid	Yes	-0.5799	5.6695	6.6614	3.4641	0.9219	0.1963	1.0104	0.6547	0.5704	-0.0153
143	Artlud	No	0.058	5.8132	6.7643	3.873	0.8623	0.1835	1.1096	0.6596	0.5944	-0.8229
144	Geum	Yes	2.3355	5.5962	6.7199	3.7417	0.8524	0.1835	0.9621	0.6559	0.4334	0.4175
145	Hespe	No	-0.3622	5.5514	6.7589	4.2426	0.811	0.2141	0.9049	0.6575	0.478	-0.3066
146	Festu	Yes	-1.5365	5.7893	7.0047	3.6056	0.8672	0.1886	1.1013	0.6603	0.8788	-0.9783
148	Artlud	No	0.2728	5.421	6.6554	3.7417	0.8844	0.2295	0.8743	0.6674	0.4115	-0.6607
150	Geum	Yes	-0.7624	5.92	7.0217	3.7417	0.8477	0.1632	1.0215	0.6676	0.6561	-0.6154
151	Geum	No	-3.2769	5.5118	6.7964	3.6056	0.8155	0.2065	1.0923	0.659	0.5824	-0.8438

#	Species	Ntmt	Comp. Intensity	Shoot Biomass	Root Biomass	Sp Rich	Even	Soil Moist	Light Intercept	Topog. Pos.	Total Nitrogen	Community Composition
152	Poa	No	-2.8073	5.3351	6.7199	4	0.8137	0.2269	0.8848	0.6599	0.5121	-0.7367
153	Festu	No	-0.214	5.7236	6.7368	3.873	0.8635	0.2218	0.9627	0.6633	0.4445	-0.8812
154	Hespe	Yes	-0.3902	5.8036	6.7752	3.873	0.7845	0.2295	0.9327	0.6639	0.478	0.2614
157	Achil	No	0.2834	5.5354	7.3635	3.7417	0.7616	0.1963	0.9172	0.6617	0.5824	-2.3474
158	Cera	Yes	0.1491	5.4315	6.5398	4.4721	0.871	0.2116	0.9146	0.6575	0.4334	0.0355
159	Solid	No	-1.246	5.0857	6.2679	3.3166	0.7799	0.2116	0.8929	0.6599	0.5352	0.8057
160	Festu	No	0.073	5.3697	6.6183	4.2426	0.8678	0.2372	0.5874	0.6648	0.5121	-0.2029
161	Rosa	No	-1.4967	5.3674	6.533	3.4641	0.8733	0.2116	0.7895	0.6704	0.5469	0.3775
162	Carex	Yes	0.0363	6.1048	6.8326	3.873	0.8501	0.1861	1.0516	0.6711	0.5824	-0.2198
163	Hespe	No	-0.4252	5.7104	6.5398	4.2426	0.8245	0.2039	0.9483	0.6603	0.5007	-0.0408
165	Poa	No	-0.0162	5.3471	6.3697	3.6056	0.8496	0.2604	0.9409	0.6473	0.5007	-0.4249
166	Achil	No	-1.326	5.2786	7.3363	4.2426	0.8146	0.2346	0.8397	0.6667	0.478	-0.0213
167	Artlud	Yes	0.2266	5.8467	6.5052	3.7417	0.8148	0.1886	0.9638	0.653	0.5236	-0.4941
168	Carex	Yes	0.1634	5.6539	6.7534	3.7417	0.7709	0.2193	0.9269	0.6626	0.5586	0.0256
169	Solid	Yes	-0.302	6.154	6.9385	4.3589	0.8383	0.1835	1.0911	0.6511	0.5007	0.1181
172	Artlud	Yes	-0.455	5.6493	6.8477	3.4641	0.839	0.1658	0.901	0.6806	0.5236	-1.1437
173	Gali	No	-0.5839	5.3008	6.56	4.1231	0.8637	0.2039	0.6549	0.6947	0.4115	-0.2345
174	Carex	Yes	0.8421	5.782	6.7424	4.2426	0.8096	0.181	0.8308	0.7056	0.4668	0.3899
175	Achil	No	-1.8183	5.6798	6.5261	4.1231	0.7884	0.1835	0.5279	0.6938	0.5121	-0.4545
177	Solid	No	-0.4605	4.9925	6.3369	3.3166	0.7074	0.2269	0.6352	0.7022	0.5704	1.0554
180	Artlud	No	-0.0693	5.2111	6.2499	4	0.7936	0.1658	0.5619	0.712	0.4668	0.7331
181	Hespe	No	-0.195	5.6423	5.8535	3.6056	0.7751	0.181	0.9009	0.7151	0.5704	0.9117
182	Artfr	No	-0.6281	5.8242	6.8173	3.3166	0.7323	0.1708	0.6977	0.6764	0.6065	0.7818
184	Festu	Yes	-0.3255	5.7875	7.0005	3.873	0.7796	0.1759	0.8426	0.6582	0.4334	1.1622
186	Cera	No	-0.1073	5.7278	5.9061	3.873	0.8769	0.2116	0.612	0.6825	0.3152	-0.3235
188	Artfr	No	-0.9408	5.6809	6.7199	3.873	0.8797	0.1988	0.5975	0.6981	0.6816	0.9842
189	Cera	No	5.4839	5.2857	6.6852	3.873	0.8386	0.2039	0.8204	0.6954	0.6065	0.2846
190	Artlud	Yes	-0.772	5.5767	6.7159	4	0.8977	0.1506	0.784	0.6898	0.6187	0.1476
191	Hespe	Yes	-0.5474	5.7014	6.9107	4.2426	0.8266	0.2346	0.8724	0.7013	0.6561	0.6203

#	Species	Ntmt	Comp. Intensity	Shoot Biomass	Root Biomass	Sp Rich	Even	Soil Moist	Light Intercept	Topog. Pos.	Total Nitrogen	Community Composition
194	Rosa	Yes	-0.0871	5.757	7.1284	4	0.8849	0.1886	0.6891	0.7006	0.5469	-0.3669
195	Artlud	No	-0.3336	5.349	6.303	4.2426	0.8788	0.1988	0.8626	0.6715	0.2942	-0.7491
197	Cera	Yes	1.2388	5.515	6.2856	3.7417	0.888	0.1861	0.8489	0.7039	0.6187	0.8261
198	Cera	No	0.5452	5.3504	6.7027	4.2426	0.8138	0.2424	0.7538	0.6633	0.5704	0.4029
199	Artlud	No	-0.3987	5.4697	6.943	4.1231	0.8713	0.2218	0.7735	0.6656	0.6561	0.1891
200	Hespe	Yes	-0.1473	5.6893	6.7698	4	0.8498	0.1861	0.6956	0.6561	0.2942	0.656
202	Rosa	Yes	0.169	5.893	7.1329	4.5826	0.8572	0.2116	0.8261	0.6986	0.7615	0.0055
203	Geum	Yes	-0.4213	5.9285	6.8869	4.3589	0.8565	0.2116	0.5678	0.6663	0.4556	-0.3772
204	Artlud	Yes	-0.6602	5.8427	7.2158	4.1231	0.8404	0.2065	0.9049	0.6583	0.6065	-0.9973
205	Poa	Yes	-0.0986	6.0992	6.9875	3.7417	0.7538	0.1759	0.5995	0.6547	0.5121	-1.5893
206	Cera	Yes	-1.4746	6.3507	7.6785	4.3589	0.8447	0.1886	0.8172	0.6722	0.7615	-1.1012
208	Hespe	Yes	0.1632	6.0808	6.9699	3.7417	0.793	0.1912	0.7937	0.6563	0.6687	-0.1513
211	Artlud	Yes	-0.4486	6.219	7.1589	3.1623	0.8634	0.1329	0.8634	0.6606	0.5944	-0.5142
212	Carex	No	5.8647	5.4161	6.8675	3.4641	0.844	0.181	0.5713	0.6609	0.4115	-0.9318
214	Poa	No	-0.1937	5.6265	7.3987	3.3166	0.8457	0.1988	0.4397	0.6571	0.3469	-0.5022
216	Poa	No	-0.7506	5.6098	6.7199	4	0.7922	0.209	1.046	0.6559	0.4334	-0.6432
218	Cera	Yes	-0.6609	5.6981	7.3121	4.4721	0.864	0.2116	0.7004	0.6662	0.4334	0.1429
220	Hespe	No	0.0228	5.9922	6.637	3.873	0.8631	0.1861	0.5876	0.6602	0.3898	0.5225
223	Geum	Yes	-0.5793	5.6974	7.0132	3.6056	0.8986	0.1607	0.9991	0.6773	0.4893	-0.1166
225	Poa	No	0.2447	5.6142	7.1625	4	0.8527	0.2014	0.9753	0.6547	0.4225	-1.0134
226	Solid	No	-0.1162	5.5691	6.6969	3.3166	0.8229	0.1861	0.698	0.6721	0.5236	1.9831
227	Geum	No	-0.1174	5.3762	6.9875	3.873	0.8256	0.2193	0.5067	0.6768	0.4445	0.1083
228	Carex	No	-0.7151	5.6269	6.3777	4	0.8709	0.1886	0.9233	0.6547	0.4225	-0.1634
229	Festu	Yes	-0.236	5.8438	6.8457	3.6056	0.8127	0.1937	0.8258	0.6719	0.2838	1.652
230	Hespe	Yes	0.4037	5.4988	6.8522	3.6056	0.8048	0.2167	0.8431	0.6535	0.4006	1.85
231	Artlud	Yes	-0.1746	5.5138	6.4989	4.1231	0.8937	0.2244	0.5998	0.65	0.4006	0.7108
232	Carex	No	-1.0157	5.7278	6.2856	3.873	0.852	0.2864	0.639	0.6685	0.4445	0.5566
234	Festu	Yes	1.1809	5.6215	6.6333	4.2426	0.8576	0.181	0.7978	0.6658	0.4225	-0.3146
236	Artfr	Yes	-0.176	5.5373	6.9293	3.6056	0.9175	0.1912	0.5259	0.7291	0.4225	1.2657

#	Species	Ntmt	Comp. Intensity	Shoot Biomass	Root Biomass	Sp Rich	Even	Soil Moist	Light Intercept	Topog. Pos.	Total Nitrogen	Community Composition
237	Artfr	Yes	0.1686	6.0285	5.263	3.7417	0.8757	0.1683	0.9731	0.7094	0.2116	1.9059
238	Geum	Yes	-0.4252	5.4549	6.8577	3.873	0.864	0.2295	0.6093	0.6956	0.4006	1.3338
239	Artfr	Yes	-0.2488	5.5362	6.7142	4.2426	0.8533	0.2244	0.8542	0.6956	0.4445	1.491
240	Cera	No	1.0909	5.2476	6.1344	3.7417	0.8829	0.2141	0.46	0.7061	0.379	0.5467
241	Hespe	Yes	-0.4432	5.3822	6.9385	3.4641	0.8932	0.1912	0.6915	0.7317	0.3047	1.0123
244	Festu	No	0.4571	4.9373	7.0507	3.3166	0.8921	0.2193	0.3822	0.7072	0.4115	1.1355
245	Cera	No	-2.0275	4.9898	6.1033	4	0.8872	0.2167	0.2133	0.7355	0.4006	0.7321
246	Hespe	No	0.3437	4.73	6.1744	3	0.8038	0.2116	0.6057	0.7039	0.3683	1.3216
248	Artfr	Yes	-1.0919	5.7028	6.8749	4.3589	0.846	0.1937	0.6886	0.6663	0.4445	0.6737
250	Poa	No	-0.192	5.7206	7.1734	3.7417	0.7225	0.1607	0.9065	0.6682	0.2942	-1.2514
251	Cera	No	3.7054	5.3433	6.8869	4.1231	0.8222	0.1886	0.8241	0.6713	0.4668	-1.305
252	Artfr	Yes	-0.4898	5.751	6.8183	3.3166	0.7411	0.1683	0.9583	0.649	0.4006	1.6115
254	Hespe	No	0.1884	5.4359	6.6674	3.7417	0.8393	0.1861	0.5329	0.6931	0.5007	0.4394
255	Festu	No	-1.9634	5.9646	7.4355	3.7417	0.8521	0.209	0.9927	0.6565	0.4668	-0.5988
256	Poa	Yes	-0.6151	5.6958	7.768	3.873	0.8051	0.1708	0.9936	0.6717	0.4334	-0.864
257	Cera	Yes	-0.0293	5.7668	7.324	3.4641	0.7604	0.1963	1.0772	0.6664	0.5944	-1.5028
259	Geum	No	-0.2118	5.9299	6.943	3.6056	0.7703	0.2167	0.8049	0.6623	0.7478	0.6424
260	Poa	Yes	-0.3861	5.8024	7.1625	3	0.8599	0.1937	1.3009	0.6582	0.4115	-1.2615
261	Poa	No	-0.6873	5.8528	7.1139	4.1231	0.7849	0.209	0.9755	0.6624	0.5121	-1.3138
264	Artfr	No	-0.4686	5.4685	7.2956	3	0.8712	0.1835	0.8756	0.6535	0.478	-1.612
265	Cera	No	0.3483	5.4446	7.413	4	0.7905	0.181	1.1408	0.547	0.4445	-0.092
266	Artlud	No	0.0299	5.8653	7.2565	4.3589	0.8923	0.2141	1.2419	0.6095	0.4893	-0.8266
267	Artfr	No	-0.6043	5.6258	6.7964	3.873	0.8224	0.1607	0.8636	0.6195	0.3683	1.8382
269	Artlud	Yes	0.0677	5.9078	7.233	3.6056	0.8481	0.1582	1.1038	0.6723	0.263	-0.4647
271	Cera	Yes	0.4732	5.8377	7.2262	3.3166	0.805	0.148	1.0782	0.6611	0.6065	-0.1004
274	Cera	Yes	-1.1629	5.9341	7.9159	3.873	0.8828	0.1759	1.1082	0.6547	0.4556	-0.7017
275	Artlud	No	-0.4146	5.5029	8.0861	3.1623	0.765	0.2218	1.2034	0.6442	0.7342	-2.1427
276	Artlud	Yes	-0.1698	5.8721	7.7274	3.873	0.9118	0.181	1.047	0.6532	0.6065	-2.3061