"But now ask the beasts, and let them teach you;
the birds of the heavens, and let them tell you.
"or speak to the earth, and let it teach you;
and let the fish of the sea declare to you.
"Who among all these does not know
that the hand of the Lord has done this."

— **Job** 12:7-9

"Nature never taught me that there exists a God of glory and of infinite majesty. I had to learn that in other ways. But nature gave the word glory a meaning for me. I still do not know where else I could have found one."

— **C. S. Lewis** (1898-1963),

"I want creation to penetrate you with so much admiration that wherever you go, the least plant may bring you the clear remembrance of the Creator. …One blade of grass or one speck of dust is enough to occupy your entire mind in beholding the art with which it has been made.

— **St. Basil the Great** (329-379)

"Some people, in order to discover God, read books. But there is a great book: the very appearance of created things. Look above you! Look below you! Read it. God, whom you want to discover, never wrote that book with ink. Instead He set before your eyes the things that He had made. Can you ask for a louder voice than that?"

— **St. Augustine** (354-430)

For to win one hundred victories in one hundred battles is not the acme of skill. To subdue the enemy without fighting is the acme of skill.

— **Sun Tzu** (6th Century BC)

University of Alberta

Mechanisms Regulating *Poa pratensis* L. and *Festuca campestris* Rybd. Within the Foothills Fescue Grasslands of Southern Alberta

by

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Abstract

Invasion of non-native species such as *Poa pratensis* L. has become a serious threat to the conservation of bunch grass communities including foothills fescue grasslands in Alberta, Canada. Conservation efforts are currently limited by a poor understanding of the ecological mechanisms responsible for regulati resistance of native grasslands to encroachment by *P. pratensis*. While invasion o *P. pratensis* has been linked to summer grazing, we lack an understanding of how environmental conditions (light, soil moisture content and soil N) may influence invasion. Four studies were conducted to determine the individual and interactive effects of environmental and disturbance mechanisms on *P. pratensis* invasion and the associated vigor of foothills rough fescue (*Festuca campestris* Rydb.).

An *in-situ* field study within a late-seral grassland suggested that conditions favoring *F. campestris* (i.e. high soil moisture content, abundant litter, winter defoliation, undefoliated conditions) suppressed *P. pratensis,* while those favoring *P. pratensis* (i.e. summer defoliation, litter removal, ambient water) reduced the vigor of *F. campestris*. Further exploration of this relationship in a variable density planting study under fallow field conditions suggested that the vigor and density of *F. campestris* were important factors regulating *P. pratensis* invasion. In a parallel greenhouse study using seedlings of both species, increased soil moisture content, defoliation, and ambient soil N, increased the ability of *P. pratensis* to suppress *F. campestris,* but this was much more significant with younger *F. campestris* plants. Finally tillage and litter removal were the most

effective methods of suppressing *P. pratensis* and increasing the vigor of *F. campestris* within heavily disturbed grassland. In the latter experiment, establishment method was also important (cuttings = plugs > seeding) in determining the vigor of *F. campestris* plants.

Observed responses suggest that maintaining the vigor of *F. campestris* within existing grasslands is the best method of suppressing invasion by *P. pratensis*. *P. pratensis* suppression may be accomplished through winter defoliation, allowing litter accumulation and minimizing soil nitrogen. Age appeared to be important in determining the competitive ability of *F. campestris* plants with immature plants appearing more likely to be detrimentally impacted by *P. pratensis* than more mature plants.

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Table of Contents

Chapter **Page**

1. INTRODUCTION 1

1.1 BACKGROUND 1

1.2 OVERVIEW OF INVASION IN FESCUE GRASSLANDS 1

1.3 NEED TO UNDERSTAND ECOLOGICAL MECHANISMS.................................... 3

1.4 THEORETICAL AND EXPERIMENTAL APPROACH... 4

1.5 LITERATURE CITED 8

2. REVIEW OF POA PRATENSIS (L.) INVASION OF *FESTUCA CAMPESTRIS* (RYBD.) COMMUNITIES.. 10

2.0 INTRODUCTION 10

2.1 INVASIVE THEORY 10

2.1.1 The Passenger Model vs. Driver Model of Invasion.......................... 11

2.1.2 Theorized Mechanisms of Invasion 13

2.1.3 Competition and Facilitation 16

2.1.4 Final Outcome.. 19

2.2 THE NEED TO UNDERSTAND ABOVE AND BELOW GROUND INTERACTIONS.. 20

2.2.1 Litter Effects 21

2.3 ABOVE GROUND INTERACTIONS.. 23

2.3.1 Light 23

2.3.1.1 Light Signals 24

2.4 BELOW GROUND INTERACTIONS.. 25

2.4.1 Soil Nutrients 25

2.4.2 Soil Nitrogen Relationships... 25

2.4.3 Soil Water 28

2.4.4 Other Soil Properties 29

2.5 DISTURBANCE... 30

2.5.1 Antropogenic Disturbance ... 31

2.5.2 Defoliation ... 32

2.6 Fescue Grasslands ... 34

2.6.1 *Festuca campestris* ... 37

2.6.1.1 *F. campestris* Response to Light ... 37

2.6.1.2 *F. campestris* Response to Nutrients ... 38

2.6.1.3 *F. campestris* Response to Water ... 39

2.6.1.4 *F. campestris* and Disturbance ... 39

2.6.1.5 *F. campestris* Response to Defoliation ... 41

2.6.2 Poa pratensis ... 42

2.6.2.1 *P. pratensis* Response to Light ... 42

2.6.2.2 *P. pratensis* Response to Nutrients ... 44

2.6.2.3 *P. pratensis* Response to Water ... 45

2.6.2.4 *P. pratensis* and Disturbance ... 45

2.6.2.5 *P. pratensis* Response to Defoliation ... 46

2.6.3 *F. campestris* Competitive Interactions with P. pratensis ... 47

2.7 Summary and Conclusions ... 49

2.7.1 Predicting the Outcomes of Invasion ... 49

2.7.1.1 Invasion on Disturbances ... 50

2.7.1.2 Invasion on Undisturbed Land ... 51

2.7.2 Expected Resource Interactions During Invasion ... 51

2.7.3 New Information Needed ... 52

2.8 Literature Cited ... 54

3. DO ENVIRONMENTAL AND DISTURBANCE REGULATE COMPOSITION WITHIN FOOTHILLS ROUGH FESCUE (*FESTUCA CAMPESTRIS* RYBD.) GRASSLANDS? ... 64

3.1 Introduction ... 64

3.2 Objectives ... 68

3.3 Methods ... 69

3.3.1 Research Site ... 69

3.3.2 Experimental Design 69
3.3.3 Measurements 72
3.3.3.1 Environmental Monitoring.. 72
3.3.3.2 Vegetation Measures 73
3.4 ANALYSES 74
3.4.1 Primary Treatment Impacts on Environment and Community........... 75
3.4.2 Detailed Plant Community Composition Responses 76
3.5 RESULTS 79
3.5.1 Treatment Induced Changes to the Environment................................ 79
3.5.2 Fescue Grassland Responses to Environment 79
3.5.3 Fescue Grassland Responses to Defoliation...................................... 84
3.6 DISCUSSION 87
3.6.1 Species Composition Responses to Nitrogen and Water 87
3.6.2 Community Responses to Litter Removal... 92
3.6.3 Defoliation Effects on Community Composition 94
3.6.4 Interactions between Species 97
3.7 CONCLUSION 99
3.8 REFERENCES.. 100

4. EFFECT OF ENVIRONMENT AND DEFOLIATION ON *FESTUCA CAMPESTRIS* (RYBD.) AND *POA PRATENSIS* (L.) VIGOR 121

4.1 INTRODUCTION 121
4.2 RESEARCH OBJECTIVES 125
4.3 METHODS 126
4.3.1 Study Site... 126
4.3.2 Experimental Design 126
4.3.3 Measurements 129
4.3.3.1 Environmental Monitoring.. 129
4.3.3.2 Vegetation Measures 130
4.4 STATISTICAL ANALYSIS 131

4.5 RESULTS 133
    4.5.1 Treatment Induced Changes to the Environment............................. 133
    4.5.2 Festuca campestris Responses 133
    4.5.3 *Poa pratensis* Responses 136
    4.5.4 Relationship between Festuca campestris and Poa pratensis 138
4.6 DISCUSSION 138
    4.6.1 *Festuca campestris* Response to Treatments.................................. 138
    4.6.1 *Poa pratensis* Response to Treatments 142
4.7 CONCLUSIONS.. 147
4.8 REFERENCES.. 148

5. FACTORS REGULATING POA PRATENSIS (L.) INVASION INTO *FESTUCA CAMPESTRIS* (RYBD.) MONOCULTURES UNDER FIELD CONDITIONS.. 165

5.1 INTRODUCTION 165
5.2 OBJECTIVES 169
5.3 METHODOLOGY 170
    5.3.1 Research Site and Plant Materials... 170
    5.3.2 Experimental Design 171
    5.3.3 Plant and Environmental Measures... 173
5.4 ANALYSIS 175
5.5 RESULTS 177
    5.5.1 *Festuca campestris* Responses.. 177
        5.5.1.1 Mortality 177
        5.5.1.2 Tillers.. 178
        5.5.1.3 Sexual Reproduction 179
        5.5.1.4 Cover 180
        5.5.1.5 Biomass... 180
    5.5.2 *Poa pratensis* Response to *Festuca campestris*............................... 181
    5.5.3 Environmental Factors 183
5.6 DISCUSSION:.. 183

5.6.1 Intraspecific Competition within *Festuca campestris* 184
5.6.2 *Festuca campestris* Response to *Poa pratensis* 187
5.7 CONCLUSION 188
5.8 REFERENCES 189

6. DOES NITROGEN OR WATER REGULATE COMPETITION BETWEEN JUVENILE *FESTUCA CAMPESTRIS* (RYBD.) AND *POA PRATENSIS* (L.) 203

6.1 INTRODUCTION 203
6.2 OBJECTIVES 206
6.3 MATERIALS AND METHODS 207
6.3.1. Experimental Design 207
6.3.2. Measurements 209
6.3.3. Statistical Analysis 210
6.4 RESULTS 210
6.4.1 Soil Nitrogen 210
6.4.2 Biomass 211
6.4.2.1 Environment 211
6.4.2.2 Plant Neighbor 213
6.4.3 Tillers 215
6.4.3.1 Environment 215
6.4.3.2 Plant Neighbor 216
6.5 DISCUSSION 217
6.5.1 *F. campestris* growth changes in the presence of *P. pratensis* 217
6.5.2 Changes in soil N and/or soil moisture alter interspecific relationships between *F. campestris* and *P. pratensis* 218
6.5.3 Defoliation, either alone, or in combination with changes in soil N and/or water, affect competition dynamics between *F. campestris* and *P. pratensis* 220
6.6 CONCLUSION 221
6.7 IMPLICATIONS 222

6.8 REFERENCES 223

7. CAN SOIL PREPARATION AND PLANTING METHOD IMPROVE *FESTUCA CAMPESTRIS* (RYBD.) ESTABLISHMENT IN *POA PRATENSIS* (L.) DOMINATED GRASSLANDS? 238

7.2 INTRODUCTION 238
7.2 OBJECTIVES 242
7.3 METHODS 242
7.3.1 Research Site 242
7.3.2 Experimental Design 243
7.3.3 Measurements 245
7.3.3.1 Environmental Monitoring 245
7.3.3.2 Vegetation Measures 246
7.3.4 Analysis 246
7.4 RESULTS 248
7.4.1 Effects of Soil Preparation on the Environment 248
7.4.2 Effects of Soil Preparation on F. campestris 249
7.4.3 Effects of Soil Preparation on Introduced Species 251
7.4.3.1 *Poa pratensis* 251
7.5 DISCUSSION 252
7.5.3 Establishment Success 252
7.5.4 Litter Removal 253
7.5.5 Tilling 256
7.5.6 Carbon Addition 257
7.6 CONCLUSIONS 258
7.7 REFERENCES 260

CHAPTER 8 SYNTHESIS AND MANAGEMENT IMPLICATIONS 270

8.1 KEY RESULTS 271
8.2 IMPLICATIONS 275
8.3 FUTURE RESEARCH 276

8.4 REFERENCES 278

APPENDIX A SUPPLEMENTAL INFORMATION FOR CHAPTER 3........ 281

APPENDIX B SUPPLEMENTAL INFORMATION FOR CHAPTER 4........ 296

APPENDIX C SUPPLEMENTAL INFORMATION FOR CHAPTER 5........ 305

APPENDIX D SUPPLEMENATAL INFORMATION FOR CHAPTER 6..... 310

APPENDIX E SUPPLEMENTAL INFORMATION ON THE ENVIRONMENT FOR CHAPTERS 3 & 4 321

APPENDIX F SUPPLEMENTAL INFORMATION FOR CHAPTER 7 328

List of Tables

Table **Page**

Table 3.1 Summary of treatments used to examine the impact of environmental conditions and disturbance on fescue grassland composition.. 107

Table 3.2 Stepwise regression analysis assessing the relationship between monthly soil moisture (SM), monthly photosynthetically active radiation (PAR), and annual soil N, with various community responses, including diversity, richness and evenness, litter and herbaceous biomass (2008 only), during each of 2006 and 2008. Analysis used only non-defoliated plots. All results are shown at P<0.1 and are considered significant at P<0.05....................................... 108

Table 3.3 Summary of significance (P) values from the Multi-Response Permutation Procedure (MRPP) analysis of plant community data associated with various treatments, including litter removal, defoliation, and water and nitrogen addition. Results are provided separately for litter modification and defoliation, alone and in combination with nitrogen and water addition.. 109

Table 3.4 Summary test results arising from the Multi-Response Permutation Procedure (MRPP) evaluating the effect of water addition, nitrogen addition, the interaction of water (+W) and nitrogen (+N) addition, and the interaction of water and litter presence (+L), on plant species composition during each of 2006, 2007 and 2008 (last year of sampling). Ambient field conditions are represented by +L, -W and -N.. 110

Table 3.5 Summary correlations (minimum r=|0.12|, |0.22|, |0.38|) between treatments, environmental factors, and key species, with each of the 3 axes arising from the NMS ordination of 2006 vegetation responses and environmental treatments. Species shown include provincially important species and those with a P value <0.1 based on the indicator species analysis. 111

Table 3.6 Summary correlations (minimum r=|0.12|, |0.22|, |0.38|) treatments, environmental factors, and key species, with each of the 3 axes arising from the NMS ordination of 2008 vegetation responses and environmental treatments. Species shown include provincially important species and those with a P value <0.1 based on the indicator species analysis. 112

Table 3.7 Summary test results arising from the Multi-Response Permutation Procedure (MRPP) evaluating the effect of various environmental treatments and their interactions, on plant community composition in each of 2007 and 2008. Effects are considered significant at p<0.05. 113

Table 3.8 Summary correlations (minimum r=|0.12|, |0.22|, |0.38|) between treatments, environmental factors, and key species, with each of the 3 axes arising from the NMS ordination of 2007 vegetation responses and defoliation treatments. Species shown include provincially important species and those with a P value <0.1 based on the indicator species analysis. 114

Table 3.9 Summary correlations (minimum r=|0.12|, |0.22|, |0.38|) between treatments, environmental factors, and key species, with each of the 3 axes arising from the NMS ordination of 2008 vegetation responses and defoliation treatments. Species shown include provincially important species and those with a P value <0.1 based on the indicator species analysis. 115

Table 4.1 Summary of treatments used to examine the impact of environment and defoliation on fescue grassland composition. 153

Table 4.2 Association of *P. pratensis* and *F. campestris* plant responses to monthly photsynthetically active radiation (PAR), soil moisture (SM), and annual available soil N sampled during each growing season from 2006 through 2008 based on a multiple regression. 154

Table 4.3 Effect of environmental conditions, including litter removal (-L), along with water (+W) and nitrogen (+N) addition, on the mean (±SE) cover and final biomass of *P. pratensis*. 155

Table 4.4 Mean density (±SE) of *P. pratensis* inflorescences (#/m^2) in response to defoliation during each year of sampling. 156

Table 4.5 Mean (±SE) cover of *P. pratensis* following nitrogen addition (+N) and defoliation, over the three years of study. 157

Table 4.6 Mean (±SE) cover, basal diameter, number of tillers, and proportion of tillers with inflorescences, of *F. campestris* plants, under varying nitrogen addition (+N) and water addition (+W) treatments, with (+L) and without litter presence, as determined in the environmental analysis. Results are averaged over all three years of the study. 158

Table 4.7 Mean (±SE) cover, basal diameter and biomass of vegetative tillers of *F. campestris* plants under varying nitrogen addition (+N) and defoliation treatments, as assessed within the defoliation analysis over the period 2007-2008. 159

Table 4.8 Mean (±SE) tiller densities (#/plant) of *F. campestris* plants to nitrogen level and defoliation treatments within the defoliation analysis during each year of sampling. During analysis, tiller densities from 2005 were run as a covariate. 160

Table 5.1 Mean (±SE) tiller counts of focal and exterior *F. campestris* plants, as well as the proportion of focal tillers with inflorescences, in response to the interaction of sampling year and *F. campestris* planting density 192

Table 5.2 Mean (±SE) biomass (g/plant) and tiller counts of focal *F. campestris* plants, invading *P. pratensis* biomass (g/m^2), and minimum distance of *P. pratensis* from adjacent exterior *F. campestris* plants, in response to the interaction of density and defoliation. 193

Table 5.3 Number of vegetative tillers and proportion of tillers with seed heads within exterior *F. campestris* plants exposed to combinations of defoliation and *P. pratensis* invasion. 194

Table 5.4 Focal *F. campestris* biomass / tiller (±SE) in response to the interaction of *P. pratensis* introduction and planting density. 195

Table 6.1 The interaction of defoliation with either sucrose addition or water addition on the final *F. campestris* focal plant shoot biomass and R:S ratios during Experiment 1. 226

Table 6.2 Plant neighbor interactions with defoliation or water addition on the final *F. campestris* focal plant shoot and root biomass during Experiment 1. 227

Table 6.3 The effects of plant neighbor interactions with presence or absence of defoliation on final root biomass, shoot biomass, and change in tillers in Experiment 2. 228

Table 6.4 The interaction of nitrogen and water on the *F. campestris* focal plant changes in tiller numbers (first 2.5 months) during Experiment 1. 229

Table 6.5 The effect of plant neighbor and nitrogen on change in tiller counts after 1 and 3 months of growth in Experiment 2. 230

Table 6.6 Summary of F and P values for the final change in tillers, root biomass, shoot biomass and R:S ratio's in Experiment 2 on water addition, sucrose addition, defoliation and plant neighbor treatments. 231

Table 6.7 Summary of F and P values for interm change in tillers, final shoot biomass, root biomass, and R:S ratios of focal *F. campestris* plants undergoing defoliation, sucrose addition, water addition and plant neighbor treatments in Experiment 1. Initial tiller counts used as a covariate for all biomass data. 232

Table 6.8 Summary of F and P values for interim change in tillers on defoliation, sucrose addition, water addition and plant neighbor treatments after 1 and 3 months in Experiment 2. 233

Table 7.1 Summary of soil preparation treatments used where (-) represents the absence of the treatment and (+) represents the presence of the treatment. 264

Table 7.2 Mean comparisons of tilling, litter removal, and carbon addition effects within planting method, on environmental conditions, including available soil N, monthly photosynthetically active radiation

(PAR), and monthly soil moisture. Data are averaged among years 2006 to 2008... 265

Table 7.3 Mean (± SE) vigor of mature cuttings and greenhouse plugs of *F. campestris*, including tiller counts, cover, final biomass, and survival from 2006 through 2008. 266

Table 7.4 Results of the multiple regression analysis within the greenhouse plug planting method between *F. campestris, H. jubatum*, and *P. pratensis* vigor measures (cover, survival, tillers, and biomass) and environment [soil moisture (SM), photosynthetically active radiation (PAR), and available soil N], in each of 2006, 2007 and 2008. Responses are averaged across all soil preparation treatments................. 267

Table 7.5 Results of the multiple regression analysis within the mature cutting planting method between *F. campestris, H. jubatum*, and *P. pratensis* vigor measures (cover, survival, tillers, and biomass) and environment [soil moisture (SM), photosynthetically active radiation (PAR), and available soil N] in each of 2006, 2007 and 2008. Responses were combined across all soil treatments. 268

Table 7.6 Effects of soil preparation techniques (carbon addition, litter removal, and tilling) on the mean (±SE) cover and biomass of *P. pratensis* within each of the experiments using mature cuttings and greenhouse plugs of *F. campestris*. 269

Table A1: Summary significance (P & F) values of mean evenness, richness, and Shannon's diversity after the initial year of treatments (2006) and after the final treatments (2008), relative to W, N, and W*N treatments within the defoliation treatments (1,3,5,7,9-16). P values < 0.1 were considered significant for all main effects................... 282

Table A2: The response of evenness to the change in cover of *F. campestr*is in the environmental treatments during 2006......................... 283

Table A3: Summary significance (P & F) values of mean evenness, richness, and Shannon's diversity after the initial year of treatments (2006) and after the final treatments (2008), relative to W, N, L and interactions within the environmental treatments (1-8). P values < 0.1 were considered significant for all main effects. 284

Table A4: Summary significance (P & F) values of mean evenness, richness, and Shannon's diversity after the initial year of treatments (2006) and after the final treatments (2008), relative to W, N,D and interactions within the defoliation treatments (1,3,5,7,9-16). P values < 0.1 were considered significant for all main effects................................ 285

Table A5: The interaction of water addition (+W) with litter removal (-L) treatments on evenness during 2006 and richness during 2007................ 286

Table A6: Indicator species analysis of the 2006-2008 environmental experiment. P values are considered significant at 0.1 for provincially important species (*P. pratensis, F. campestris, S. occidentalis, B. inermis*) and 0.05 for all other species.. 287

Table A7: Indicator species analysis of the 2006 environmental experiment. P values are considered significant at 0.1 for provincially important species (*P. pratensis, F. campestris, S. occidentalis, B. inermis*) and 0.05 for all other species.. 288

Table A8: Indicator species analysis of the 2008 environmental experiment. P values are considered significant at 0.1 for provincially important species (*P. pratensis, F. campestris, S. occidentalis, B. inermis*) and 0.05 for all other species.. 289

Table A9: Indicator species analysis of the 2007 defoliation experiment. P values are considered significant at 0.1 for provincially important species (*P. pratensis, F. campestris, S. occidentalis, B. inermis*) and 0.05 for all other species. 290

Table A10: Indicator species analysis of the 2008 defoliation experiment. P values are considered significant at 0.1 for provincially important species (*P. pratensis, F. campestris, S. occidentalis, B. inermis*) and 0.05 for all other species. 291

Table A11: Summary correlations (minimum r=|0.12|, |0.22|, |0.38|) between treatments, environmental factors, and key species, with each of the 3 axes arising from the NMS ordination of 2006-2008 vegetation responses and environmental treatments. Species shown include all those with a P value <0.1 based on the indicator species analysis. 292

Table B1: Temporal variation in the vigor of *F. campestris* and *P. pratensis* plants during each year of sampling (2006, 2007 and 2008). Data are from plants sampled within the environmental treatments (1-8) only. 297

Table B2: Mean *F. campestris* basal diameter associated with N addition for each of the 3 years of sampling. Data are from the environmental treatments (1-8) only. 298

Table B3: Mean proportion of tillers with inflorescences within *F. campestris* focal plants following water addition during each of the 3 years of sampling. Data are the environmental treatments (1-8) only. 299

Table B4 Summary significance (P & F) values of mean *F. campestris* cover, basal diameter, proportion of tillers with inflorescences, total tillers counts, and biomass, from 2006 through 2008, relative to the environmental treatments (1-8). Biomass data were only available from 2008. Analyses of data (except biomass) used 2005 tiller counts as a covariate. P values were considered significant at P<0.1 for all main effects. 300

Table B5 Summary significance (P & F) values of mean *F. campestris* cover, basal diameter, proportion of tillers with inflorescences, and total tiller counts in each of 2006, 2007, and 2008, relative to the defoliation treatments. Biomass data were only available for 2008. Analyses of all data (except biomass) use 2005 tiller counts as a covariate. P values were considered significant at P<0.1 for all main effects. 301

Table B6 Summary significance (P & F) values of mean *P. pratensis* cover, inflorescences density, vegetative tiller heights, and final biomass in relation to the environmental treatments in each of 2006, 2007 and 2008. Biomass data were available only for 2008. For all analyses but that of biomass, cover from 2005 was used as a covariate for all vigor measures. P values were considered significant at P<0.1 for all main effects. 302

Table B7 Summary significance (P & F) values of mean *P. pratensis* cover, inflorescence density, vegetative tiller heights, and final biomass within the defoliation treatments in 2006, 2007 and 2008, with initial cover from 2005 used as a covariate. Biomass data were available only for 2008. Values were considered significant at P<0.1 for all main effects. .. 303

Table B8 **S**ummary significance (P & F) values of mean *P. pratensis* cover, inflorescence density, vegetative tiller heights, and final biomass within the defoliation treatments in 2006, 2007 and 2008, with initial cover from 2005 used as a covariate. Biomass data were available only for 2008. Values were considered significant at P<0.1 for all main effects.. 304

Table C1: Effect of distance from the focal *F. campestris* plant and its interaction with planting density and defoliation, on *P. pratensis* and *F. campestris* cover. 305

Table C2: Effect of variable planting density and defoliation on the cover of *F. campestris*, and the distance *P. pratensis* invaded towards the focal *F. campestris* plant.. 306

Table C3: Effect of sampling year, planting density, defoliation and *P. pratensis* introduction, on total number of tillers and the proportion of tillers with inflorescences within focal and exterior *F. campestris* plants.. 307

Table C4: Effect of plant density, defoliation, and *P. pratensis* introduction on the total biomass and biomass/tiller of *F. campestris* focal and exterior plants, and the effects of density and defoliation on *P. pratensis* biomass. 308

Table D1: The interaction of nitrogen and water on the *F. campestris* focal plant tiller heights (3.5 months) and tillers numbers (2.5 months) during Experiment 1. Letters that differ denote differences significant at <0.05 in each column. 313

Table D2: Plant neighbor interactions with defoliation on the final *F. campestris* focal plant tiller heights during Experiment 1. Letters that differ within a column and abiotic factor denote differences significant at <0.05. 314

Table D3: The effects of plant neighbor interactions with presence or absence of defoliation on final root and shoot biomass, tiller counts and tiller heights. Letters that differ within a column denote differences significant at <0.05. 315

Table D4: Summary of the F and P values for Tiller heights on defoliation, sucrose addition, water addition and plant neighbor treatments after one and thee months in Experiment 2. 316

Table E1: The effects of water addition and one time litter removal (-L) on measured soil moisture (%) and light transmittance (% PAR) during each of the 2006, 2007 and 2008 growing seasons. 323

Table E2: Precipitation at the Cochrane weather station including 2006, 2007, 2008, 30 year normal and percentage of the 30 year normal precipitation experienced in each month. 2008 data is underestimated as data points were missing from the weather station. 324

Table F.1: Summary of significance tests for available soil N, as well as May, June and July photosynthetically active radiation (PAR), within the soil preparation treatments (carbon addition, litter removal and tilling treatments) and planting methods (mature cuttings and greenhouse plugs). P values <0.1 are considered significant........ 329

Table F1.1: Summary of the P-values of Environmental measures (May, June, July and August soil moisture) within the soil preparation treatments (carbon addition, litter removal and tilling treatments) and planting methods (mature cuttings, and greenhouse plugs). P values <0.1 are considered significant. 329

Table F2: Summary of the P-values of *F. campestris* vigor measures including Tillers (2007, 2008, and total) and Cover (2007, 2008 and Total) within the soil preparation treatments (carbon addition, litter removal and tilling treatments) and planting methods (mature cuttings, and greenhouse plugs). P value<0.1 are considered significant. 330

Table F2.1: Summary of the P-values of *F. campestris* vigor measures including final biomass and survival (2006, 2007, 2008 and Total) within the soil preparation treatments (carbon addition, litter removal and tilling treatments) and planting methods (mature cuttings, and greenhouse plugs). P values <0.1 are considered significant.................... 330

Table F3: Summary of the P-values of *P. pratensis* vigor measures including final biomass and Cover (2007, 2008 and Total) within the soil preparation treatments (carbon addition, litter removal and tilling treatments) and planting methods (mature cuttings, and greenhouse plugs). P values <0.1 are considered significant. 331

Table F4: Summary of the P-values of *H. jubatum* Cover (2006, 2007, 2008 and Total) within the soil preparation treatments (carbon addition, litter removal and tilling treatments) and planting methods (mature cuttings, and greenhouse plugs). P values <0.1 are considered significant.. 331

Table F5: Results of the multiple regression analysis within the greenhouse plug planting method between, *H. jubatum*, vigor measures (cover, survival, tillers, and biomass) and environment [soil moisture (SM), photosynthetically active radiation (PAR), and available soil N], in each of 2006, 2007 and 2008. Responses are averaged across all soil preparation treatments. 332

Table 5.1: Results of the multiple regression analysis within the mature cutting planting method between F. campestris, H. jubatum, and P. pratensis vigor measures (cover, survival, tillers, and biomass) and environment [soil moisture (SM), photosynthetically active radiation (PAR), and available soil N] in each of 2006, 2007 and 2008. Responses were combined across all soil treatments. 332

Table F6: Effect of soil preparation techniques (carbon addition, litter removal, and tilling) on the mean (±SE) cover of *H. jubatum* within each of the experiments using mature cuttings and greenhouse plugs of *F. campestris*. **333**

List of Figures

Figure **Page**

Figure 1.1: Theoretical model depicting transitional dynamics for *F. campestris* communities in relation to *P. pratensis* invasion and abiotic site controls. 9

Figure 3.1 Experimental design of plots, including areas treated with for defoliation and litter modification (1.5 x 1.5 m), water and nitrogen addition (1 x 1 m), and the permanent sampling areas (0.5 x 0.5 m). 116

Figure 3.2 Non-metric multi-dimensional scaling ordination of the environmental analysis with overlays of environmental variables (Moss=Moss cover, Litter=Litter cover, Ri=Species richness, Ev=Evenness, Sh=Shannon's diversity index, JunL=June %PAR, MayL= May %PAR, AugL=August %PAR, JunM=June soil moisture and MayM=May soil moisture) and plant cover, (Astealp=*Aster alpinus*, Elymlan=*E. lancolatus*, Pascsmi=*Pascopyrum smithii*, Astelae=*Aster laevis*, Brompum=*Bromus pumpellianus*, Careobt=*Carex obtusata*, Carepen=*Carex pensylvanica*, Ceraara=*Cerastum arvense*, Festcam=*F. campestris*, Galaari=*Galardia aristata*, Gentama=*Gentiana amarella*, Geumtri= *Geum triflorum*, Potepen *Potentilla pensylvanica* and Sympocc=*Symphoricarpos occidentalis*) during 2006. Key species show trends in overlays of the ordinations at a cut off r^2 value of 0.15.Key Environmental factors show trends in overlays of the ordinations at a cut off r^2 value of 0.05. +W = water addition, -W = ambient water, +N = nitrogen addition, -N = ambient nitrogen, -L = litter removal, and +L = ambient litter. 117

Figure 3.3 Non-metric multi-dimensional scaling ordination of the environmental analysis with an overlay of the environmental variables (Moss=Moss cover, Litter=Litter cover, Richness=Species richness Ev=Evenness Sh=Shannon's diversity index, Ri=Species Richness, MayL= May %PAR, JunM=June soil moisture, AugM=August soil moisture, FCB=*F. campestris* biomass, GB=other grass biomass, PPB=*P. pratensis* biomass, SB=Shrub biomass and LB=Litter biomass) and plant cover variables (Astelae=*Aster laevis*, Bromine=*Bromus inermis*, Careobt=*Carex pensylvanica*, Festcam=*F. campestris*, Sympocc=*Symphoricarpos occidentalis*, and Poaprat=*P. pratensis*) in 2008. Key species show trends in overlays of the ordinations at a cut off r^2 value of 0.15. Key Environmental factors show trends in overlays of the ordinations at a cut off r^2 value of 0.035. +W = water addition, -W = ambient water, +N = nitrogen addition, -N = ambient nitrogen, -L = litter removal, and +L = ambient litter. 118

Figure 3.4 Non-metric multi-dimensional scaling ordination of the defoliation analysis with an overlay of environmental variables (N=Plant available N, MayM=May soil moisture, AugM=August soil moisture, JulM=July soil moisture, Ri=species richness, Ev=Evenness, Sh=Shannon's diversity index, Litter=litter cover and Soil=bare soil) and plant cover values (Carepen=*Carex pensylvanica*, Festcam=*F. campestris*, Sympocc=*Symphoricarpos occidentalis*, and Poaprat=*P. pratensis*) in 2007..Key species show trends in overlays of the ordinations at a cut off r^2 value of 0.15. Key Environmental factors show trends in overlays of the ordinations at a cut off r^2 value of 0.05. +W = water addition, -W = ambient water, +N = nitrogen addition, -N = ambient nitrogen, UD = undefoliated plots, WD = dormant season defoliation, and SD = summer defoliation. 119

Figure 3.5 Non-metric multi-dimensional scaling ordination of the defoliation analysis with an overlay of environmental variables (Moss=Moss cover, Litter=Litter cover, Ri=Species richness Ev=Evenness Sh=Shannon's diversity index, JunM=June soil moisture, FCB=*F. campestris* biomass, GB=other grass biomass, PPB=*P. pratensis* biomass, SB=Shrub biomass, FB=Forb biomass, and N=plant available N) and plant cover (Bromine=*Bromus inermis*, Carepen=*Carex pensylvanica*, Festcam=*F. campestris*, Sympocc=*Symphoricarpos occidentalis*, Solimis=*Solidago missouriensis*, Tara off=*T. officinale* and Poaprat=*P. Pratensis*) in 2008. Key species show trends in overlays of the ordinations at a cut off r^2 value of 0.15. Key Environmental factors show trends in overlays of the ordinations at a cut off r^2 value of 0.05. +W = water addition, -W = ambient water, +N = nitrogen addition, -N = ambient nitrogen, UD = undefoliated plots, WD = dormant season defoliation, and SD = summer defoliation. 120

Figure 4.1 Experimental design of plots, including areas treated with defoliation and litter modification (1.5 x 1.5 m), water and nitrogen addition (1 x 1 m), and the permanent sampling area (0.5 x 0.5 m). 161

Figure 4.2 Mean basal diameter (±SD) of *F. campestris* plants within the environmental study to water addition (+W), nitrogen addition (+N), and litter removal (-L) during the 2008 growing season. Means use original data with different letters indicating those that differ ($P<0.05$) based on analysis with transformed data while error bars are untransformed. +W = water addition, -W = ambient water, +N = nitrogen addition, -N = ambient nitrogen, +L = ambient litter, and –L = litter removal. 162

Figure 4.3 The association of changes in *P. pratensis* cover to *F. campestris* cover in each of the undefoliated (UD, n=32), summer defoliated (SD, n=32) and winter defoliated (WD, n=32) plots, during the three year period 2006 to 2008 within the defoliation experiment. UD = undefoliated, WD = winter defolation, and SD = summer defoliation. 163

Figure 4.4 The association of changes in *P. pratensis* cover to *F. campestris* cover within each of the ambient litter (+L, n=32) and litter removal (-L, n=32) treatments of the environmental experiment, during the three year period 2006 to 2008. +L = ambient litter, and –L = litter removal. ... 164

Figure 5.1 Standardized configuration of *F. campestris* and *P. pratensis* plants in the variable density study. 196

Figure 5.2 Standardized configuration of *F. campestris* and *P. pratensis* plants and measurements taken within the variable density study............ 197

Figure 5.3 Mean (±SE) tiller counts of focal *F. campestris* plants in response to combinations of planting density, defoliation and *P. pratensis* introduction. Within a density, means with different letters differ significantly $P<0.05$. Density of *F. campestris* is divided into: High = 0.15 m spacing, Medium = 0.30 m spacing, Low = 0.45 m spacing. +D = defoliated plots, -D = undefoliated plots. +B = Plots with *P. pratensis* and –B = Plots without *P. pratensis* 198

Figure 5.4 The interaction of planting density and distance from the focal plant on the cover of *F. campestris* seedlings as measured during the final assessment in 2008. Points represent the mean of all samples within a density x distance combination. Density of *F. campestris* is divided into: High = 0.15 m spacing, Medium = 0.30 m spacing, Low = 0.45 m spacing 199

Figure 5.5 The relationship between mean *P. pratensis* biomass (g/m^2) and *F. campestris* plant biomass per plot in high, medium, and low density plantings. Density of *F. campestris* is divided into: H = 0.15 m spacing, M = 0.30 m spacing, L= 0.45 m spacing. 200

Figure 5.6 The mean distance (±SE) of *P. pratensis* encroachment from the perimeter into the plot towards focal *F. campestris* plants at each of 3 different planting densities. Letters show significant differences P<0.05. Density of *F. campestris* is divided into: High = 0.15 m spacing, Medium = 0.30 m spacing, Low = 0.45 m spacing 201

Figure 5.7 The interaction of distance from the focal *F. campestris* plant and defoliation on the cover of *P. pratensis* within stands planted with *F. campestris* at high (top), medium (middle) and low (bottom) density. Means and error bars are from the mixed model analysis. +D = defoliated plots, -D = undefoliated plots 202

Figure 6.1 Concentration of available N (ug g-1) in soil exposed to sucrose addition (i.e. low N) and no sucrose addition (i.e. high N) in Experiment 1. Time = months since adding sucrose............................... 234

Figure 6.2 Concentration of available N (ug g-1) in soil exposed to sucrose addition (i.e. low N) and no sucrose addition (i.e. high N) in Experiment 2. Time = months since sucrose was added. 235

Figure 6.3 Changes in the R:S ratio of *F. campestris* when exposed to varying nitrogen, water and neighbor treatments in Experiment 1. Means with different letters differ. P<0.05+N = ambient addition, -N = low nitrogen, +W = field capacity, -W = low water, Mixture = Festuca focal plant with Poa exterior plants, Monoculture = Festuca focal and exterior plants.. 236

Figure 6.4 Change in tiller counts after 1 month of growth under sucrose addition and water addition treatments on *F. campestris* plants with *F. campestris* and *P. pratensis* neighbors during Experiment 2. Means with different letters differ P<0.05. +N = ambient addition, -N = low nitrogen, +W = field capacity, -W = low water, Mixture = Festuca focal plant with Poa exterior plants, Monoculture = Festuca focal and exterior plants.. 237

Figure 8.1 Plant community invasion dynamics between *Festuca campestris* and *Poa pratensis* 280

Figure A1: The response of evenness to changes in *F. campestris* cover during the 2006 growing season within the environmental analysis.......... 293

Figure A2: Non-metric multi-dimensional scaling ordination of the environmental analysis of plant available nitrogen, soil moisture, and PAR, categorized by water addition and nitrogen addition treatments in 2006-2008. Moss=Moss cover, Litter=Litter cover, Richness=Species richness Ev=Evenness Sh=Shannon's diversity index, Ri=Species Richness, MayL= May %PAR, JunM=June soil moisture, AugM=August soil moisture, FCB=*F. campestris* biomass, GB=other grass biomass, PPB=*P. pratensis* biomass, SB=Shrub biomass, LB=Litter biomass. Key environmental factors show trends in overlays of the ordinations at a cut off r^2 value of 0.045..[1]Treatments labels are as follows: +W indicates water addition, -W ambient water; + L indicates litter remained intact, -L litter removed; +N 294

Figure A3: Non-metric multi-dimensional scaling ordination of the environmental analysis with plant cover overlays and categorized by water addition and nitrogen addition treatments in 2006-2008. Festcam=*F. campestris,* Sympocc=*Symphoricarpos occidentalis,* Geumtri= *Geum triflorum,* Careobt=*Carex obtusata,* Astelae=*Aster laevis,* Bromine=*Bromus inermis,* Brompum=*Bromus pumpellianus* Poaprat=*P. pratensis*. Key species show trends in overlays of the ordinations at a cut off r^2 value of 0.15. Treatments labels are as follows: +W indicates water addition, -W ambient water; + L indicates litter remained intact, -L litter removed; +N indicates nitrogen addition, -N indicates no nitrogen addition. 295

Figure C1: The relationship between mean *P. pratensis* cover in the outer 30 cm of each plot and *F. campestris* tiller counts per plant in each planting density. 309

Figure D1: Changes in final tiller heights of *F. campestris* when exposed to varying nitrogen, water, and neighbor treatments in Experiment 1. Means with different letters differ. P<0.05.......... 317

Figure D2: Change in tiller counts after 1month of growth under sucrose addition and water addition treatments on *F. campestris* plants with *F. campestris* and *P. pratensis* neighbors. 318

Figure D3: Changes in final tiller heights of *F. campestris* when exposed to varying water, defoliation and neighbor treatments in Experiment 1. Means with different letters differ. P<0.05.......... 319

Figure D4: Changes in tiller heights (3.5 months) of *F. campestris* when exposed to varying nitrogen, defoliation and neighbor treatments in Experiment 1. Means with different letters differ. P<0.05.......... 320

Figure E1: Average soil moisture levels 1.5 hrs after addition of 12.7 mm of water to each of 4 plots repeated six consecutive times.......... 325

Figure E2: Mean soil moisture values 2 hrs after water addition at each of five separate levels (n=4). The 64 mm treatment was also assessed 24 hrs after water addition. 326

Figure E3: Precipitation data for the Cochrane weather station for 2006, 2007, 2008, and 30 year climate normals. The 2008 data was missing data points and is likely an underestimate of precipitation levels in the area. 327

List of Abbreviations

CEC	Cation Exchange Capacity
D	Defoliation
GP	Greenhouse Plugs
L	Litter
MC	Mature Cuttings
N	Nitrogen
PAR	Photosynthetically Active Radiation
SD	Summer Defoliation
SE	Seeding
SM	Soil Moisture
UD	Undefoliation
W	Water
WD	Winter Defoliation

Chapter 1 INTRODUCTION

1.1 Background

Invasive species have become an increasingly important consideration in managing ecosystems. There are few places in the world where invasive species are not a current threat to ecological integrity. Understanding the causes for vascular plant invasion is critical for management of natural ecosystems to be effective for economic and intrinsic values. Factors that affect invasion can include abiotic factors (light, nitrogen, and water), biotic factors (i.e. litter, biological interactions with other plants), and defoliation (i.e. animals and insects). These forces can be determinants of invasion success and as such must be understood.

1.2 Overview of Invasion in Fescue Grasslands

Festuca campestris Rydb. (foothills rough fescue) is the dominant plant species in the montane and foothills fescue grasslands of southwestern Alberta (Dormaar et al. 1990; Willms et al. 1998). Invasion by non-native species has, however, become increasingly common, with *Poa pratensis* L. (Kentucky bluegrass) dominating many areas today. Remaining *F. campestris* grasslands are threatened by invasion of species such as *P. pratensis* (Looman 1969). Invasions by *P. pratensis* are of particular concern due to the potential for native species to be displaced. To date, little is understood about the mechanisms allowing invaders such as *P. pratensis* to dominate native plant communities, but this species has been found to be a common invader within fescue grasslands (Tyser 1992). Without a clear understanding of the factors regulating the vigor of these species when growing in conjunction with one another, it is unlikely that practical management strategies can be developed to limit the establishment and growth of *P. pratensis*, and optimize the abundance of *F. campestris.*

The process of invasion of *F. campestris* grasslands by *P. pratensis* has been documented on many public lands, where long-term, permanent monitoring areas (exclosures) have been in place to allow Alberta Sustainable Resource Development to assess the ongoing condition of these grasslands. Within these benchmark sites approximately 10 by 20 m in size, grasslands have been excluded from large herbivore grazing, allowing comparison to the surrounding grazed areas. While the occurrence of *P. pratensis* was initially low inside exclosures compared to adjacent grazed areas, suggesting that grazing was a key factor increasing the rate of invasion (Solid arrow in Figure 1.1) (Looman 1969; Alexander and Willoughby 2005), the cessation of grazing has not prevented invasion, even with late-seral *F. campestris* present. Moreover, although protection from grazing shows signs of slowing the invasion process, instances where marked decreases in *P. pratensis* have occurred irrespective of grazing history suggesting that other triggers, potentially abiotic site controls (i.e. resources such as water, nutrients, and light - bottom dashed arrow in Figure 1.1), may also be responsible for controlling *P. pratensis* abundance.

1.3 Need to Understand Ecological Mechanisms

Grassland ecosystems contain diverse interactions between plants and their interactions with herbivores and parasitic organisms. These interactions occur through biotic and abiotic mechanisms that are capable of determining positive and negative plant interactions. Each species has a minimum amount of each resource necessary for survival and an optimum amount at which point it maximizes its growth potential. Differences between species in their resource requirements allows competitive exclusion in the ecosystem, but also means that co-existence may be possible if no individual species is able to become a superior competitor for all resources. The resources available in the environment are therefore the mechanisms by which a plant community assemblage is built and maintained and is therefore critical to understand. If we identify which mechanisms or combinations of them leads to a shift in plant community composition, we can predict future plant interactions as well as direct plant community succession in disturbances and restoration projects.

The maintenance and protection of remaining *F. campestris* grasslands requires an understanding of how and why these areas may change composition with disturbance, climate change, nitrogen deposition, among other mechanisms. Alternatively, an understanding of the specific mechanisms regulating interspecific competition between *F. campestris* and *P. pratensis* can be used to modify land use activities such as grazing to promote the conservation of *F. campestris* and its associated grasslands**.** In addition to simply understanding the mechanisms, these experiments are designed in a manner capable of identifing the interactions between mechanisms at different levels and determine how they will impact native plant community dynamics with *P. pratensis* invasion. Understanding how much nitrogen, soil moisture content, defoliation, and light is necessary to shift competition will allow more effective and pragmatic field methods to manage invasion as well as a greater understanding of what causes invasion by exotic perennial grasses.

1.4 Theoretical and Experimental Approach

Invasion of *P. pratensis* and *F. campestris* and associated subdominant species in native grasslands may occur due to competitive interactions between species, or suppression of native species due to environmental factors that in turn allow *P. pratensis* to invade native grasslands. Interactions between species due to changing environmental conditions are well documented, but understanding the specific mechanisms that shift the composition of these grasslands is not well understood. To determine the potential mechanisms regulating invasion of *P. pratensis* into *F. campestris* grasslands, four complementary experiments were undertaken.

Experiments were divided into an *in-itu* field study, two outdoor microcosm studies, and one greenhouse microcosm study. They were conducted to determine how soil moisture content, nutrients and light, and defoliation, affect interspecific competition between *P. pratensis* and *F. campestris,* and the native grasslands they co-habitate. Each study design was modified to examine a unique aspect of the interspecific relationship between these two species.

The first experiment (addressing #1 in Figure 1.1) is a community-based field study that was initiated in April 2005 and continued during the 2006, 2007 and 2008 growing seasons. This experiment isolated the specific influence of soil moisture content, nitrogen, and defoliation, together with litter removal, on the condition and composition, including *P. pratensis* and *F. campestris*, within a relatively pristine *F. campestris* grassland. The study site was located northwest of Cochrane, Alberta in a late-seral grassland with minimal invasion. Eight replications of 16 treatments were divided into two separate complete factorial designs. The first included the environmental treatments (i.e. N x W x L) while the second experiment tested the interaction of defoliation on environmental treatments (i.e. N x W x D). This experiment is discussed in two chapters:

Chapter 3) The interaction of water addition, nitrogen addition and litter removal on shifts in plant community cover to determine if community composition changes, including how *P. pratensis* and *F. campestris* are impacted. The second half of the chapter addresses how these environmental factors interact with defoliation in shifting community structure.

Chapter 4) The interaction of water addition, nitrogen addition, litter removal and defoliation on the health and abundance of *P. pratensis* and *F. campestris* within the plant community.

The second study (addressing #2 in Figure 1.1) is a controlled 2-way plant density study that began in April 2005. In this study cuttings from mature *F. campestris* plants were divided into 756 plugs and transplanted into a fallow field in 3 density configurations to examine the ability of *F. campestris* to resist *P. pratensis* invasion. Each plot included 7 *F. campestris* plugs (6 perimeter plants in a hexagon around a focal plant), with 3 different spacing's between plugs of 15cm, 30cm, or 45cm. A total of 12 treatments with 9 replications were used. This experiment will allow us to directly test the resistance of *F. campestris* stands established at various densities, to *P. pratensis* invasion, which in turn, will reflect varied intensities of interspecific competition with *P. pratensis*. This experiment was done with and without defoliation in a controlled environment excluding all other species. Abiotic site factors were not manipulated in this study. This study is found in:

Chapter 5) Effect of Plant density on interspecific competition with *P. pratensis* and *F. campestris.*

The third study (addressing #4 in Figure 1) involved a series of greenhouse studies. These investigations examined, under controlled conditions, how water, nitrogen and defoliation influence competition between *F. campestris* and *P. pratensis*, individually and collectively. This work complemented study #2 because of the lack of other plant species, thereby isolating *F. campestris -P. pratensis* interactions. Moreover, this experiment allowed individual and combined testing of the role of key abiotic factors regulating competition between *F. campestris* and *P. pratensis*, thereby complementing studies #2 and #3. The greenhouse study was conducted in a factorial design allowing for the isolation of these influences on *P. pratensis* and *F. campestris* from all other species, which was not possible in the field and restoration/reclamation studies. This study is reported in:

Chapter 6) Effect of sugar addition, drought, and defoliation on *F. campestris* and *P. pratensis* competition.

The fourth and final study (addressing #3 in Figure 1) consists of a restoration experiment assessing the ability of various site preparation treatments to promote *F. campestris* establishment in areas now dominated by *P. pratensis*. This work took place on a well-site undergoing reclamation near the AAFC - Stavely Research Station. Treatments at this site included various site and soil treatments designed to alter soil resources, with the intent of favoring *F. campestris* over *P. pratensis*. This study focused on active restoration using different plant propagation techniques (i.e. life stages) of *F. campestris*. In such situations restoration through natural processes may no longer be feasible. This study is found in:

Chapter 7) Effect of sawdust, tilling and litter on seedling, plug, and mature cutting survival and the effect of sawdust, tilling and litter, on *P. pratensis* invasion rates.

Collectively, these 4 studies allow for an improved understanding of the factors regulating interspecific competition between *P. pratensis* and *F. campestris*, and ultimately will provide an improved framework for conserving native *F. campestris* grasslands.

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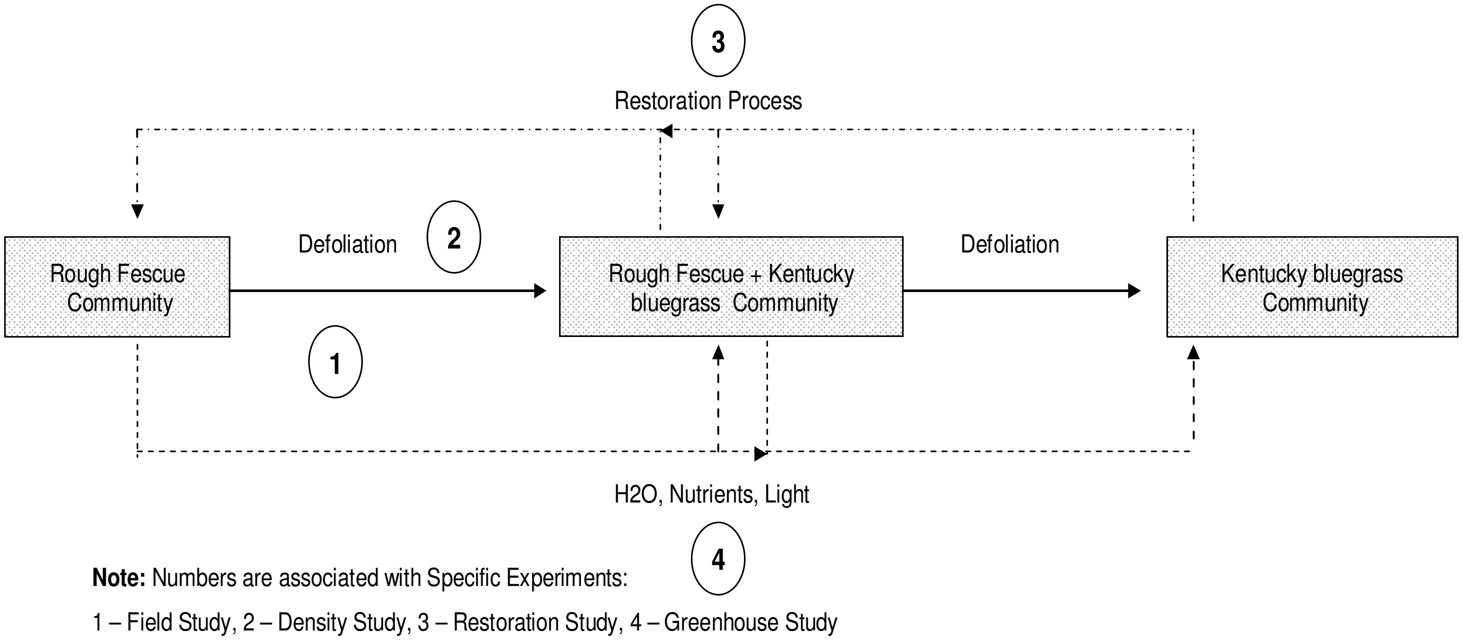

Figure 1.1: Theoretical model depicting transitional dynamics for *F. campestris* communities in relation to *P. pratensis* invasion and abiotic site controls.

Chapter 2 REVIEW OF *POA PRATENSIS* (L.) INVASION OF *FESTUCA CAMPESTRIS* (RYBD.) COMMUNITIES

2.0 Introduction

Long-term conservation and sustainable management of fescue grasslands requires an understanding of the mechanisms allowing *P. pratensis* to invade *F. campestris* communities. This chapter reviews and synthesizes current scientific literature pertinent to plant community invasions with a focus on *P. pratensis* and potential outcomes of interactions with *F. campestris*. This information includes below and above ground mechanisms together as theorized links between *P. pratensis* and *F. campestris* in competition during invasion.

2.1 Invasive Theory

Exotic invasive species are considered among the top five environmental concerns world wide due to their association with species decline (Didham et al. 2005). Displacement of native plant communities through exotic invasive species is occurring at a global scale in bunchgrass type communities (Mack 1989). The aggressive nature of many exotic species present significant management problems for land managers and complicate restoration and reclamation projects (D'Antonio and Meyerson 2002).

Exotic invaders in the Rocky Mountain region include agriculturally useful species such as *P. pratensis*, and noxious weeds that have no economic uses like *Bromus tectorum* (Tyser 1992). It is therefore important to understand invasive species because of their ability to alter regional and global ecosystem function (D'Antonio and Vitousek 1992). It has been noted by Carl M. D’Antonio that grass invasions are particularly important because: 1) grasses are actively moved by humans, 2) exotic grasses compete effectively with native species in many ecosystems, 3) dominant grasses may change nutrient cycling and regional microclimates, and 4) many grass species change fire dynamics (D'Antonio and Vitousek 1992). Of these four categories the first three may be significant reasons why *P. pratensis,* the subject of this research, is invasive.

2.1.1 The Passenger Model vs. Driver Model of Invasion

A key issue surrounding invasive species is whether the former are driving species decline or are filling in empty niches left by habitat alteration (Didham et al. 2005). Invasion by exotic species in much of North America has been thought to be driving ecosystem change (driver model), but invasive species have also been filling in niches left after anthropogenic disturbances (passenger model) (Didham et al. 2005; MacDougall and Turkington 2005). Given this, the management of invasive species will depend on whether a species is a passenger or a driver of ecosystem change. Preliminary evidence suggests that the passenger model is likely applicable in heavily disturbed areas, but invasion may also be occurring due to fire suppression, grazing regimes and other anthropogenic changes to the natural ecosystem. The basis of determining whether a species is a driver or passenger can be obtained through species removal studies, where indigenous species are removed from plots and compared to plots without removal. If *P. pratensis* is able to invade only areas with species removal, then the passenger model applies; however if invasion happens in both scenarios the driver model applies (MacDougall and Turkington 2005). In determining which model is most appropriate we can theorize the most probable mechanism(s) causing invasion. Passenger model invasion suggests that disturbance is the cause and if stopped invasion can be reversed, while if the driver model applies then other mechanisms will have to be explored.

Historical results from Alberta Sustianable Resource Development's benchmark exclosures show invasion is occurring with the removal of livestock grazing, suggesting the driver model, but the passenger model may also be exacerbating this situation (Alexander and Willoughby 2005). Thus, *P. pratensis* may be acting as both a driver and passenger of community change. *Poa pratensis* invasion is reduced but not stopped in the benchmark studies where anthropogenic influences are minimized. Where anthropogenic disturbances occur, *P. pratensis* invasion is greatly increased. These observations suggest a weak driver model and strong passenger model may be possible for *P. pratensis* invasion, yet a full exploration of the possible mechanisms responsible for the invasion process is still required.

2.1.2 Theorized Mechanisms of Invasion

Novel weapons and enemy release theories may play a part in invasions (Colautti et al. 2004; Callaway and Vivanco 2005) and should thus be considered in interpreting invasion patterns. Many species may either have biological weapons that they can utilize, or associations with micro-organisms that allow them to either access new resources or steal resources from indigenous plants. Grasses can be involved in both the use of and susceptibility to such weapons (Carey et al. 2004). It is possible that *P. pratensis* may be able to utilize such methods in competition, but to date no major evidence exists that this is the mechanism allowing *P. pratensis* to invade grasslands.

There are also more novel weapons than the ability to steal from other plants. Evolutionary pathways in the original habitat of an invasive species may have allowed surrounding plants to adapt genetic methods to resist chemical and biological associations within a plant while indigenous species of the new range are not adapted to these new weapons (Callaway and Aschelhoug 2000). *P. pratensis* could be interacting with the soil biochemistry as well as with microorganisms, thereby providing it advantages over *F. campestris* and its associated community. Indigenous plants may be able to fight back against invaders with their own allelopathic compounds. As *F. campestris* litter contains just such compounds, grazing of this species may reduce tallelopathic suppression (Dormaar and Willms 1992) allowing improved vigor of invasive species.

Release from natural enemies has been hypothesized as a method by which a species can become invasive (Blumenthal 2006). This theory states that the original habitat had predatory species that suppressed the ability for a species to take over. Once the species has moved to a new habitat, the indigenous species of this habitat are not adapted to resist this species and so the invader no longer is suppressed. Many predators such as insects can be responsible for such suppression, but it is possible that chemical warfare between plants may lead to the suppression of a species and when released the invader becomes much more aggressive (Callaway and Aschelhoug 2000). While the novel weapons hypothesis shows the biological functions within the invader drives the invasion process while the enemy release hypothesis suggests that exterior forces drive plant invasion.

The empty niche hypothesis states that invasive species become a problem because there are empty niches in the ecosystem that no other species is filling (Prieur-Richard and Lavorel 2000). By accessing these niches, invasive species are able to establish and compete in a new ecosystem. This theory has been frrought with difficulties as invasions typically cause changes to the plant community instead of simply filling empty gaps, suggesting they would occur even without empty niches (Prieur-Richard and Lavorel 2000). It is possible that *P. pratensis* invasion is dependant on finding an empty niche in the ecosystem to establish before it can start effectively competing with the indigenous plants, although this may only speed up the rate of invasion and therefore is an unsatisfactory explanation for invasion. Community complexity would also be linked to the empty niche theory with saturation of the community reducing invasibility (Prieur-Richard and Lavorel 2000). However, this does not fit well with the most resistant fescue communities, which have fewer species as *F. campestris* tends to outcompete most other species.

More competitive – Some species may simply be more competitive than their indigenous counterparts allowing them to dominate the community (Seabloom et al. 2003). Grazing resistant species exposed to centuries of heavy grazing may be more tolerant to grazing than native species allowing human alterations to the disturbance regime to shift competitive advantages in favour of invaders. Similarly, a species may come from a harsh environment and have tolerances beyond that of the indigenous species allowing the former to simply be more efficient at resource acquisition and utilization. Experimental work on this theory completed in California documented the opposite effect whereby native species started to outcompete invaders once their poor establishment was overcome (Seabloom et al. 2003).

Manipulation of environment – The environment can be manipulated by a plant through resource use. Light absorption and interception can pre-empt other species trying to access light. Water uptake can be manipulated by either taking up water more efficiently or changing the water holding capacity of the soil to benefit a plant. Nutrient uptake and cycling can increase or decrease available nutrients, changing the competitive environment (D'Antonio and Vitousek 1992).

2.1.3 Competition and Facilitation

Interactions among organisms are controlled by a complex interaction of biotic and abiotic forces. These forces interact in any number of combinations of positive and negative forces upon plant communities (Callaway and Walker 1997). Positive forces on a species are facilitative or mutualistic, while negative forces are competitive or even parasitic. These complex interactions between negative and positive interactions make studying individual processes difficult or even inaccurate unless these interactions are taken into account. This is clearly evident in Callaway's (1991) study of *Quercus douglasii*, wherein increased soil nutrients did not relate clearly to increased herb production under *Q. douglassii* stands due to rooting depth of these trees. Competition for nutrients interacted with facilitative nutrient additions to create either a net positive or a net negative interaction depending on the location (Callaway et al. 1991). All ecosystem functions must be accounted for in combination with each other in order for the net balance to be determined between positive and negative forces (Callaway and Walker 1997). Unfortunately the balance between these forces is not clearly understood, and each combination of species in combination with environmental conditions will dictate the nature of thatbalance.

Competition is a negative force allowing one species to win against another in resource acquisition. It has been debated as to whether competition is important in determining plant community structure in arid ecosystems. Fowler (1986) indicates that although arid ecosystems rely heavily on competition to structure plant communities, it differs from that found in productive ecosystems

(Fowler 1986). Competition occurs for all resources within an ecosystem. Any resource that can be accessed by two or more organisms will undergo competition. These interactions lead to a net winner and a net loser if the relationship remains linear for any one resource. Moreover, this relationship becomes much more complicated once additional resources are added, with no single overall winner typically leading to coexistence.

In addition to the competitive interactions capable of suppressing species it is clear that facilitative relationships also occur in these ecosystems. Facilitation is the process whereby one organism aids another, and in some cases, allows another to exist in an ecosystem that it would otherwise fail to survive within. In the fescue grasslands there is a possibility of both competitive and facilitative interactions structuring plant communities and this could also be affecting the relationship between *P. pratensis* and *F. campestris* in this community (Callaway 1995).

Facilitative interactions allow species to move beyond their normal environmental thresholds. These interactions add a great deal of complexity to the natural system as there is no longer a strict threshold at which a plant will no longer be able to compete in the system (Callaway and Walker 1997). This can be seen in water relations whereby a species can be facilitated in dry conditions by staying in the understory and using less water through transpiration. Humidity levels in the understory can be raised, increasing the chance of a plant surviving in these conditions. On the opposite end of water relations some species are capable of drawing down soil moisture content allowing species that need these conditions to survive and compete. Such relations complicate plant interactions as one plant may outcompete the other for soil nutrients, but can not extirpate the latter because it must have that species to reduce soil moisture content. Such interactions remove the linear nature to competition (Seabloom et al. 2003).

Light competition can also influence facilitative relationships. *Centaurea maculosa* can take carbon from surrounding grasses to aid its own growth (Ridenour and Callaway 2004). This relationship is almost parasitic as it allows the plant to outcompete surrounding plants, but nevertheless shows the possibility of facilitative relationships whereby overstory species can support understory species in a sward.

Carbon is one of the most important resources required for plant growth. Plants can develop mutualistic relationships with microorganisms unable to produce their own sugars for growth while providing soil nutrients at a much more efficient level than a plant can normally access them. Such relationships can facilitate plant growth under low nutrient conditions where it otherwise could not survive.

These relationships with soil organisms can allow plants to facilitate neighbouring plants. Nitrogen fixing plants such as legumes commonly facilitate the growth of species that require high amounts of nitrogen. These interactions can then be complicated by competition for other resources that allow nitrogen fixing plants to persist in plant communities that would otherwise be able to outcompete them.

2.1.4 Final Outcome

Establishment can be divided into three types of outcomes, 1) dominance of the indigenous plant community or 2) coexistence with the indigenous plant community (Seabloom et al. 2003), or 3) exclusion from the indigenous plant community. These outcomes are important as the consequences of each determine the appropriate management to deal with invasion, as well as the economic and environmental impact invasion will have on an ecosystem.

Dominance and suppression of the native community by *P. pratensis* may lead to economic and ecological losses. Isolation of the mechanisms that allow this is critical and thresholds capable of allowing for such suppression must be understood. The second form of successful invasion that leads to coexistence is important to understand. This can happen if the invading species is a more successful competitor for one resource, but is an inferior competitor for a second resource at which point the invader will reach equilibrium and the invader can no longer expand but remains within the community (Seabloom et al. 2003). This type of community may have an economic and an ecological loss. The damage of this result will be determined by what percentage of the community is replaced by the invasive species. Stopping the invasion or even excluding *P. pratensis* from the plant community is generally desired by managers. To do this understanding the mechanisms allowing for persistence of *P. pratensis* is essential if reversal of invasion is to occur. Once the mechanisms are understood, it is possible to determine what the most economical result may be and what result can most easily be achieved.

2.2 The Need to Understand Above and Below Ground Interactions

To control the ongoing invasion of *F. campestris* grassland by *P. pratensis*, a greater understanding is required of the relative importance of the dominant disturbance (grazing) and abiotic factors in regulating interspecific competition between these species. Where complete shifts have occurred from *F. campestris* to *P. pratensis*, either with prolonged periods of heavy grazing (Looman 1969), or following disturbances (cultivation), active restoration is likely necessary (dash-dotted line in Fig. 1.1) to re-establish *F. campestris*, including the abiotic site conditions conducive to its survival and dominance within the plant community.

Collectively, disturbance and environmental variables likely lead to a slow replacement of native species like *F. campestris* with *P. pratensis* in many areas. While numerous studies have documented the impact of factors like heavy grazing on *F. campestris* (Johnston 1961; Looman 1983; Willms et al. 1985), other mechanisms (water, nutrients, light), although theorized, remain un-investigated. Specific attention must be directed to determine what environmental mechanisms aid invasion, and in what combinations these mechanisms function to determine the outcome of competition between *F. campestris* and *P. pratensis*, both with and without defoliation. The model in Figure 1 outlines the theorized pathways for key shifts in species composition, and specifically invasion, within *F. campestris* grasslands. These include both hypothesized environmental mechanisms and known disturbance mechanisms thought to regulate invasion by *P. pratensis*.

A theoretical framework showing shifts in species composition should closely reflect the biological adaptations of each plant. For example, tall plants with broad leaves are more competitive for light and can outcompete short, fine leaved species (Berendse et al. 1992). Conversely, the former are uncompetitive with shorter species when nutrients and soil moisture content are limited. In conditions where disturbance interacts with below and above ground resources, tall competitive plants have the most above ground biomass to lose and therefore are at a competitive disadvantage when their large photosynthetic leaf area is lost during defoliation (Fynn et al. 2005).

2.2.1 Litter Effects

Plant litter has a critical role in the ecological function of grasslands because it affects both above and below ground resources. Litter provides insulation that controls soil temperature (Weaver and Rowland 1952), erosion (Thurow et al. 1988), soil hydraulic function, nutrient holding capacity, carbon source for microorganisms (Bardgett and Wardle 2003), light inhibition. In most fescue grasslands, removing litter marginally increases productivity in the first 3 years (Willms et al. 1986), which is more common in productive environments (Bardgett and Wardle 2003). There are, however, benefits of maintaining litter in grasslands that may outweigh the reduced productivity that is sometimes experienced, especially in dryer climates such as the mixed grass prairie (Willms et al. 1986; Bardgett and Wardle 2003). Litter provides increased soil moisture retention through lowering evapotranspiration, reduced runoff, increasing soil aggregation, aggregate stability and infiltration rates through increases in soil organic matter and reduced erosion (Naeth et al. 1991; Naeth and Chanasyk 1995). These factors drastically aid in increasing the long-term soil water holding capacity of the soil, but may also reduce the amount of moisture that actually reaches the soil. Thus, depending on the plant community and climate, soil moisture may act either to increase or decrease soil moisture depending on the time of year and precipitation event. Modifications to litter will change soil moisture content, and thus may shift the competitive advantage between species within the community.

Litter also has an impact on nutrient cycling. Nutrients that are immobilized in litter is released through microbial activity and leaching (Risser 1984; Bardgett and Wardle 2003). Depending on the composition of the litter, decomposition can increase or decrease nutrient cycling (Bowman et al. 2004). Some plants can compete effectively by using their litter layer to slow or enhance the nutrient cycle. Removal of litter will either reduce available nutrients or increase the rate of nutrient cycling through grazing and fire (Naeth et al. 1991). These effects are capable of shifting community composition, and in the case of some invasive species, can be a mechanism for invasion.

Light levels are also impacted by the amount of litter. Litter impacts on light can cause changes in tiller development (Willms et al. 1986), germination and competition. Plants capable of growing through a thick litter layer may utilize this layer to suppress other species by reducing light and germination (Haslam 1971). Such competitive advantages may lead to reduction and eventually exclusion of other species, as is often seen in how *F. campestris* dominates fescue grasslands under grazing suppression.

2.3 Above Ground Interactions

2.3.1 Light

One of the main abiotic factors contributing to plant growth is photosynthetically active radiation (PAR). Plant growth is directly related to access to carbohydrates, either stored or synthesized. In most cases, intercepted light directly affects leaf area and therefore, photosynthetic rates. Competition for light among neighbouring plants is asymmetric whereby the plant with the greatest ability to pre-empt light interception has the ability to become the most competitive. Competition for light is also not a simple linear relationship, as species in the understory can compete by increasing their efficiency of light capture through the use of shade leaves. These alternate, competitive strategies mean that a plant pre-empting high quality light interception may not always result in the same net competitive advantage. Plants alter shoot architecture as well as biomass allocations due to shading (Aphalo et al. 1999). This has been linked to the ability of a species to compete effectively for nutrients (Tilman 1988; Coomes and Grubb 2000). Competition for light has been strongly debated by Grime (1973) who argued that above ground competition is the dominant form of competition (Grime 1973; Craine 2005). Such competition for light may be critical for the process of invasion by *P. pratensis* into fescue grasslands, and ultimately its competition with *F. campestris* for dominance.

2.3.1.1 Light Signals

Light competition hinges on plant plasticity and as such, is essential to the survival of plants (Aphalo et al. 1999). Plants recognize neighbor plants through light signals allowing them to react plastically (Aphalo et al. 1999). The proportion of light absorbed and reflected determines the signal a plant receives. Wavelengths of red light are absorbed by plants while far-red light is reflected and transmitted by plants. Phytochromes, the photoreceptors able to detect these wavelengths, determine how plants will respond to changes in the ratio of red to far red light (Smith 1994). Plant responses to changes in this ratio can include tillering rate, flowering, and changes to leaf morphology (Aphalo et al. 1999). These responses explain how plants can interact with one another competitively, including how differences between *P. pratensis* and *F. campestris* will determine the outcome of light competition.

2.4 Below Ground Interactions

2.4.1 Soil Nutrients

Soil nutrients are capable of limiting plant growth and determining the outcome of interactions between plant species (Berendse et al. 1992). Such interactions include facilitation and mutualism that can extend the range of survival of a species, or competition capable of suppression or exclusion of a species. In grassland ecosystems competition for soil nutrients has been considered as strong as or even stronger than competition for light (Casper and Jackson 1997). Our understanding of below ground competition for soil nutrients is generally poorly understood (Cahill 2003). To understand the influence of soil nutrients, three different techniques have been utilized to assess the outcome of competition: nutrient addition (fertilizer), nutrient reduction (ie: immobilization through carbon additions), and plant removal studies.

2.4.2 Soil Nitrogen Relationships

Soil N can be found in inorganic and organic forms. Inorganic N pools include NO_3 and NH_4 in soil solution and bound to clay and other particles. Organic N can be in the form of amino acids and proteins in soil solution and that in plant and microbial biomass. Organic forms in living and dead tissues are unavailable for plant uptake (Booth et al. 2005). Depending on the carbon to N ratio, soil microorganisms will either immobilize soil N if the soil C:N ratio is high, or mineralize N if the C:N ratio is low. Strong correlations have been shown between carbon concentrations and N mineralization. As growing microbial biomass breaks down carbon for energy, the C:N ratio drops increasing mineralization rates (Booth et al. 2005). Soil microorganisms are stronger competitors for N than plants, and thus will determine N availability for plants. These dynamics control the level of soil N available for plant use.

Plant uptake of N has traditionally been seen as an inorganic pathway that relies on the rate of N mineralization to release N to plants. More recently it has been noted that in many areas organic forms of N are being taken up by plants and plants with this capability may have an advantage over species that can not do this (Bardgett et al. 2003). Other methods of competing effectively for N have been shown in microbial associations. Plants have many microbial associations and these associations can be beneficial in increasing access to nutrients.

Nutrient uptake is tied to root configuration. Plants with large, deep root systems will be able to access deep nutrients while plants with shallow root systems will be able to access shallow nutrients. Fertilization typically aids shallow rooted species because they are able to intercept the majority of surface applied N. In addition to rooting depth, biomass and area must be considered. A large root biomass only helps the plant if it increases rooting area. Many fine roots are more beneficial for N capture than a few large roots. Microbial associations also can greatly aid in N uptake in poor nutrient conditions (Berendse et al. 1992).

Nutrient addition, specifically of N, can increase above ground productivity and effectively shift competitive advantages away from low N requiring species to high N requiring species if they are more competitive for other resources such as light or water (Aerts 1999; Berendse 1990). Fertilization has the ability to replicate areas with high nutrient availability, switching competition from below ground to above ground competition. Under such systems, plants that allocate more production above ground are more likely to dominate (Aerts 1999). However, this is not always the case as in some interactions N addition appears more important than light in reducing diversity through competitive exclusion (Rejmanek 1989). Finally, increases in N do not have to be related directly to fertilization, but can also arise due to N cycling rates such as mineralization and immobilization rates (Berendse 1994; Aerts 1999).

Nutrient reduction studies have been increasingly used to reverse the shifts in competitive interactions occurring between plants (Perry et al. 2004). This is because the tradeoffs between species from nutrient poor and nutrient rich habitats are mutually exclusive (Aerts 1999). Such methods are more difficult to implement, but have successfully shown that reduction in N can reverse competitive interactions and allow previous plant community dynamics to be restored (Perry et al. 2004; Eschen et al. 2007). This may be partly due to the re-establishment of previous nutrient cycling regimes (Prober et al. 2005). Under nutrient poor conditions plants must be able to either maximize assimilation of nutrients, or minimize their loss (Berendse et al. 1992; Aerts 1999). *Festuca rubra* effectively out-competes taller species adapted to more nutrient rich environments under low nutrient conditions. This was also accelerated by defoliation, which removed more N from plants using high N than low ones (Berendse et al. 1992).

2.4.3 Soil Water

The soil water holding capacity of a specific site may be highly variable and seasonal water deficits are common in fescue grasslands. Water is important for germination and seedling establishment, and this can be especially important in early successional communities (Henry et al. 2005). Water regulates nutrient uptake through transportation and is essential for many plant functions. Plants retain only a small percentage of the water they take up, while also being unable to efficiently recycle water, making them much more susceptible to drought conditions than low nutrient conditions (Henry et al. 2005). This suggests that soil moisture could easily become a limiting factor for plant growth. The rooting habit of plants can greatly change their ability to access soil moisture and possibly reduce or increase the competitive effects on other plants (Feddes et al. 2001). Areas with high soil moisture content are more susceptible to invasion, yet plant diversity among other factors may interact to complicate this relationship (Maron and Marler 2007). In addition, rooting habit is affected by nutrient availability, which can reduce water uptake efficiency in some plants by increasing growth and subsequently increasing evapotranspiration (Ho et al. 2004; Henry et al. 2005).

Hydraulic lift has been noted to exist in shrubs and trees (Caldwell et al. 1998), and allows species with deep roots to access water during the night from deep in the soil profile (while plants are not actively photosynthesising) and store it for use during the day. This water is pumped up into the surface layers of the soil where the majority of plant roots lie. This allows deep rooted trees and shrubs to access a large percentage of their daily water requirements from parts of the soil profile that they can only efficiently access with very few roots (Caldwell et al. 1998). By pumping water up into the shallow parts of the soil profile these species also provide a service to other plant species who gain access to this moisture, but may also give these species a competitive advantage during drought. Hydraulic lift has been observed most commonly in arid landscapes (Caldwell et al. 1998). Such benefits may facilitate species to become competitors for other resources. Theoretically the possibility of a deep rooted bunchgrass species taking part in this phenomenon could explain the drought tolerance of species such as *F. campestris*, and subsequently provide a competitive mechanism that they can utilize in out-competing other species.

2.4.4 Other Soil Properties

Soil properties that can influence soil moisture holding capacity include soil bulk density and organic matter content. These soil properties may be critical in competitive interactions and allow different soil moisture conditions to exist and persist into drought periods. Soil compaction reduces the rate of infiltration of soil moisture. Such properties can be influenced by grazing and other land uses (Liacos 1962). Litter volume and organic matter in the surface of the soil may cause soils to be insulated from the surface conditions, reducing water losses due to transpiration (Naeth and Chanasyk 1995). Temperature changes at the surface of the soil greatly impact transpiration rates and are a means by which a plant can influence its microenvironment to counter drought.

2.5 Disturbance

Human caused disturbance has become the single largest form of disturbance on earth (Vitousek et al. 1997). Biological invasions benefit from disturbance because they fundamentally change ecosystem functions in ways natural disturbances never have (Vitousek et al. 1997). The reason for this is that disturbance increases resources and decreases competition, leaving freeing up resources for the first plant able to get to them (Prieur-Richard and Lavorel 2000). Some of these impacts are large scale soil tilling, fertilization, mowing, irrigation, and grazing. All of these practices fundamentally change the relationship between plants and their environment, as well as their biological interactions. When multiple disturbances occur, an increased rate of invasion may result (Prieur-Richard and Lavorel 2000). In the fescue grasslands several of these disturbance regimes have become increasingly prevalent. Human caused disturbances such as tilling, urban expansion, industrial development and cropping disturbs the soil environment in new and unique ways, to which indigenous plants are not adapted.

Grazing, historically common in these grasslands, has fundamentally changed to a much higher intensity system focused on the growing season instead of the dormant season. This fundamental change puts the native flora at a disadvantage to more grazing tolerant invasive species.

2.5.1 Antropogenic Disturbance

Most human-caused disturbances of grasslands involve some form of mechanical manipulation of the soil or destruction of the original plant community. Such a drastic modification of the plant community leads to the modification of light, soil water, and nutrient conditions of the environment, while drastically altering the species available to compete by killing live plant material. This process favors plant species capable of propagation from seed and rhizomes, typically colonizers. Tilling and planting of tame and invasive species has destabilized the natural ecosystem, creating large sources from which invasion would be initiated (Tyser 1992). Highway development has initiated large linear disturbances into which invasive species adapted to colonization can readily invade, although in many cases tame and invasive species are used to revegetate these areas. Industrial development has historically caused many linear disturbances that have been revegetated with invasive species (Tyser 1992). Even when this practice was stopped, a combination of colonization and already established invasive species allow for easy access to disturbances, disrupting the restoration process (Tyser 1992).

Once established, these invasive species do not necessarily stop their progression into the native ecosystem. Many of them continue to alter their nutrient environment, fire regimes and light capture (Vitousek et al. 1997). These changes can accelerate conversion of the plant community from the indigenous to a new invasive community. In these cases, disturbance is not just the cause of invasion but also facilitates further invasions.

2.5.2 Defoliation

Defoliation, like fire, is a process capable of influencing multiple resource levels, subsequently adding a complexity of multiple mechanisms interacting to facilitate invasion (Prieur-Richard and Lavorel 2000). Defoliation is one of the more difficult processes for which to isolate specific competitive mechanisms. Grazing in fescue grasslands is a historically important process that increased plant diversity, reduced water infiltration and retention (Naeth and Chanasyk 1995), increased nutrient cycling (Dormaar et al. 1990), reduced soil organic matter (Naeth et al. 1991; Dormaar and Willms 1992), and increased light levels. These changes, alone and in combination, may be responsible for shifting competitive interactions between species, and as such each factor must be analyzed individually and in combination to determine what, if any, mechanism is capable of altering the plant community.

One possible reason for the changes to diversity after initiation of grazing is the suppression of key dominant species in the plant assemblage. This allows species adapted to grazing to increase in prominence (Belsky 1992). Adaptations to grazing include a low growth form (Berendse et al. 1992), unpalatable foliage, toxicity, defensive structures, or fast regrowth (Berendse et al. 1992), of which *P. pratensis* has a low growth form and fast regrowth. Such species spend large amounts of energy on leaf area protection and growth, but may not be the most efficient competitor for light in the absence of disturbances.

Increases in diversity can be seen when dominant species are artificially eliminated or fire occurs in the ecosystem (Belsky 1992). This suggests that the positive influence of defoliation on diversity may be correlated with the loss of key species dominating the plant community. Release from grazing shows an increase in tall perennials and a subsequent reduction in short, typically grazing resistant plants (Belsky 1992). This suggests that suppression instead of competition may be responsible for shifts in plant community composition.

One method of describing community organization is testing the response of each species to the physical and biotic factors organizing the community (Belsky 1992). These studies are difficult undertakings that require complex multivariate analysis of all environmental and physical variables structuring the community, and therefore most research focuses on artificial communities limited to only a few species. These studies, while important, fail to replicate the true complexity of the natural system.

The specific method by which a dominant species is suppressed by grazing may be linked to nutrient cycling, soil moisture, light capture, regrowth ability and avoidance of defoliation. While any one resource may have a limited impact on the outcome of invasion and subsequent competition, the combination of these factors may markedly shift competitive advantages. Species that allocate large amounts of N to produce above ground biomass tend to be poor competitors under defoliation and low N regimes, suggesting interactions between mechanisms (Berendse et al. 1992). Other interactions have been shown between plants when they are defoliated and may suggest that a simple linear relationship is impossible with grazing.

2.6 Fescue Grasslands

Fescue grasslands dominated by *Festuca scabrella* (*Festuca campestris*, *Festuca hallii* and *Festuca altacia*) are a unique grassland type (Coupland and Brayshaw 1953). The Foothills Fescue Grasslands are dominated by *F. campestris* (foothills rough fescue (Looman 1983) and exist primarily in the Northwestern United States and Canada. Extensive tracts of these grasslands are found along the east and west slopes of the Rocky Mountains while outlying *F. campestris* grasslands exist where environmental conditions have created suitable niches for this unique grassland type (Looman 1969). These grasslands extend primarily along the east and west slopes of the Rocky Mountains in British Columbia (McLean and Marchand 1968), Alberta, Washington (Hodgkinson and Young 1973), Oregon, Idaho and Montana (Stickney 1961), and eastern populations at high elevations in Alberta and Saskatchewan (Hitchcock et al. 1969; Anonymous 1973).

Populations of *F. campestris* are found up to high elevations (~2000m) where they transition to *Festuca altacia* grasslands, and transition into *Festuca hallii* at lower elevations (~800 m) in the Parkland (Darbyshire and Pavlick 2009). While there are several different geographic regions in which foothills fescue grasslands can be found, the eastern slopes of the Rocky Mountains contain a large region of these grasslands with a unique climate, geology and history, making them of special interest for study (Looman 1969). In Alberta the foothills fescue natural subregion comprises 1.95% of Alberta and 13.45% of the grassland natural region (ASIC, 2001), of which approximately 16.8% remains intact (Adams et al. 2003). In addition to this area the Foothills Parkland, Montane, Subalpine and parts of the Lower Foothills all contain *F. campestris* grasslands.

Foothills fescue grasslands in southwestern Alberta were historically dominated by *F. campestris* (Willms, King, Dormaar 1998), with cover between 36-85% (Adams et al. 2003) in climax communities, providing more than 15% of the forage yield (Hodgkinson and Young 1973). Co-dominant species, including *Festuca idahoensis* (Elmer), and *Danthonia parryii* (Scribn), are common in these grasslands along with many minor species (Daubenmire and Daubenmire 1968). The current status of these grasslands is largely unknown though there are many that are noted to be at risk (Allen 2008).

F. campestris grasslands receive 397-589 mm/year of precipitation (Adams et al. 2003), with 50-60 % falling between May and August, the greatest of which occurs before July (Looman 1969; Looman 1983). The summer moisture deficit begins in July as precipitation decreases and temperatures rise. For these reasons, most species in the foothills complete growth before mid-July (Looman 1983). While summer temperatures can reach highs of 40 ^{o}C, winter temperatures can drop below -40 ^{o}C (Looman 1969), but can increase above freezing in a few hours due to Chinook winds that come over the Rocky Mountains (Looman 1983). These drastic changes in temperature during the dormant season demand that vegetation be winter hardy. The range of the fescue foothills grasslands is largely dependant on climate and more importantly, precipitation levels. Fescue communities can be found on north slopes only in drier climatic zones (Looman 1983). The frost free period is between 88-113 days (Adams et al. 2003).

The topography of these grasslands is unique as it is based on sandstone that has been folded up along the eastern edge of the Rocky Mountains (Glaister 1959). This has created rolling foothills with a relatively high elevation compared to the surrounding plains. These changes in altitude act to increase moisture levels, making the climate cooler and wetter than adjacent grasslands (Looman 1983). Soils in fescue grasslands are classed as Black Chernozems. The cation exchange capacity (CEC) typically ranges from 18.5 to 27.0 mcq/100g. The parent materials are largely calcareous in nature allowing 50-60 % of the CEC to be calcium. Average nutrient concentrations are as follows; potassium is high at 1.5 %, while NO_3-N and $NaHCO_3$-P are low at 5.5 and 13 ppm (Looman 1969). Soil field capacity averages 46 % with ranges from 35-56 %.

During the last ice age these grasslands received little or no glaciations, allowing for a larger diversity of species to be preserved. Since the last ice age, *Bison bison* made up a large component of the grazing history, utilizing the wind swept slopes free of snow in the winter and moving out into the plains and lower valleys in summer where there was more lush vegetation available. This created a grazing history that allowed plants to adapt to dormant season grazing while remaining relatively sensitive to grazing during the growing season. Fire also played an important component to these grasslands, removing shrubs and trees and allowing the grassland ecosystem to dominate, even in areas normally wet enough for forest cover.

2.6.1 *Festuca campestris*

2.6.1.1 *F. campestris* Response to Light

In the absence of disturbance *F. campestris* dominates the cover of fescue grasslands. Without disturbance *F. campestris* continues to dominate the community unless woody species establish. *F. campestris* therefore appears well adapted to preventing other species from accessing light by over-topping them and producing abundant litter to reduce light levels. Light may limit the overall growth of grasslands (Willms et al. 1986; Grace 1995), and may be more important than moisture in the foothills region where rainfall is > 450 mm. In the Mixed Prairie the opposite effect was found (Willms et al. 1986), likely because moisture is more limiting for growth than light (Willms et al. 1993). Such an interaction suggests the litter accumulation common in foothills grasslands is beneficial not for moisture retention, but in competition for light. Light also has a part in determining the number of *F. campestris* tillers in combination with defoliation (Willms 1988).

Light has a marked impact on soil conditions by increasing soil temperatures and subsequently impacts some below ground relations with plants. Soil temperature is important for ensuring the germination and growth of seedlings. Moderate temperatures are most effective for germination (Romo et al. 1991). Falling temperatures reduce germination and amplify the effects of water stress (Romo et al. 1991). This suggests that *F. campestris* is optimally suited for spring germination and growth. These requirements for establishment can severely restrict the ability of *F. campestris* to establish after disturbance.

2.6.1.2 *F. campestris* Response to Nutrients

Soil nutrients are critical for any plant growth. Current literature is limited when it comes to understanding *F. campestris* and associated nutrient requirements, but a number of observations are worth noting to suggest further study is warranted. It has, however, been noted that *F. campestris* appears to establish in subsoil piles with low nutrient conditions much more efficiently than it does in rich top soils where there is strong competition for light. It also appears that *F. campestris* can compete under low nutrient conditions for light more efficiently than other species. If this is true, immature *F. campestris* plants may have a competitive advantage over invasive species like *P. pratensis*. Another aspect of these nutrient relationships is that *F. campestris* may be capable of binding nutrients in litter to reduce access and slow rates of N cycling. Slowed rates of cycling may reduce acquisition rates for nutrients. A species that can slowly access nutrients, but is also slow to release them, can out-compete a fast cycling species if the former is allowed to accumulate biomass and retain this biomass (Berendse 1994). This can occur when grazing suppression occurs, such as when *F. campestris* shades out its competitors while binding up large portions of soil nutrients in its own biomass, both dead and alive.

2.6.1.3 *F. campestris* Response to Water

Unlike *P. pratensis*, *F. campestris* has deep roots with a high tolerance to drought. Litter loss in these native grasslands is known to inflate soil temperature and increase the soil moisture deficit (Willms et al. 1986), reducing water use efficiency. *F. campestris* is very responsive to soil moisture conditions, with moisture deficits causing reduced heights and biomass of tillers. Soil moisture may also be limiting for *F. campestris* at different life stages. In *F. hallii* (plains rough fescue), a close relative to *F. campestris*, germination decreases have been directly tied to reduced osmotic potential (Romo et al. 1991). For this reason, establishing *F. campestris* from seed may be extremely difficult especially in combination with neighboring (invasive) species that are not as susceptible in the seedling stage to moisture deficits.

2.6.1.4 *F. campestris* and Disturbance

Fire adaptation of *F. campestris* consists of the ability to increase the number of tillers and reduce the size of the tillers. Fire does exhibit a negative effect on *F. campestris*, but this species can handle early spring grazing after wild fires due to slowed growth, suggesting that it has a moderate tolerance to the combined force of these two disturbance types (Bogen et al. 2003). Nevertheless, *F. campestris* is generally not well adapted to most human initiated disturbances. Within industry trials, seedling survival of *F. campestris* is extremely low in disturbed environments subject to reclamation (Adams 2008). It has been theorized that limited recrutment may be due to poor drought tolerance, poor germination, fungal interactions, slow rates of growth, and competition.

Overall, *F. campestris* is uncompetitive in disturbed environments with no way to vegetatively propagate itself and poor sexual propagation. Expansion into disturbed areas by *F. campestris* is restricted to sexual propagation, which only tends to occur episodically under ideal environmental conditions, and must be followed by ideal establishment conditions with three to five years for a seedling to reach maturity (Desserud 2006). Where seed is not needed, *F. campestris* can re-establish to some degree. This is evident in sod salvage trials and low disturbance (i.e. ploughing-in) of small diameter pipelines that have had mixed success, together with the use of greenhouse started plugs (Petherbridge 2000; Desserud 2006; Tannas 2009). Such success suggests that mature *F. campestris* plants are competitive and resilient, and are indicative of a climax species rather than a colonizer. Therefore it is theorized that restoration to *F. campestris* on disturbed sites will depend on invasive species control, overcoming establishment difficulties, and the restoration all components of the ecosystem (i.e. soils, climate, biology, etc.). For this reason understanding all aspects of this species within the ecosystem is critical. The only real revegetation success has been shown in areas where small diameter pipelines have been plowed in without striping the top soil and some sod salvage have been encouraging (Petherbridge 2000).

2.6.1.5 *F. campestris* Response to Defoliation

In contrast to *P. pratensis*, *F. campestris* is a deep rooted, slow growing bunch grass. These adaptations make *F. campestris* ideally suited to handling adverse environmental conditions, such as drought and low nutrient levels, but reduce its ability to respond to herbivory. Heavy grazing of fescue grasslands reduce range condition (Johnston et al. 1971), productivity, and have led to the requirement for long rest periods from grazing to recover (Willms et al. 1985). At moderate defoliation intensities *F. campestris* cover is reduced, while at heavy grazing intensities it can be eliminated from a community (Willms et al. 1985; Looman 1983; Johnston et al. 1971).

Defoliation has many effects on *F. campestris*. Following defoliation, increased light intensity at the plant crown may contribute to *F. campestris* growth via enhanced tiller development, although prompt removal of leaf area may lead to a net reduction in biomass of this species (Bogen et al. 2003). When *F. campestris* experiences repeated defoliations, asexual reproduction shifts towards increases in tiller numbers, decreased tiller sizes (Willms et al. 1986; Willms 1988) and decreased biomass production (Willms and Fraser 1992). This response to grazing allows more tillers to gain access to light, but the smaller size of resulting tillers may limit the ability of this species to compete with adjacent competitors, particularly when the latter are not defoliated. Forb production in these grasslands has also increased in some trials (Johnston et al. 1971; Willms et al. 1986), demonstrating the ability of other mid-seral species to compete with *F. campestris* once defoliation occurs.

In addition to these effects, *F. campestris* is capable of greater regrowth at low to moderate temperatures than high temperatures (King et al. 1998). This suggests defoliation in summer and fall may lead to marked differences in the ability of *F. campestris* to respond to competition (Willms and Fraser 1992). Clipping in May to late June causes high mortality and reduces vigour in *F. campestris* (McLean and Wikeem 1985; Mengli et al. 2005). Dormant season grazing, however, does not have the same negative affect on *F. campestris* growth, and consequently does not reduce its competitive ability as severely (Willms and Fraser 1992). This adaptation may be due to the historical dormant season grazing *F. campestris* experienced when herds of bison and other large grazers moved off the plains into the foothills for the winter.

2.6.2 *Poa pratensis*

2.6.2.1 *P. pratensis* Response to Light

In contrast to *F. campestris, P. pratensis* is a dominant herbaceous understory and overstory species. In neighbour removal experiments around

North America, *P. pratensis* increases its relative growth rate specifically after top growth removal (Wilson and Tilman 1991; Reader et al. 1994). This suggests there is a strong relationship between light availability and growth of *P. pratensis*. Interactions between N and light have been shown where there is a minimum threshold for N required by *P. pratensis* to effectively compete for above ground resources (Wilson and Tilman 1991). Light levels with and without competition may be important to this relationship, yet biomass of neighbours did not strongly influence *P. pratensis* growth on most sites (Reader et al. 1994). *P. pratensis* commonly maintains greater survivorship of young plants when grown with neighbours than without competitors (Wilson and Tilman 1991). This suggests that young *P. pratensis* plants need shelter from high intensities of light until mature. Moreover, fast growing species such as *P. pratensis* can pre-empt light interception by other plants, effectively out-competing them (D'Antonio and Vitousek 1992). Long photo periods maximize rhizome development of *P. pratensis,* suggesting that both long days and reduced shading will maximize growth potential (Moser et al. 1968). For this reason, grazing may interact with light to enhance growth of this species. *P. pratensis* is known to be grazing resistant (Cole 1995), mainly due to a prompt leaf area increase in response to defoliation, effectively allowing it to out-compete surrounding vegetation (Lemeziene et al. 2004). *P. pratensis* may also benefit from its plastic nature that allows it to tolerate diverse environments with differing light levels (Reader et al. 1994).

2.6.2.2 *P. pratensis* Response to Nutrients

Limited nutrient supply adversely affects shallow rooted, N-adapted species such as *P. pratensis,* which have a lower threshold of tolerance for these factors than their native counterparts (Martin and Chambers 2001). *P. pratensis* traditionally grows in medium to high N grasslands (Wilson and Tilman 1991). A decline in N may negatively impact *P. pratensis* due to lower competitive ability of N utilization. This is because *P. pratensis* generally has a faster cycling rate of N mineralization than slower growing N competitive species, increasing its need for available N compared to other species (Wedin and Tilman 1990). Conversely, invasive species may become highly competitive when resources are abundant (Liancourt 2005). *P. pratensis* increases in biomass with N addition, irrespective of grazing treatment (Martin and Chambers 2001). This is likely due to the shallow rooting nature of *P. pratensis* allowing it to be perfectly situated to intercept any fertilization (Bookman and Mack 1982).

The question therefore remains as to whether altered N availability in *F. campestris* grasslands will change *P. pratensis* abundance. Increases in N, clipping and grazing cause increases in *P. pratensis*, while exclusion from grazing stops and may even reverse invasion (Wilson and Tilman 1991; Martin and Chambers 2001). Moreover, evapo-transpiration within *P. pratensis* is highly correlated with nutrient addition (Ebdon et al. 1999). If *P. pratensis* uses more water with N abundance, plentiful N may increase the likelihood of induced ‘drought’. Conversely, low N conditions may reduce the ability of *P. pratensis* to utilize an abundance of soil water, limiting growth in this species. Either such effects could benefit native plants if they are capable of using surplus N under these same circumstances.

2.6.2.3 *P. pratensis* Response to Water

Limited water supply adversely affects shallow rooted species such as *P. pratensis* (Jiang and Huang 2001), which have a lower threshold of tolerance for these factors than their native counterparts. As discussed with nutrient additions, evapo-transpiration within *P. pratensis* is correlated with N addition (Ebdon et al. 1999). If *P. pratensis* uses more water with N abundance, increased N may increase the likelihood of induced 'drought', while low N conditions may reduce the ability of *P. pratensis* to utilize water, subsequently limiting its competitive ability. This relationship may benefit native plants if they are capable of using water when *P. pratensis* cannot.

2.6.2.4 *P. pratensis* and Disturbance

Symptoms of the response of *P. pratensis* to disturbances in Foothills Fescue Grasslands have likely been progressing for the past century. *P. pratensis* is capable of quickly establishing after disturbances such as tilling. This capability at recolonization allows *P. pratensis* to quickly invade native ecosystems upon human-caused disturbances using both rhizomes and seed (Moser et al. 1968). From this entry point, *P. pratensis* typically will utilize favorable grazing management regimes to continue invasion into the native grassland as well as invasion in unfavorable grazing regimes.

2.6.2.5 *P. pratensis* Response to Defoliation

The response of *P. pratensis* to grazing is fairly well understood. This species comes from a long Eurasian history of grazing and has been developed as an agronomic for grazing in many countries (Mack and Thompson 1982). It is widely recognized that *P. pratensis* has a high grazing tolerance (Cole 1995). In heavily grazed pastures and intensive grazing systems *P. pratensis* is able to effectively compete and increase in prominence (Kruess and Tscharntke 2002). One reason for this resistance to grazing is likely the low growth form of the species, although this also leads to low overall productivity (Jameson 1963). *P. pratensis* is adapted to defoliation through its creeping root system, which allows for defoliated parts of the plant to be supported during regrowth (Moser et al. 1968). This also allows the plant to reproduce and spread vegetatively without having to rely on seed production. Such advantages make this species highly competitive during grazing and have led to its classification as an increaser species that typically increases under grazing (Kruess and Tscharntke 2002).

Much of this grazing adaptation may be linked with the ability of *P. pratensis* to effectively access soil nutrients such as N and water (Bardgett and Wardle 2003), and as such may be dependant on specific levels of availability for it to respond positively to grazing pressure.

2.6.3 *F. campestris* Competitive Interactions with *P. pratensis*

Interspecific competition is largely driven by one or more of the following abiotic resources: light, water, and nutrients (Tilman 1987; Grace 1995). Notably, *F. campestris* grasslands continue to experience invasion by species such as *P. pratensis*, regardless of disturbance. *Poa pratensis* can invade even in the absence of grazing (i.e. within exclosures), but under high rainfall (Facelli and Pickett 1991). This suggests abiotic factors (i.e. moisture, nutrients, light) are at least partly responsible for regulating observed grassland dynamics (Weaver et al. 2001). Additionally, competitive outcomes are further modified by disturbances, including defoliation, and associated competitive shifts.

Moisture, light and nutrients can be altered indirectly though litter removal under grazing and associated microclimate modification. Moisture may also vary naturally due to drought, as is common in the plains of western Canada (Willoughby 2001). Relative to *P. pratensis* dominated areas, *F. campestris* grasslands are less dependent on precipitation during the growing season (Willms et al. 1986; Willms et al. 1996) suggesting water addition may lead to competitive exclusion (Liancourt et al. 2005). The effect of increased moisture aiding invasion has been used to explain differences in invasion between the dry mixed grass prairie and foothills/parkland sites (Adams 2008). However, given that invasion occurs with both high and low moisture conditions, other factors may be driving competition between these species.

Grazing decreases *F. campestris* prominence, even under moderate grazing (Willms et al. 1985), with replacement by *P. pratensis*. This may occur because of grazing-induced drought, resulting from lower root biomass in *F. campestris* (King et al. 1998). *F. campestris* also allocates abundant energy to regrowth making it vulnerable to repeated defoliation (King et al. 1998). It is generally believed that heavy grazing will favor *P. pratensis* provided other environmental conditions are optimal (Trottier 1986). Grazing also has dramatic indirect impacts on soil moisture by impacting infiltration and evapo-transpiration (Naeth et al. 1991; Naeth and Chanasyk 1995). Due to the prevalence of grazing within these communities, it is imperative to understand how defoliation and moisture impacts interspecific competition and the overall health of these grasslands. Given that fescue grasslands are typically moisture stressed for at least a portion of the year (Naeth and Chanasyk 1995), it is also important to understand how moisture impacts invasion by *P. pratensis* into *F. campestris* grassland. Although a light-moisture dynamic is probable in *F. campestris* grassland, the question remains as to whether *P. pratensis* can compete as well as *F. campestris* under varying litter conditions, with either high or low moisture availability.

Lastly, soil N may increase in heavily grazed areas, although the form of N may not be readily available for plant use (Dormaar et al. 1990). When combined with individual plant species requiring different N levels (Dormaar et al. 1990) and which have different N use efficiencies, further competitive shifts may occur with defoliation. Unfortunately, individual nutrient requirements of invader species and native bunchgrasses are relatively unknown in these grasslands (Dormaar et al. 1990), as are the cumulative community responses to nutrient levels. To manipulate soil N, a number of techniques have been utilized in the past. Nitrogen enrichment favors invasive non-indigenous species in a variety of habitats (Vinton and Burke 1995). As a result, N supplementation may negatively impact the competitive ability of rough fescue. There has also been heightened interest in carbon loading of soils using substrates such as sucrose and/or sawdust to reduce plant available N and alter plant community development (Corbin and D'Antonio 2004). When N in the soil is naturally high, the addition of carbon can reduce plant available N through immobilization. Some native grasses increase in competitiveness with the addition of sawdust in the first year and show no negative impacts due to carbon loading when competing with annual grasses (Corbin and D'Antonio 2004).

2.7 Summary and Conclusions

2.7.1 Predicting the Outcomes of Invasion

All the different models explaining invasion have a net result of the invader being able to access the indigenous plant community and establish successfully. However, different models and pathways have different consequences, and therefore require different management regimes to control. The most likely methods that must be dealt with in *P. pratensis* invasion are that *P. pratensis* is: more competitive given specific environmental conditions, experiencing an empty niche or filling in niches voided due to environmental and physical ecosystem changes, or is manipulating the environment for its own benefit (nutrients and light). If the specific thresholds necessary for invasion are isolated and manipulated, *P. pratensis* will no longer experience the advantage it is gaining over the indigenous species. Because environmental conditions are linked to multiple invasion theories, understanding these thresholds and how they interact is critical in determining which theory applies to *P. pratensis* invasion, including whether the driver or passenger model is capable of explaining invasion.

2.7.1.1 Invasion on Disturbances

P. pratensis invasion of native fescue grasslands is widespread in the foothills, and it has been noted that much of this invasion may be due to its historical use, such as road and trail revegetation, and for agronomic purposes (Tyser 1992). Such introductions have allowed *P. pratensis* to invade fescue grasslands wherever disturbance occurs. Disturbance is an important mechanism causing invasion. Grazing resistance is one reason that *P. pratensis* is successful in invasion of fescue grasslands, and this may be in part due to its long Eurasian grazing history, allowing for it to be better adapted to grazing than its North American counterparts (Mack and Thompson 1982). It is expected that tilling and grazing will aid *P. pratensis* invasion. As tilling eliminates all vegetation this benefits the fastest growing species, which is *P. pratensis* rather than *F. campestris*.

2.7.1.2 Invasion on Undisturbed Land

Invasion into undisturbed land has historically occurred from entry points such as those left by disturbance. Once *P. pratensis* has entered a fescue grassland, it cancontinue expanding in conditions that appear to have no anthropogenic disturbance (Mack 1986). The absence of grazing and anthropogenic influences has not abated some invasions (Tyser 1992; Larson et al. 2001), including that of *P. pratensis*. Outside of disturbance, the most likely causes for invasion are increases in N and soil moisture during the growing season. Both of these factors favor *P. pratensis* and may be key components of competition shifts. Reduction in these resources may decrease invasion or even reverse invasion.

2.7.2 Expected Resource Interactions During Invasion

Resource interactions during invasion are likely important in the fescue grassland ecosystem. It is very likely that defoliation plays a large role in the outcome of invasion and subsequent competition that occurs in these grasslands. Water levels have positive impacts on *P. pratensis* invasion, and thus it is likely that defoliation and water may interact to increase the likelihood of successful invasion and dominance. Nitrogen concentrations have also been linked to *P. pratensis* growth and to water use by the plant. Light levels are also modified by defoliation and may give *P. pratensis* a competitive advantage over slower growing species. Increases in both above and below ground resources could therefore easily interact to increase the competitive ability of *P. pratensis*.

In the same way, decreases in N and water can have negative impacts on *P. pratensis* invasion because it cannot readily compete with *F. campestris* under these conditions. Reduced defoliation may also combine with drought to allow *F. campestris* the ability to increase litter loads and reduce the impact of drought while also reducing light levels. It is therefore possible that these resources may be highly linked, with interactions of resources much more important than any one resource in the ecosystem.

2.7.3 New Information Needed

Information that we currently are lacking includes the specific mechanisms that drive invasion of *P. pratensis* into fescue grasslands. We do not understand what allows for *P. pratensis* persistence and why in some communities this species dominates the community, while in others it coexists or ends up being suppressed or eliminated. A test of the passenger and driver models is needed to determine if *P. pratensis* is driving invasion or if it is filling in empty niches left by ecosystem changes. It is also possible that the driver model allows establishment, but the passenger model is taking effect when grazing causes mortality in *F. campestris* tussocks. Shifts in environmental factors or their interactions with grazing may also be responsible for shifting competitive interactions and invasion dynamics between *P. pratensis* and the native fescue grassland community. Understanding what mechanisms are driving these shifts in community structure, regardless of the driver or passenger model, must occur with a secondary focus on whether *P. pratensis* is driving change or if *P. pratensis* is simply filing in empty niches left by anthropogenic changes.

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Chapter 3 DO ENVIRONMENTAL AND DISTURBANCE REGULATE COMPOSITION WITHIN FOOTHILLS ROUGH FESCUE (*FESTUCA CAMPESTRIS* RYBD.) GRASSLANDS?

3.1 Introduction

Invasion by non-native plants is a world wide problem in bunchgrass dominated plant communities (Mack 1986; Tyser 1992), and has often led to the replacement of endemic vegetation with an invasive community (Mack 1989). The mechanisms responsible for plant invasions include direct physical or mechanical disturbances such as tillage and grazing (Mack 1981; Tyser 1992; D'Antonio 1993), although responses may vary inversely with species diversity (Davies et al. 2007; Maron and Marler 2007). Invasions may also be influenced by environmental conditions (Tyser 1992), including available nitrogen (Ebdon et al.1999), water (Larson et al.2001; Maron and Marler 2007) or light. Moreover, these environmental mechanisms may act alone, interact with one another, or combine with disturbance to facilitate invasion (Fridley et al. 2007).

Understanding the impacts of environmental and disturbance factors on plant invasions requires examining invasion processes within the context of naturally occurring plant communities. While difficult to undertake, long-term field studies provide the most realistic method of determining how a community responds to invasion under varying environmental and disturbance regimes (Peters 1991). This is particularly important given that increasing community diversity can negatively impact invasion (Maron and Marler 2007; Davies et al.

2007), suggesting more diverse communities are more resistant to species change. However, results supporting this theory have been mixed (Elton 1958; Levine and D'Antonio 1999). Rather than diversity being the mechanism conferring resistance, the presence of specific species or functional plant groups that resist invasion may be more important, the latter of which are more likely present in diverse communities (Dukes 2002). In this case, understanding the role of each species in regulating community composition may be critical in preventing invasion.

In addition to assessing how diversity impacts invasion, it is also important to determine the roles of extrinsic factors regulating invasion. Disturbance has an important role in manipulating plant community structure by shifting the competitive advantage among neighboring species towards more stress tolerant plants (Passenger Model) (MacDougall and Turkington 2005), and away from those that are susceptible, including ruderals or colonizers (Grime 1974). Moreover, variation in the intensity and type of disturbance may favor different invasive plants (Baker 1974; Mack et al.2000). By reducing the presence, size or vigor of existing vegetation, disturbance may facilitate invasion by creating empty niches for invader colonization (Didham et al. 2005). In this situation, invasion merely remains symptomatic of disturbance processes (MacDougall and Turkington 2005). Conversely, once initiated, invasion may lead to further changes in the environment, and thus drive community change (Driver Model) (MacDougall and Turkington 2005). Under this model, invasion continues regardless of ongoing changes to disturbance regimes and the associated environment.

In SW Alberta, the invasion of native foothills rough fescue (*Festuca campestris* Rybd.) grasslands by *Poa pratensis* (L). has become increasingly prevalent (Looman 1969). This area also coincides with many land use activities, including livestock grazing, oil and gas development, recreation, and urban sprawl. As a result, conserving remaining *F. campestris* grasslands is considered a priority in land management within the region.

Poa pratensis (Kentucky bluegrass), an introduced species, has been widely used in agronomic (Tyser 1992) and urban landscapes of North America. However, this species can be invasive within adjacent native ecosystems because of its fast growth rates, high productivity and prolific reproduction, from seeds and rhizomes (Lemeziene et al. 2004). These traits also make *P. pratensis* difficult to control. Conditions likely to promote the invasion of *P. pratensis* include defoliation (Looman 1969), soil nitrogen (N) concentrations (Wedin and Tilman 1990; Liancourt et al.2005), and soil moisture (Ebdon et al. 1999; Martin and Chambers 2001). Moreover, these mechanisms may operate alone or in combination. Nutrient addition and defoliation may have the largest potential to interact during invasion (Liancourt et al. 2005) because of the ability of *P. pratensis* to respond rapidly to defoliation, which in turn, would be exacerbated by abundant soil moisture and N availability.

Defoliation of fescue grasslands historically (pre-settlement) was concentrated during the dormant season (Hodgkinson and Young 1973), and may be why grazing during the growing season has been linked to a decrease in the competitive ability of *F. campestris* (Hodgkinson and Young 1973; Willms et al. 1998). Moreover, growing season defoliation may allow for grazing tolerant and opportunistic species such as *P. pratensis* to replace less plastic species such as *F. campestris*. Although initially establishing from seed, *P. pratensis* does not require seed production to colonize a community once established, and can effectively dominate a community through vegetative (i.e. rhizome) propagation (Bookman and Mack 1982). This differs sharply from *F. campestris*, which has limited ability to spread spatially, and instead must colonize interspaces from seed.

Nitrogen addition and accelerated nutrient cycling have also been associated with increased growth of *P. pratensis* (Wedin and Tilman 1990), while the same may not be true of native plant species. Many native grasses are bunchgrasses, and have limited response to N addition (Wilson et al. 1966; Monaco et al. 2003). In contrast, *P. pratensis* is a sod forming species with a relatively shallow root system (Moser, Anderson and Miller 1968), potentially allowing this species to better capture increasing N from fertilization, deposition during grazing, or atmospheric inputs. Under this scenario, N capture could pre-empt N available for deeper rooted species such as *F. campestris* (Bookman and Mack 1982), placing the latter at a competitive disadvantage. Finally, under conditions of increased water and nutrient availability, *P. pratensis* may be able to colonize adjacent areas through vegetative means.

Water addition (W) increases the competitive ability of *P. pratensis*, and may be increasingly important later in the growing season as *P. pratensis* is susceptible to summer drought (Jiang and Huang 2001). Although not drought tolerant, water uptake in this species depends on nitrogen (N) use, with the latter potentially increasing the susceptibility of *P. pratensis* to drought (Ebdon et al. 1999). The link between N and water availability and use may therefore have important implications on how *P. pratensis* invades these grasslands.

Understanding the individual and collective influence of environmental conditions and physical disturbances on rough fescue grassland composition, including invasive species such as *P. pratensis*, is necessary to develop specific management strategies that conserve these native grasslands and minimize the threat of future invasion.

3.2 Objectives

The goal of this study was to determine the role of grassland diversity in conferring community resistance to species invasion by *P. pratensis*, and investigate the role of environmental (i.e. abiotic) conditions and disturbance (i.e. grazing) in regulating this invasion. More specifically, this study assessed:

1) How nitrogen (N) and water (W) addition, alone or in combination, alters species richness, diversity and composition within a foothills rough fescue grassland, including the abundance of native and non-native vegetation.

2) How summer or winter defoliation, either alone, or in combination N and W addition, modify community composition and diversity.
3) How litter removal alters community composition and diversity, including the environmental factors responsible for these changes.

3.3 Methods

3.3.1 Research Site

This study was conducted within a native grassland in the Foothills Fescue natural region northwest of Cochrane, Alberta (51°14'42.02"N, 114°31'9.85"W). The site was well-drained, situated on an elevated, west-facing terrace, and had a history of moderate grazing by cattle and occasional use as a native hay field for several decades. At the initiation of the study, *P. pratensis* cover was low throughout the study site with an average of 8%, though it ranged from 0-70% among plots. Soil at the site was an Orthic Black Chernozem (Series: Dunvargan / Hatfield), with 5.9 pH, 24.1% organic matter, cation exchange capacity of 22.7meq/100g and a clay loam texture (43% sand, 19% silt, 38% clay).

3.3.2 Experimental Design

A total of 16 treatments, each replicated 8 times, were used in an incomplete factorial design to examine community responses to the manipulation of nitrogen (N), water (W), litter, and seasonal defoliation, between 2005 and 2008 (Table 3.1). All combinations of N, W and litter were assessed. However, summer and winter defoliation were assessed only in combination with W and N. The total of 128 plots represented a wide range of initial conditions, including the abundance of *F. campestris* and *P. pratensis*.

The study site was fenced in July 2005 to prevent livestock access and unintended defoliation. All plots were established in a systematic manner and permanently marked to facilitate relocation. Each plot contained a series of nested plots of larger size, within which measurements or specific treatments were undertaken. Sample plots were 0.5 x 0.5 m in size. Additions of N and W additions occurred within a larger 1x1 m plot nested overtop of the sample plot (Fig. 3.1). Similarly, litter and defoliation were done within a larger 1.5x1.5 m area to minimize the influence of treatment edge effects. All plots were separated by a minimum distance of 0.25 m.

Defoliation treatments were conducted in either November 2005 (winter defoliation) or June 2006 (summer defoliation). At the time of defoliation, all above ground material was clipped to 2 cm height, and separated into live (standing) and dead fractions (litter) (November), or further stratified into *P. pratensis*, *F. campestris*, other grasses, forbs, or shrubs (June). All samples were oven dried at 50 ^{o}C to constant mass and weighed.

Selected treatments included an *in-situ* check where no treatment occurred (Table 3), and a litter removal treatment intended to indirectly modify the microenvironment. Litter was removed in November of 2005, with all loose and detached coarse material hand scraped from plots. The average weight of litter removed was 68.40 ± 4.4g /m^2. Both check and litter removal treatments were repeated (Table 3.1) within W and N addition treatments.

Plots with W addition were brought up to field capacity every 2 weeks from May 1 to August 31 of each year (2006 through 2008). The amount of water necessary to reach field capacity was determined using measured soil moisture values obtained with a Delta-T^{TM} ML2X moisture probe, coupled with calibrated relationships between moisture addition and observed measures of moisture for soil conditions at the site (Appendix E, Fig E1-E2). During calibration, water was added in 2.5 cm increments and left for 24 hr before soil moisture readings were taken. This process was repeated until saturation of the soil was reached.

Another set of four treatments were used to examine the combined manipulation of the availability of W and N, the dominant nutrient limiting plant growth in grasslands (Vitousek 1982) (Table 3.1). The addition of N on one half of the plots occurred annually each spring (May) by broadcasting granular urea (46-0-0) to the surface of each plot. Rates of urea addition were 100, 50 and 50 kg ha^{-1} in 2006, 2007, and 2008, respectively. Reduced rates were used after 2006 based on soil tests that indicated mineral N levels remained elevated (Appendix E).

Finally, defoliation treatments at two separate times of the year were imposed in a factorial design with the W and N treatments (Table 3.1). Defoliation occurred non-selectively within affected plots by removing all current years' growth to 2 cm height, without altering existing litter on the soil surface. Defoliation was done at a single time in either winter (November 2005) or summer (July 2006). Biomass removed at defoliation was sorted to grass, forb, and shrub components, and litter (litter removal experiment only), bagged, oven dried (50 °C) for 36 h and weighed to determine the severity of defoliation impact.

3.3.3 Measurements

3.3.3.1 Environmental Monitoring

Volumetric soil moisture in the upper 15 cm of soil was recorded at 2 week intervals from May 10 to August 31 in 2006 and 2007 using an ML2X moisture probe. These measures were taken 2 weeks after each water addition treatment and a minimum of 24 hr after precipitation. Measurements were also taken in 2008, but ended in July at final biomass sampling. Individual soil moisture values were sampled non-destructively in each plot approximately 10 cm from the center of the sampling plot in 4 random locations. A rain gauge was used to record local rainfall throughout the growing season, and compared to regional temperature and rainfall data obtained from the Cochrane weather station, approximately 2 km southeast of the study site.

Photsynthetically active radiation (PAR, in the 400 to 700 nm wavebands) was measured using a Decagon AccuPAR^{TM} ceptometer. PAR was recorded over a 3 hr period around solar noon on uniformly overcast days using the average of 10 readings above each plot, and 10 at the soil surface under all standing plant biomass and litter; an equal number of readings were taken at a 90 degree angle at each position. PAR readings were repeated monthly for each plot between May 1 and August 31 in 2006 and 2007, and from May 1 to July 30th in 2008.

Soil samples were collected in each plot during the last week of August of each year, using three, 2.5 cm diameter cores to a depth of 15 cm. Sub-sample cores from each plot were combined, frozen, and a subset was later analyzed for available NO_3-N and NH_4-N by spectral absorption after extraction from soil using a 5:1 mixture of 2*M* KCl (Maynard and Kalre 1993).

3.3.3.2 Vegetation Measures

Vegetation sampling included non-destructive cover assessments of all plant species within the permanent sampling plots. Canopy cover assessments started in early August 2006 when the crown cover (i.e. % of plot occupied) of each species was measured: this measurement was repeated in 2007 and 2008. Estimates of bare ground, moss/lichen, and litter cover were also obtained for each plot.

Above ground net primary production (ANPP) of *F. campestris, P. pratensis*, grasses, forbs, shrubs, and litter were assessed within each permanent sample plot at the beginning of August 2008 at final sampling. Material was clipped at 2 cm height, sorted to component, dried at 50^{o}C to constant mass and weighed. Biomass removed during initiation of the defoliation treatments was also collected in November 2005 and July 2006, with all biomass similarly sorted to *P. pratensis*, *F. campestris*, other grasses, forbs, shrubs, and litter components, oven dried (50 ^{o}C) for 36 h and weighed**.**

3.4 Analyses

Due to the incomplete design of the experiment, data were examined using two separate procedures, including that of the environmental impacts (i.e. treatments 1-8 in Table 3.1) and the effects of defoliation (i.e., treatments 1,3,5,7, and 9-16 in Table 3.1). Environmental treatments were examined separately for each of 2006, 2007 and 2008. Defoliation was assessed both individually, and with the additive effects of N and W addition to the defoliation treatments. Defoliation effects were only evaluated on data from 2007 and 2008 due to the summer defoliation in July 2006, which precluded sampling that year. Moreover, emphasis in the latter analysis was placed on defoliation and interactions with environmental factors, rather than main effects of the latter. Plant compositional data from each plot were summarized using PC-Ord 5.10, to species richness, evenness (E=H/R) and Shannon's diversity index [H = -sum (Pi*R(Pi)], where R = richness and Pi = the proportion of total species cover in a plot consisting of species 'i'. Similarly, environmental data from each plot were summarized for each sampling time including mean monthly soil moisture in each year, mean monthly PAR transmittance, and annual soil N measured in August.

All community level plot responses, including diversity, richness, evenness,as well as litter and biomass removed at the start of the study and again at final harvest, together with measures of soil moisture, PAR transmittance, and soil N, were assessed for normality and homogeneity of variances prior to analysis. Assumptions of normality were met for all data except species richness assessed from 2006-08 in the environmental analysis, and again in 2008 within the defoliation analysis. As attempts to normalize these data were unsuccessful (i.e. using various transformations), the original (i.e. untransformed) data were analyzed to maintain comparability and simplify interpretation of the results.

3.4.1 Primary Treatment Impacts on Environment and Community

Direct effects of the fixed factors of soil N, W addition, litter removal, and defoliation, together with interactions among these factors as outlined in the previous section (i.e., using separate environmental and defoliation analyses), on community responses (richness and diversity), and environmental conditions (observed soil N, soil moisture availability and PAR interceptance), were examined using an ANOVA with Proc Mixed in SAS statistical software v9.2 (SAS Institute Inc 2008). Block was considered random in all models, with the main effects and interactions significant at $P<0.05$. All analyses were conducted using LS means, and post-hoc mean comparisons were conducted on all significant effects with a Tukey test using $P<0.05$.

A stepwise regression using Proc Reg in SAS v9.2 (SAS Institute Inc 2008) was used to evaluate the association between environmental conditions and observed plant community responses in each of 2006, 2007 and 2008. Dependent variables included species richness, diversity, evenness, *P. pratensis* biomass, *F. campestris* biomass, shrub biomass, other grass biomass, forb biomass and litter biomass. Independent variables included monthly soil moisture (SM), monthly photosynthetically active radiation (PAR), and yearly available N for each respective year. Regression rather than correlation was used as the former provides *B*-coefficients for significant variables, which provide an indication of the empirical nature of the relationship between variables.

3.4.2 Detailed Plant Community Composition Responses

Detailed plant species responses were examined using multivariate analysis techniques in PC-Ord v5.1 (McCune and Grace 2002). This included a combination of Multi-Response Permutation Procedures (MRPP) to directly tie species composition to the fixed experimental treatments (Mielke 1979; McCune and Grace 2002), and Non-metric Multi-dimensional Scaling (NMS) ordinations. MRPP has the advantage of being robust to distributional assumptions (McCune and Grace 2002) (normality and homogeneity of variance).

Multivariate analysis included assessment of species responses in each year of sampling (2006 through 2008, inclusive). However, species composition during 2006 was not assessed in relation to the defoliation treatments, as recent defoliation in July of that year within the summer defoliation treatments precluded assessment that year. Additionally, vegetation responses were assessed from 2006 to 2008 as the specific change in abundance of each plant species. The latter had the advantage of adjusting for differential species presence among experimental plots at the start of the study, and enabled species dynamics to be directly tied to individual treatments over the three year period. Due to the presence of negative values for those species that declined in abundance over the study period, all ‘change’ data were linearly rescaled to positive values by adding the minimum cover value necessary to bring all species cover levels above 0. Examination of these results suggested little additional information was provided, so these results are provided as supplemental information in Appendix A.

For all multivariate analysis the Sorensen’s distance metric was used because it is robust for ecological analysis (McCune and Grace 2002). Similar to the univariate analysis, the MRPP was conducted in two discrete stages to simplify the complexity of the experiment into questions involving: 1) the impact of environment (litter, N and W) on community composition, and 2) the impact of combinations of defoliation with environment (N and W) on composition. In the MRPP analysis $A = 1$ (observed delta/expected delta) where $A_{max} = 1$ means that items are identical within groups, $A=0$ means that heterogeneity equals expectation within the groups, and $A<0$ means that there was more heterogeneity within the group than expected. Significance for all MRPP analyses was set at $P<0.05$, with post-hoc mean comparisons of treatment levels assessed using $P<0.05$.

Ordination with NMS (Kruskal 1964; Mather 1976) was used to further support the MRPP analysis. Ordination reduces the dimensionality of complex multivariate relationships, and was used to visually assess and identify patterns in species composition among plots, which in turn, could then be further interpreted relative to environmental factors (soil moisture, N level, and light availability), disturbance (i.e. seasonal defoliation), or community characteristics (e.g. richness, diversity, biomass, and ground cover). NMS was selected because it is capable of handling large numbers of zeros (i.e. species absence within plots) and does not require normality of sampling distributions or linearity of relationships (McCune and Grace 2002).

All NMS ordinations were configured with 1000 runs using real data and 1000 runs with randomized data. The stability criterion used was P<0.0001 over the last 15 iterations. This was repeated at least 3 times, and the most frequent result utilized in the final analysis. Results were interpreted using dimensionality, stress and instability scores, associated axis p-values and axis r value (Appendix A). All species composition data were used without relativization to reduce the impact of rare species. Overlays were used to visually interpret those plant species with an r value above |0.39| in relation to the experimental treatments, with provincially important species included as well. The latter included *F. campestris*, the dominant historical graminoid in fescue grasslands, and *P. pratensis,* the primary invasive species. Additionally, *Bromus inermis* was examined, as this species has been identified as an invasive grass in other regions of western Canada (Grilz et al. 1994; Otfinowski and Kenkel 2008), along with *Symphoricarpos occidentalis*, which is a shrub that is capable of expanding its abundance within grasslands throughout much of the Aspen Parkland and Foothills Fescue region of western Canada (Wilson 1998; Partel and Wilson 2002). Finally, those environmental responses (moisture, light, and N) and summary cover variables (litter, bare ground, moss, and diversity measures:

richness, evenness and Shannon diversity index) with r values above |0.22| were plotted.

3.5 Results

3.5.1 Treatment Induced Changes to the Environment

Treatment induced changes to the environment, including the impact of litter removal on soil moisture, PAR and soil N, are reviewed in Appendix A. In general, litter removal increased light transmittance, particularly during 2006. Litter removal also decreased soil moisture initially, although these effects diminished through 2007, and litter removal even led to increased soil moisture in 2008. As expected, W addition increased soil moisture, while addition of N reduced soil moisture. Defoliation had variable effects on soil moisture. Finally, N addition predictably led to increased soil N in August of each year (Appendix E).

3.5.2 Fescue Grassland Responses to Environment

A total of 52 plant species were present across the study site during this investigation in the environmental study (i.e. treatments 1-8), including 19 grasses, 31 forbs and 2 shrubs. In 2006, 42 species were observed, which increased to 48 by 2008. Similarly, the defoliation study had a total of 50 species, including 44 in 2007 and 48 in 2008, respectively. A total of 18 grasses, 30 forbs, and 2 shrubs were documented throughout the study period in defoliation plots.

Species richness was not affected by W or N addition at any time (Appendix A). However, evenness and Shannon's diversity were similarly affected by these treatments. Diversity declined with W addition during the first year of treatment (2006) from 1.56±0.05 to 1.40±0.05 (P = 0.03), a response that was paralleled by a reduction in evenness from 0.66±0.02 to 0.60±0.02 (P= 0.04). In contrast, N addition increased diversity in 2006 from 1.40±0.05 to 1.56±0.05 (P =0.03), with a similar increase in evenness from 0.60±0.02 to 0.66±0.02 (P =0.02). Evenness was negatively associated with *F. campestris* cover (P=0.02). Closer examination indicated this relationship was less important within the ambient W (P=0.08) and litter (P=0.08) conditions, but eveness was significant for the W addition (P=0.01), N addition (P=0.03), ambient N (P=0.02) and litter removal treatments (P=0.01) (Appendix A).

During the final year of sampling (2008), both N and N by W effects remained evident. Although evenness declined from 0.70±0.01 to 0.65±0.01 (P =0.03) with N addition, plots with added N and ambient W had greater (P <0.02) evenness (0.72±0.03) than all other combinations of N and W (evenness ≤ 0.60±0.03). Diversity exhibited a similar increase (P<0.02) under N addition and ambient water (1.72±0.07) compared to all other treatments (1.40±0.07). Litter removal had no effect on evenness, richness or diversity in 2006 or 2008 (P >0.05).

Stepwise regressions revealed that diversity, evenness and richness were associated with levels of PAR and SM (Table 3.2). During 2006, June PAR was positively related to diversity (*B*= 0.32), largely to a parallel relationship with species richness (*B*= 0.37). In 2008 however, May PAR was positively related to diversity (*B*= 0.32) and evenness (*B*= 0.41). June SM was also negatively related to diversity (*B*= -0.27) and evenness (*B*= -0.31) in 2008 which was similar to the response in 2006 (*B*= -0.26) (Table 3.2). Total biomass was not associated with any of the environmental variables, but litter biomass was negatively associated with available N (*B*= -0.22), forbs with soil moisture (*B*= -0.23) and shrubs had a weak negative relationship with available N (*B*= 0.24). Grass biomass was divided into three categories: while the majority of grass species together had no relationship with environmental variables, *P. pratensis* had a negative association with May SM (*B*= -0.27), while *F. campestris* was associated with available N, (*B*= -0.24), May PAR (*B*= -0.22) and May SM (*B*= 0.31).

The MRPP analysis of the environmental treatments in 2006 indicated the greatest effects on plant species composition involved the addition of W, either alone ($P<0.001$), or in combination with N addition ($P<0.01$), or litter removal ($P=0.01$) (Table 3.3): however, the effect of W addition remained weak ($A \leq 0.05$; Table 3.4). Closer examination of the N*W interaction revealed that the only significant divergence in community composition was generated by the addition of W, and only when accompanied by simultaneous N addition (Table 3.4). Similarly, the interaction of W x L indicated that W addition was effective in changing species composition, but only in the presence of intact litter (Table 3.4). By 2007, the effect of W addition all but disappeared, with only the main effect being marginally significant ($P=0.1$; Table 3.4). At the end of the study in 2008, plant composition was no longer dependent on W addition. Instead, effects of N addition were observed based on the MRPP in 2008 (P=0.06), although effect sizes remained relatively weak (A=0.01, Table 3.4).

The 2006 indicator species analysis (see Appendix A for complete results) revealed that litter removal correlated with increases in *Elymus lanceolatus* (-L: P=0.03). While N addition correlated with *Geum triflorum* (+N: P=0.04), ambient N correlated with *Taraxacum officinale* (-N: P=0.04), particularly when accompanied by added W (-N+W: P=0.04). Water addition also correlated with *F. campestris* (+W: P=0.004), particularly when litter was intact (+W+L: P=0.01) or N was added (+W+N: P=0.01). Water addition was also associated with *Solidago missouriensis* under a range of conditions (+W:P=0.02, +W-L:P=0.004, +W+N:P=0.01), as was *Agroelymus bowdenii* (+W: P=0.04, +W+L: P=0.03, +W+N: P=0.01). In contrast, ambient water correlated with increases in *P. pratensis* (-W; P=0.07) and *Thermopsis rhombifolia* (-W: P=0.01) (Appendix A).

The 2006 NMS indicated a 3-dimensional solution (all axes P <0.03). Axis 1, 2 and 3 represented 24.5, 31.3, and 35.4% of species variance, respectively. Ordination overlays illustrate the relationship between environmental factors, community responses, and key species along these axes (Figs. 3.2). Axis 1 was associated primarily with levels of N (r=0.27) and W (r=-0.15), while axes 2 (r=-0.33) and 3 (r=-0.25) were associated with the W treatments only (Table 3.5). Notably, *P. pratensis* and *F. campestris* exhibited strongly divergent responses within the community, primarily along axis 2 (Fig. 3.2). In general, *F. campestris* was associated with the cover of litter and May soil moisture in 2006, while *P. pratensis* was associated with the cover of moss, and to a lesser extent, species evenness and diversity (Fig. 3.2, Table 3.5).

Indicator species analysis during the final year of sampling in 2008 revealed that intact litter was associated with *Elymus lanceolatus* ssp. *riparium* (+L: P=0.004), particularly under high W (+L+W: P=0.02) and high N (+L+N: P=0.002) levels (see Appendix A). In contrast, litter removal was associated with *Elymus lanceolatus* (-L: P=0.02). Nitrogen application was associated with increases in *Symphoricarpos occidentalis* (+N; P=0.04)*, Elymus trachycaulus* (-L+N:P=0.04), and *Elymus lanceolatus* ssp. *riparium*. (+N: P=0.05). Finally, W application generally favored *Achillea millefolium* (+W: P=0.02, +W+L: P=0.01), *Festuca campestris* (+W: P=0.04)*, Solidago missouriensis* (+W: P<0.05, +W+N: P=0.04) and *Artemisia ludoviciana* (+W-L: P=0.05), while ambient W levels were associated with *Rosa woodsii* (-W: P=0.002, -W-L: P=0.03, -W+N: P=0.02) (Appendix A).

Analysis with NMS of the 2008 data indicated a 3-dimensional solution (P=0.03), where axis 1, 2 and 3 represented 28.1, 22.9, and 38% of species variance, respectively (Table 3.6). Axis 1 was not associated with any environmental treatment, while axis 2 was associated with N (r =-0.32). Both axes 2 (r =0.15) and 3 (r =-0.14) were associated with W addition (Table 3.6, Figs. 3.4-3.5). Among provincially important species, *B. inermis* was associated with axis 1 (r =-0.76), as was evenness (r =0.27) and diversity (r =0.24), albeit in opposite directions. Similarly, *S. occidentalis* (r =-0.73) and *F. campestris* (r =0.74) demonstrated divergent responses on axis 2. Also of note was that axis 2 reflected a number of environmental factors and plant community measures (Table 3.6). Finally, *P. pratensis* (r =0.91) and *F. campestris* (r =-0.61) were strongly associated with axis 3, but in opposite directions (Table 3.6). Both *P. pratensis* and *F. campestris* appeared unrelated to plant community characteristics based on the ordination (Fig. 3.3, Table 3.6). While the treatments did not demonstrate a strong correlation, the environmental overlay's (W, N, and L) did suggest relationships between plant species, diversity measures and environmental variables (Fig 3.3).

3.5.3 Fescue Grassland Responses to Defoliation

Winter defoliation (WD) increased (P =0.0003) diversity in 2006 relative to undefoliated (UD) plots from 1.48±0.06 to 1.66±0.06, a pattern that was associated both increased richness (P <0.0001, 10.6±0.42 to 12.0±0.42 species / plot) and evenness (P =0.03, 0.63±0.02 to 0.67±0.02). By 2007, no effect of WD remained, but the effects of summer defoliation (SD) the previous year were now evident on all measures of diversity compared to both the UD and WD treatments: the SD treatment had greater total diversity (P =0.0003, 1.97±0.05 vs. 1.73±0.05 /1.66±0.05), which in turn was associated with greater richness (P =0.0001, 12.5±0.42 vs 11.6±0.42 /10.7±0.42 species / plot), and evenness (P =0.001, 0.79±0.02 vs 0.71±0.02). Modest increases in diversity (P =0.09) remained evident in 2008 within the SD treatment (1.72±0.05), but only in comparison to

UD plots (1.55±0.05). Additionally, UD plots had lower (P =0.04) evenness (0.64±0.02) compared with WD and SD treatments (0.69±0.02).

The MRPP analysis indicated that in 2007 defoliation impacted plant community dynamics (P <0.0001), with additional interactions of defoliation with N (P <0.001) and W (P =0.002) addition (Table 3.3). Overall, SD plots were differentiated from both UD and WD (Table 3.7). Seasonal defoliation effects were present among all treatments with N addition, but only between UD and SD treatments under ambient N: similarly, the relative effect of N addition remained greatest in UD plots (Table 3.7). Defoliation effects were also consistent between SD and WD plots regardless of W treatment, with an additional difference between UD and SD treatments but only under high W (Table 3.7). Within defoliation treatments, W addition did not significantly alter plant community composition. One year later in 2008, both N addition and WxN addition effects remained evident, with no effects of defoliation (Table 3.7). It is noteworthy that the latter result contrasts directly with the environmental analysis, where WxN effects were not as apparent (P =0.43): the increase in significance in this response may be attributed to the larger sample size (n=12 rather than 8 treatments) in the defoliation analysis.

Indicator species analysis of the initial response to the defoliation treatments (2007) revealed that the WD treatment was associated with *F. campestris* (WD: P =0.03) and *Geranium viscosissimum* (WD-W: P =0.05). Undefoliated conditions were similarly associated with *F. campestris*, but only under ambient N (UD-N: P =0.06). Summer defoliation was correlated with numerous other species under a range of conditions, including *Elymus trachycaulus* (SD: P =0.05), *Agroelymus bowdenii* (SD: P =0.002, SD+W: P =0.002, SD+N: P =0.002), *Carex pensylvanica* (SD: P =0.004, SD+W: P =0.02, SD-N: P =0.004), *Stipa curtiseta* (SD: P =0.002, SD+W: P =0.006, SD-N: P =0.008), *Elymus lanceolatus* (SD+W: P =0.02, SD+N: P =0.02), and *Achillea millefolium* (SD+N: P =0.02, SD+W: P =0.02) (Appendix A).

Analysis with NMS of the 2007 data indicated a 3-dimensional solution (P =0.03). Axis 1, 2 and 3 represented 36.6, 24.8, and 22.3% of species variance, respectively (Fig 3.4, Table 3.8). Axis 1 was weakly associated with SD (r =0.17), which in turn, was also associated with *P. pratensis*, *F. campestris*, and decreases in soil moisture (May, July, August): notably, *P. pratensis* and *F. campestris* had strongly divergent vectors on this axis. Axis 2 was associated with the SD (r =0.34), WD (r =-0.24), and N addition (r =0.16) treatments, and reflected litter and associated PAR (Table 3.8). Axis 2 was also associated with all measures of community diversity, with additional divergent responses in *C. pensylvanica* (r =0.76) and *F. campestris* (r =-0.65). Axis 3 revealed separation of UD (r =0.24) from SD (r =-0.19) treatments, and demonstrated N effects (r =0.23), with divergent responses between *Symphoricarpos occidentalis* (r =0.73) and *F. campestris* (r =-0.44).

Indicator species analysis of the final measured responses in 2008 indicated the UD treatments were correlated with *Bromus pumpellianus* (UD: P =0.03), and *F. campestris* (UD-N: P =0.07). Summer defoliation was correlated with *Agroelymus bowdenii* (SD: P =0.03), *Carex pensylvanica* (SD-W: P =0.03), *Geranium viscosissimum* (SD+W, SD+N; P=0.06, 0.08) and *Pascopyrum smithii* (SD+W: P =0.03).

Analysis with NMS of the 2008 data again indicated a 3-dimensional solution (P =0.03), where axis 1, 2 and 3 represented 14.7, 24, and 49.5% of species variance, respectively (Fig 3.5). Axis 1 was associated with the UD (r =0.12) and N (r =-0.33) treatments, with most plant community characteristics (e.g. richness, evenness, and shrub, forb and grass biomass) and several herbaceous species (*C. pensylvanica*, *S. missouriensis*, and *S. occidentalis*) associated with N addition and availability (Table 3.9, Fig 3.5). In contrast, axis 2 was linked only with W addition (r =-0.29), with similar responses for species evenness (r =0.2), other grass biomass (r =0.6), and the abundance of several species, including *B. inermis* (r =0.6), but not *F. campestris* (r =-0.5). Finally, axis 3 was not associated with any treatment, but it did correlate with June soil moisture, with divergent responses observed once again between *F. campestris* (r =0.6) and *P. pratensis* (r =-0.9).

3.6 Discussion

3.6.1 Species Composition Responses to Nitrogen and Water

Overall, this community responded to N and W addition, although the magnitude and temporal extent of the response varied between treatments. Water impacts on diversity were negative, immediate, and persisted for a relatively short period of time, largely disappearing by the second year. This may be related to precipitation in 2006 being 116% of normal, while in 2007 it was 152%

(Appendix E). The plant community examined here appeared to increase productivity with W addition under normal precipitation, but not elevated precipitation, suggesting moisture limited production under normal summer rainfall.

Soil N effects on evenness were positive, and although evident early on, tended to peak after 3 years of treatment. Notably, the greatest effects on species composition arose from the combined effects of N and W addition, suggesting both of these resources may be limiting alone or only in the presence of the other resource (Ebdon et al.1999). Interpretation of these responses must be tempered by the specific size of the plot assessed in this investigation, as evenness can reflect plot size in grasslands (Kwiatkowska and Symonides 1986).

The negative relationship of W addition with diversity, specifically evenness, was supported by species-level responses. Changes in evenness were driven by a relatively small subset of species that were indicators of either positive (n=7 species) or negative (n=3 species) responses to added W. Species that responded (+/-) to W addition were predominantly rhizomatous grasses and creeping rooted forbs, and one tap rooted forb and a caespitose grass (*F. campestris*) (Moss and Packer 1983). This supports findings that species with functionally distinct characteristics (i.e. shallow, rhizomatous species) from those of the dominant-species, *F. campestris* (Coupland and Brayshaw 1953) responded more markedly to treatments (MacDougall and Turkington 2005). The lone exception, *F. campestris,* which responded positively to W addition, may also have driven the negative effects on evenness by suppressing subdominant species.

Such effects of dominance are recognized as an important function in how evenness, a measure which responds quickly, can eventually lead to losses in species richness (Hillebrand et al. 2008). Although this did not occur, the lack of change in species richness may be due to the short timeframe of the present study combined with the long-lived nature of the plant community, which would limit actual displacement or addition of new plant species (Debinski and Holt 2001). Alternatively, the ability of species replacement to stabilize richness appeared to occur uniformly over treatments (e.i. species lost, -W: 7, +W: 8; species gained, -W: 10, +W:10).

Not surprisingly, soil moisture was related to W addition, but because this parameter was quantified two weeks after adding W, other abiotic (i.e. litter biomass, evaporation) and biotic (i.e. differential response to water among species present) factors may also have impacted this measure. Soil moisture appeared to be an important resource affecting species composition in 2006 when precipitation was near normal (116%), suggesting this community was capable of exploiting abundant soil moisture when available. Soil moisture remained an important factor associated with the final biomass of several variables, including that of forbs, and the key grasses *F. campestris* and *P. pratensis*. However, *F. campestris* and *P. pratensis* also exhibited strong divergence in the ordination, as did *F. campestris* and another common invasive grass, *B. inermis* (Otfinowski et al. 2007) which was not strongly associated with any treatment in our study.

Observed reductions in diversity (i.e. evenness) coincided with increases in the dominant species (i.e., *F. campestris*), which in turn was favored by increased soil moisture, from W addition. These results suggest localized suppression of subdominant species by *F. campestris* may have been linked to moisture availability. Moreover, this response was also found under ambient litter conditions and suggests the potential for litter to simulate the effects of W addition, presumably due to the ability of litter to trap snow (Willms and Chanasyk 2006), reduce evaporation (Facelli and Pickett 1991)(Naeth et al. 1991), and minimize runoff (Naeth et al. 1991; Chanasyk et al. 2003). With the demonstrated ability of *F. campestris* to withstand soil moisture deficits (Chapter 6), this species is ideally suited to dominate this plant community, particularly in the absence of defoliation (Johnston et al. 1971).

In contrast, low soil moisture content appeared to favor an increase in *P. pratensis*, which is typically a moisture loving species (Ebdon et al.1999). This observation did not initially support our hypothesis that *P. pratensis* would be better adapted to exploit increased soil moisture than endemic native plant species such as *F. campestris*. Furthermore, *P. pratensis* did not appear to drive reductions in diversity as the association of this species with diversity was initially weak in this investigation, responses similar to that of Meiners et al. (2001). By 2008 however, the current study revealed a more pronounced negative association between *P. pratensis* cover and diversity in the NMS, similar to MacDougall and Turkington (2005). The other introduced species, *B. inermis*, also expanded in cover from 2006 to 2008, but based on the NMS, was found to prefer locations without *F. campestris* or *P. pratensis*. There was no clear association of *B. inermis* with environmental factors except a weak association with low W. This is a unique response give that *B. inermis* is known to respond positively to increases in W (Nernberg and Dale 1997) and N (Foster and Gross 1998). Similar to the response of *P. pratensis, B. inermis* may be suppressed in its preferred habitat by dominant species like *F. campestris*, particularly under W addition. Such suppressive responses are capable of reducing evenness and species richness and are widely understood to occur by dominant species (Hillebrand et al. 2008).

Although overall changes in community composition to N addition took several years to fully manifest themselves, the initial effect of N in 2006 was to increase species evenness, presumably by increasing the biomass of existing plants (Lamb 2008) because soil N is often a limiting factor for growth in grasslands (Vitousek and Howarth 1991; Lamb et al. 2007). Therefore, immediate impacts of N addition appeared to favor changes in species abundance rather than their presence or absence. Indicator species analysis corroborated this as species associated specifically with N addition in 2006 were limited, suggesting most or all plant species in this community responded favorably to added N.

By 2008, those species responding to N addition included 2 subdominant grasses, a response consistent with graminoids being more efficient in the uptake of N (Bowman et al. 1994), and *S. occidentalis,* a native, clonal shrub commonly found across the Parkland and Fescue Prairie regions (Romo et al. 1993). This suggests that *S. occidentalis* abundance may be constrained by N availability, and compares favorably with studies from the Aspen Parkland where woody invasion has been correlated with N addition (Kochy and Wilson 2001). Moreover, the majority of plant species responding to N addition in this study did so only in the presence of high W, either directly through addition or indirectly through litter retention. The interaction of NxW suggests that both of these resources are necessary for growth to be optimized in this ecosystem. Conversely, either resource added alone may leave the other one limiting for plant growth (Ebdon et al.1999). Similarly, the interaction of N with litter may be attributed to increased soil moisture with the retention of litter (Weaver and Rowland 1952; Fowler 1986; Facelli and Pickett 1991). While N levels did not appear limiting for the dominant species, *F. campestris*, it appeared to be limiting for many other species, but only in the presence of W or conditions known to increase soil moisture (i.e. litter accumulation). It is therefore important to limit N additions into these grasslands to maintain late seral communities dominated by *F. campestris.* This may be achieved by limiting fertilization or N deposition from the atmosphere (Kochy and Wilson 2001) which is more difficult to control.

3.6.2 Community Responses to Litter Removal

Litter removal was not directly linked to changes in species richness, evenness, or diversity in this investigation. Although litter and soil moisture appeared correlated with each other (NMS) and litter removal appeared to counteract the effect of water addition, potentially through reduced evaporation (Weaver and Rowland 1952; Fowler 1986; Facelli and Pickett 1991), the indicator analysis indicated that most species responses were tied to W treatments independent of litter. In this study, the direct effects of litter on diversity were limited by the one time litter removal treatment wherein the strongest effects were seen in 2006, with diminishing effects by 2008 when litter had re-accumulated to 98% of ambient litter. The relatively weak effects of litter on species composition contrast those of other studies where litter had much more significant impacts on plant diversity (Lamb 2008).

The only individual plant species that served as an indicator of litter removal was *E. lanceolatus*, perhaps because of its adaptation to arid and semi-arid prairie habitats where favorable PAR and low moisture (Maxwell and Redmann 1978) would be more similar to the litter removal treatments in this experiment. Species responding favorably to ambient litter, either alone (*A. riparium* in 2008) or together with added W (*F. campestris* in 2006), potentially due to their tolerance of lower PAR, may have resulted from suppression of other species, leading to a reduction in evenness. This suggests that *F. campestris* (the most productive species making up 55% of herbaceous biomass in 2008) may be capable of exploiting litter biomass, much of which is its own, as a mechanism to compete more effectively with its neighbours. Indeed, this has been found in other studies (Facelli and Pickett 1991). The marked association of *F. campestris* with litter cover and soil moisture suggests that moisture effects on diversity may also be linked to *F. campestris* vigor. In contrast, litter removal may reduce the vigor and associated ability of this species to suppress neighbors, as has been found to occur in other dominant species (Facelli and Facelli 1993), ultimately resulting in increased diversity under conditions of small amounts of litter (Haslam 1971).

3.6.3 Defoliation Effects on Community Composition

In general, the greatest impact of defoliation was observed on species composition up to one (summer defoliation, SD) or two (winter defoliation, WD) growing seasons after disturbance: by 2008, environmental conditions rather than defoliation appeared to affect species composition based on the MRPP. Nevertheless, defoliation in summer and winter resulted in divergence in the abundance of select species during both years, with summer defoliation effects more pronounced through 2008. Increases in species richness one growing season after defoliation are consistent with responses in other grasslands (Vujnovic et al. 2002), and indicate that defoliation promptly facilitated the entry of new species. The appearance of new species may be tied to increased PAR, bare soil, and suppression of dominant species common after a defoliation event in grasslands with high W and N availability (Olff and Ritchie 1998). Notably, observed richness responses disappeared, suggesting strong resilience in this community to one-time defoliation.

Species responses in SD plots relative to the others (particularly the undefoliated treatments (UD)) were more dependent on added water. Abundant W would likely compensate for increased evaporation experienced after SD when there is the greatest risk of a soil moisture deficit in the region. In contrast, vegetation development in the absence of defoliation may have progressed relatively rapidly during spring and early summer, with senescence at a time when temperatures were still optimal for growth of *F. campestris* (King et al. 1998). In essence, defoliation during the growing season may have altered community phenology in such a way that resident plants were differentially able to utilize resources (Kahlert et al. 2005) (i.e. water), with those possessing superior regrowth capabilities during high temperatures of summer most capable of responding positively to summer defoliation. In the case of *F. campestris*, this species is very early growing in spring (Mengli et al. 2005) and typically responds with poor regrowth (Chapter 5,6) (King et al. 1998).

Application of N also differentially impacted community composition, and further separated SD and WD treatments. Similar to with added W, available soil N is most likely to be utilized by vegetation that remains in an active stage of growth (Kahlert et al. 2005), and may again account for why SD exhibited maximum differentiation from the other defoliation treatments. Moreover, as WD occurred well into dormancy, the removal of insulating litter biomass at that time may have enabled earlier growth and greater production the following year (Willms et al. 1986), thereby allowing compensation for biomass removed. Litter and standing biomass removal is known to increase spring soil temperature and associated rates of growth (Willms et al.1986; Facelli and Pickett 1991). In general, the effects of W and N addition on this plant community appear tied to defoliation in mid growing season and its impact on sustaining plant growth.

Both SD and WD treatments showed increases in evenness relative to the undefoliated plots. This finding has been observed by others (Bai et al., 2001) and suggests that removal of standing biomass may create conditions that promote a more uniform mix of species. In the absence of disturbance late seral grasslands are often lower in species richness and evenness due to dominance of a small group of species that suppress neighboring vegetation (Whittaker 1972). Undefoliated and WD treatments were associated with *F. campestris*, the historical dominant species in this community (Hodgkinson and Young 1973), specifically under low disturbance (McLean and Wikeem 1985), and is consistent with the notion that this grassland is representative of a late seral grassland. In this study, defoliation may have suppressed *F. campestris* and in the process released early and mid seral plant species (Willms et al. 1985) thereby accounting for the increased evenness. While evenness remained elevated in 2008, much of the initial effects of WD appeared to have disappeared by the final year of the study, supporting the notion that fescue grasslands are resilient to WD (Johnston and MacDonald 1967; Willms et al. 1985;). Overall, community resilience appeared to be related to the vigor of *F. campestris*, which in turn, has been positively associated with WD in past studies (Johnston and MacDonald 1967; Willms et al. 1985) and has been found to be a favorable indicator of recovery within fescue grasslands (Lamagna 2006).

Increased diversity in the SD treatment appeared to be tied to a number of disturbance tolerant species (*E. trachycaulus, A. bowdenii, C. pensylvanica, G. viscosissimum and E. lanceolatus*), and one climax species (*S. curtiseta*). Most of these species are known as grazing resistant species and may respond favorably to one-time defoliation, or even have niches dependant on defoliation. Increases in the subdominant species may also have coincided with competitive release associated with reductions in *F. campestris* under SD, as discussed earlier (Johnston et al. 1971; Willms et al. 1985). Notably, the effects of SD were longer lasting than WD, consistent with other work on the detrimental effects of defoliation at this time of year in fescue grassland communities, particularly at high stocking rates (Johnston et al. 1971; Willms et al. 1985).

3.6.4 Interactions between Species

Of special note was the markedly divergent response of *F. campestris* from the introduced grasses, *P. pratensis and B. inermis*. This observation suggests the introduced species were favored by conditions unlike those preferred by *F. campestris* or that there was a suppressive effect between these species. One reason to suspect a suppressive effect is that *P. pratensis* has been well established to benefit from increases in soil moisture and N but the opposite was seen in a parallel study (Chapter 4), with a further negative association of *P. pratensis* with *F. campestris* vigor after 3 years of growth (Chapter 4). This suggests that *F. campestris* dominance may be controlling invasibility and is supported by the abnormal reductions in the vigor of *P. pratensis* and concurrent increases in the vigor of *F. campestris* under W addition as seen in the NMS. Therefore, it appears that *F campestris* was more readily able to exploit excess W than *P. pratensis* in the absence of disturbance. While litter removal also appeared to reduce *F. campestris* vigor slightly there was a much more pronounced increase in *P. pratensis* vigor with litter removal, but only in the absence of W addition (Chapter 4). This addition of W may have compensated for loss of SM due to litter removal (Weaver and Rowland 1952; Fowler 1986; Facelli and

Pickett 1991) allowing *F. campestris* to effectively compete for increases in PAR. These responses suggest that *P. pratensis* is likely a passenger, while *F. campestris* vigor determines invasion potential (MacDougall and Turkington 2005) within this grassland.

The complexity of species composition did not limit interactions to only these two species as N addition, which benefited neither species, appeared to increase the vigor of forbs and *Symphoricarpos occidentalis*, a native shrub (Moss and Packer 1983) suggesting that other species in the community have a role in suppressing invaders. This makes sense because graminoids are more efficient in N uptake than forbs (Bowman et al. 1994) and therefore would be less likely to benefit from surplus N.

Defoliation also had a significant affect on the relationship between *F. campestris* and *P. pratensis*. Defoliation, particularly during summer, tended to weaken the apparent negative effects of *F. campestris* on *P. pratensis* (Chapter 4). This is supported in previous studies of *F. campestris* wherein this species was poorly suited to summer grazing (McLean and Wikeem 1985; Willms et al. 1998; Mengli et al. 2005) but better adapted to winter grazing (McLean and Wikeem 1985). As such, although not appearing as an indicator, *P. pratensis* was favored by summer defoliation, especially during N addition when *F. campestris* cover was reduced (Chapter 4). This would account for observations elsewhere that this species increases under summer grazing (Kruess and Tscharntke 2002). *P. pratensis* is well adapted to tolerate defoliation during the growing season because of its low growth form (Jameson 1963) and reproduction from rhizomes (Moser et al. 1968).

3.7 Conclusion

All environmental factors examined (PAR, soil moisture, soil N) affected species composition in this grassland ecosystem. Though litter removal and W addition effects dissipated quickly, they were replaced by effects of soil N, which took longer to appear. Similarly, defoliation was a significant determinant of community composition, with SD associated with stronger and longer-term responses than WD. Overall there was a strong association of environmental resources with *F. campestris* within the community, which in turn, appeared to be an important determinant of plant composition in this grassland, including other key species such as *P. pratensis* and *B. inermis*. Invasion and diversity within this grassland appeared linked to the vigor of the dominant species *F. campestris*, and its associated suppression of neighboring species. Abundance of invasive species within these grasslands can best be limited by enhancing the abundance of *F. campestris*, and includes maintaining litter, avoiding growing season grazing, and minimizing soil N through fertilization or nutrient redistribution within these grasslands.

3.8 References

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Table 3.1 Summary of treatments used to examine the impact of environmental conditions and disturbance on fescue grassland composition.

Category	Treatment	Description
Water	1	*In-situ* Check
	2	No litter (litter removal in mid Nov of 2005)
	3	*In-situ* + Water (W) (monthly to field capacity)
	4	No litter + Water
Nitrogen	5	1 + Nitrogen (N) (100kg/ha 2006+50kg/ha 2007/2008)
	6	2 + N
	7	3 + N
	8	4 + N
Defoliation	9	1 + Summer Defoliation, July of 2006 (SD)
	10	3 + SD
	11	5 + SD
	12	7 + SD
	13	1 + Winter Defoliation, November of 2005 (WD)
	14	3 + WD
	15	5 + WD
	16	7 + WD

Table 3.2 Stepwise regression analysis assessing the relationship between monthly soil moisture (SM), monthly photosynthetically active radiation (PAR), and annual soil N, with various community responses, including diversity, richness and evenness, litter and herbaceous biomass (2008 only), during each of 2006 and 2008. Analysis used only non-defoliated plots. All results are shown at P<0.1 and are considered significant at P<0.05.

Year	Community Response	Independent Variable	Partial R^2	Model R^2	B[a]	Prob>|F|[b]
2006	Diversity	PAR, June	0.10	0.1	0.32	**0.01**
	Evenness	SM, May	0.05	0.05	-0.26	0.06
	Richness	PAR, June	0.13	0.14	0.37	**<0.01**
2008	Diversity	PAR, May	0.09	0.09	0.32	**0.02**
		SM, June	0.07	0.16	-0.27	**0.03**
	Evenness	PAR, May	0.14	0.14	0.41	**<0.01**
		SM, June	0.1	0.24	-0.31	**<0.01**
	Richness	None				>0.10
	Litter Biomass	Available N	0.05	0.05	-0.22	**0.09**
	Forb Biomass	SM, June	0.05	0.05	-0.23	0.07
	P. pratensis Biomass	SM, May	0.07	0.07	-0.27	**0.03**
	F. campestris Biomass	Available N	0.09	0.09	-0.24	**0.01**
		SM, May	0.07	0.17	0.31	**0.03**
		PAR, May	0.05	0.22	-0.22	**0.05**
	Other Grass Biomass	None				>0.10
	Shrub Biomass	Available N	0.06	0.06	0.24	0.06
	Total Biomass	None				>0.10

Table 3.3 Summary of significance (P) values from the Multi-Response Permutation Procedure (MRPP) analysis of plant community data associated with various treatments, including litter removal, defoliation, and water and nitrogen addition. Results are provided separately for litter modification and defoliation, alone and in combination with nitrogen and water addition.

	2006	**2007**	**2008**
Litter	0.84	0.84	0.72
Nitrogen	0.61	0.61	**0.06**
Litter*Nitrogen	0.67	0.30	0.38
Water	**<0.001**	**0.10**	0.17
Water*Litter	**0.01**	0.28	0.48
Water*Nitrogen	**<0.01**	0.43	0.14
Defoliation[1]		**<0.0001**	0.23
Nitrogen		0.25	**0.02**
Nitrogen*Defoliation		**<0.001**	0.16
Water		0.18	0.31
Water*Defoliation		**<0.01**	0.48
Water*Nitrogen		0.12	**0.02**

[1] 2006 defoliation data were not analyzed as defoliation treatments occurred in that year and therefore confounded vegetation measures. Responses to environment (N, W, and N x W) in that year also showed the same trends as in the environmental study, and were therefore not included. Measures from 2007 represented the first year responses to defoliation.

Table 3.4 Summary test results arising from the Multi-Response Permutation Procedure (MRPP) evaluating the effect of water addition, nitrogen addition, the interaction of water (+W) and nitrogen (+N) addition, and the interaction of water and litter presence (+L), on plant species composition during each of 2006, 2007 and 2008 (last year of sampling). Ambient field conditions are represented by +L, -W and -N.

					2006			**2007**			**2008**		
Treatment		**Groups Compared**			**T**	**A**	**P Value**	**T**	**A**	**P Value**	**T**	**A**	**P Value**
Water		-W	vs.	+W	**-6.6**	**0.03**	**<0.001**	**-1.3**	**0**	**0.1**	-0.9	0	0.2
Nitrogen		-N	vs.	+N	0.5	0	0.60	0.4	0	0.6	**-1.7**	**0.01**	**0.07**
Nitrogen vs Water	+W	-N	vs.	+N	-0.1	0	0.4	0.1	0	0.4	-0.3	0	0.3
	-W	-N	vs.	+N	0.3	0	0.5	1.1	0	0.9	-0.6	0	0.2
	+N	-W	vs.	+W	**-5.6**	**0.05**	**<0.001**	-0.1	0	0.4	-1.0	0	0.2
	-N	-W	vs.	+W	-0.8	0	0.2	-0.4	0	0.3	0.7	0	0.7
Litter vs Water	+L	-W	vs.	+W	**-5.0**	**0.05**	**0.001**	-0.4	0	0.3	-0.3	0	0.3
	-L	-W	vs.	+W	-1.3	0	0.1	-1.4	0	0.09	-0.3	0	0.3
	-W	+L	vs.	-L	0.3	0	0.5	0.3	0	0.5	1.0	0	0.9
	+W	+L	vs.	-L	0.1	0	0.5	0.2	0	0.5	-0.1	0	0.4

[1] +W = water addition, -W = ambient water, +N = nitrogen addition, -N = ambient nitrogen, -L = litter removal, and +L = ambient litter.

Table 3.5 Summary correlations (minimum r=|0.12|, |0.22|, |0.38|) between treatments, environmental factors, and key species, with each of the 3 axes arising from the NMS ordination of 2006 vegetation responses and environmental treatments. Species shown include provincially important species and those with a P value <0.1 based on the indicator species analysis.

		2006 Ordination Axes (% Variance Represented)		
		1 (24.5%)	2 (31.3%)	3 (35.4%)
Factor & Description		r	r	r
Treatment Vectors[1]				
Light		-0.05	0.06	-0.01
Nitrogen		**0.27**	-0.11	0.02
Water		**-0.15**	**-0.33**	**-0.25**
Environmental Factors[2]				
Mmay	May soil moisture	0.18	**-0.45**	0.1
Ljun	June light	0.2	0.1	**0.29**
Laug	August light	0.0	**-0.2**	0.1
Litter	Litter cover	0.0	**-0.50**	**-0.25**
Plant Community Measures[2]				
Ri	Species richness	**0.25**	0.2	**0.58**
Ev	Evenness	**0.53**	**0.56**	**0.51**
Sh	Shannon's diversity index	**0.50**	**0.49**	**0.64**
Key Species[3]				
Agrodas	*Elymus lanceolatus*	**0.42**	-0.1	0.2
Careobt	*Carex obtustata*	0.3	-0.1	**0.62**
Festcam	*Festuca campestris*	**-0.39**	**-0.74**	**-0.62**
Geumtri	*Geum triflorum*	**0.67**	-0.1	0
Poaprat	*Poa pratensis*	-0.2	**0.85**	0
Moss	Moss cover	0.0	**0.42**	0.1

[1] Treatment vectors show trends in overlays of the ordinations at a cutoff r value of |0.12|
[2] Key variables show trends in overlays of the ordinations at a cutoff r value of |0.22|
[3] Key species show trends in overlays of the ordinations at a cutoff r value of |0.38|

Table 3.6 Summary correlations (minimum r=|0.12|, |0.22|, |0.38|) treatments, environmental factors, and key species, with each of the 3 axes arising from the NMS ordination of 2008 vegetation responses and environmental treatments. Species shown include provincially important species and those with a P value <0.1 based on the indicator species analysis.

		2008 Ordination Axes (% Variance Represented)		
		1 (28.1%)	2 (22.9%)	3 (38%)
Factor & Description		r	r	r
Treatment Vectors[1]				
Light		0.09	0.02	-0.02
Nitrogen		-0.11	**-0.32**	-0.08
Water		0.09	**0.15**	**-0.14**
Environmental Factors[2]				
Lmay	May light	0.0	**-0.28**	0.0
Mmay	May soil moisture	-0.1	0.1	**-0.3**
N	Available N	-0.1	**-0.26**	0.0
Litter	Litter cover	0.2	**0.34**	0.0
LB	Litter biomass	0.0	**0.39**	-0.1
Diversity Measures[2]				
Ri	Species richness	0.1	**-0.39**	-0.1
Ev	Evenness	**0.27**	**-0.60**	0.1
Sh	Shannon's diversity index	**0.24**	**-0.62**	0.1
Plant Community Measures[2]				
SB	Shrub biomass	-0.1	**-0.67**	0.1
FB	Forb biomass	**0.27**	**-0.42**	-0.1
GB	Other grass biomass	**-0.57**	-0.2	-0.2
PPB	*Poa pratensis* biomass	0.1	0.2	**0.79**
FCB	*Festuca campestris* biomass	**0.29**	**0.64**	**-0.39**
Key Species[3]				
Bromine	*Bromus inermis*	**-0.76**	-0.1	0.0
Festcam	*Festuca campestris*	0.3	**0.74**	**-0.61**
Poaprat	*Poa pratensis*	0.0	0.1	**0.91**
Sympocc	*Symphoricarpos occidentalis*	-0.3	**-0.73**	0.1
Moss	Moss cover	-0.2	**-0.32**	0.1

[1] Treatment vectors show trends in overlays of the ordinations at a cutoff r value of |0.12|

[2] Key variables show trends in overlays of the ordinations at a cutoff r value of |0.22|

[3] Key species show trends in overlays of the ordinations at a cutoff r value of |0.38|

Table 3.7 Summary test results arising from the Multi-Response Permutation Procedure (MRPP) evaluating the effect of various environmental treatments and their interactions, on plant community composition in each of 2007 and 2008. Effects are considered significant at $p<0.05$.

					2007			2008		
Treatment		Groups Compared			T	A	p	T	A	p
Nitrogen		-N [1]	vs.	+N	0.36	0.00	0.42	**-2.73**	**0.01**	**0.02**
Nitrogen vs Water	+W	-W-N	vs.	+W-N	-0.6	0.0	0.2	-0.6	0.0	0.2
	-W	-W-N	vs.	-W+N	-0.7	0.0	0.2	**-3.18**	**0.02**	**<0.01**
	+N	-W-N	vs.	+W+N	-1.4	0.0	0.09	-1.2	0.0	0.1
	-N	+W-N	vs.	-W+N	0.0	0.0	0.4	-1.8	0.0	0.1
Defoliation		UD	vs.	SD	**-6.2**	**0.0**	**0.0001**	-2.0	0.0	0.05
		UD	vs.	WD	0.6	0.0	0.7	0.6	0.0	0.7
		SD	vs.	WD	**-6.6**	**0.0**	**<0.0001**	0.1	0.0	0.5
Nitrogen vs Defoliation	+N	UD	vs.	SD	**-1.9**	**0.0**	**0.04**	-0.5	0.0	0.3
		UD	vs.	WD	**-1.9**	**0.0**	**0.05**	0.4	0.0	0.6
		SD	vs.	WD	**-5.0**	**0.0**	**<0.001**	0.2	0.0	0.5
	-N	UD	vs.	SD	**-5.5**	**0.0**	**<0.001**	-0.6	0.0	0.2
		UD	vs.	WD	0.8	0.0	0.8	0.8	0.0	0.8
		SD	vs.	WD	-1.7	0.0	0.1	0.4	0.0	0.6
	UD	-N	vs.	+N	**-2.3**	**0.0**	**0.03**	-1.2	0.0	0.1
	SD	-N	vs.	+N	1.0	0.0	0.8	-0.2	0.0	0.4
	WD	-N	vs.	+N	-0.6	0.0	0.2	0.0	0.0	0.4
Water vs Defoliation	+W	UD	vs.	SD	**-4.3**	**0.0**	**<0.01**	-0.9	0.0	0.2
		UD	vs.	WD	0.0	0.0	0.4	0.0	0.0	0.4
		SD	vs.	WD	**-3.4**	**0.0**	**<0.01**	0.7	0.0	0.7
	-W	UD	vs.	SD	-1.0	0.0	0.1	-0.4	0.0	0.3
		UD	vs.	WD	0.6	0.0	0.7	0.8	0.0	0.8
		SD	vs.	WD	**-2.9**	**0.0**	**0.01**	0.3	0.0	0.6
	UD	-W	vs.	+W	-0.4	0.0	0.3	-0.3	0.0	0.3
	SD	-W	vs.	+W	0.2	0.0	0.5	0.3	0.0	0.5
	WD	-W	vs.	+W	0.3	0.0	0.6	1.0	0.0	0.9

[1] +W = water addition, -W = ambient water, +N = nitrogen addition, -N = ambient nitrogen, UD = undefoliated plots, WD = dormant season defoliation, and SD = summer defoliation.

Table 3.8 Summary correlations (minimum r=|0.12|, |0.22|, |0.38|) between treatments, environmental factors, and key species, with each of the 3 axes arising from the NMS ordination of 2007 vegetation responses and defoliation treatments. Species shown include provincially important species and those with a P value <0.1 based on the indicator species analysis.

		2007 Ordination Axes (% Variance Represented)		
		1 (28.1%)	2 (22.9%)	3 (38%)
Factor & Description		r	r	r
Treatment Vectors[1]				
UD	Undefoliated	-0.04	-0.10	**0.24**
SD	Summer defoliated	**0.17**	**0.34**	**-0.19**
WD	Winter defoliated	-0.13	**-0.24**	-0.05
N	Nitrogen	-0.01	**0.16**	0.12
W	Water	-0.03	-0.08	-0.03
Environmental Factors[2]				
Mmay	May soil moisture	**-0.30**	0.2	-0.2
MJun	June soil moisture	-0.1	0.1	0.0
MJul	July soil moisture	**-0.32**	0.0	-0.2
MAug	August soil moisture	**-0.30**	0.0	-0.1
LMay	May light	0.1	**0.27**	-0.1
LJun	June light	0.0	**0.30**	-0.2
LJul	July light	0.1	**0.30**	-0.2
N	Available soil N	0.1	0.2	**0.23**
Litter	Litter cover	0.0	**-0.36**	0.2
Soil	Bare soil	-0.1	**0.40**	**-0.31**
Plant Community Measures[2]				
Ri	Species richness	0.0	**0.49**	-0.1
Ev	Evenness	0.2	**0.56**	**0.29**
Sh	Shannon's diversity index	0.1	**0.65**	0.2
Key Species[3]				
Carepen	*Carex pensylvanica*	-0.4	**0.76**	-0.3
Festcam	*Festuca campestris*	**-0.50**	**-0.65**	**-0.44**
Poaprat	*Poa pratensis*	**0.85**	-0.1	0.1
Sympocc	*Symphoricarpos occidentalis*	0.1	-0.3	**0.73**

[1] Treatment vectors show trends in overlays of the ordinations at a cutoff r value of |0.12|

[2] Key variables show trends in overlays of the ordinations at a cutoff r value of |0.22|

[3] Key species show trends in overlays of the ordinations at a cutoff r value of |0.38|

Table 3.9 Summary correlations (minimum r=|0.12|, |0.22|, |0.38|) between treatments, environmental factors, and key species, with each of the 3 axes arising from the NMS ordination of 2008 vegetation responses and defoliation treatments. Species shown include provincially important species and those with a P value <0.1 based on the indicator species analysis.

		2008 Ordination Axes (% Variance Represented)		
		1 (14.7%)	2 (24%)	3 (49.5%)
Factor & Description		r	r	r
Treatment Vectors[1]				
UD	Undefoliated	**0.12**	-0.07	-0.05
SD	Summer defoliated	-0.11	0.10	-0.01
WD	Winter defoliated	-0.02	-0.03	0.05
N	Nitrogen	**-0.33**	0.06	-0.07
W	Water	-0.06	**-0.29**	0.04
Environmental Factors[2]				
MJun	June soil moisture	0.0	0.1	**0.3**
N	Available N	**-0.3**	0.0	-0.1
Plant Community Measures[2]				
Moss	Moss cover	**-0.2**	-0.2	-0.1
Ri	Species richness	**-0.3**	0.2	0.2
Ev	Evenness	**-0.4**	**0.2**	0.1
Sh	Shannon's diversity index	**-0.5**	**0.3**	0.2
LB	Litter biomass	**0.2**	-0.1	0.0
SB	Shrub biomass	**-0.5**	**-0.4**	**-0.3**
FB	Forb biomass	**-0.4**	0.1	**0.2**
GB	Other grass biomass	**-0.2**	**0.6**	**0.3**
PPB	*Poa pratensis* biomass	0.1	0.0	**-0.7**
FCB	*Festuca campestris* biomass	**0.5**	**-0.3**	**0.3**
Key Species[3]				
Artelud	*Artemisia ludoviciana*	-0.2	**0.4**	0.1
Bromine	*Bromus inermis*	0.0	**0.6**	0.0
Carepen	*Carex pensylvanica*	**-0.6**	**0.4**	0.4
Festcam	*Festuca campestris*	**0.6**	**-0.5**	**0.6**
Poaprat	*Poa pratensis*	0.1	0.0	**-0.9**
Solimis	*Solidago missouriensis*	**-0.3**	0.0	0.1
Sympocc	*Symphoricarpos occidentalis*	**-0.6**	**-0.5**	**-0.4**
Taraoff	*Taraxacum officinale*	-0.2	0.1	**0.3**

[1] Treatment vectors show trends in overlays of the ordinations at a cutoff r value of |0.12|
[2] Key variables show trends in overlays of the ordinations at a cutoff r value of |0.22|
[3] Key species show trends in overlays of the ordinations at a cutoff r value of |0.38|

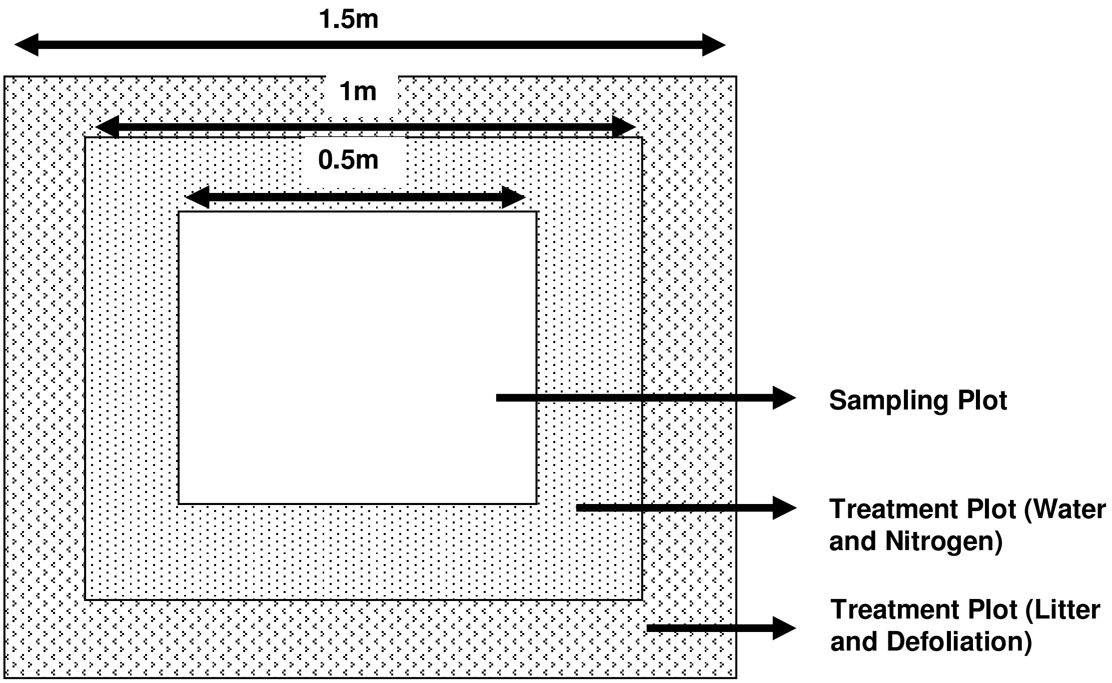

Figure 3.1 Experimental design of plots, including areas treated with for defoliation and litter modification (1.5 x 1.5 m), water and nitrogen addition (1 x 1 m), and the permanent sampling areas (0.5 x 0.5 m).

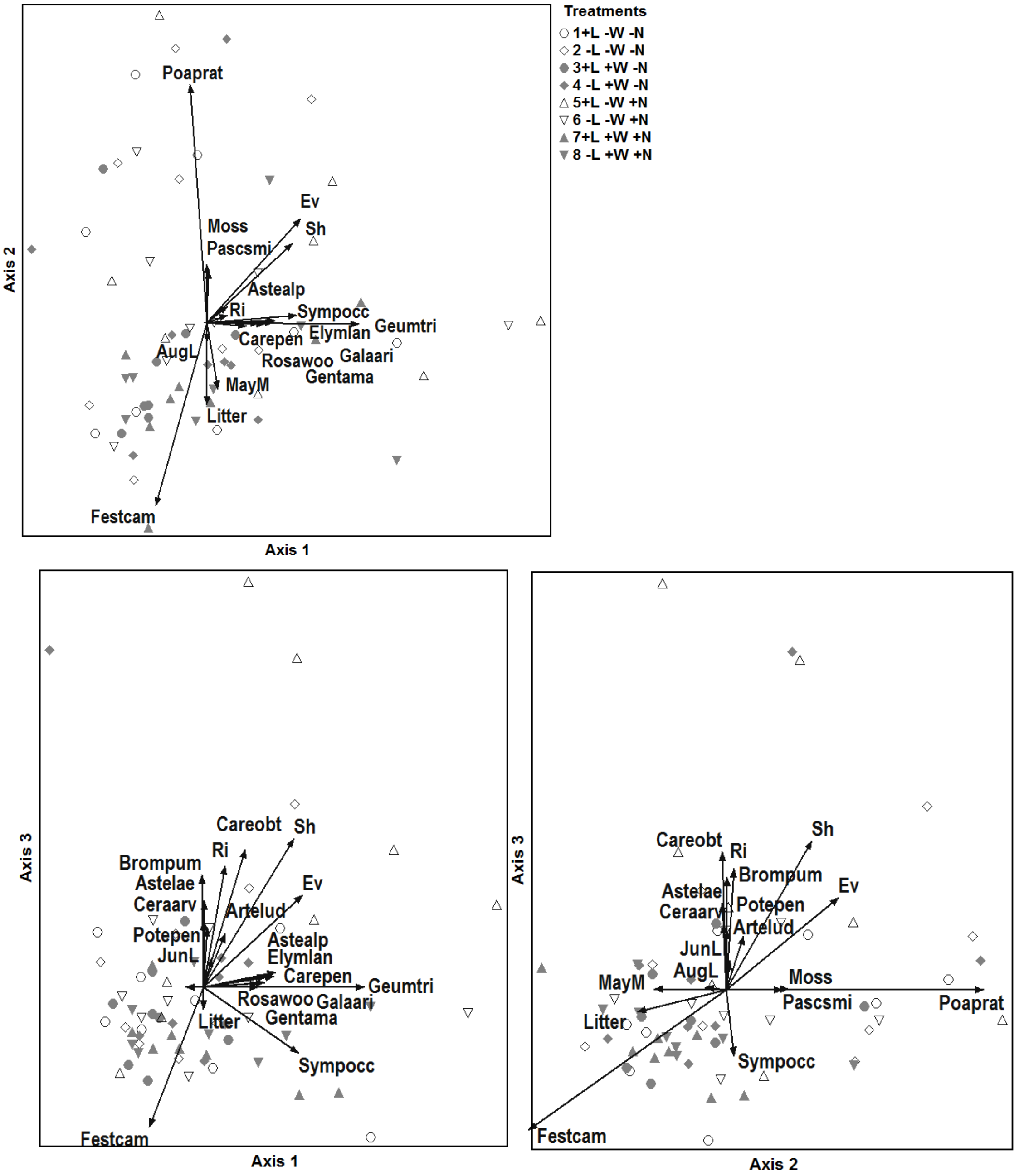

Figure 3.2 Non-metric multi-dimensional scaling ordination of the environmental analysis with overlays of environmental variables (Moss=Moss cover, Litter=Litter cover, Ri=Species richness, Ev=Evenness, Sh=Shannon's diversity index, JunL=June %PAR, MayL= May %PAR, AugL=August %PAR, JunM=June soil moisture and MayM=May soil moisture) and plant cover, (Astealp=*Aster alpinus*, Elymlan=*E. lancolatus*, Pascsmi=*Pascopyrum smithii*, Astelae=*Aster laevis*, Brompum=*Bromus pumpellianus*, Careobt=*Carex obtusata*, Carepen=*Carex pensylvanica*, Ceraara=*Cerastum arvense*, Festcam=*F. campestris*, Galaari=*Galardia aristata*, Gentama=*Gentiana amarella*, Geumtri= *Geum triflorum*, Potepen *Potentilla pensylvanica* and Sympocc=*Symphoricarpos occidentalis*) during 2006. Key species show trends in overlays of the ordinations at a cut off r^2 value of 0.15.Key Environmental factors show trends in overlays of the ordinations at a cut off r^2 value of 0.05. +W = water addition, -W = ambient water, +N = nitrogen addition, -N = ambient nitrogen, -L = litter removal, and +L = ambient litter.

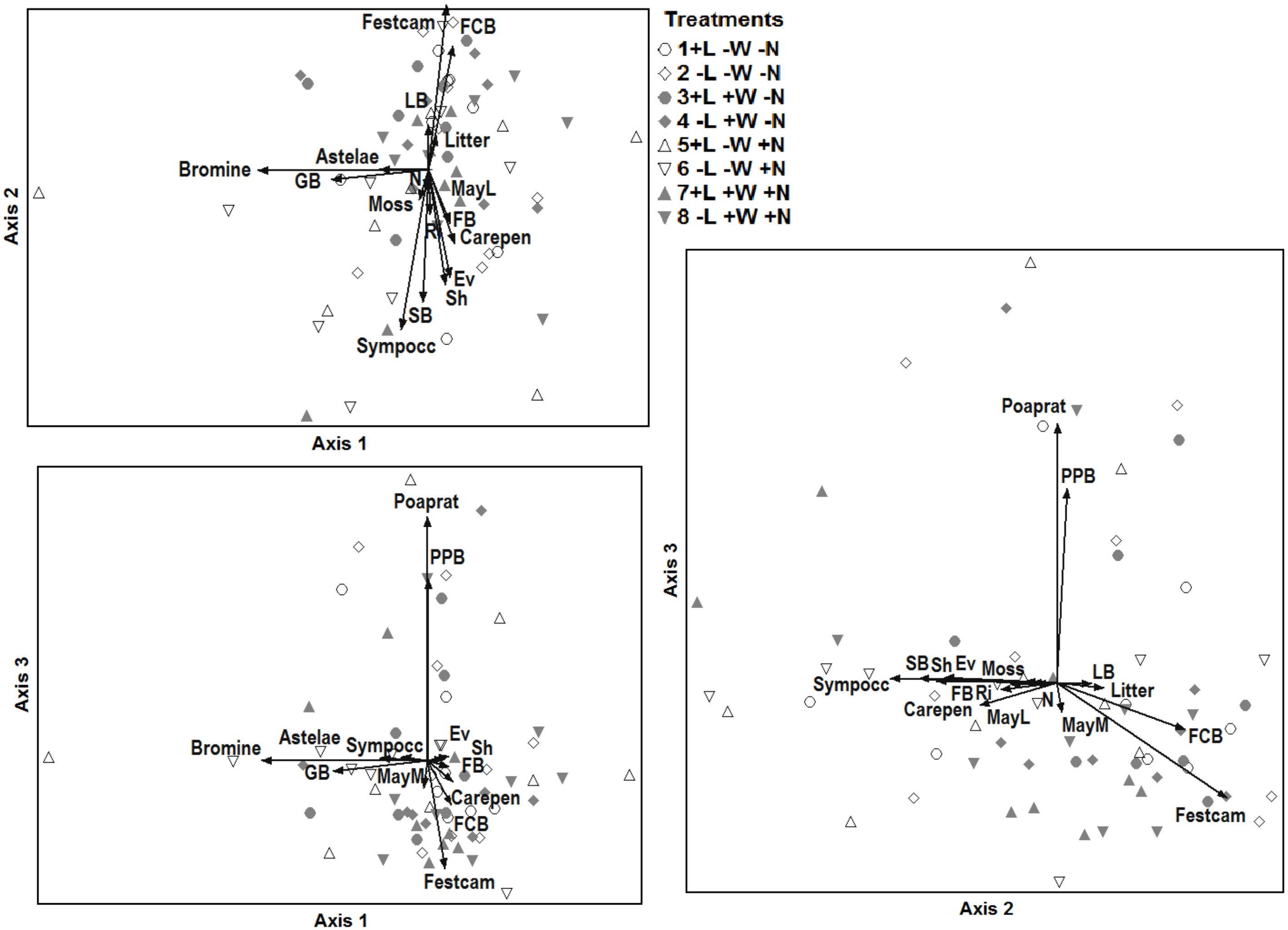

Figure 3.3 Non-metric multi-dimensional scaling ordination of the environmental analysis with an overlay of the environmental variables (Moss=Moss cover, Litter=Litter cover, Richness=Species richness Ev=Evenness Sh=Shannon's diversity index, Ri=Species Richness, MayL= May %PAR, JunM=June soil moisture, AugM=August soil moisture, FCB=*F. campestris* biomass, GB=other grass biomass, PPB=*P. pratensis* biomass, SB=Shrub biomass and LB=Litter biomass) and plant cover variables (Astelae=*Aster laevis*, Bromine=*Bromus inermis*, Careobt=*Carex pensylvanica*, Festcam=*F. campestris*, Sympocc=*Symphoricarpos occidentalis*, and Poaprat=*P. pratensis*) in 2008. Key species show trends in overlays of the ordinations at a cut off r^2 value of 0.15. Key Environmental factors show trends in overlays of the ordinations at a cut off r^2 value of 0.035. +W = water addition, -W = ambient water, +N = nitrogen addition, -N = ambient nitrogen, -L = litter removal, and +L = ambient litter.

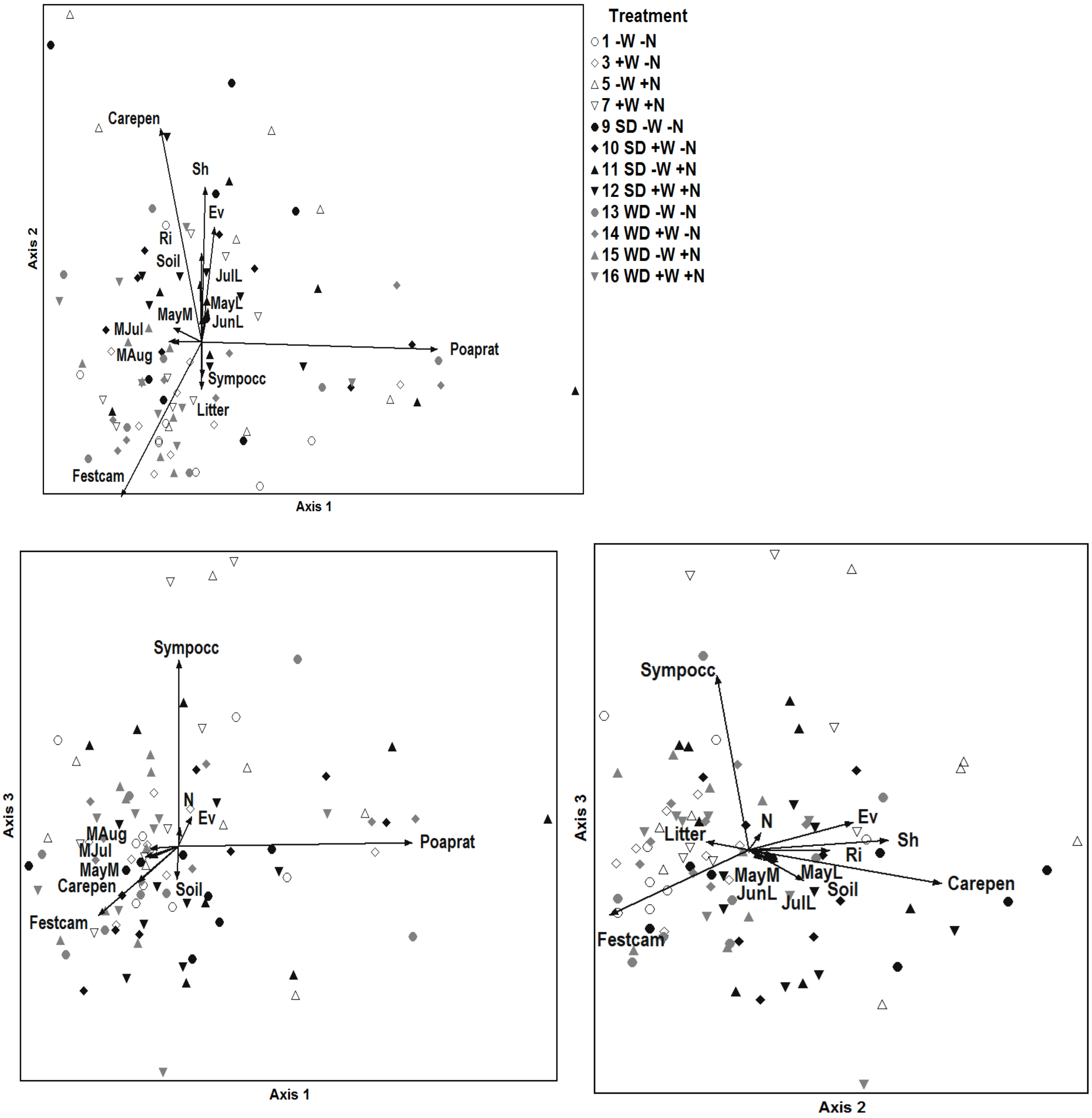

Figure 3.4 Non-metric multi-dimensional scaling ordination of the defoliation analysis with an overlay of environmental variables (N=Plant available N, MayM=May soil moisture, AugM=August soil moisture, JulM=July soil moisture, Ri=species richness, Ev=Evenness, Sh=Shannon's diversity index, Litter=litter cover and Soil=bare soil) and plant cover values (Carepen=*Carex pensylvanica*, Festcam=*F. campestris*, Sympocc=*Symphoricarpos occidentalis*, and Poaprat=*P. pratensis*) in 2007..Key species show trends in overlays of the ordinations at a cut off r^2 value of 0.15. Key Environmental factors show trends in overlays of the ordinations at a cut off r^2 value of 0.05. +W = water addition, -W = ambient water, +N = nitrogen addition, -N = ambient nitrogen, UD = undefoliated plots, WD = dormant season defoliation, and SD = summer defoliation.

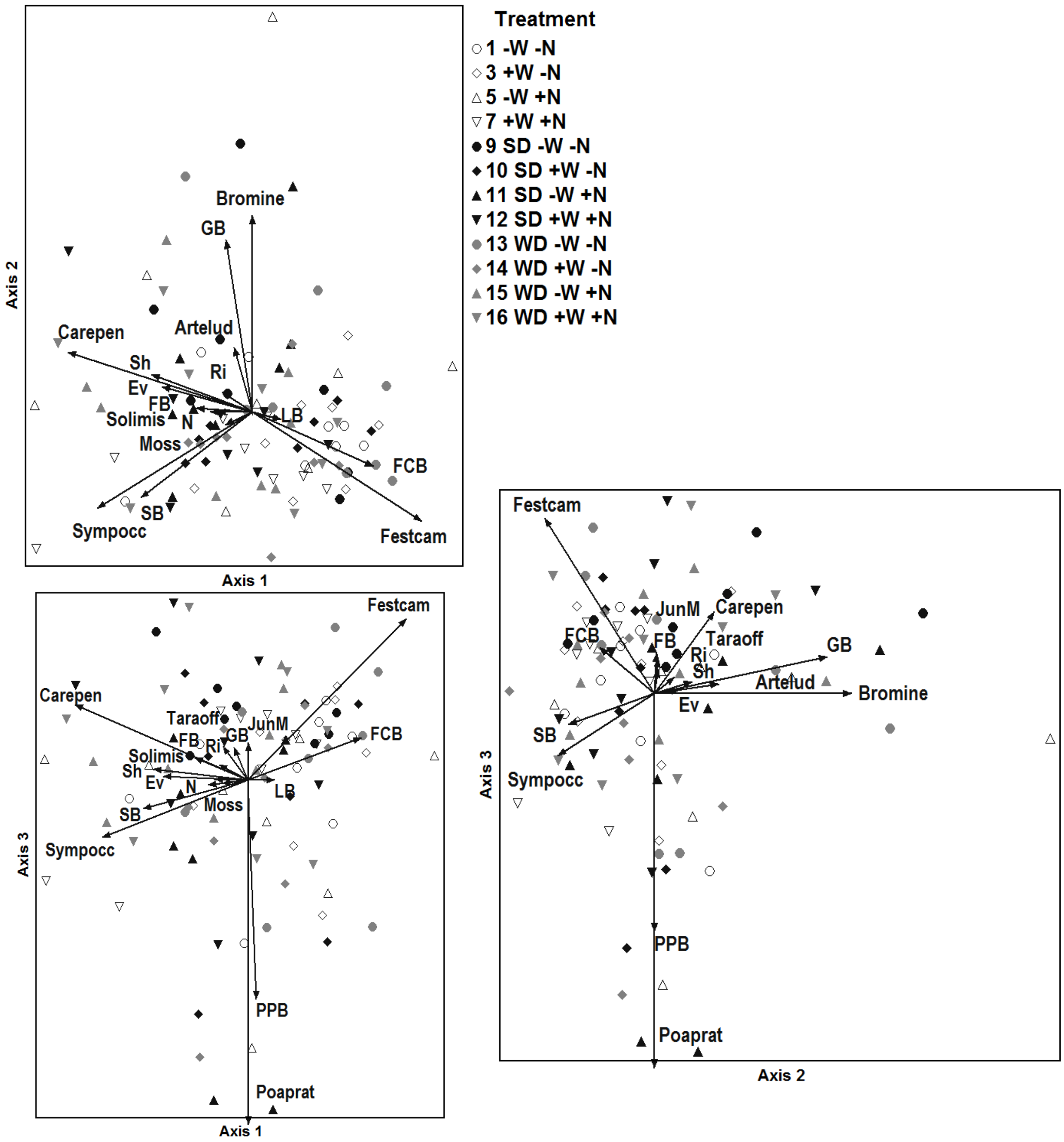

Figure 3.5 Non-metric multi-dimensional scaling ordination of the defoliation analysis with an overlay of environmental variables (Moss=Moss cover, Litter=Litter cover, Ri=Species richness Ev=Evenness Sh=Shannon's diversity index, JunM=June soil moisture, FCB=*F. campestris* biomass, GB=other grass biomass, PPB=*P. pratensis* biomass, SB=Shrub biomass, FB=Forb biomass, and N=plant available N) and plant cover (Bromine=*Bromus inermis*, Carepen=*Carex pensylvanica*, Festcam=*F. campestris*, Sympocc=*Symphoricarpos occidentalis*, Solimis=*Solidago missouriensis*, Tara off=*T. officinale* and Poaprat=*P. Pratensis*) in 2008. Key species show trends in overlays of the ordinations at a cut off r^2 value of 0.15. Key Environmental factors show trends in overlays of the ordinations at a cut off r^2 value of 0.05. +W = water addition, -W = ambient water, +N = nitrogen addition, -N = ambient nitrogen, UD = undefoliated plots, WD = dormant season defoliation, and SD = summer defoliation.

Chapter 4 EFFECT OF ENVIRONMENT AND DEFOLIATION ON *FESTUCA CAMPESTRIS* (RYBD.) AND *POA PRATENSIS* (L.) VIGOR

4.1 Introduction

Invasive plants have become a world wide problem in bunchgrass communities (Mack 1986; Tyser 1992). Past invasions have led to the loss of endemic plant communities and their replacement with those dominated by invasive species (Mack 1989). Potential mechanisms responsible for these invasions include direct physical disturbance of the soil and overlying vegetation through mechanical means, or perturbation of the plant community under grazing (Mack 1981; Tyser 1992; D'Antonio 1993). Invasions may also be influenced by environmental factors, including changes in available nitrogen (Stohlgren et al. 1999), water (Larson et al. 2001; Maron and Marler 2007) or light, which can be key determinants in the success of invasion (Tyser 1992). Moreover, these environmental mechanisms may act alone, interact with one another, or combine with physical disturbances to facilitate invasion (Fridley et al. 2007).

Understanding the impacts of disturbance and environment on plant invasion requires examining the processes of invasion within the context of naturally occurring plant communities. The use of microcosms can aid in showing the relationship between two species, but may not accurately represent the response of diverse plant communities where interspecific relations among species are complex (Drake et al. 1996). While logistically difficult to undertake, field studies provide the most realistic method to determine how a plant community may react to an invasive species under varying disturbance and environmental regimes (Peters 1991). This is particularly important given that increasing community diversity can have a negative impact on invasion (Davies et al. 2007; Maron and Marler 2007). Field studies to support this theory have been mixed, however, as other studies have indicated there is no relationship between diversity and the risk of invasion (Elton 1958; Levine and D'Antonio 1999), while yet others have concluded that greater diversity may increase invasion (Robinson et al. 1995; Palmer and Maurer 1997).

Disturbance plays important roles in manipulating plant community structure by changing competitive relationships among neighboring species (Hobbs and Huenneke 1992). Native species, especially those tolerant of environmental stress (i.e.*, Festuca campestris* Rybd.), may not be adapted to the intensity or type of disturbance to which invaders are adapted (Baker 1974; Mack et al. 2000). In such a case, disturbance may drive invasion by creating empty niches for an invader (Didham et al. 2005), where the latter represents an opportunistic ‘passenger’ in the invasion process following disturbance (MacDougall and Turkington 2005). Alternatively, it is possible for an invader to drive change by controlling the environment (e.g. altering nutrient cycling) during invasion, and in the process favor its own growth (Bowman et al. 2004).

In SW Alberta, native grasslands of the Foothills Fescue and adjacent Montane Natural Sub-regions have been historically dominated by foothills rough fescue (*Festuca campestris*) (Hodgkinson and Young 1973; Hill et al. 1997). *F. campestris* is recognized for its deep-rooted, caespitose growth habit (Willms and

Fraser 1992), which increases its drought tolerance, but also renders the species grazing susceptible (Johnston et al. 1971; Willms et al. 1985). Although soils underlying *F. campestris* often have low available nutrients similar to other climax grasslands (Chapin III et al. 1993), this species remains competitive under environmental extremes, including summer drought (Looman 1983).

In contrast to *F. campestris*, Kentucky bluegrass (*Poa pratensis* L.) is an introduced species that has been highly utilized in agronomic (Tyser 1992) and urban landscapes of North America. However, this species can be invasive within adjacent native ecosystems because of its fast growth rates, high productivity and prolific reproduction, both from seed and rhizomes (Lemeziene et al. 2004). *P. pratensis,* a sod forming species, with a relatively shallow root system, is therefore not drought tolerant (Moser et al. 1968). Water uptake in this species depends on nitrogen (N) use, with increased N potentially increasing the susceptibility of *P. pratensis* to drought (Ebdon et al. 1999). Previous studies have demonstrated marked invasion of Foothils Fescue Grasslands by *P. pratensis*, a process attributed at least in part to the influence of heavy grazing (Looman 1969), particularly during the summer growing season (Willms and Fraser 1992).

The most likely mechanisms that assist invasion by *P. pratensis* include defoliation (Johnston et al. 1971) together with increases in nitrogen (Wedin and Tilman 1990; Liancourt et al. 2005) and soil moisture (Ebdon et al. 1999; Martin and Chambers 2001). These mechanisms may operate alone or interact with each other to influence invasion. For example, nutrient addition and defoliation may increase *P. pratensis* (Liancourt et al. 2005) because of the ability of this species to respond quickly to defoliation, coupled with its high demand for water and N during growth.

Nitrogen is the dominant nutrient limiting plant growth in grasslands (Vitousek 1982). Nitrogen addition and accelerated nutrient cycling are associated with increased growth of *P. pratensis* (Wedin and Tilman 1990), while the same may not be true of *F. campestris*. Late successional species adapted to low nutrient concentrations are often poorly adapted to utilize nutrients due to a morpho-physiology that conserves the latter (Chapin III 1991; Chapin III et al. 1993). In contrast, roots of *P. pratensis* are highly concentrated in the top soil (i.e. few centimetres) (Veresoglou and Fitter 1984), potentially allowing this species to better capture N additions from fertilization, atmospheric inputs or surface decomposition. Industrial sources of nutrient addition have been implicated in the increase of *P. pratensis* within the central Parkland region of western Canada (Kochy and Wilson 2001). Under this scenario, N captured by shallow rooted *P. pratensis* could pre-empt interception by deeper rooted species such as *F. campestris* (Bookman and Mack 1982), placing the native grass at a competitive disadvantage.

Similarly, water addition is thought to increase the competitive ability of *P. pratensis*, and this may be increasingly important during the growing season as this grass is susceptible to summer drought due to its shallow root system (Veresoglou and Fitter 1984). Furthermore, the impact of N addition may increase water use, thereby enhancing *P. pratensis* susceptibility to drought (Ebdon et al. 1999). Thus, changes in water and nutrient availability may confer an advantage to species like *P. pratensis*, enabling it to spread and colonize areas containing new resources.

In the absence of disturbance, *F. campestris* typically dominates climax grasslands and may occupy up to 85% of the plant community's cover (Adams et al. 2003). Defoliation of these grasslands has historically (i.e. pre-settlement) occurred during the dormant season (Hodgkinson and Young 1973), and likely accounted for the retention of the dominant grass, which remains susceptible to decline under growing season defoliation (Johnston et al. 1971). Reduced competitive ability of *F. campestris* (Hodgkinson and Young 1973; Willms et al. 1998) under growing season use may allow for more grazing tolerant and opportunistic species such as *P. pratensis* to replace *F. campestris* (Willms and Quinton 1995). Although initially establishing from seed, *P. pratensis* does not require seed production to occupy a site, and once established, can effectively dominate a community through vegetative spread (Bookman and Mack 1982). This differs sharply from *F. campestris*, which has a limited ability to spread spatially through vegetative means, and instead must colonize interspaces between plants from seed.

4.2 Research Objectives

The goal of this study was to determine how environmental factors and physical disturbance, either alone or together, affect the abundance and vigor of *P. pratensis* and *F. campestris* within an existing native community. More specifically, this experiment was conducted to determine if:

1) Environmental conditions, specifically soil water, soil N availability, and litter presence, alter the relative abundance and vigor of *P. pratensis* and *F. campestris*
2) Defoliation (summer, winter, or no defoliation) and the environment have independent or synergistic (i.e. additive) effects on the abundance and vigor of *P. pratensis* and *F. campestris*.

4.3 Methods

4.3.1 Study Site

This study was conducted within a native grassland situated in the Foothills Fescue Natural Subregion, approximately 7 km northwest of Cochrane, Alberta (51°14'42.02"N, 114°31'9.85"W). The site was well-drained, located on an elevated west-facing terrace, and had a history of light to moderate grazing by cattle and occasional use as a native hay field for several decades. Soil was an Orthic Black Chernozem (Series: Dunvargan / Hatfield), with 5.9 pH, 24.1% organic matter, cation exchange capacity (CEC) of 22.7meq/100g and a clay loam texture (43% sand, 19% silt, 38% clay).

4.3.2 Experimental Design

A total of 16 different treatments, each replicated 8 times, were used in an incomplete factorial design to examine community responses to the manipulation of nitrogen (N), water (W), litter, and seasonal defoliation, between 2005 and 2008 (Table 3.1). All combinations of N, W and litter were evaluated. However, summer and winter defoliation were assessed only in combination with W and N. The total of 128 plots represented a wide range of initial conditions, including the abundance of *F. campestris* and *P. pratensis*: for example, *P. pratensis* cover averaged 8% but ranged from 0-70% among plots.

The study site was fenced in July 2005 to prevent livestock access and unintended defoliation. Plots were established in 8 blocks in a systematic layout, and permanently marked to facilitate relocation. Each plot contained a series of nested plots of progressively larger size, within which measurements or specific treatments were undertaken (Fig. 3.1). Centrally located sample plots were 50 x 50 cm in size, and N and W additions occurred within a larger 1 x 1 m plot nested overtop the sample plot. Similarly, litter and defoliation were done within a larger 1.5 x 1.5 m area to minimize the influence of edge effects on all measures within the sample plots. Plots were separated by a minimum distance of 0.25 m.

Selected treatments included an *in-situ* check where no treatment occurred and a litter removal treatment intended to examine the effect that removing biomass after dormancy has on the microenvironment (Table 3.1). Litter was removed in November of 2005, with all loose and detached coarse material hand scraped from plots. The average weight of litter removed was 68.4±4.4 g m^{-2}. Both check and litter removal treatments were repeated in combination with the W and N addition treatments (Table 3.1).

Plots with water addition were brought up to field capacity every 2 weeks from 1 May to 31 August of each year (2006 through 2008). The amount of water necessary to reach field capacity was determined using measured soil moisture values obtained with a Delta-T^{TM} ML2X moisture probe, coupled with calibrated relationships between moisture addition and observed measures of moisture for soil conditions at the site (Appendix E, Figs. E1-E2). Water was added in 2.5 cm increments and left for 24 hr before soil moisture readings were taken. This process was repeated until saturation of the soil was reached.

Another set of four treatments were used to examine the combined effects of manipulating W and N (Table 3.1). Addition of N to half the plots occurred annually each spring (May) by broadcasting granular urea (46-0-0) to the surface of each plot. Rates of urea addition were 100, 50 and 50 kg ha^{-1} in 2006, 2007, and 2008, respectively. Reduced rates were used after 2006 based on soil tests that indicated mineral N levels remained moderate (Appendix E).

Finally, two initial defoliation treatments were imposed to emulate one-time winter grazing (November 2005) or summer grazing (July 2006) in a factorial design with the W and N addition treatments (Table 3.1). Defoliation occurred non-selectively within affected plots by removing all current years' growth to 1 cm height, without altering existing litter on the soil surface. Biomass removed at defoliation was sorted into live (i.e. green) and dead (i.e. senescent) fractions (winter defoliation), or further stratified into grass, forb, and shrub components (summer defoliation), then bagged, dried and weighed to quantify the severity of defoliation.

4.3.3 Measurements

4.3.3.1 Environmental Monitoring

Volumetric soil moisture in the upper 15 cm of soil was sampled non-destructively within each plot at 2 week intervals from 10 May to 31 August in 2006 and 2007 using an ML2X moisture probe. Individual moisture values were taken approximately 10 cm from the center of the sampling plot in 4 random directions, and coincided with periods after each W addition treatment and a minimum of 24 hr after precipitation. Measurements were also taken in 2008 but ended in July at final biomass sampling. A rain gauge was used to record local rainfall throughout the growing season, and compared to regional rainfall data from the Cochrane weather station, approximately 2 km southeast of the study site.

Photosynthetically active radiation (PAR, in the 400 to 700 nm wavebands) was measured using a Decagon AccuPAR^{TM} ceptometer. PAR was recorded over a 3 hr period around solar noon on uniformly overcast days using the average of 10 readings above each plot, and 10 at the soil surface under all standing plant biomass and litter: an equal number of readings were taken at a 90 degree angle at each position. PAR readings were repeated monthly for each plot between 1 May and 31 August in 2006 and 2007, and from 1 May to 30 July in 2008.

Soil samples were collected in each plot during the last week of August of each year, using three, 2.5 cm diameter cores to a depth of 15 cm. Sub sample cores from each plot were combined, frozen, and later analyzed for available NO_3-N and NH_4-N by spectral absorption after extraction using a 5:1 mixture of 2*M* KCl (Maynard and Kalre 1993).

4.3.3.2 Vegetation Measures

Vegetative sampling included non-destructive measures, which were repeated annually from 2005 (pre-treatment) to 2008 (final sampling year). Repeated sampling of each permanent plot included the cover of *F. campestris* and *P. pratensis*, and the total density of *F. campestris* plants within each 1 x 1m plot. All sampling was conducted at peak biomass in the second half of July.

Additional sampling was conducted on focal *F. campestris* plants. Focal plants were randomly selected and permanently marked in each sampling plot at the start of the study (August 2005). Focal plants were assessed annually for basal diameter, total tiller counts, the proportion of tillers with inflorescences, and the average height of total tillers and tillers with inflorescences. Sampling of *P. pratensis* included average tiller height within the permanent sampling plot, and the number of inflorescences and average inflorescence height within each sampling plot.

Final above ground net primary production (ANPP) was assessed within each permanent sample plot at the beginning of August 2008 at final sampling. All material was removed at 1 cm height, sorted to *F. campestris, P. pratensis*, other grasses, forbs, shrubs, and litter, dried at 50^{o}C to constant mass and weighed. Biomass removed during imposition of the defoliation treatments was also collected in November 2005 and July 2006.

4.4 Statistical Analysis

All plant vigor response measures together with repeated measures of soil moisture content, PAR transmittance, and soil N, were assessed for normality and homogeneity of variances prior to analysis. Assumptions of normality were met for most variables except *F. campestris* basal diameter (square root transformation) and tiller density (natural log transformation) in the environmental study, and in the defoliation study, *F. campestris* biomass (square root transformation). Similarly, square root transformations were completed on *P. pratensis* cover, the proportion of tillers with inflorescences, and *P. pratensis* biomass in the environmental study, and on cover in the defoliation study. In addition a natural log transformation was completed on the proportion of inflorescences of *P. pratensis* species found in the defoliation study.

Univariate analyses used a two-stage approach to analyze the 16 treatments. First, combinations of the fixed environmental factors of litter removal, N addition and W addition (i.e. treatments 1-8 in Table 3.1) were assessed for their impacts on plant responses with an ANOVA using Proc Mixed in SAS software v9.2 (SAS Institute Inc 2008). Second, effects of the defoliation treatments (i.e. treatments 9-16 in Table 4.1) were combined with the undefoliated treatments where litter remained intact (see Table 4.1) to assess the additive effect of defoliation on plots with varying N and W addition. Block was considered random in all assessments, with the main effects and interactions in each analysis considered significant at $P<0.05$. All analyses were conducted separately for each year, with 2005 data (i.e. pre-treatment sampling) used as a covariate (i.e. initial tiller counts for *F. campestris*, and cover for *P. pratensis*). All analyses used LS means, with post-hoc mean comparisons conducted using a Tukey test ($P<0.05$).

A univariate analysis was conducted to quantify the impact of treatments on *P. pratensis* cover, tiller height, inflorescence density, inflorescence height and biomass measures, and for *F. campestris* cover, basal diameter, tiller counts, tiller heights, proportion of tillers with inflorescences, inflorescence height, and above ground biomass in each of the 3 treatment years (2006, 2007 and 2008). The 2005 sampling of each measure (excluding biomass) was utilized as a covariate in all analyses. Environmental variables such as available soil N, moisture and light were analyzed similarly.

Stepwise regression using Proc Reg in SAS v9.2 (SAS Institute Inc 2008) was utilized in the environmental analysis of data collected in 2006, 2007, and 2008, to assess the relationship between plant response variables and environmental conditions. Specifically, *P. pratensis* cover, number of inflorescences/m^2, vegetative and inflorescence tiller heights, and final biomass, were analyzed. Dependant variables for *F. campestris* included cover, basal diameter, total tillers / plant, tiller heights, proportion of inflorescences, and biomass. Independent variables included mean monthly soil moisture (SM) and photosynthetically active radiation (PAR) over the 3 years of data collection, and annual available soil N measured in August of each year.

4.5 Results

4.5.1 Treatment Induced Changes to the Environment

Treatment induced changes to the environment, including litter removal on soil moisture, PAR and soil N levels, are reviewed in Appendix E. In general, litter removal increased light transmittance, particularly during 2006. Litter removal also initially decreased soil moisture, although these effects diminished through 2007, and eventually led to increased moisture in 2008. As expected W addition increased soil moisture, while addition of N reduced soil moisture. Defoliation had variable effects on soil moisture. Finally, N addition predictably led to increased soil N in August of each year (Appendix E).

4.5.2 *Festuca campestris* Responses

Abundance of *F. campestris* varied markedly through all years of the study (Appendix B). Cover of *F. campestris* species declined from 2006 to 2008, although tiller counts within focal plants increased over this period. Other vigor measures indicated *F. campestris* plants were generally larger in 2007 than 2006 or 2008. Most characteristics of *F. campestris* were also associated with soil moisture measures from May through August, with responses both positive (i.e. proportion of tillers with inflorescences, cover, tiller height, and basal diameter) and negative (tiller density) (Table 4.2). Final *F. campestris* biomass was positively associated with May SM and negatively associated with available N and May PAR (Table 4.2).

Nitrogen addition reduced *F. campestris* plant biomass (P<0.01, +N: 44.8±6.3 g, -N: 70.2±6.3 g), tillers (P<0.01, +N: 133.3±11.4 tillers/plant, -N:

167.9±11.4 tillers/plant), average tiller heights (P=0.02, +N: 53.1±1.2 cm, -N: 56.1±1.2 cm), and basal diameter (P<0.01, +N: 14±0.7 cm, -N: 15.8±0.7 cm). Although N addition did not impact basal diameter initially (i.e. during the first 2 years), this response became significant (Y*N; P=0.03) by the final year, at which time plants with ambient N had greater basal diameter (Appendix B).

Litter removal interacted with N addition to affect *F. campestris* cover (P=0.001), basal diameter (P=0.01), and total tiller numbers (P<0.0001). *F. campestris* plants were generally smallest within plots with added N and ambient litter (i.e. +L) compared to all other treatments (Table 4.6). Conversely, *F. campestris* plant vigor was greatest under ambient N conditions in the presence of *in-situ* litter. With litter removal, N addition had little impact on *F. campestris* vigor (Table 4.6).

Water addition increased *F. campestris* cover (P<0.001;-W: 58±1.9, +W: 66.4±1.9), biomass (P<0.01; -W: 44±6.3, +W: 71±6.3), basal diameter (P<0.01; -W: 13.8±0.6, +W: 16±0.6) and tillers (P<0.01; -W: 129.6±11.8, +W: 171.6±11.8). Water addition also increased inflorescence production of *F. campestris,* but not until 2007 (W*Y; P=0.07); however, this relationship had reversed by 2008 (Appendix B).

Water addition also interacted with litter removal to affect basal diameter (P=0.09), number of inflorescences (P=0.02), and the tiller numbers (P=0.08) of *F. campestris* plants. Treatments with added W and litter removed led to the greatest number of tillers, proportion of inflorescences, and plant basal diameter of *F. campestris* (Table 4.6). Conversely, plants in treatments with ambient W and litter removed had the smallest basal diameter and proportion of inflorescences. Tiller counts were lowest with ambient W and *in-situ* litter (Table 4.6).

A complex interaction of W*N*L*Y occurred on *F. campestris* basal diameter (P=0.06): closer examination indicated that the W*N*L (P=0.03) effect found in Appendix B was confined to 2008 (Fig. 4.2). In general, addition of W increased basal diameter in all conditions except the presence of N addition and abundant litter. In contrast, N addition in the absence of W addition suppressed basal diameter but only in the presence of litter (Fig. 4.2).

Defoliation significantly affected tiller counts (P=0.02) and cover (P<0.0001) of *F. campestris*, with SD (110.8±13.4 tillers/plant, 49±2.2% cover) treatments lower than the WD (147.9±13.4 tillers/plant, 61.4±2.2%) and UD (141.8±13.4 tillers/plant, 60.4±2.2%) treatments. Cover of *F. campestris* was also affected by the interaction of defoliation and year (P=0.001), and revealed that during 2006, the UD (70.9±3.3%) and WD (69.4±3.3%) treatments had more cover than SD (45.6±3.3%) treatments. This increased cover continued into 2007 with SD (50.8±3.3%) treatments being lower than WD (62.4±3.3%) treatments in *F. campestris* cover, but not lower than UD (56.5±3.3%) treatments. By 2008 the cover effect had disappeared (UD: 53.9±3.3%, SD: 50.5±3.3%, WD: 52.5±3.3%).

There was also an N*D interaction on *F. campestris* cover (P=0.02), basal diameter (P=0.001), tiller counts (P<0.0001) and final biomass (P=0.04). The largest plants were generally those left undefoliated in the absence of N addition. Under ambient N, although the final biomass of *F. campestris* did not differ with defoliation, SD plots had lower cover and basal diameter than the other treatments

(Table 4.7). With N addition, defoliation had no effect on *F. campestris* biomass or basal diameter, but cover differed widely among treatments (WD>UD>SD) (Table 4.7). Examined another way, N addition tended to reduce *F. campestris* vigor, but only in SD and UD plots (Table 4.7).

A similar interaction between N and D but which included year (P=0.05) existed on *F. campestris* tiller counts. Although tiller counts first responded in 2007, peaking in WD treatments with added N, by 2008 tiller counts were greatest in UD plots with ambient N and lowest in UD plots with added N (Table 4.8). All other treatments were intermediate in tiller counts.

Finally, tiller counts were affected by the interaction of D*W (P=0.01). *F. campestris* tiller counts were greater in UD treatments with added W (170.6±17.0 tillers/plant) than those under ambient (i.e. –W and UD) conditions (113±16.9 tillers/plant). However, W addition had no effect on tiller counts within SD (+W: 114.9±16.6, -W: 106.8±16.9) or WD (-W: 131.1±16.7, +W: 164.6±16.8) treatments.

4.5.3 *Poa pratensis* Responses

P. pratensis exhibited substantial inter-annual variability throughout the study. Overall, *Poa* had greater abundance and vigor in 2008 than previous years (Appendix B). Measures of *Poa* vigor were generally directly and negatively associated with soil moisture throughout the growing season (Table 4.2). *Poa pratensis* cover was associated with soil moisture (2006 May, 2007 July) and inflorescence height (2007, June). Inflorescence height was also associated with

PAR (2006, July) (Table 4.2). Final biomass of *P. pratensis* was directly related to early season (May) soil moisture during 2008.

Nitrogen addition reduced *P. pratensis* cover (P=0.02) from 11.0±1.8% to 7.4±1.8%, reproductive tiller density (P=0.09) from 2.5±0.7 stems/m^2 to 1.7±0.7 stems/m^2, and final biomass (P=0.05) from 45.5±15.6 g/m^2 to 24.9±15.6 g/m^2. The interaction of N addition with year (P=0.07) resulted from N addition decreasing tiller height in 2007 from 28.2±2.9 cm to 22.3±2.5 cm, but increasing tiller height in 2008 from 43.2±2.5 cm to 47.3±2.6 cm.

Litter removal increased *P. pratensis* inflorescence densities (P=0.08) from 5.8±3.0 heads/m^2 to 12.2±2.7 heads/m^2. A more complex interaction was apparent between N and W addition with litter removal, on both *P. pratensis* cover (p=0.03) and biomass (p=0.08). Closer examination of these interactions revealed that *P. pratensis* cover and biomass tended to be greater under ambient levels of both W and N, but only in the absence of litter, compared to all other treatment combinations (Table 4.3). Conversely, an increase in availability of either W or N, or the presence of *in-situ* litter levels, all appeared equally effective in limiting *P. pratensis*. Water addition alone reduced *P. pratensis* biomass (P=0.04) from 47.9±15.6 g/m^2 to 22.5±15.6 g/m^2. Similarly, water addition reduced vegetative tiller heights (P=0.02) from 38.4±1.8 cm to 32.4±2.0 cm.

Defoliation affected *P. pratensis* final biomass (P=0.09): summer defoliation (SD) led to greater biomass (61.3±18.4 g/m^2) than in winter defoliated (WD: 27.4±18.4 g/m^2) or undefoliated (UD: 34.9±18.4 g/m^2) plots. A similar relationship among defoliation treatments was evident in the density of *P.*

pratensis inflorescences (P=0.02), although it took until 2008 for treatment effects to fully develop (Table 4.4). Finally, defoliation interacted with N addition to alter *P. pratensis* cover (P=0.007). Under ambient N, *P. pratensis* was more abundant in the WD treatment than either the SD or UD treatments (Table 4.5). However, with the addition of N, SD treatments tended to have more *P. pratensis* cover than both WD and UD treatments (Table 4.5).

4.5.4 Relationship between *Festuca campestris* and *Poa pratensis*

Changes in the abundance of *P. pratensis* over the 3 year study showed a weak negative association with the cover of *F. campestris* during the same period in both the defoliation (R^2 = 0.08, P =0.03) and environmental treatments (R^2 = 0.08, P = 0.06). However, the significance of the relationship between *P. pratensis* and *F. campestris* was determined largely by plots within the undefoliated and *in-situ* litter treatment rather than the –L, SD, and WD treatments (Fig 4.3, 4.4).

4.6 Discussion

4.6.1 *Festuca campestris* Response to Treatments

F. campestris responded positively to W addition, likely an opportunistic response to allow this competitive species (Coupland and Brayshaw 1953) to exploit soil moisture. Although we anticipated that the extensive fibrous root system of *F. campestris* (Hodgkinson and Young 1973; Moss and Packer 1983) would allow this species to demonstrate a strong tolerance to low soil moisture content, this same adaptation could allow *F. campestris* to benefit from surplus soil moisture, similar to that observed in a parallel greenhouse study where immature *F. campestris* plants performed better in monocultures with high W (see Chapter 6). While immature plants in the greenhouse were suppressed by interspecific competition (see Chapter 6), mature *F. campestris* plants in this field study appeared to exploit hyper-abundant water, and this benefit may have been at the expense of neighbors such as *P. pratensis*, which did not benefit from W addition (see Section 4.5.2 below).

These responses suggest that *F. campestris* is a highly opportunistic species capable of exploiting periods of increased rainfall, which in turn may make it a strong competitor under these conditions (Driver Model) and capable of decreasing the vigor of other species (see Chapter 3) (MacDougall and Turkington 2005). It is also important to note however, that the benefit of high water in the current study was at least partly negated by defoliation, particularly during summer, as evidenced by the limited increase in tillers within these treatments. Therefore, ongoing chronic disturbances such as summer grazing across the region may limit the ability of *F. campestris* to benefit from periods of high precipitation.

Ambient litter favored *F. campestris*, but only under ambient rainfall. In contrast, W addition appeared to compensate for litter removal in benefiting this species. These responses highlight the role of litter in conserving soil moisture (Weaver and Rowland 1952; Fowler 1986; Facelli and Pickett 1991) to the benefit of *F. campestris*, and is consistent with other studies suggesting litter removal may reduce production by as much as 40% in fescue grasslands (Willms et al. 1986). Moreover, as *F. campestris* is tolerant of reduced PAR and produces the largest portion (41%) of living biomass in the community (Appendix E), this species contributes directly to litter accumulation over time, and suggests positive feedback may exist between *F. campestris* and soil moisture conservation, as mediated by litter. Although improved soil moisture may be the primary benefit associated with litter retention, litter may also have some detrimental impacts on *F. campestris*. Tiller numbers were positively related to PAR in this study, including the proportion of tillers with inflorescences, which in turn were associated with litter removal. The association of light and tillers is not surprising given that floral induction in *F. campestris* is regulated by light availability at the plant crown, particularly during fall (Johnston and MacDonald 1967). Such effects of light may explain why other studies have shown high light levels lead to increases in the biomass of *F. campestris* (Willms et al. 1986; Naeth et al. 1991).

In contrast to the impact of W, N addition had a decidedly negative effect on *F. campestris* vigor, including tiller numbers, a trend that strengthened throughout the 3 year study, and also was most apparent in the SD treatment. Notably, these responses support those from a parallel investigation into the species-level responses to N addition (see Chapter 6) where *F. campestris* had no response to N addition. Reductions in *F. campestris* with added N may be linked to the suppressive effects of other species, largely forbs and *Symphoricarpos occidentalis* (Chapter 3), a native shrub (Moss and Packer 1983), which demonstrated a marked positive response to added N. Similarly, although *P.*

pratensis generally remained indifferent to N, this competitor was favored by N addition under SD, and could therefore have played a role in limiting *F. campestris* responses to N under those specific treatment conditions. Finally, the effect of N addition in reducing *F. campestris* was markedly stronger than the beneficial role of retaining litter, suggesting the conservation of this species is more closely tied to minimizing N enrichment or mineralization in the soil. For example, non-uniform nutrient deposition of animal wastes or atmospheric inputs of N, rather than litter depletion through ongoing grazing, is likely more important for *F. campestris* conservation.

The overall inability of *F. campestris* to exploit high N in this study and parallel investigations (Chapter 6), suggests that this species is not strongly dependant on available N to maintain its growth and dominance within the community. Consequently, soil amendments to slow the N cycle (i.e. reduce mineralization) may benefit *F. campestris* over those competing species more reliant on high N, as seen with other bunchgrasses (Bowman et al. 2004; Berendse 1990). Although evidence points to the possibility of such a relationship, the question remains as to whether *F. campestris* is able to modify N cycles to maintain its dominance within the plant community. Large biomass and associated litter accumulation by *F. campestris*, both above ground in the standing litter pool and below ground in its extensive fibrous root system (Hodgkinson and Young 1973; Moss and Packer 1983), may immobilize large amounts of N and limit soil N availability. This is further likely given the morphology of *F.*

campestris leaves (i.e. rolled structure and sclerenchymatous layer), which is believed to limit degradation and decay (Willms et al. 1998).

Festuca campestris is poorly suited to SD (Willms et al. 1998; McLean and Wikeem 1985; Mengli et al. 2005), responses clearly supported by the current study. Recovery from the SD took until the second full growing season after defoliation. In contrast, *F. campestris* appeared much better adapted to dormant season defoliation (McLean and Wikeem 1985), although N addition increased the susceptibility of *F. campestris* to decline under any season of defoliation relative to the undefoliated control. It should also be noted that the one time defoliation treatments tested here do not account for the potential additive effects of long-term grazing, with repeated defoliation within a season and between successive years known to be particularly detrimental to *F. campestris* (Willms et al. 1985).

4.6.1 *Poa pratensis* Response to Treatments

Poa pratensis, a shallow rooted (Bookman and Mack 1982; Veresoglou and Fitter 1984; Jiang and Huang 2001) rhizomatous species (Moss and Packer 1983) typically found in medium to high N grasslands (Wilson and Tilman 1991), did not benefit from W and N addition as in previous studies (Ebdon et al. 1999). Instead, *P. pratensis* was unexpectedly favored by ambient N and W. While the moderate to high *in-situ* W and N present in untreated soils of this grassland during the study period may help explain the lack of response to resource addition, it does not explain why vigor of *P. pratensis* decreased under high resource availability.

Benefits of abundant resources to *P. pratensis* may have been negated by the simultaneous response of neighbouring vegetation to resource addition. For example, N and W addition favored *Symphoricarpos occidentalis* (Chapter 3) and *F. campestris* (see 4.5.2), respectively. As both *S. occidentalis* (Moss and Packer 1983) and *F. campestris* (Hodgkinson and Young 1973) are dominant species of late seral communities within the Foothills Fescue Subregion, increases in these species may have suppressed *P. pratensis* through competitive processes; a conclusion further supported by the negative association between changes in the abundance of *P. pratensis* and *F. campestris*. The suppression of *F. campestris* may also account for why the lone positive response of *P. pratensis* to N addition occurred in conjunction with SD: a sharp decline in *F. campestris* and other grazing sensitive species under SD may have enabled *P. pratensis* to exploit added N more effectively under reduced competition. Dependence of *P. pratensis* on the vigor of other species in the community supports the passenger model of species dynamics (MacDougall and Turkington 2005).

The positive effect of litter removal on *P. pratensis* suggests that ambient amounts of litter in this grassland had the ability to suppress this species. Litter in this grassland averaged 3,862 kg/ha, similar to that in other fescue grasslands and plant community types, which average 2,690 kg/ha and range from 1800 to 4707 kg/ha (Adams et al. 2003), suggesting these amounts of litter were not unusual, but rather were representative of the region. Suppressive effects of litter on the creeping rooted *P. pratensis* can be attributed, at least in part, to the impacts of litter modification on soil moisture, responses supported by the similar effects of these treatments. For example, litter removal reduces soil moisture through increased evaporation (Weaver and Rowland 1952; Fowler 1986; Facelli and Pickett 1991), and may therefore create drier conditions similar to those of the ambient W treatment, to which *P. pratensis* appeared better adapted within this community. These responses are surprising given previous work indicating *P. pratensis* prefers ample soil moisture (Ebdon et al. 1999; Martin and Chambers 2001). These contradictory results are difficult to explain, but rather than *P. pratensis* responding specifically to the drier conditions under ambient W and/or litter removal, this species may also be benefiting from a reduction in competition intensity from adjacent vegetation including *F. campestris*, whose abundance demonstrated a strong positive association with water availability. Abundant litter retention in the ambient treatment is likely to maintain soil moisture content (Weaver and Rowland 1952; Fowler 1986; Facelli and Pickett 1991) and associated competition from neighbors, thereby reinforcing that *P. pratensis* is only able to increase within this grassland under conditions where the dominant species are stressed and/or under decline.

The interaction of litter removal with W and N addition on *P. pratensis* suggests that responses in this species may also be attributed to mechanisms outside of soil resource availability, and involve factors such as light. In general, *P. pratensis* appeared to be positively related to light availability, consistent with previous studies (Bookman 1983), which in turn would be regulated by litter mass

(Facelli and Pickett 1991). Moreover, given that litter removal was effective in increasing *P. pratensis,* but only under ambient W and N, this response suggests that *P. pratensis* may have a relatively narrow niche of ecological adaptation within this particular plant community. Of special note was the increase in *P. pratensis* inflorescence density with litter removal, as this could enhance the reproductive capacity of this species, and more specifically, increase the potential for its spread to adjacent gaps in the community. Similar to increasing in biomass under increased light (Bookman and Mack 1983), this species may likewise increase inflorescence production. Previous studies have shown that *P. pratensis* forms a significant component of the seed bank in *F. campestris* grasslands (Willms and Quinton 1995), and that re-establishment of this species on drastically disturbed land is favored by litter removal (Chapter 7). Thus, litter retention may remain an important strategy to minimize seed production of *P. pratensis* and thereby limit the potential movement of this grass into adjacent, uninvaded areas. The use of appropriate stocking rates and promotion of uniform grazing strategies may all be critical in retaining litter within rough fescue grasslands under livestock grazing.

P. pratensis has typically been considered an increaser in response to grazing during summer (Cole 1995), with rhizomes (Moss and Packer 1983) and favorable regrowth (Wilson and Tilman 1991; Reader et al. 1994) allowing this species to rapidly exploit gaps in the plant community. In this study *P. pratensis* abundance and vigor were likewise favored by SD over the WD and UD treatments, and was further enhanced by N addition. The latter observation differs somewhat from previous findings that *P. pratensis* responds readily to N addition regardless of the presence or timing of defoliation (Martin and Chambers 2001). As *P. pratensis* is known to be more defoliation tolerant than many native grasses in this ecosystem (Looman 1969), this grass may benefit more than other species during regrowth by being able to capitalize on added N. This observation is particularly important as it highlights the importance of avoiding N enrichment in fescue grasslands to minimize *P. pratensis*, as well as ensuring that grazing and subsequent nutrient deposition is not concentrated in the landscape using appropriate animal distribution techniques (Bailey and Welling 1999).

The effectiveness of the UD and WD treatments in reducing *P. pratensis* biomass was not surprising given the prominent role of dormant season grazing and low stocking rates in maintaining native fescue grassland composition, including minimizing the invasion of species such as *P. pratensis* (Willms and Fraser 1992). However, the observed responses also indicated that WD favored an increase in *P. pratensis* cover under low N conditions. While the mechanism for allowing *P. pratensis* to increase during WD and low N remains unclear, we speculate that the removal of dormant and standing dead biomass in this treatment may have had a similar impact to litter removal, and favored *P. pratensis* through increases in light and temperature. Notably, the fact that *P. pratensis* was not increased by WD in the simultaneous presence of N addition suggests that more rapid responses in other plant species within the community during early spring may have offset any benefit to *P. pratensis*.

4.7 Conclusions

Festuca campestris and *P. pratensis* appeared favored by a relatively unique set of environmental conditions. While *F. campestris* was favored by high W and either the absence of defoliation or defoliation during the dormant season only, *P. pratensis* increased with summer defoliation and ambient levels of W. Both species also tended to demonstrate greater vigor under low N, although *P. pratensis* exhibited the ability to exploit added N under SD, and exhibited increases in inflorescence production with litter removal. In summary, conditions that favored *F. campestris* were often those that did not benefit *P. pratensis*, and vice versa.

These responses suggest that management strategies that reduce soil N, such as ensuring uniform grazing activities, and shifting defoliation to the dormant season (i.e. winter grazing) are likely to conserve *F. campestris* while limiting increases in *P. pratensis*. Similarly, the maintenance of abundant litter may be a useful tool for conserving water, thereby maintaining conditions that maximize the vigor and competitiveness of *F. campestris*, particularly during droughts. Litter retention also has the potential to limit the production of seed by *P. pratensis*, which in turn may reduce the risk of invasion by this species into adjacent grasslands.

4.8 References

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Table 4.1 Summary of treatments used to examine the impact of environment and defoliation on fescue grassland composition.

Category	Treatment	Description
Water	1	*In-situ* Check
	2	No litter (litter removed in mid Nov of 2005)
	3	*In-situ* + Water (monthly additions to field capacity)
	4	No litter + Water
Nitrogen	5	1 + Nitrogen (100kg/ha 2006+50kg/ha 2007/2008)
	6	2 + N
	7	3 + N
	8	4 + N
Defoliation	9	1 + Summer Defoliation, July of 2006 (SD)
	10	3 + SD
	11	5 + SD
	12	7 + SD
	13	1 + Winter Defoliation, November of 2005 (WD)
	14	3 + WD
	15	5 + WD
	16	7 + WD

Table 4.2 Association of *P. pratensis* and *F. campestris* plant responses to monthly photsynthetically active radiation (PAR), soil moisture (SM), and annual available soil N sampled during each growing season from 2006 through 2008 based on a multiple regression.

Species	Year	Dependant variable	Independent Variable	Model R^2	Partial R^2	B[a]	Prob>|F|[b]
P. pratensis	2006	Cover	SM, May	0.11	0.11	-0.34	<0.01
		Inflorescence height	PAR, July	0.97	0.97	-0.46	0.01
	2007	Cover	SM, July	0.08	0.08	-0.19	0.03
		Inflorescence height	SM, June	0.49	0.49	-0.70	0.05
	2008	Biomass	SM, May	0.07	0.07	-0.27	0.029
F. campestris	2006	Inflorescences (%)	SM, August	0.07	0.07	0.24	0.03
		Tillers / plant	SM, May	0.06	0.06	-0.25	0.04
		Max Tiller Height	SM, June	0.06	0.06	0.24	0.05
		Basal Diameter	SM, May	0.15	0.15	0.37	<0.01
	2007	Cover	SM, July	0.18	0.12	0.38	<0.01
			PAR, July		0.06	-0.20	0.04
		Tillers / plant	PAR, July	0.16	0.1	-0.28	0.01
			SM, June		0.06	-0.28	0.03
	2008	Biomass	Available N	0.22	0.09	-0.22	0.01
			SM, May		0.07	0.31	0.03
			PAR, May		0.05	-0.22	0.05

[a] Regression coefficient

[b] Probability of whether inclusion of this variable improves the overall fit of the regression model.

Table 4.3 Effect of environmental conditions, including litter removal (-L), along with water (+W) and nitrogen (+N) addition, on the mean (±SE) cover and final biomass of *P. pratensis*.

Nitrogen	Litter	Water	Cover (%)	Biomass (g/m^2)
+N[2]	+L	+W	7.4 (±2.8) b[1]	2.4 (±22) b
		-W	7.0 (±2.8) b	47.6 (±22) ab
	-L	+W	8.7 (±2.8) b	20 (±22) b
		-W	6.7 (±2.8) b	30 (±22) ab
-N	+L	+W	9.2 (±2.8) b	48.4 (±22) ab
		-W	6.3 (±2.8) b	41.2 (±22) ab
	-L	+W	9.6 (±2.8) b	19.2 (±22) b
		-W	18.9 (±2.8) a	73.2 (±22) a

[1] Within columns, means with different letters differ, $P<0.05$.

[2] +W = water addition, -W = ambient water, +N = nitrogen addition, -N = ambient nitrogen, +L = ambient litter, and –L = litter removal.

Table 4.4 Mean density (±SE) of *P. pratensis* inflorescences (#/m^2) in response to defoliation during each year of sampling.

Defoliation	Year	Inflorescences / m^2
UD[2]	2006	3.7 (±7.4) a[1]
SD		-3.0 (±7.9) a
WD		1.1 (±7.9) a
UD	2007	3.9 (±6.3) b
SD		13.7 (±6.3) a
WD		12.6 (±6.8) ab
UD	2008	26.5 (±6.2) b
SD		34.4 (±6.0) a
WD		16.4 (±6.4) b

[1] Within a year, means with different letters differ, P<0.05.

[2] UD = undefoliated, WD = winter defolation, and SD = summer defoliation

Table 4.5 Mean (±SE) cover of *P. pratensis* following nitrogen addition (+N) and defoliation, over the three years of study.

Nitrogen	Defoliation	Cover (%)
+N[2]	UD	8.1 (±2.3) b[1]
	SD	11.4 (±2.3) ab*
	WD	6.1 (±2.3) b*
-N	UD	8.9 (±2.3) b
	SD	10.6 (±2.3) b
	WD	16.5 (±2.3) a

[1] Means within a nitrogen treatment with different letters differ, P<0.05.

* Means differ at P=0.054.

[2] +N = nitrogen addition, -N = ambient nitrogen, UD = undefoliated, WD = winter defolation, and SD = summer defoliation

Table 4.6 Mean (±SE) cover, basal diameter, number of tillers, and proportion of tillers with inflorescences, of *F. campestris* plants, under varying nitrogen addition (+N) and water addition (+W) treatments, with (+L) and without litter presence, as determined in the environmental analysis. Results are averaged over all three years of the study.

Variable	Litter	Cover (%)	Basal Diameter (cm)	Tillers (#/plant)	Inflorescences (%)
+N[2]	+L	54.7 (±2.7) b	13.0 (±0.8) c	101.5 (±15.6) c	-
	-L	66.7 (±2.7) a	14.9 (±0.8) b	165.1 (±15.6) ab	-
-N	+L	66.8 (±2.7) a	16.7 (±0.8) a	191.5 (±15.5) a	-
	-L	60.4 (±2.7) ab	14.9 (±0.8) b	144.4 (±15.5) b	-
+W	+L	-	15.5 (±0.8) ab	167.9 (±15.7) ab	2.3 (±0.8) ab
	-L	-	16.6 (±0.8) a	175.3 (±15.8) a	3.4 (±0.8) a
-W	+L	-	14.3 (±0.8) cb	125 (±16) b	2.7 (±0.8) ab
	-L	-	13.2 (±0.8) c	134.2 (±15.6) ab	1.9 (±0.8) b

[1] Within a variable and column, means with different letters differ, P<0.05.

[2] +W = water addition, -W = ambient water, +N = nitrogen addition, -N = ambient nitrogen, +L = ambient litter, and –L = litter removal.

Table 4.7 Mean (±SE) cover, basal diameter and biomass of vegetative tillers of *F. campestris* plants under varying nitrogen addition (+N) and defoliation treatments, as assessed within the defoliation analysis over the period 2007-2008.

Nitrogen	Defoliation	Cover	Basal Diameter	Biomass
+N[2]	UD	54.5 (±2.8) bc[1]	12.6 (±0.7) b	37.6 (±7.4) b
+N	SD	45.2 (±2.8) d	13.9 (±0.7) b	35.1 (±7.4) b
+N	WD	62.2 (±2.8) a	13.7 (±0.7) b	49.9 (±7.4) ab
-N	UD	66.4 (±2.8) a	16.5 (±0.7) a	75.4 (±7.4) a
-N	SD	52.8 (±2.8) c	13.9 (±0.7) b	56.5 (±7.4) ab
-N	WD	60.7 (±2.8) ab	13.6 (±0.7) b	51.2 (±7.4) ab

[1] Within a column, means with different letters differ, $P<0.05$.

[2] +N = nitrogen addition, -N = ambient nitrogen, UD = undefoliated, WD = winter defolation, and SD = summer defoliation

Table 4.8 Mean (±SE) tiller densities (#/plant) of *F. campestris* plants to nitrogen level and defoliation treatments within the defoliation analysis during each year of sampling. During analysis, tiller densities from 2005 were run as a covariate.

		Vegetative Tiller Densities		
Nitrogen	Defoliation	2006	2007	2008
+N[3]	UD	103.0 (±25.7) a[1]	66.5 (±25.7) b	116.9 (±25.7) c
+N	SD	85.4 (±25.8) a	67.9 (±25.8) b	195.4 (±25.8) b
+N	WD	117.8 (±25.7) a	140.0 (±25.7) a	214.8 (±25.7) b
-N	UD	125.0 (±25.7) a	130.2 (±25.7) ab[2]	309.3 (±25.7) a
-N	SD	68.5 (±25.8) a	73.6 (±25.8) ab	174.2 (±25.8) bc
-N	WD	105.0 (±25.7) a	81.8 (±25.7) ab	227.7 (±25.7) b

[1] Within a column, means with different letters differ, $P<0.05$.

[2] Differs from UD+N, SD+N, and SD-N at $P<0.10$.

[3] +N = nitrogen addition, -N = ambient nitrogen, UD = undefoliated, WD = winter defolation, and SD = summer defoliation

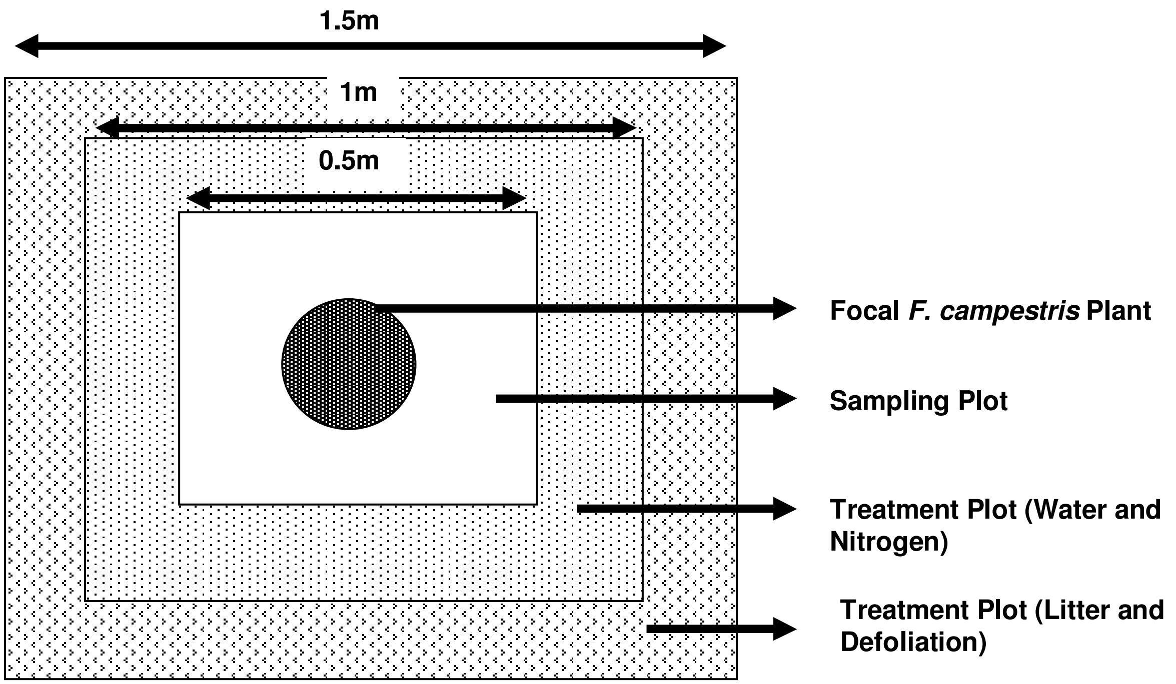

Figure 4.1 Experimental design of plots, including areas treated with defoliation and litter modification (1.5 x 1.5 m), water and nitrogen addition (1 x 1 m), and the permanent sampling area (0.5 x 0.5 m).

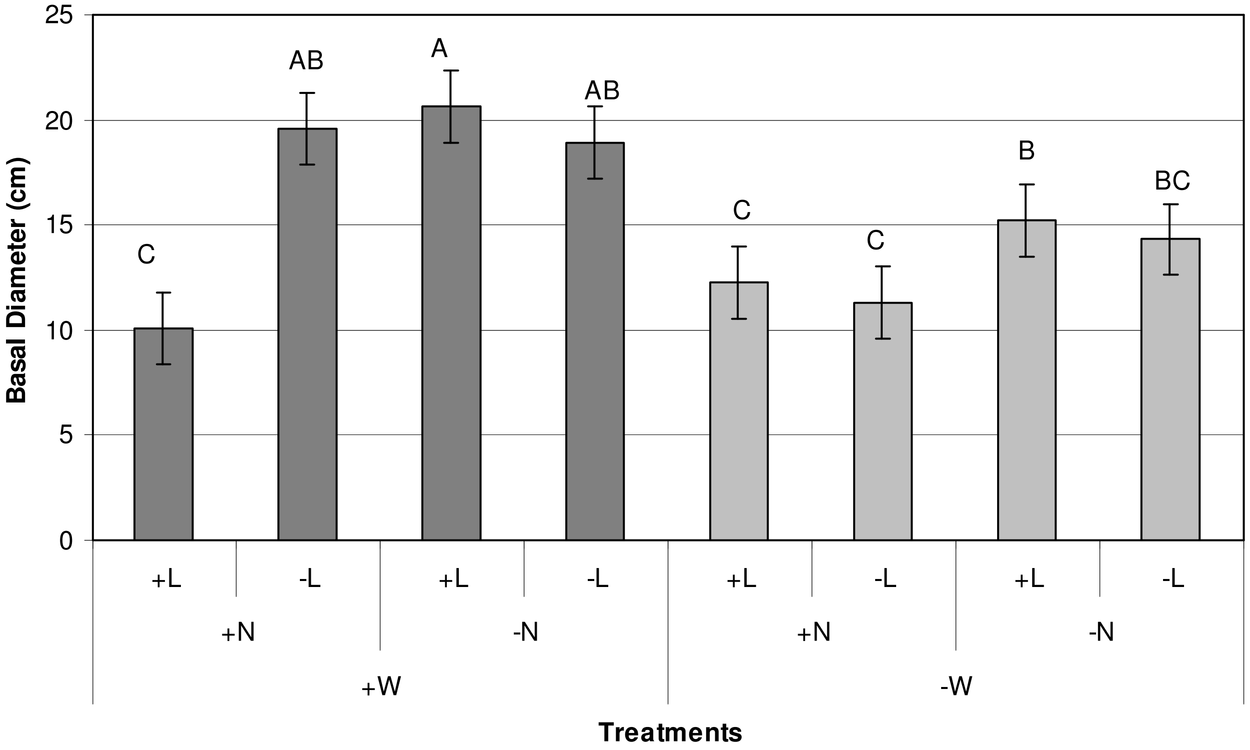

Figure 4.1 Mean basal diameter (±SD) of *F. campestris* plants within the environmental study to water addition (+W), nitrogen addition (+N), and litter removal (-L) during the 2008 growing season. Means use original data with different letters indicating those that differ ($P<0.05$) based on analysis with transformed data while error bars are untransformed. +W = water addition, -W = ambient water, +N = nitrogen addition, -N = ambient nitrogen, +L = ambient litter, and –L = litter removal.

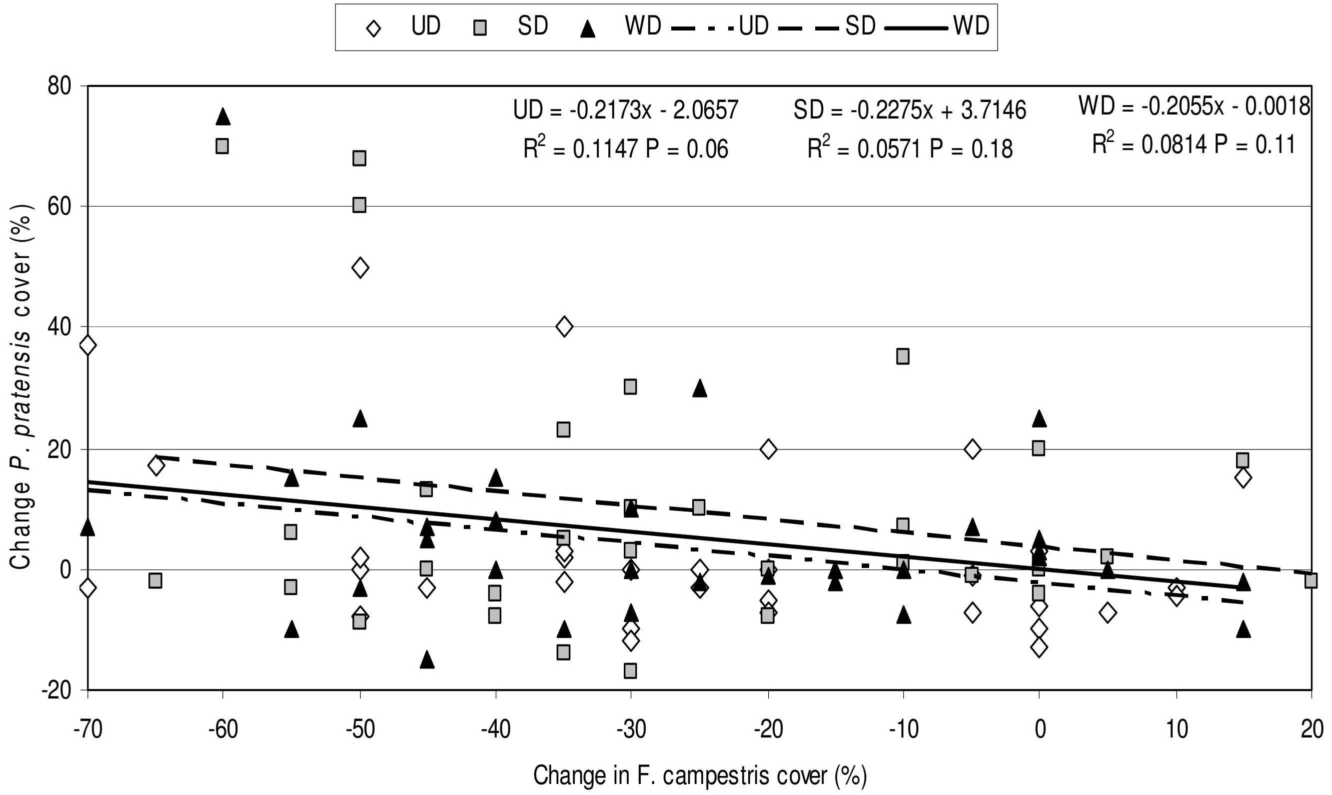

Figure 4.2 The association of changes in *P. pratensis* cover to *F. campestris* cover in each of the undefoliated (UD, n=32), summer defoliated (SD, n=32) and winter defoliated (WD, n=32) plots, during the three year period 2006 to 2008 within the defoliation experiment. UD = undefoliated, WD = winter defolation, and SD = summer defoliation.

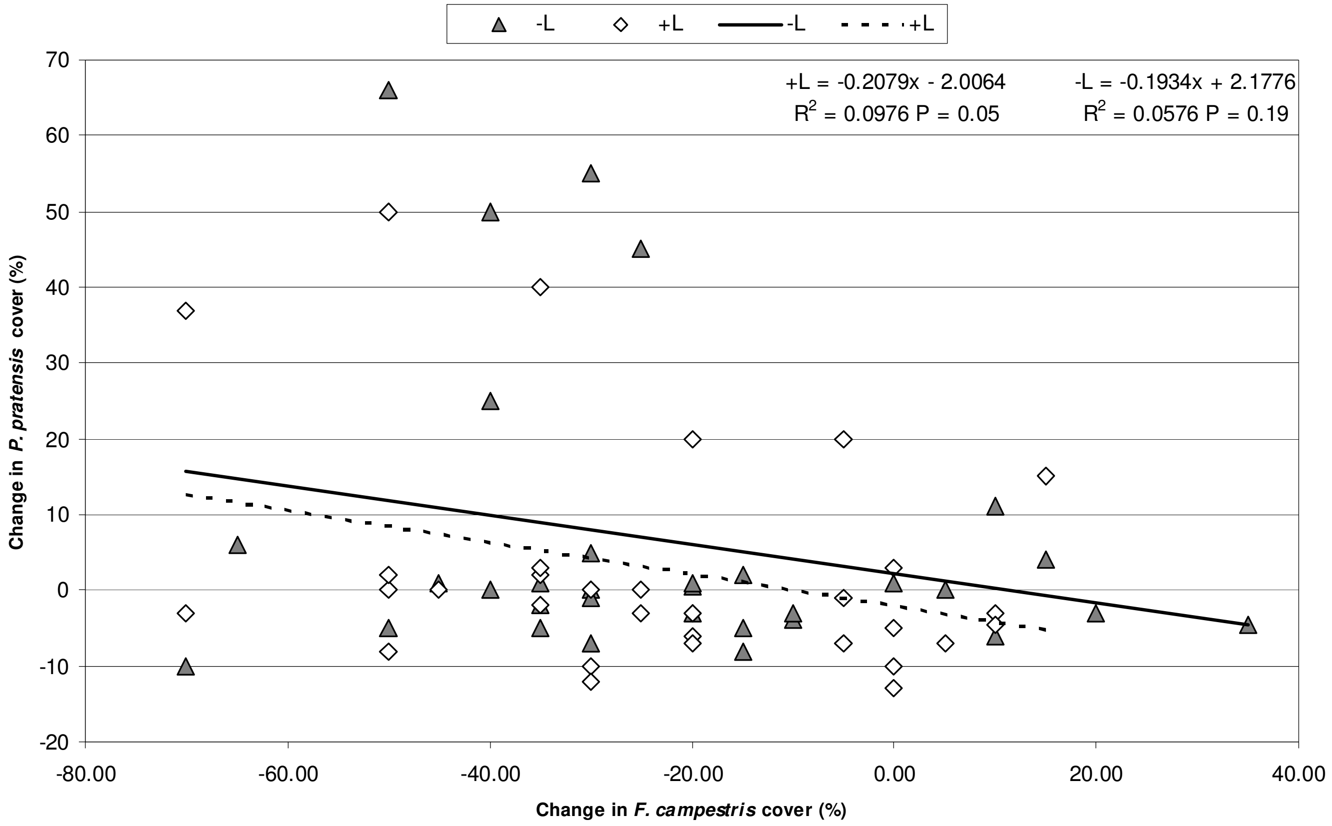

Figure 4.3 The association of changes in *P. pratensis* cover to *F. campestris* cover within each of the ambient litter (+L, n=32) and litter removal (-L, n=32) treatments of the environmental experiment, during the three year period 2006 to 2008. +L = ambient litter, and –L = litter removal.

Chapter 5 FACTORS REGULATING *POA PRATENSIS* (L.) INVASION INTO *FESTUCA CAMPESTRIS* (RYBD.) MONOCULTURES UNDER FIELD CONDITIONS

5.1 Introduction

Invasive species have the potential to severely disrupt ecosystems (Gurevitch and Padilla 2004). Plant invasions in particular have become a common problem world wide (Didham et al. 2005), with bunchgrass communities being a significant concern for many such invasions (Mack 1989). The effect of invasive species on indigenous species is known to be affected by many factors, including the type and intensity of disturbance, and environmental conditions (Gurevitch and Padilla 2004). Understanding the invasibility of a system must occur within the context of external factors capable of affecting invasion. To either prevent future invasions or contain existing invasions within endemic bunchgrass communities, an understanding is necessary of the fundamental ecological mechanisms regulating invasion processes.

Several contrasting theories exist to explain species invasion (Hierro et al. 2005). Of specific interest in the context of exotic species invasion into bunchgrass communities has been the “empty niche hypothesis”, which purports that communities with unutilized resources are more susceptible to invasion due to availability of resources needed by newly establishing species (Elton 1958). Further to this, the concept of ‘species packing’ has been proposed to maximize the number of endemic plants present to occupy vacant niches, and in the process, potentially increase community resistance to invading species (Elton 1958). Conceptually, greater species diversity appears to increase the likelihood of invasion resistance, although this theory has been met with mixed results (Elton 1958; Levine and D'Antonio 1999). An alternative notion to species packing is that a few highly competitive functional groups present in moderate to high density populations may be just as effective as species rich guilds in preventing invasion (Dukes 2002). Under the latter model, diversity may not be beneficial in preventing invasion, but rather exert a positive influence on preventing invasion through the increased likelihood of finding specific plant functional groups capable of preventing invasion. Should this be the case, once the functional groups or plant species capable of suppressing invasion are identified, diversity may be less important than the abundance and condition of plant species found in communities susceptible to invasion.

After initial establishment of the invasive species, successful invasion must favor continued expansion of the invader into the indigenous community. Three models explain how this invasion can occur. The driver model suggests that the invader drives plant community change by manipulating the environment. The passenger model suggests that the environment symotaniously manipulates both the community and the invader to allow it to invade empty spaces left when the indigenous species are suppressed (Didham et al. 2005). Finally the opportunistic model suggests that changes in the environment shift the community allowing for invasion (Chabrerie *et al.* 2008).

Disturbance has a key role in manipulating plant community composition by shifting the competitive advantage from stressed to non-stressed plants. As defoliation is a common land use and disturbance in grasslands, and is known to be patchy in nature, compositional changes arising from competitive shifts include those from defoliated to non-defoliated species, and from those plants with low regrowth potential (i.e. recovery) following defoliation to those with high regrowth potential. Plant species indigenous to North American grasslands however, may not be well adapted to the current timing and intensity of disturbance associated with contemporary land use practices (i.e. summer grazing in fescue grasslands), particularly with the accompanying presence of more stress-tolerant introduced species, which have the potential to become invasive given the opportunity (Grime 1974; Baker 1974; Mack et al. 2000). Such novel disturbance intensities and types may be driving invasion by disproportionately stressing indigenous species and creating empty niches for invaders to subsequently occupy (Didham et al. 2005). In this case invasive species are simply occupying empty niches left by modified disturbance regimes (MacDougall and Turkington 2005). In the fescue grasslands of southwestern Alberta, *Festuca campestris* (Rybd.) is considered the most competitive native bunchgrass, and is known to exclude other species in late seral and climax communities (Willms et al. 1998). In native grasslands, *F. campestris* can make up 36-85% of vegetative cover, while being absent or nearly absent in early seral grassland (Adams et al. 2003). Within fescue grasslands, *Poa pratensis* is a common invader and is particularly prevalent in early seral communities following moderate to heavy grazing during the growing season (Looman 1969). Grazing is therefore hypothesized to be a key mechanism effecting *F. campestris* decline, in turn facilitating replacement by grazing resistant *P. pratensis,* consistent with the passenger and opportunistic models of species invasion (MacDougall and Turkington 2005; Chabrerie *et al.* 2008).

P. pratensis is also known to invade in the absence of grazing (Martin and Chambers 2001), suggesting grazing may simply accelerate invasion, or invasion may depend further on unrelated environmental factors, such as the availability of light, water or nutrients, and their impact on the resistance of *F. campestris* grassland to invasion. Select environmental factors may be responsible for increasing the competitive ability and associated invasibility of *P. pratensis*. Should high densities of *F. campestris* not fully occupy the available niches in existing grasslands, *P. pratensis* may be more competitive under select environmental conditions (Seabloom et al. 2003), allowing *P. pratensis* invasion regardless of the niches present (MacDougall and Turkington 2005).

Our current understanding of the biology of the two predominant plant species in *F. campestris* grasslands suggests that both the driver and passenger models (Didham et al. 2005) offer plausible mechanisms for the regulation of invasion by *P. pratensis*. Moreover, under changing environmental variables *P. pratensis* may become a driver while under disturbance it may be a passenger. *P. pratensis* has undergone centuries of adaptation to grazing (Mack and Thompson 1982) and may therefore be better adapted to heavy summer defoliation (i.e. the current predominant grazing regime) than indigenous plant species. This may lead to *P. pratensis's* increased ability to occupy empty niches left by declining *F.*

campestris swards. *F. campestris* is well adapted to drought conditions (Chapter 6) and may lack the ability to utilize soil resources (water and nutrients) made available within early seral communities or recently disturbed soil. This leaves *P. pratensis,* a highly opportunistic species that is well adapted to high nutrient (N) (Martin and Chambers 2001) and water conditions (Bookman and Mack 1982; Jiang and Huang 2001), with a vacant niche into which to invade. Under these conditions, *F. campestris* may be unable to pre-empt *P. pratensis* from accessing resources, regardless of plant densities. In this situation, above ground competition would be the only means by which *F. campestris* could slow or stop invasion by *P. pratensis.* This resistance to invasion would be accomplished through increased plant density (interspecific competition) and litter accumulation (light competition).

5.2 Objectives

The overall goal of this study was to determine the extent to which *P. pratensis* abundance and invasion are affected by characteristics of the *F. campestris* community, including plant density and vigor as affected by defoliation. To isolate and test this question, plant responses were assessed in fallow field conditions where interspecific responses could be isolated. Specific objectives of this study include determining how:

1) *F. campestris* is impacted by intraspecific competition from cogeners, under varied planting densities and defoliation

2) *F. campestris* response varies as a function of *P. pratensis* presence

3) *P. pratensis* invasion varies as a function of *F. campestris* plant density

4) *P. pratensis* invasion varies as a function of *F. campestris* plant vigor, as regulated by defoliation

5.3 Methodology

5.3.1 Research Site and Plant Materials

This study was conducted in a fallow field near Cremona, Alberta, Canada (114^o 27’ 20” W 51^o 29’ 48” N) from May 2005 through August 2008. The field had been in fallow for the preceding 3 years to provide weed control. Soil is a deep, fertile Orthic Black Chernozem (Antler Series), with 15.9% organic matter, 7.0 pH, and clay texture (34% sand, 24% silt, 42 % clay) and a CEC of 24.5meq/100g. The site was nearly level (<2% slope) with an easterly aspect.

The study site is located in the Foothills Fescue Natural Subregion of Alberta, where the historic vegetation for the region was a fescue grassland. Mean annual precipitation for this region is 466 mm, with 61% falling during the growing season, which extends from approximately May 1 to August 30 (Adams et al. 2003).

In May 2005, *F. campestris* plants, 10-20 cm in basal diameter, were removed to 10 cm depth from a native grassland 30 km west of Cremona (114^o 47’ 31” W, 51^o 34’ 40” N). *F. campestris* plants from the immediate study area were not available due to the widespread conversion of fescue grasslands to cultivated cropland over the last century. Conditions at the location from where *F. campestris* plants were removed were similar to those at the study site, with a Black Chernozemic soil. Seed for *P. pratensis* was wild harvested in August 10 2005 from within 1 km of the study site, and had a germination of 84%. *Poa pratensis* plants were harvested from an invaded grasslandconsidered representative of local, naturally occurring ecovars in the region and actively invading *F. campestris* grasslands.

5.3.2 Experimental Design

This study was conducted using a microcosm design employing the two focal species *F. campestris* and *P. pratensis*. Microcosm experiments have been used in the past to successfully examine interspecific relationships between plant species (Drake et al. 1996), and were considered appropriate here given the objective of testing specific mechanisms governing *P. pratensis* invasion and/or *F. campestris* resistance to invasion. Moreover, simple binary mixtures of plant species were used to isolate the interspecific relationships between these species to the exclusion of other vegetation (the latter is being examined elsewhere in related studies - see Chapter 3). At the start of the study, broadleaf (dicot) species were largely eliminated for the duration of the study with the application of Grazon (containing the active ingredients picloram + 2,4-D), a herbicide providing residual properties for long-term broadleaf weed control. In addition, volunteer grassy weeds (annuals and perennials) were hand pulled throughout the study, as required.

On May 4 2005, *F. campestris* bunchgrass plants extracted from the native grassland were cut into quarters (approximately 5 cm diameter x 10 cm deep), and 756 cuttings planted in a standard planting configuration including a single *F. campestris* focal plant surrounded by 6 exterior plants (Fig 5.1). These plants were then allowed to establish over 2 growing seasons. During the first year, any transplants that died were replaced. The 12 treatments (Table 5.2) consisted of 3 combinations of separate fixed factors: plant density (15, 30 or 45 cm), defoliation (presence or absence) and *P. pratensis* (presence or absence), in a full factorial design with 9 replications (N=108). High density (15 cm spacing) to low density (45 cm spacing) treatments were considered representative of early seral to late seral fescue grassland communities, respectively, which in turn were hypothesized to fundamentally differ in the presence of vacant niches in the plant interspaces, and which were susceptible to *P. pratensis* invasion.

Plots from each planting density were further separated into those where *F. campestris* was either defoliated in mid summer or undefoliated, and either exposed to *P. pratensis* invasion or not, in a crossover randomized complete block design, resulting in a total of 12 treatment combinations, each replicated 9 times. *P. pratensis* invasion was examined by seeding this species around the full perimeter of these plots (i.e. adjacent to exterior *F. campestris* plants) (Fig. 5.1). Within plots where *P. pratensis* was seeded, seed was hand broadcast on May 7, 2007 at a rate of approximately 15 kg/ha of pure live seed, thereby exposing *P. pratensis* seedlings to competition from adjacent *F. campestris* plants. Defoliation was conducted as a one time event on August 1, 2007, to simulate a typical mid-summer grazing event. Defoliation occurred 2.5 cm above ground on all plants in each plot. Although all vegetation was defoliated non-selectively, *P. pratensis* was generally not tall enough to be defoliated.

5.3.3 Plant and Environmental Measures

Over the 4 year study period, environmental conditions were monitored monthly (soil moisture, light penetration, and precipitation) during the growing season. Volumetric soil moisture in the top 10 cm of soil was recorded monthly using a Delta-T^{TM} model ML2X theta moisture probe (Cambridge, UK) beginning May 10th each year, and continuing through August 31st in 2006 and 2007, and ending in July 2008 after final destructive sampling of vegetation. A rain gauge was located on site to record precipitation from mid-April through October 1. Year round temperature and precipitation data were also available from the nearest Environment Canada weather station, located at Maden, 14 km southeast of the study site.

Photsynthetically active radiation (PAR, in the 400 to 700 nm wavebands) was measured using a Decagon AccuPAR^{TM} ceptometer. PAR was recorded using 5 averaged samples above each plot, and compared to the average of 5 samples collected at the soil surface at the mid point between the focal and exterior *F. campestris* plants. All light measures were converted to % of PAR in the open for analysis. Measurements of PAR were repeated twice for each plot at 90 degree angles once a month between May 1 and August 31 in 2006 and 2007, and through July 2008. All light measurements were conducted around solar noon (±2 hr) on uniformly overcast days.

Vegetation sampling included yearly non-destructive measurements of *F. campestris* vigor, as reflected by tiller numbers, maximum tiller height per plant, the number of inflorescences per plant, the maximum height of inflorescences per plant and average basal diameter per plant (two perpendicular measures taken at 90^o were averaged). These measures, together with mortality, were taken yearly from June 1, 2005 through July of 2008 during the growing season of each year. Biomass removed during implementation of the defoliation treatments in 2007 was quantified, as well as the final standing biomass of both *P. pratensis* and *F. campestris* (August 1, 2008). Biomass of *F. campestris*, both focal and exterior plants, was assessed. *P. pratensis* biomass (g/m^2) was sampled in the exterior 30 cm of each plot at each density (High=0-30, Medium=10-40, Low=20-50).

Seedling establishment of *P. pratensis* and *F. campestris* was monitored through cover assessments on July 15, 2008. Counts were conducted within contiguously placed 10 x 10 cm quadrats from the edge of the focal *F. campestris* plant, through the central interspace of exterior *F. campestris* plants (see Fig. 5.1), and was repeated for all directions around the focal plant. This procedure resulted in a variable number of quadrats being assessed for each planting density (i.e., n=3, 4 and 5 for high density, moderate density, and low density plots, respectively). Additionally, two distance measures were taken July 15-18, 2008 to assess the spatial extent of encroachment by *P. pratensis*. The first was encroachment from the plot perimeter towards the focal plant. For this measure the distance from the original planting location of the *P. pratensis* to its closest distance to the focal *F. campestris* plant was assessed. The second distance measure was the minimum distance between the exterior *F. campestris* plants and adjacent *P. pratensis* plants.

5.4 Analysis

Response variables included that of focal *F. campestris* plants, exterior *F. campestris* plants and seeded *P. pratensis*. All data from exterior *F. campestris* plants were averaged in each plot (n=6) prior to analysis. Similarly, measures of *P. pratensis* taken within the interspaces between exterior *F. campestris* plants were averaged for each plot (n=6). All data were analyzed using SAS statistical software version 9.2 (SAS Institute Inc 2008).

Normality and equality of variances were examined for all data prior to analysis. A square root transformation was performed on *F. campestris* seedling cover, *P. pratensis* cover, focal *F. campestris* tiller counts and the proportion (i.e. %) of focal *F. campestris* tillers with inflorescences. No transformations were needed for distance measures of encroachment by *P. pratensis*, exterior *F. campestris* tiller counts or inflorescences, the final biomass of *F. campestris* and *P. pratensis*, July light transmittance, or July soil moisture content.

Mortality data were assessed with a Chi-Square analysis for the effects of planting location (exterior vs. focal), planting density, defoliation, and the presence of *P. pratensis*. Analysis of all other responses, including biomass, tiller counts, plant cover, July light transmittance, July soil moisture content, and the distance metrics assessing encroachment by *P. pratensis* into plots (Fig 5.2), was done using an ANOVA with mixed model procedures for a randomized complete block design. All data were analyzed for 2008, except for tiller data, which were analyzed for both 2007 and 2008. Tiller counts from 2006 were used as a covariate for all analyses to adjust for differences in initial *F. campestris* plant size, but had no effect on the biomass model ($p > 0.63$), and was therefore removed in the final analysis of those data. Finally, regression analysis was used to assess changes in the cover of *F. campestris* seedlings and *P. pratensis* ramets encroaching at varying distances from the focal plant. Regression was also used to assess changes in final *P. pratensis* biomass and cover analysis in relation to neighboring *F. campestris* biomass and tiller counts.

Preliminary assessment of the plots indicated there were inconsistencies in *P. pratensis* establishment among plots, with some unexpected growth (<30g/m^2) in unseeded check (-B) plots (n=7), presumably due to volunteers, and little *P. pratensis* in others that were seeded with this species (+B; n=7). A threshold of 10 g/m^2 was used as a cutoff for plots delineating those with and without *P. pratensis*. Moreover, this resulted in minimal changes to final sample sizes among treatment combinations (N range of 8-10 per treatment combination).

Tiller counts of *F. campestris* were analyzed as 4 variables, including the total number of tillers of focal plants or exterior plants, and the proportion of tillers with inflorescences at both the focal plant and exterior plant locations. Two procedures were used in the analysis of cover. First, density and defoliation effects were assessed with cover data from the exterior 30 cm of each plot. This was done by averaging cover from the three 10 x 10 cm quadrat measures nearest the perimeter of plots from each density (i.e. High=0-10cm, 10-20cm, 20-30cm; Medium=10-20cm, 20-30cm, 30-40cm; Low=20-30cm, 30-40cm, 40-50cm) (see Fig. 5.2). The second cover analysis was on the effects of distance from the focal plant and its interactions with defoliation and density. For this analysis all cover quadrats within the plot were utilized (High=10-30cm, Medium=10-40, Low=10-50).

5.5 Results

Key results are summarized in this section. A comprehensive list of all P-values including that of non-significant variables can be found in Appendix C.

5.5.1 *Festuca campestris* Responses

5.5.1.1 Mortality

At the end of the study in 2008, mortality remained relatively low for all *F. campestris* plants. Nevertheless, plant mortality differed between planting locations (P=0.002) and planting density (P<0.0001). Focal plants had greater mortality (12.0%) compared to exterior plants (4.5%), and mortality was greater for plants within high density plots (10.7%) than either medium density (4.4%) or low density (1.6%) plots. No difference (P>0.05) was found between *F. campestris* mortality in plots with (5.6%) and without (5.6%) *P. pratensis*.

5.5.1.2 Tillers

Tiller counts on focal *F. campestris* plants were affected by planting density (P<0.0001), density x year (P=0.002), defoliation (P<0.0001), the interaction of density x defoliation (P=0.09), and a 3-way interaction of density, defoliation and *P. pratensis* (P=0.02). Tiller numbers of exterior *F. campestris* plants responded to density, density x year, defoliation, and density x defoliation in the same way as focal plants. In addition there was an interaction of *P. pratensis* and defoliation (P=0.09).

Focal *F. campestris* plants had fewer tillers within high density (83.2±18.9) compared to medium (157.4±18.5) and low (196.6±18.9) density plots, although this took until 2008 (the final year of sampling) to appear (Table 5.1). Focal plants also produced more tillers in response to defoliation (+D:184.3±16.5 vs -D: 107.2±16.5), although this effect was evident only within the medium and low density plots (Table 5.2). Within exterior plants this defoliation effect only occurred in the absence of *P. pratensis* (Table 5.3). Closer examination of the 3-way interaction of density, defoliation and *P. pratensis* presence (Fig. 5.3) indicated that at medium planting densities, defoliation alone increased tillers in *F. campestris*, but only in the absence of *P. pratensis*. While the same trend occurred within low density plots, the response to defoliation alone remained non-significant, and instead *F. campestris* focal plants exposed to both defoliation and *P. pratensis* had the greatest number of tillers (Fig. 5.3).

5.5.1.3 Sexual Reproduction

Sexual reproductive effort of focal *F. campestris* plants, as assessed by the proportion of tillers producing inflorescences, was affected by the year of sampling (P<0.0001), as well as by the interaction of density and year, which was not significant (P=0.013). The proportion of *F. campestris* tillers with inflorescences was markedly greater in 2007 (29.8±2.2) than 2008 (14.3±2.3). During 2007, the proportion of tillers with inflorescences declined from low to medium and through high density plots (Table 5.1). Although the opposite trend occurred one year later in 2008, with high planting densities increasing the likelihood of tillers producing inflorescences, no differences were found in the proportional production of reproductive tillers (Table 5.1). Despite this, the markedly lower number of tillers within high density plots during 2008 led to a sharp reduction in the actual number of inflorescences per plant in both years. For example, the low, medium and high density treatments in 2007 were associated with 34.5, 30 and 13 inflorescences/plant, respectively. During 2008, these same treatments were associated with 34.7, 28 and 19.5 inflorescences/plant.

Exterior *F. campestris* plants also demonstrated a response in inflorescence production, including an interaction of defoliation x *P. pratensis* (P=0.10). Defoliation tended to reduce *F. campestris* inflorescence production, but only in the absence of *P. pratensis* (Table 5.2). Conversely, inflorescences of *F. campestris* plants grown with *P. pratensis* had little response to defoliation.

5.5.1.4 Cover

Seedling cover of *F. campestris* within the interspaces in August 2008 reflect the establishment of new *F. campestris* plants from seed produced by adjacent plants. Seedling cover was affected by density (P=0.001) and defoliation (P=0.06). Planting density affected the cover of *F. campestris*, with low density plots having greater cover (11.2±1.5%) than either medium (6.1±1.6%) or high density plots (9.7±1.7%). Defoliation increased the cover of *F. campestris* from 8.2±1.5% to 9.9±1.5 %.

Spatial variation in seedling recruitment also occurred within plots (Fig. 5.4). *F. campestris* seedlings generally peaked in cover at sampling distances farthest away from all parent plants, particularly at high and moderate planting densities. At low planting densities, seedling cover was generally high (i.e. 10-12%) throughout the interspace between *F. campestris* plants. In contrast, seedling recruitment appeared to peak about 30 cm and 20 cm from focal *F. campestris* plants, within moderate and high density plots, respectively (Fig. 5.4).

5.5.1.5 Biomass

Biomass of *F. campestris* was influenced by density (P<0.0001), defoliation (P=0.004) and an interaction of the two (P=0.07). Increased planting densities reduced the size of *F. campestris* plants at the end of the study from 65.3±6.7 g/plant under low density, to 50.5±6.7 g/plant under medium density, to 22.6±6.7 g/plant under high density. In addition, the biomass of *F. campestris* plants was reduced by defoliation from 56.3 ±5.8 g/plant to 36.0 ±5.8 g/plant.

This relationship was particularly strong within the low density treatment, thereby reducing effects of density (Table 5.3). Individual tiller biomass responded to defoliation (P=0.05) by reducing biomass from 0.22±.015 g/tiller to 0.19±0.015 g/tiller.

In general, *F. campestris* plant biomass was markedly reduced by *P. pratensis*, for both focal (P=0.02; 54.5±5.9 vs 37.7±5.9 g/plant) and exterior (p=0.05; 47.8±3.6 vs 41.2±3.6 g/plant) plants. The biomass per tiller of *F. campestris* was also affected by *P. pratensis* (P=0.01) and the interaction with plant density (P=0.02). *P. pratensis* reduced biomass per tiller from 0.23±0.015 g/tiller to 0.18±0.015 g/tiller. In addition, the introduction of *P. pratensis* at high and moderate densities reduced biomass per tiller while at low densities there was no significant effect of *P. pratensis* (Table 5.4).

5.5.2 *Poa pratensis* Response to *Festuca campestris*

The average biomass of *F. campestris* plants significantly altered the invasion of *P. pratensis*, although this effect varied among planting densities (Fig 5.5). At high densities, there was no relationship between *F. campestris* biomass and *P. pratensis* biomass. At medium and low densities, however, *P. pratensis* biomass varied inversely with *F. campestris* biomass. Similarly, *P. pratensis* final cover within interspaces was related to the size of *F. campestris* plants as reflected by tiller counts, but only at low planting densities (Appendix C) where *F. campestris* plants were larger.

Encroachment by *P. pratensis* into the interior of plots was assessed through distance measures from the outer perimeter of plots (i.e. original seeded location) to the extent of *P. pratensis* entry towards focal *F. campestris* plants. Density had a significant effect on invasion ($P \leq 0.0001$). Distance of *P. pratensis* entry into plots was greatest within low density plots, while high density plots not only prevented *P. pratensis* entry, but limited *P. pratensis* to areas outside of seeded areas resulting in negative encroachment (Fig. 5.6). Medium density plots showed moderate encroachment of *P. pratensis* (Fig 5.6).

Changes in *P. pratensis* cover across varying distances from the focal plant indicated that *P. pratensis* cover decreased under a high density planting, but only within plots that remained undefoliated (Fig 5.7). In contrast, defoliation facilitated a large increase in *P. pratensis* cover, similar to that observed in medium and low density plots, regardless of defoliation treatment.

Final *P. pratensis* biomass was influenced by density ($P=0.06$) and the interaction of density and defoliation ($P=0.09$. *P. pratensis* biomass increased from high (177.6±20.6 g/m^2) to medium (214.2±21.4 g/m^2) and finally to low density (242.4±21.3 g/m^2), although only the high and low densities differed significantly. *P. pratensis* had the greatest biomass where *F. campestris* was planted at low densities and was defoliated (Table 5.3). However, this increase was only significant relative to defoliated plots grown under moderate and high densities. In the absence of defoliation, *P. pratensis* biomass remained uniformly high (212.3±27.1 to 238.9±28.0 g/m^2).

5.5.3 Environmental Factors

July soil moisture was altered by plant density (P<0.0001), year (P<0.0001) and defoliation (P=0.002). Increasing density significantly reduced soil moisture (Low: 18.7±0.3%, Medium 15.8±0.3%, High: 12.3±0.3%), while defoliation increased soil moisture from 15.1±0.2% to 16.0±0.2%. In 2007, soil moisture content was lower (12.60±0.2%) than in 2008 (187±0.2%). July light levels were only affected by plant density (P=0.01) with low density treatments having significantly higher light infiltration (23.6±1.5%) than medium (18.5±1.5%) or high (17.6±1.5%) density treatments.

5.6 Discussion:

The design of this project, which uses a microcosm with only two focal species, does not represent the diversity of the fescue grasslands and therefore the responses in this investigation must be interpreted within the context of the experiment. Microcosms are however, effective in isolating interspecific relationships between plant species (Drake et al. 1996). Responses in the present study may therefore be used to help understand potential relationships observed within the complexity of natural ecosystems (Chapter 3). These responses also have implications within reclamation systems where species diversity can be reduced to only a few dominating species (Chapter 7).

5.6.1 Intraspecific Competition within *Festuca campestris*

Survival and vigor of *F. campestris* plants, as evidenced by tiller number, sexual reproductive effort, and biomass, declined with increasing initial planting density. Within high density plots, *F. campestris* demonstrated particularly strong intraspecific competition (Archer and Detling 1984), which may be associated with how *F. campestris* plants grew into each other. Moreover, focal plants had reduced growth compared to exterior *F. campestris* plants. Closer spacing among plants was associated with a reduction in available soil moisture, and to a lesser extent light, and likely represents intensified competition for limited resources. In contrast, low density plots appeared to have fewer negative interactions among *F. campestris* plants, as exemplified by high growth. In any case, these responses highlight that *F. campestris* is susceptible to intraspecific competition, much the same way as *Festuca idahoensis* (Sheley et al. 2006). Observed responses may also explain why *F. campestris* grows in a systematic (i.e. dispersed) pattern, whereby neighbors and resources may determine the distance between tussocks. These responses assume only intraspecific competition or competition with only one other species is occurring, and while this may be fairly realistic in reclamation situations (Chapter 7) it is not the case in natural ecosystems (Chapter 3) where over 50 species may be coexisting in a given community. These responses must therefore be explained in light of more complex communities (Chapter 3).

As this study examined *F. campestris* growth within fallow fields, this investigation provided the opportunity to assess seedling recruitment under optimal conditions (i.e. low competition from neighboring vegetation). Seedling recruitment within plant interspaces was reduced under increasing planting densities. Patterns of *F. campestris* seedling recruitment were complex, and likely reflect a combination of varying density of seed rain, coupled with opportunities for germination and emergence of seedlings based on competition from other plants, including conspecifics.

Like many other grasses, seed rain from *F. campestris* has a limited dispersal distance and consequently the seed bank is large below and adjacent to parent plants (Cook 1980; Houle 1995; Willms and Quinton 1995; Bakker et al. 1996). Nevertheless, seed availability did not appear to limit *F. campestris* establishment, as evidenced by ample seedling recruitment at all locations of plots, regardless of planting density. Concentrated deposition of seed however, may help account for the maximal abundance of *F. campestris* seedlings in high density plots, but only at the mid-point of the interspace between interior and exterior *F. campestris* plants.

Sharp reductions in seedling abundance near parent plants in medium and high density plots suggests recruitment declined under more intense competition near established plants. Although other studies have suggested that seedlings may require shelter from parent plants for successful establishment (Houle 1995), this did not appear to be the case in the presence study. As bunchgrass recruitment is known to be relatively slow (Page and Bork 2005), and mature bunchgrasses like *F. campestris* tend to have very large fibrous root systems (Moss and Packer 1983) capable of effectively capturing resource like soil water, competition from parent plants may be an important mechanism to limit the establishment of conspecifics near established plants (i.e. through self-thinning), which in turn, may reduce the vigor of the overall population. However, given that seedling recruitment was greatest and relatively uniform within the interspace of low density plantings, seedlings of *F. campestris* may be relatively resistant to intraspecific competition provided the latter is limited in spatial pattern to one side of seedlings.

This study appears to be the first documenting *F. campestris* seedling emergence over time. *F. campestris* plants are long-lived, and likely to survive for several decades, much like other bunchgrasses in western North America. Although high recruitment of seedlings is unlikely to occur in existing *F. campestris* grasslands, observed responses do highlight the ability of *F. campestris* to colonize available microsites (i.e. bare soil) provided competition is limited. Periodic availability of microsites for *F. campestris* recruitment, particularly at locations segregated from parent plants, may lead to large increases in seedling recruitment, and in the process could explain the increase in 'pulse' reproductive efforts in this species following disturbance such as fire (Bogen et al. 2003).

Festuca campestris plants responded to one-time defoliation by increasing tiller numbers despite decreased plant biomass, responses consistent with other studies (Bogen et al. 2003; May et al. 2003). These findings reinforce the adaptation of *F. campestris* by allowing this species to reallocate resources to more but smaller tillers, and could be an important strategy to minimize short-term exposure to future disturbances including defoliation and fire (Bogen et al. 2003). In contrast, long-term grazing reduces *F. campestris* (Willms et al. 1985), suggesting that this adaptation has limited benefit to repeatedly defoliated plants (Mengli et al. 2005).

5.6.2 ***Festuca campestris* Response to *Poa pratensis***

P. pratensis was only able to suppress *F. campestris* tillering under defoliated conditions, wherein *F. campestris* attempted to compensate for losses in biomass through increased tillering. Such inability to drive change suggests that *P. pratensis* invasion may be primarily opportunistic within the current environmental conditions. In contrast it appears that P. pratensis relies on external factors such as defoliation events to weaken *F. campestris* stands before invasion can proceed (Looman 1969). Exterior plants appeared to react in this way regardless of density which may be explained by lower intraspecific competition. Focal plants at medium density responded in the same way as exterior plants, but at low and high density there was no significant affect of *P. pratensis* regardless of defoliation. At low density the lack of an effect can be explained by the fact that *P. pratensis* cover had not yet reached the focal plants at this density. At high densities, intraspecific competition pressure was so high the addition of a new competitor had little effect on plant growth. Suppression of *F. campestris* by *P. pratensis* is therefore ineffective at high densities of *F. campestris* and therefore dense stands of *F. campestris* may potentially resist invasion.

5.7 Conclusion

The responses observed in this study suggest *F. campestris* is a strong competitor with the ability to competitively exclude other plants through interspecific and intraspecific competition. Density of *F. campestris* plants appeared to be the most significant factor influencing the vigor of grass plants regardless of plant age. This competitive exclusion may have been caused by reductions in soil moisture and photosyntheitically active radiation observed with increasing plant density. The interactions of *P. pratensis* with *F. campestris* suggest that where *F. campestris* plants were suppressed by summer defoliation, is it possible for *P. pratensis* to have a suppressive effect on *F. campestris*. Even then, these responses were tempered at high density where there was no effect on focal plants (i.e. only exterior plants). The responses in this study suggest that *P. pratensis* is an opportunistic species that is suppressed by *F. campestris* plants at high density. Management strategies that avoid summer defoliation and enhance *F. campestris* density appear to be best suited in suppressing *P. pratensis* vigor.

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Table 5.1 Mean (±SE) tiller counts of focal and exterior *F. campestris* plants, as well as the proportion of focal tillers with inflorescences, in response to the interaction of sampling year and *F. campestris* planting density .

		Focal *F. campestris* Plants		Exterior Plants
Year	Density	Tiller Numbers (# plant^{-1})	Proportion Tillers With Inflorenscens (%)	Tiller Numbers (# plant^{-1})
2007	High [2]	59.8 (±23.9) c [1]	21.7 (±3.7) c	74.6 (±14.2) d
	Medium	99.4 (±23.6) c	30.1 (±3.7) b	79.5 (±13.9) d
	Low	91.2 (±23.9) c	37.8 (±3.6) a	90.5 (±14.3) d
2008	High	106.7 (±23.9) c	18.4 (±3.9) c	145.8 (±14.2) c
	Medium	215.5 (±23.6) b	13 (±3.8) c	197.7 (±13.9) b
	Low	302 (±23.9) a	11.5 (±3.7) c	254.3 (±14.2) a

[1] Within a column, means with different letters differ, $p<0.05$.

[2] High = 0.15 m spacing, Medium = 0.30 m spacing, and Low = 0.45 m spacing

Table 5.2 Mean (±SE) biomass (g/plant) and tiller counts of focal *F. campestris* plants, invading *P. pratensis* biomass (g/m^2), and minimum distance of *P. pratensis* from adjacent exterior *F. campestris* plants, in response to the interaction of density and defoliation.

Defoliation	Density	Focal *F. campestris* Biomass (g)	Focal Tiller No/Plant	*P. pratensis* Biomass (g/m^2)	Minimum Distance Between *P. pratensis* and Exterior *F. campestris* (cm)
+D [3]	High [2]	19.3 (±8.9)d [1]	89.5 (±24.1) cd	143 (±28)c	4.93 (±0.85) b
	Medium	44.6 (±9) bc	190.8 (±23.6) b	189.5 (±29.3)bc	7.7 (±0.85) a
	Low	44 (±8.9)bc	272.7 (±24.1) a	264.8 (±27.6)a	7.4 (±0.86) ab
-D	High	25.9 (±9) cd	76.9 (±23.7) d	212.3 (±27.1)ab	7.83 (±0.85) a
	Medium	56.3 (±8.9)b	124.1 (±23.6) c	238.9 (±28)ab	7.88 (±0.85) a
	Low	86.6 (±9) a	120.4 (±23.7) c	220 (±29.7)ab	7.96 (±0.85) a

[1] Within each column, means with different letters differ, $p<0.05$ ($p<0.06$ for *P. pratensis*).[2] Density of *F. campestris* is divided into: High = 0.15 m spacing, Medium = 0.30 m spacing, Low = 0.45 m spacing

[3] +D = defoliated plots, -D = undefoliated plots

Table 5.3 Number of vegetative tillers and proportion of tillers with seed heads within exterior *F. campestris* plants exposed to combinations of defoliation and *P. pratensis* invasion.

Defoliation	*P. pratensis*	Tillers	% Tillers Flowering
+D [2]	+B [3]	146.4 (±12.5) ab[1]	23.3 (±2.3) ab
	-B	166.8 (±12.4) a	20.7 (±2.3) b
-D	+B	129.2 (±12.4) bc	24.6 (±2.3) ab
	-B	119.2 (±12.5) c	27.3 (±2.3) a

[1] Within a column, means with different letters differ, $p<0.05$.

[2] +D = defoliated plots, -D = undefoliated plots

[3] +B = Plots with *P. pratensis* and –B = Plots without *P. pratensis*

Table 5.4 Focal *F. campestris* biomass / tiller (±SE) in response to the interaction of *P. pratensis* introduction and planting density.

Level	Density	*F. campestris* Biomass / Tiller (g)
+B[3]	High[2]	0.17 (±0.02)b[1]
	Medium	0.16 (±0.02)b
	Low	0.21 (±0.02)ab
-B	High	0.23 (±0.03)a
	Medium	0.25 (±0.02)a
	Low	0.20 (±0.02)ab

[1] Means with different letters differ, $p<0.05$.

[2] Density of *F. campestris* is divided into: High = 0.15 m spacing, Medium = 0.30 m spacing, Low = 0.45 m spacing

[3] +B = Plots with *P. pratensis* and –B = Plots without *P. pratensis*

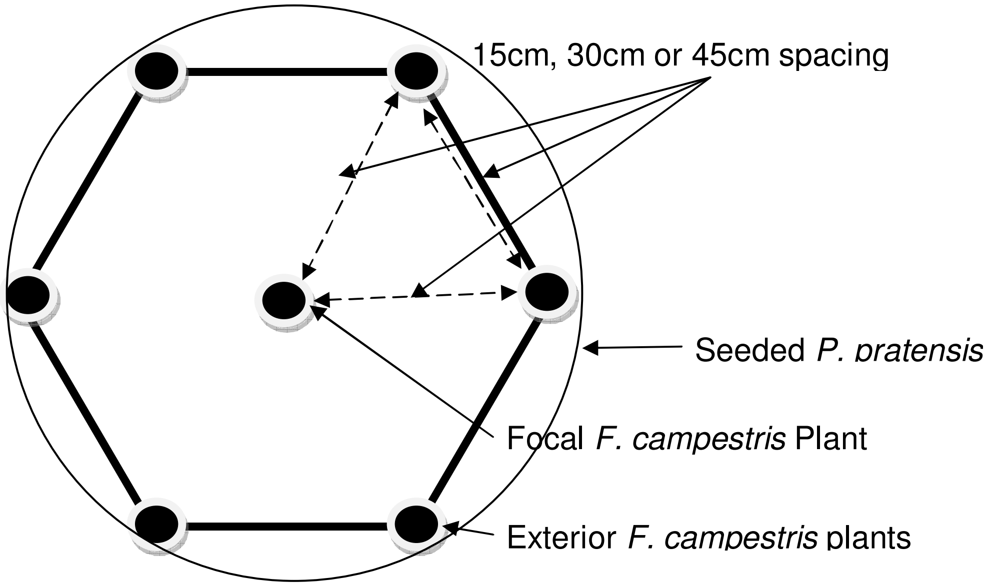

Figure 5.1 Standardized configuration of *F. campestris* and *P. pratensis* plants in the variable density study.

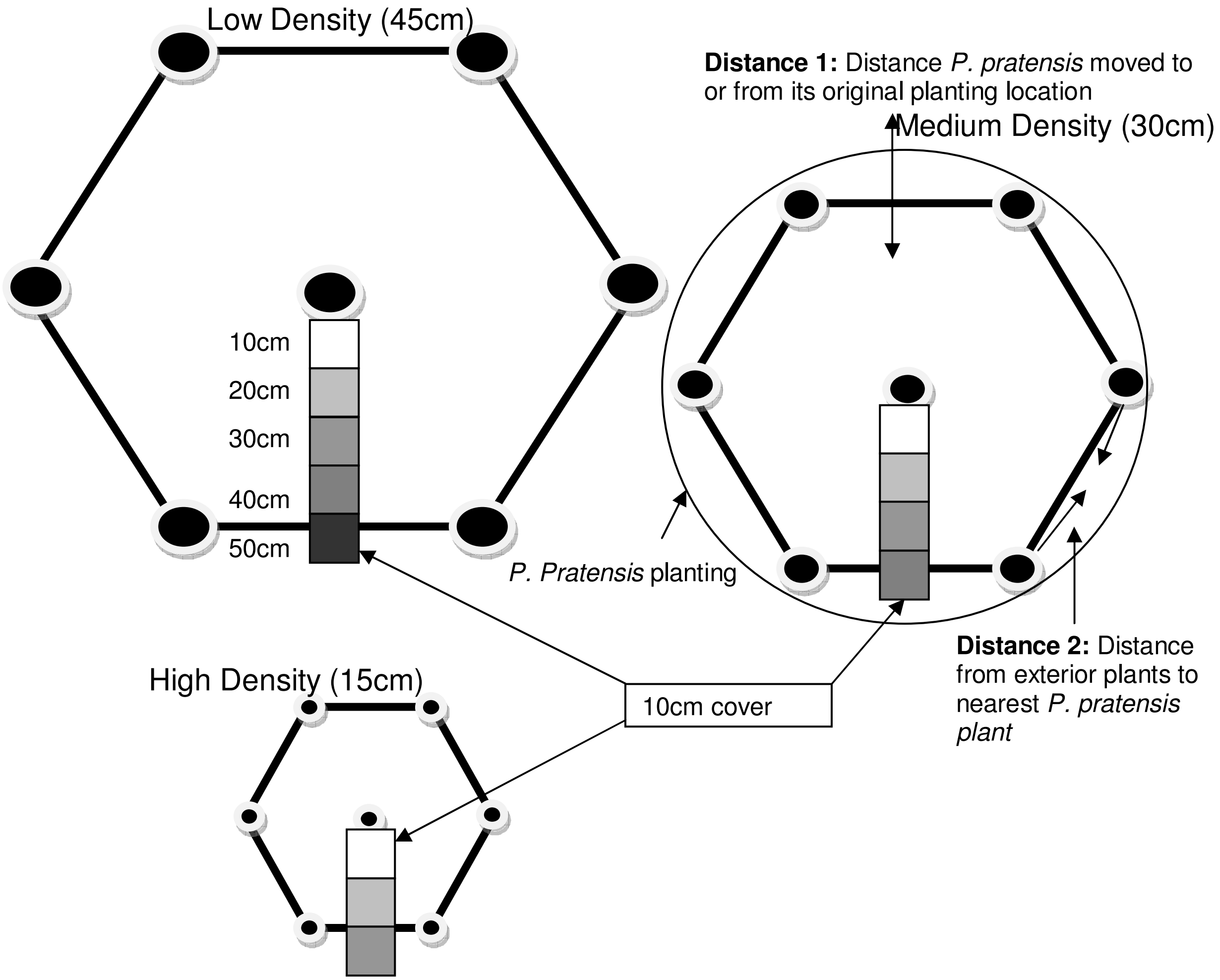

Figure 5.2 Standardized configuration of *F. campestris* and *P. pratensis* plants and measurements taken within the variable density study.

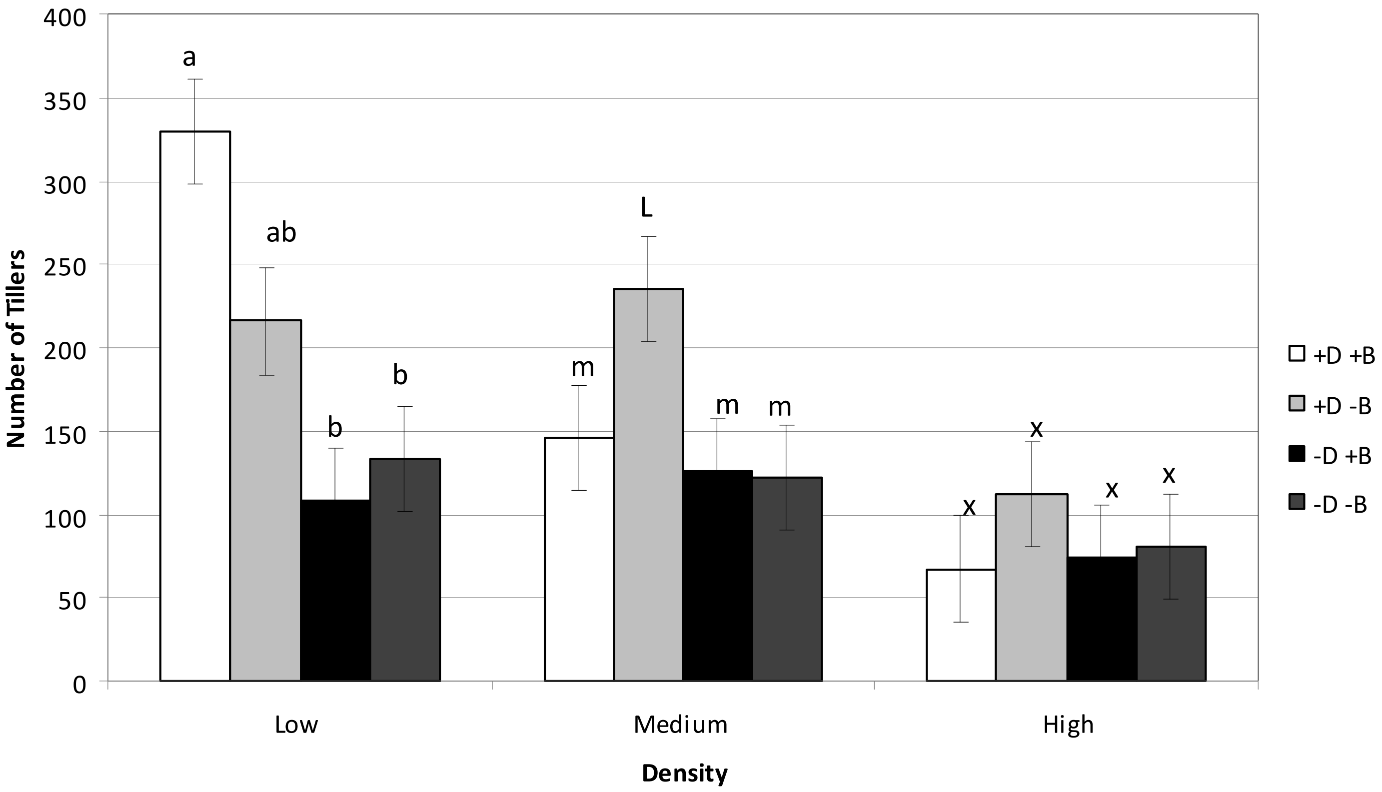

Figure 5.3 Mean (±SE) tiller counts of focal *F. campestris* plants in response to combinations of planting density, defoliation and *P. pratensis* introduction. Within a density, means with different letters differ significantly P<0.05. Density of *F. campestris* is divided into: High = 0.15 m spacing, Medium = 0.30 m spacing, Low = 0.45 m spacing. +D = defoliated plots, -D = undefoliated plots. +B = Plots with *P. pratensis* and –B = Plots without *P. pratensis*

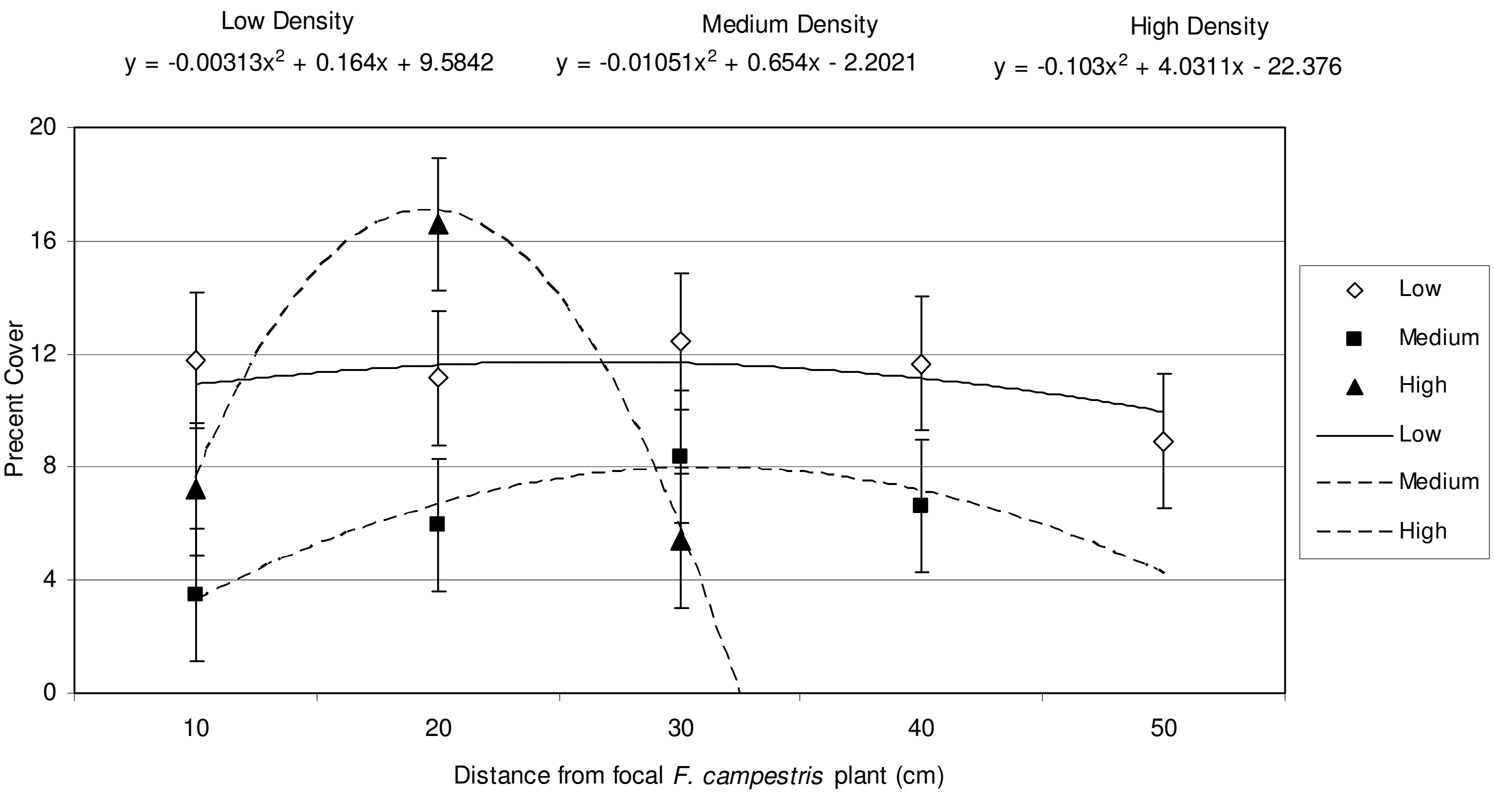

Figure 5.4 The interaction of planting density and distance from the focal plant on the cover of *F. campestris* seedlings as measured during the final assessment in 2008. Points represent the mean of all samples within a density x distance combination. Density of *F. campestris* is divided into: High = 0.15 m spacing, Medium = 0.30 m spacing, Low = 0.45 m spacing

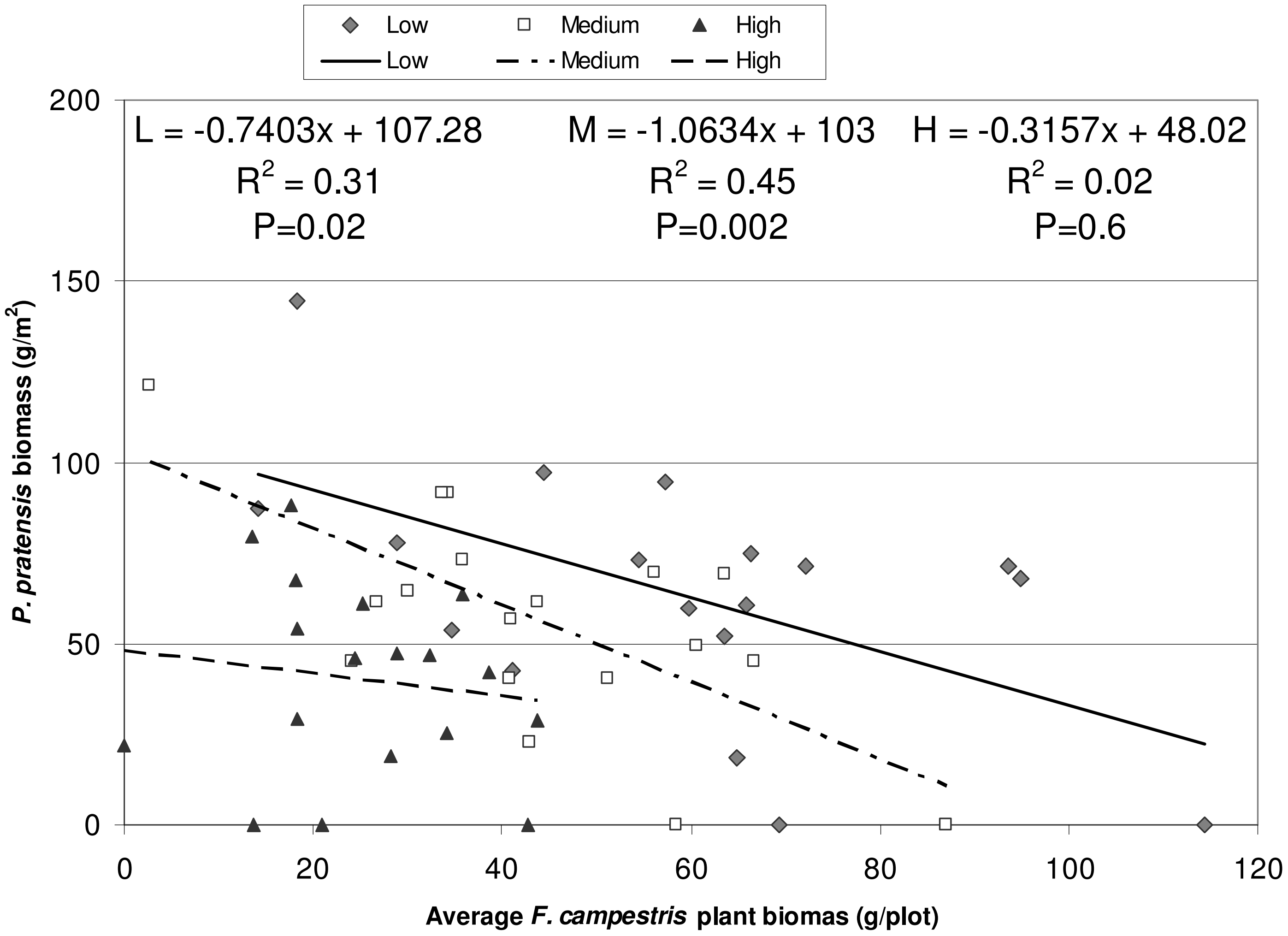

Figure 5.5 The relationship between mean *P. pratensis* biomass (g/m^2) and *F. campestris* plant biomass per plot in high, medium, and low density plantings. Density of *F. campestris* is divided into: H = 0.15 m spacing, M = 0.30 m spacing, L= 0.45 m spacing.

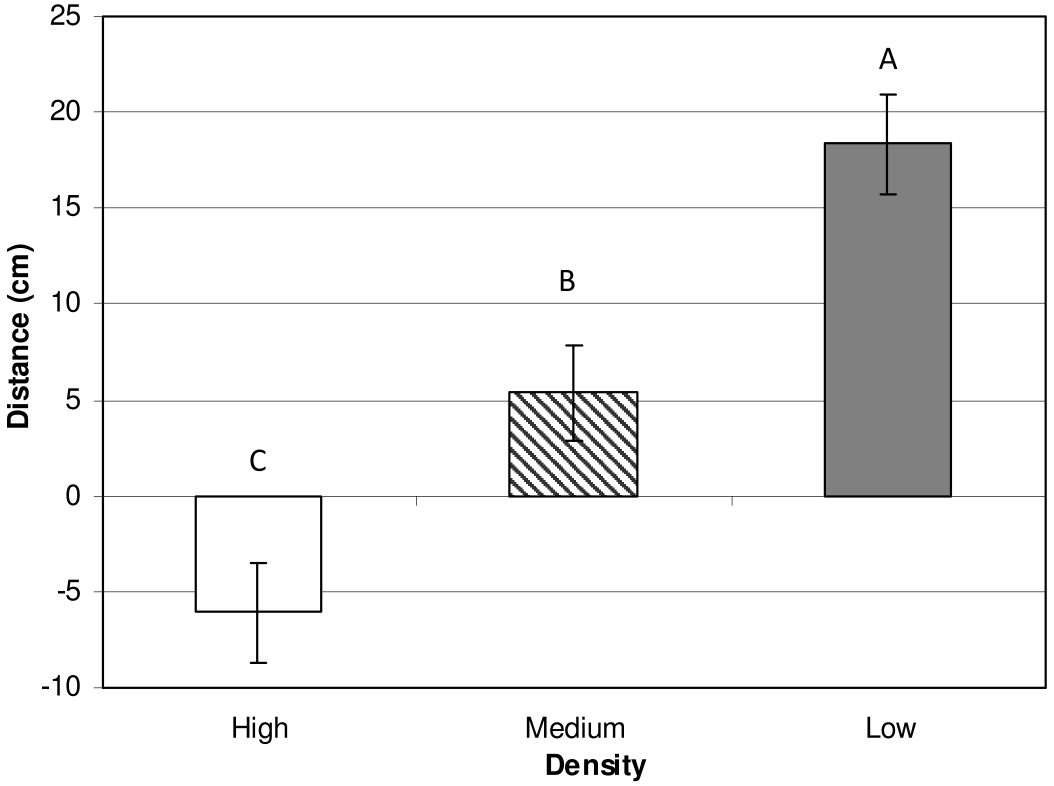

Figure 5.6 The mean distance (±SE) of *P. pratensis* encroachment from the perimeter into the plot towards focal *F. campestris* plants at each of 3 different planting densities. Letters show significant differences P<0.05. Density of *F. campestris* is divided into: High = 0.15 m spacing, Medium = 0.30 m spacing, Low = 0.45 m spacing

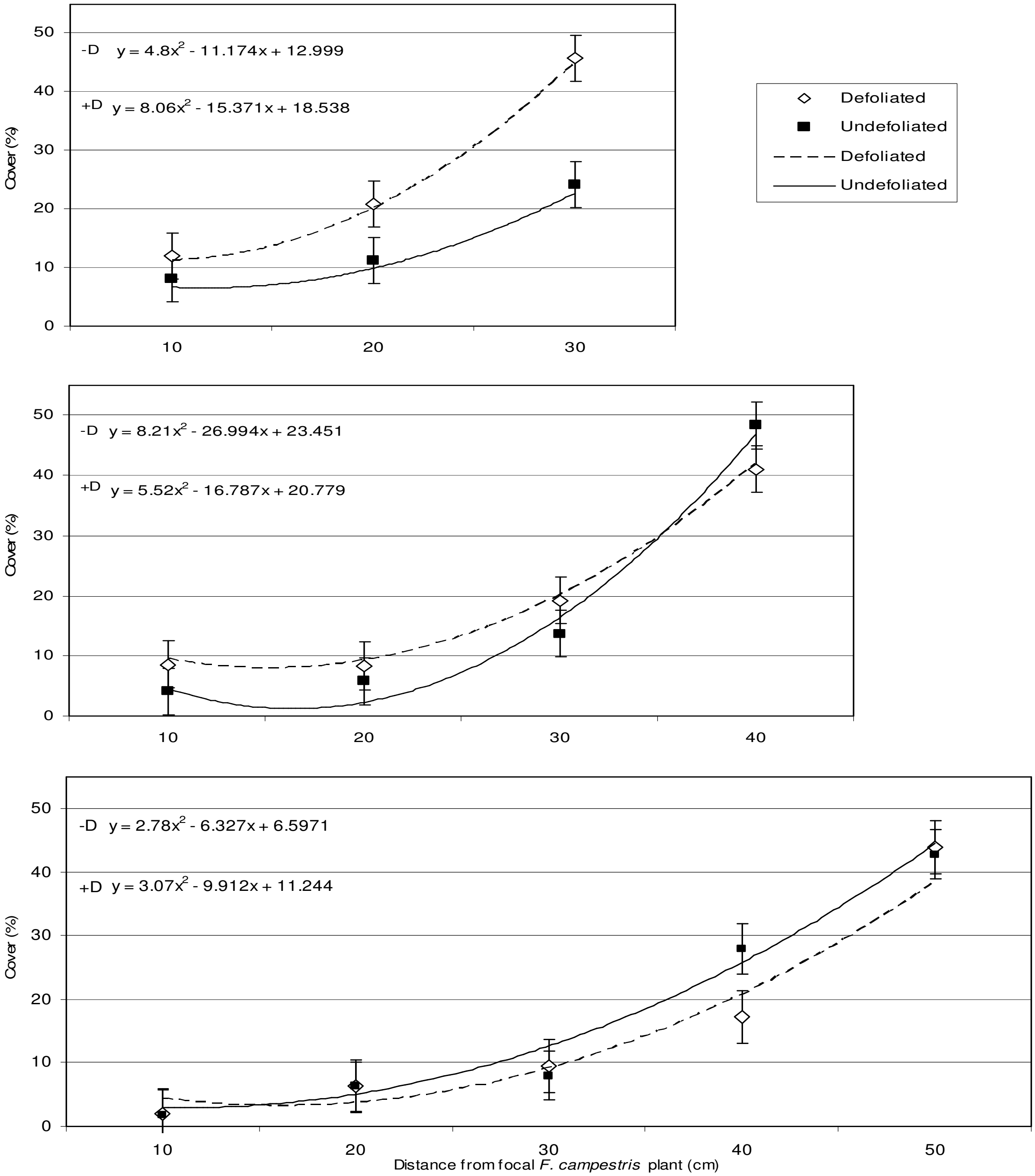

Figure 5.7 The interaction of distance from the focal *F. campestris* plant and defoliation on the cover of *P. pratensis* within stands planted with *F. campestris* at high (top), medium (middle) and low (bottom) density. Means and error bars are from the mixed model analysis. +D = defoliated plots, -D = undefoliated plots

Chapter 6 DOES NITROGEN OR WATER REGULATE COMPETITION BETWEEN JUVENILE *FESTUCA CAMPESTRIS* (RYBD.) AND *POA PRATENSIS* (L.)

6.1 Introduction

Plant community structure is determined by the interaction of each component population of the community with its environment and each other. Physical disturbance and environment determine the competitive ability of each component of a community, and thereby determine overall community structure. Physical disturbance of industrial activity has led to the complete removal of indigenous plant communities, severely disrupting ecological process (Hobbs and Hopkins 1990). Restoration of these communities to their previous natural diversity and function is usually desired (Herath et al. 2009).

Restoration can be complicated by invasion of non-indigenous species. Invasive species, especially those already present in the pre-disturbance plant communities, pose a threat to restoration after disturbance (Mack 1981; Tyser 1992; D'Antonio 1993). Resource availability is linked to the success of invasive species. Resource availability affects complex facilitative and competitive interactions among plants (Callaway and Walker 1997). The fluctuating resource hypothesis proposes that high resource availability facilitates invasion (Davis et al. 2000), and disturbance, by increasing resource availability, can thereby increase invasibility. If the reverse is true, and suppression of invasive species under low-resource conditions is possible, controlling resource availability may be a critical tool in limiting and managing invasions (Funk and Vitousek 2007).

For this reason, study of resource levels on invasive species and invaded communities is necessary.

Resources regulating invasion include: light (Funk and Vitousek 2007), water (Larson et al. 2001; Maron and Marler 2007), nutrients (i.e. nitrogen) (Stohlgren et al. 1999), disturbance (i.e. defoliation) (Willms et al. 1985; Willms and Fraser 1992), and competition from plant neighbors. Each factor influences competitive interactions between species, and eventually determines the success of an invasion (Tyser 1992). Invasion dynamics in establishing communities may be dramatically different than those in established communities. Establishment order and propagule growth rates (Ross and Harper 1972) are two factors capable of changing the outcome of invasion in disturbed environments. This is because differing system mechanics such as plant age and size (Drake 1991) changes the competitive ability of each plant.

To understand invasion dynamics, the invasion of *Poa pratensis* into establishing *Festuca campestris* plants was studied. Invasion of *P. pratensis* into *F. campestris* reclamation projects has become a major problem during reclamation efforts (Adams 2008) in the Foothills Fescue Grasslands of Southern Alberta. Theorized conditions capable of shifting competition between these two species include soil nutrients (Martin and Chambers 2001), soil moisture (Adams 2008), and defoliation (Willms et al. 1985; Willms and Fraser 1992).

Fast growing species like *P. pratensis* (L.) that are adapted to quickly capturing and utilizing nutrients, benefit from increases in soil N at the expense of slower growing species such as *F. campestris* (Rybd.) (Corbin and D'Antonio

2004). Therefore, environments with high plant available N may be more susceptible to invasion by *P. pratensis* than environments with low N (Wilson and Tilman 1991; Alpert et al. 2000). In contrast, reduced N may inhibit *P. pratensis* growth and favor *F. campestris* (Martin and Chambers 2001). For this reason successful restoration of habitats rich in N may first require reducing available N to restore the competitive balance (Corbin and D'Antonio 2004). Reductions of plant available N through carbon additions (sucrose) have proven effective (Alpert and Maron 2000) while maintaining the complex trophic relationships within the soil. Carbon addition theoretically allows less plastic indigenous species to become more competitive against highly plastic invasive species, specifically grasses (Alpert and Maron 2000; Paschke et al. 2000; Blumenthal et al. 2003). This is accomplished by decreasing the growth rate of invaders below the growth rate of slower growing indigenous species, thereby enabling indigenous species to gain an advantage over invasive species (Corbin and D'Antonio 2004).

Drought appears to favor indigenous plant communities over *P. pratensis* (Adams 2008). Once established, *F. campestris* is a superior competitor under drought conditions perhaps due to its large root system (Bradley 2003; Adams 2008). *P. pratensis* has a shallow, rhizomatous root system that makes this species unable to cope with drought (Bookman and Mack 1982; Jiang and Huang 2001). This characteristic may also make it more susceptible to competition from native bunchgrasses (Martin and Chambers 2001), and provides a possible explanation for the ability of mature stands of *F. campestris* to prevent *P. pratensis* invasion on dry sites, and why drought conditions reverse invasion as observed here. However, the behaviour of juveniles for these two species is not known. This becomes even more complicated as previous research indicates *F. hallii,* a close relative to *F. campestris,* requires abundent moisture during germination and establishment (Romo et al. 1991).

Defoliation can shift competition in favor of *P. pratensis* in mature grasslands (Trottier 1986), however its affect on juvenile plants in competition is not well understood. Grazing responses of juvenile *P. pratensis* and *F. campestris* during colonization may not be the same as in mature grasslands. In addition these grazing responses may interact in unique ways with N and soil moisture contents.

6.2 Objectives

The goal of this study was to determine the role of environmental factors, including growing conditions, defoliation, and competition from *P. pratensis*, on the growth of juvenile *F. campestris*. Specific objectives included determining if reduced soil N, W, and defoliation can enhance the competitive ability of juvenile *F. campestris*, either alone or grown with *P. pratensis*. This experiment was designed to determine if:

1) F. campestris growth changes in the presence of neighboring *P. pratensis.*

2) Changes in soil N and/or soil moisture alter interspecific relationships between *F. campestris* and *P. pratensis.*

3) Defoliation, either alone, or in combination with changes in soil N and/or water, affect competition dynamics between *F. campestris* and *P. pratensis.*

6.3 Materials and Methods

6.3.1. Experimental Design

Testing competition during establishment is most effective in the controlled conditions of a greenhouse 'microcosm' environment. A microcosm was utilized to simplify competition dynamics while allowing for the examination of individual and multiple environmental factors. This approach increases the ability to experimentally test controlled factors, yet produces results that remain comparable (indirectly) with similar studies conducted in the field (Drake et al. 1996). A total of 2 greenhouse experiments were run, each approximately 6 months long. The first experiment ran from October 2007 to April 2008, while the second one ran from May 2008 to November 2008. Greenhouses at the University of Alberta were used for both experiments. Plants were placed in a greenhouse at 21 °C, and exposed to 16 hours of light intensity and 8 hours of darkness each day.

Each experiment used a full factorial design. Treatments included 2 plant neighbors, 2 nitrogen (N) levels, 2 watering (W) levels, with or without defoliation (D) (Fig. 6.1). All treatments were replicated 9 times.

Seed for both species was obtained from populations currently found within invaded fescue grasslands. *Festuca campestris* and *P. pratensis* seed were planted in 7.5 cm deep root trainers and grown in a greenhouse, prior to Experiment 1, for 4 months and 2 months, respectively. Both were grown for 3 months prior to Experiment 2. Plants in root-trainers were thinned to 1 plant after emergence. All plugs were then transplanted into 24 cm diameter and 13 cm deep pots containing Black Chernozem soil removed from a cultivated field near Cremona, Alberta. Each pot was weighed to ensure uniform amounts of soil were added to each treatment. Five grass plugs were planted in each pot (Fig. 6.1) using one of 2 planting configurations. In the first configuration, a single *F. campestris* focal plant was surrounded by 4 con-specifics, while in the second, a single *F. campestris* plant was surrounded by 4 *P. pratensis* plants. These configurations facilitated the comparison of intraspecific and interspecific competitive influences on *F. campestris*, with all other treatments (N, W and D) added to these configurations using all possible combinations.

Nitrogen reduction treatments utilized sucrose additions to immobilize plant available N through microbial biomass. One-half of pots in each treatment received 0.012 g/cm^3 of sucrose mixed into the soil at planting. This level of carbon addition was selected with the goal of achieving a sucrose level of 1500 g/m^2, similar to that used in previous studies (Corbin and D'Antonio 2004). This relatively high rate of carbon addition was chosen to suppress N for the 6 month duration of the experiment.

Water addition treatments were based on soil water holding capacity. Soil samples were dried for 3 days at 40 ^{o}C and weighed to determine dry weight. These samples were then saturated with water for 24 h and weighed to determine field capacity. During the experiment, half the pots were watered to field capacity (high water treatment) while the other half received 50% this amount of water (low water treatment near wilting point). Each pot was watered twice a week to its forementioned water level.

Defoliation of half the pots occurred 3 months after initial planting. Plants were defoliated at 1cm above the ground to ensure an intensive defoliation treatment and maximize the ability of detecting interactions between defoliation and the environment on *F. campestris*-*P. pratensis* relationships. All biomass removed during defoliation was retained, oven dried (50^{o}C) to constant mass and weighed.

6.3.2. Measurements

Soil N sampling occurred monthly on the four environmental treatments including: carbon addition (presence = -N vs absence +N) and its interaction with the water addition treatments (high = +W vs low -W) using small control pots with no growing plants. Soil samples were frozen for later analysis. Available NO_3-N and NH_4-N was determined by spectral absorption after extraction from soil with a 5:1 mixture of 2*M* KCl (Maynard and Kalre 1993).

Vegetative sampling included tiller heights and tiller numbers. An initial tiller number and height was taken for each plant at planting for later use as a covariate. Tiller numbers were subsequently counted once during Experiment 1 and every 2 months during Experiment 2. Maximum tiller heights were determined monthly in both trials. Three months after planting, the above ground biomass of one-half of the plants was measured through the defoliation treatment. Above ground biomass and below ground biomass of all plants were measured at the end of each experiment. All biomass samples were dried at 40^{o}C for 36 hours and weighed.

6.3.3. Statistical Analysis

Tiller data were analyzed by taking the difference between the initial number of tillers and the final tiller numbers. This change in tiller numbers was analyzed using SAS statistical software (SAS Institute Inc 2008). Biomass was analyzed using initial tiller counts as a covariate. Tiller heights were analyzed using initial heights as a covariate. All statistical analysis was completed in SAS using Proc Mixed. Data were transformed in order to meet normality and heteroscedascticity using square root experiment 1: changes in tiller densities [May to September and May to November] and root biomass, experiment 2: root to shoot ratio) and natural log (experiment 1: shoot biomass) transformations of the data as necessary.

6.4 Results

Supplemental results on tiller heights and plant neighbour interactions can be found in Appendix D.

6.4.1 Soil Nitrogen

In Experiment 1, adding sucrose significantly reduced available N in the soil for the entire experiment (Fig.6.1). However this did not occur in Experiment 2 where soil N was naturally higher. After 3 months, the significant difference in N content between treatments no longer existed (Fig 6.2). The loss of the N effect likely reflects a die-off in the soil microbial biomass, which would lead to decomposition and a release of N back into the soil. For this reason, the effect of sucrose addition was only analyzed for the first 3 months of Experiment 2.

6.4.2 Biomass

6.4.2.1 Environment

Defoliation had a clear effect on the R:S ratio of *F. campestris* in Experiment 1 (P=0.04) and Experiment 2 (P=0.03). Defoliation did not change root biomass in Experiment 1 or shoot biomass in either experiment. However in Experiment 2, defoliation reduced root biomass (P=0.0007) from 1.26g (±0.09g) to 0.73g (±0.09g). This reduction likely resulted in the subsequent reduction in the R:S ratio from 0.62(±0.06) to 0.45(±0.06) in Experiment 2. In Experiment 1, the R:S ratio was similarly reduced from 1.01 (±0.06) to 0.79 (±0.06) by defoliation. This suggests that while the older plants in Experiment 1 could tolerate defoliation, they still experienced negative effects on root and shoot biomass.

Drought reduced shoot biomass of *F. campestris* plants during Experiment 1 after 3 months (P=0.002) (+W: 1.17 g ± 0.06 g, -W: 0.88 g ± 0.06 g), and after 6 months (P=0.002) from 4.21g (±0.23g) under high water conditions to 2.89g (±0.23g) under drought conditions. While root biomass was not altered, the R:S ratio (P=0.059) increased from 0.83 to 0.96 (±0.06), driven largely by changes in shoot biomass. Younger *F. campestris* plants in Experiment 2 did not experience significant changes in root biomass, shoot biomass or R:S ratios.

In Experiment 1, sucrose addition had a significant effect on shoot biomass (P=0.096), root biomass (P=0.01) and the R:S ratio (P=<0.001) of *F. campestris*. Adding sucrose reduced shoot biomass from 3.9g (±0.23g) to 3.21g (±0.23g), and increased root biomass from 2.17g (±0.26g) to 3.14g (±0.25g). The R:S ratio subsequently increased from 0.72 to 1.08 (±0.06). No final biomass data were analyzed for sucrose addition treatments during Experiment 2 due to the loss of the effect of sucrose addition on available N levels after 3 months.

Sucrose addition interacted with water addition to effect the R:S ratio (P=0.03) in Experiment 1. With sucrose addition *F. campestris* had the highest R:S ratio regardless of water treatment (+W-N=1.08±0.08, -W-N=1.08±0.08). When no sucrose was added plants in low moisture conditions had significantly higher R:S ratios (0.85±0.08) than high water conditions (0.59±0.08), yet both were significantly lower than conditions where sucrose was added.

A significant water and defoliation interaction affected the R:S ratio (P=0.01) whereby drought conditions without defoliation had significantly higher R:S ratios than all other conditions (Table 6.1). A similar effect was seen when sucrose additions and defoliation interacted to affect the R:S ratio (P=0.02). Undefoliated plants with sucrose addition had significantly higher R:S ratios compared to all other conditions. Shoot biomass had a different interaction with sucrose addition and defoliation on the R:S ratios (P=0.001), whereby undefoliated conditions without sucrose addition were larger than all other conditions.

6.4.2.2 Plant Neighbor

In Experiment 1, *P. pratensis* neighbors, in contrast to *F.campestris* neighbors, reduced the shoot biomass of *F. campestris* focal plants at 3 months (P=0.004) from 1.16g (±0.06g) in monocultures to 0.9 (±0.06g) with *P. pratensis* neighbors, and at 6 months (P=<0.0001) from 4.32g (±0.23g) to 2.77g (±0.23g). Root biomass showed similar reductions (P=0.01) from 3.11g (±0.25g) to 2.19g (±0.25g). The R:S ratio (P=0.003) increased significantly with *P. pratensis* neighbors (1.00±0.06) compared to monocultures of *F. campestris* (0.79±0.06).

In Experiment 2 shoot biomass (P=<0.0001), root biomass (P=<0.0001) and the R:S ratio (P=<0.0001) were all significant. Interspecific competition had a larger negative effect on shoot biomass (0.94g±0.20g) and root biomass (0.65g±0.09g) than intraspecific competition (shoot=4.2g±0.21g, root=1.34±0.09). When exposed to interspecific competition from *P. pratensis*, shoot biomass was reduced more than root biomass, resulting in a larger R:S ratio (0.75±0.06) than when exposed to intraspecific competition (0.32±0.06).

Plant neighbor interactions with watering treatments increased the shoot biomass (P=0.05) and root biomass (P=0.07) of *F. campestris* under intraspecific competition when there was high water levels. However, root and shoot biomass did not increase under stronger interspecific competition from *P. pratensis* neighbors in Experiment 1 (Table 6.2). In Experiment 2, root biomass was affected by the interaction of water and plant neighbor (P=0.04). Under high water conditions, intraspecific competition led to significantly greater root biomass (1.50g ±0.13g) than did interspecific competition (0.64g ±0.13g). In contrast under drought conditions interspecific competition did not significantly reduce root biomass (F+F-W: 1.175g, F+P-W: 0.65g ±0.13g).

In Experiment 1, plant neighbor identity interacted with water and sucrose addition (P=0.04) to alter the R:S ratio of focal *F. campestris* plants (Fig. 6.3). Under high resource conditions (+W+N), *F. campestris* maintained a low R:S ratio while under low resource conditions (-W-N) it maintained a high R:S ratio, regardless of neighbor. Under –W+N conditions and +W-N conditions, the R:S ratio increased for plants with *P. pratensis* neighbors over those with *F. campestris* neighbors.

In Experiment 1, plant neighbor interacted with defoliation to alter shoot (P=0.005) and root biomass (P=0.02). With *P. pratensis* neighbors, shoot biomass decreased significantly under defoliated conditions but not under undefoliated conditions. Root biomass only decreased under defoliation when *P. pratensis* was a neighbor. The strength of interspecific competition over intraspecific competition and the additive effect of defoliation to interspecific competition are illustrated in Table 6.2.

In Experiment 2, defoliation and plant neighbor had a significant affect on shoot (P=0.0002) and root biomass (P=0.0004) (Table 6.3). Under intraspecific competition, the shoot biomass of *F. campestris* plants was significantly greater than those exposed to interspecific competition. The shoot biomass of defoliated *F. campestris* plants exposed to intraspecific competition was smaller than that of undefoliated plants. Root biomass was significantly larger for undefoliated *F. campestris* plants exposed to intraspecific competition.

6.4.3 Tillers

6.4.3.1 Environment

In Experiment 1, defoliation at 3 months did not have a significant effect on tiller densities. In Experiment 2, with younger *F. campestris* plants, defoliation reduced tiller densities (P=0.001) from 28.74±2.56 to 14.68±2.56.

Tiller densities were reduced in Experiment 1 (P=0.02) from 14.1 (±1.6) to 8.7 (±1.6) after 3 months of drought. In Experiment 2, the opposite effect was found as drought increased tiller densities after 1 month (P=<0.0001) from 5.9±0.8 to 9.2±0.8 and after 3 months (P=0.01) from 22.6±2.5 to 30.7±2.5 tillers. This main effect became insignificant after 6 months at which point the water and plant neighbor interaction started increasing in significance.

In Experiment 1, adding sucrose reduced tiller densities (P=0.003) from 15.0 (±1.6) to 7.9 (±1.6). During the first 3 months of Experiment 2 sucrose addition had no effect on tiller counts unless plant neighbor was a factor.

Sucrose addition interacted with water addition treatments on tiller counts (P=0.07). Adding sucrose reduced tiller densities. This reduction was only significant under high water conditions as drought suppressed *F. campestris* under high N conditions more than those under low N conditions (Table 6.4).

6.4.3.2 Plant Neighbor

In Experiment 1, plant neighbor had no effect on tiller densities after 3 months (P=0.7). In Experiment 2, plant neighbor significantly altered tiller densities after 1 month (P=<0.0001), 3 months (P=<0.0001), and 6 months (P=<0.0001) of growth. Interspecific competition had a stronger influence on *F. campestris* plants than intraspecific competition after 1 month (*P. pratensis* =4.7±0.8, *F. campestris* =10.5±0.8), 3 months (*P. pratensis* =8.6±2.4, *F. campestris* =44.6±2.5) and by month 6 led to a loss in tillers from 45.2±2.6 with *F. campestris* as a neighbor to -1.8±2.5 when *P. pratensis* was a neighbor.

Plant neighbor interactions with sucrose addition occurred after 1 month (P=0.004) and 3 months (P=0.01) of growth in Experiment 2. Focal *F. campestris* was suppressed by sucrose addition (Table 6.5). With *P. pratensis* as a neighbour, this trend was reversed after 1 month, and although after 3 months this relationship was no longer significant more tillers remained in the sucrose addition treatments (Table 6.5).

In Experiment 2, plant neighbor interacted with defoliation to alter tiller counts in *F. campestris* plants (P=<0.0001). In monocultures, undefoliated *F. campestris* plants had more tillers compared to defoliated plants. Plants with *P. pratensis* neighbors were significantly smaller than those in monocultures. These plants lost tillers when undefoliated while tiller densities did not change when defoliated (Table 6.3).

After 6 months in Experiment 2, the water affect on tiller counts disappeared, but the water by plant neighbor effect became more pronounced

(P=0.11). With *P. pratensis* as a neighbour there was no difference between high water (-3.0±3.5) and low water (-0.05±3.5) conditions; however, under monocultures of *F. campestris*, high water conditions led to plants with 40.3±3.59 tillers compared to 49.9±3.5 tillers in plants under low water conditions. There was also a 3 way interaction of sucrose addition, water addition, and plant neighbor (P=0.01) on tiller counts in Experiment 2. *P. pratensis* neighbors reduced tiller counts under all conditions except under low water and sucrose additions (Fig 6.4).

6.5 Discussion

6.5.1 *F. campestris* growth changes in the presence of *P. pratensis*

Interspecific competition of *P. pratensis* reduced *F. campestris* focal plant growth. While tiller growth rates were not altered in Experiment 1, this resistance was not evident in the younger plants of Experiment 2. In addition, shoot and root biomass were suppressed by *P. pratensis* in both experiments. There was however, a disproportionate reduction in shoot biomass, as shown by the R:S ratios. These negative impacts of *P. pratensis* were again amplified in younger plants of Experiment 2. Therefore, plant age may be a key component in determining resistance to *P. pratensis* invasion. Despite this, the use of older plants was unable to reverse these negative effects. This strong negative effect on *F. campestris* suggests that *P. pratensis* impacts on the former are not consistent with the passenger model, but instead the non-native grass appears to be driving plant community changes (MacDougall and Turkington 2005). Such a negative effect suggests competitive suppression was occurring within these experiments (Callaway and Walker 1997; Liancourt et al. 2005), and indicates *P. pratensis* has the capability of competitively driving plant community change under these specific conditions.

6.5.2 Changes in soil N and/or soil moisture alter interspecific relationships between *F. campestris* and *P. pratensis*

In Experiment 1, sucrose addition significantly reduced available N (Fig. 6.1) during the entire experiment, but for only 3 months in Experiment 2 (Fig 6.2). This reduction in N was most likely responsible for the unique responses in plant growth to sucrose addition during the two experiments. In Experiment 1, shoot biomass was reduced, tiller development suppressed, and root biomass increased. This plastic ability of *F. campestris* to shift between above and below ground biomass suggests an adaptation to low N conditions (Callaway et al. 2003). *Festuca campestris* commonly grows in low N environments and therefore it is not unreasonable for it to be adapted to such conditions.

In Experiment 2 low N suppressed tiller growth during intraspecific competition, but increased it during interspecific competition, accounting for the interaction of plant neighbor identity with sucrose addition. This reversal in growth suggests that young *F. campestris* plants can adapt and compete effectively under low N conditions with *P. pratensis*. This finding also supports field observations of the greatest *F. campestris* establishment in low N environments (Neville 2007). The negative effect of low N on *P. pratensis*

(Wedin and Tilman 1990) may be reducing interspecific competition below that of intraspecific competition. *P. pratensis* is not considered to be adapted to low N conditions, and under these conditions its relationship with *F. campestris* became neutral or facilitative (Callaway et al. 2003).

Drought had a negative effect on older *F. campestris* plants (Experiment 1) suggesting that water limited plant biomass and tillers densities. In contrast, young *F. campestris* plants (Experiment 2) did not appear to be influenced by water treatments. When plant neighbor did interact with watering treatments there was a significant effect of water content in both Experiments 1 (Table 6.2) and 2. Under drought conditions, there was no effect of *P. pratensis* neighbors on focal *F. campestris* plants, while there was clear suppression of *F. campestris* under the high water treatments. Drought conditions therefore allowed *F. campestris* to more effectively compete with *P. pratensis*, which is not adapted to such environments (Jiang and Huang 2001)

Water and sucrose addition interacted to effect R:S ratios and tiller growth rates of *F. campestris* focal plants. Only drought conditions with low available N were able to maintain tiller development rates of *F. campestris* when *P. pratensis* was a neighbor. As a result, the negative effects of drought and sucrose additions on *P. pratensis* had an additive effect on shifting the competitive balance between these two species. The combined reductions of water and N during establishment appeared to give *F. campestris* a competitive advantage over *P. pratensis* under these conditions (Wedin and Tilman 1990; Jiang and Huang 2001).

6.5.3 Defoliation, either alone, or in combination with changes in soil N and/or water, affect competition dynamics between *F. campestris* and *P. pratensis*

Defoliation has historically been considered detrimental to *F. campestris* (Johnston et al. 1971; Willms, et al. 1985; Willms et al. 1986; Willms and Fraser 1992; Willms et al. 1998; Bogen et al. 2003). Responses observed in the present study show that these negative effects also change with plant age and neighbor type. Older *F. campestris* resisted the negative effects of defoliation, but younger *F. campestris* plants were unable to tolerate defoliation. Plant age may therefore be a significant determinant in whether defoliation has a negative effect on *F. campestris*. This said the short-term and long-term effects of defoliation may be different. Reduction of the R:S ratio suggests that defoliation could reduce the ability of *F. campestris* to capture below ground resources. Such plastic changes will eventually reduce the competitive ability of smaller plants (Willms and Fraser 1992). Therefore, a single defoliation that has limited immediate effects on establishing plants, may lead to larger long-term effects (Willms et al. 1985).

When plant neighbor interacted with defoliation, *P. pratensis* as a neighbor negated the effects of defoliation. Interspecific competition on establishing *F. campestris* plants, especially young ones appeared much more important than defoliation. Older *F. campestris* plants suffered additive effects from defoliation and interspecific competition. This suggests that while these older plants could resist defoliation alone, the added presence of competition from

P. pratensis resulted in a clear additive effect detrimental to the native grass, an effect seen in other species (Ang et al. 1994).

6.6 Conclusion

The most important factor determining the health of *F. campestris* was whether or not *P. pratensis* was a neighbor. *Poa pratensis* reduced below and above ground growth and in some cases *F. campestris* even became smaller. The effects *P. pratensis* had on *F. campestris* were limited by reductions in N and drought. Both of these environmental factors were able to mitigate or eliminate the effects of *P. pratensis* on establishing *F. campestris*. The interaction of water and N also affected the interaction of *P. pratensis* with *F. campestris*. Drought conditions combined with low N environments have the ability to eliminate the effects of *P. pratensis* on *F. campestris*. Defoliation interacted with plant neighbor to reduce the competitive ability of older *F. campestris* plants, but defoliation did not have an affect on younger plants while they were establishing. Plant age also played a role, with older *F. campestris* plants generally being more resistant than younger plants to *P. pratensis* under most environmental conditions tested.

6.7 Implications

During establishment of *F. campestris* stands, it is critical that *P. pratensis* be controlled. *Poa pratensis* has clear negative effects on the growth of *F. campestris*. In the presence of *P. pratensis,* water and N additions, which normally would aid in the growth of *F. campestris* in monoculture, have the opposite effect. *P. pratensis* appears to more readily utilize abundant resources, and in turn competes more effectively with *F. campestris*. For this reason, low N conditions and dry sites are necessary to establish *F. campestris* in the presence of *P. pratensis*.

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Table 6.1 The interaction of defoliation with either sucrose addition or water addition on the final *F. campestris* focal plant shoot biomass and R:S ratios during Experiment 1.

Environmental Factor	Defoliation	Shoot biomass	R:S Ratio
+N[1]	+D	2.9(±0.32)b	0.7(±0.08)b
	-D	4.88(±0.34)a	0.74(±0.08)b
-N	+D	3.43(±0.33)b	0.88(±0.08)b
	-D	2.99(±0.32)b	1.28(±0.08)a
+W	+D		0.82(±0.08)b
	-D		0.85(±0.082)b
-W	+D		0.76(±0.08)b
	-D		1.17(±0.08)a

Letters denote differences significant at <0.05 in each column and within each abiotic factor

[1] +W = field capacity, -W = low water, +N = ambient nitrogen, -N = low nitrogen, +D = defoliation, -D = undefoliated.

Table 6.2 Plant neighbor interactions with defoliation or water addition on the final *F. campestris* focal plant shoot and root biomass during Experiment 1.

Abiotic Factor	Level	Neighbor	Shoot Biomass	Root Biomass
Defoliation	+D	*Festuca+Poa*	2.99(±0.18)c	1.86(±0.35)b
		Festuca+Festuca	4.52(±0.19)a	3.03(±0.37)a
	-D	*Festuca+Poa*	3.72(±0.18)b	2.53(±0.35)a
		Festuca+Festuca	4.33(±0.19)ab	3.2(±0.35)a
Water	+W	*Festuca+Poa*	3.04(±0.33)b	2.03(±0.36)b
		Festuca+Festuca	5.38(±0.33)a	3.53(±0.36)a
	-W	*Festuca+Poa*	2.51(±0.33)b	2.35(±0.35)b
		Festuca+Festuca	3.26(±0.32)b	2.7(±0.35)b

Letters denote differences significant at <0.05 in each column and within each abiotic factor

[1] +W = field capacity, -W = low water, +D = defoliation, -D = undefoliated.

Table 6.3 The effects of plant neighbor interactions with presence or absence of defoliation on final root biomass, shoot biomass, and change in tillers in Experiment 2.

Neighbor	Neighbor	Shoot Biomass	Root Biomass	Final Tiller counts
+D[1]	*Festuca+Poa*	1.15(±0.3)c	0.64(±0.13)b	-0.02(±3.57)c
	Festuca+Festuca	3.28(±0.3)b	0.82(±0.13)b	29.39(±3.67)b
-D	*Festuca+Poa*	0.74(±0.3)c	0.65(±0.13)b	-3.64(±3.62)c
	Festuca+Festuca	5.12(±0.3)a	1.86(±0.13)a	61.11 (±3.62)a

Letters denote significant differences at <0.05 in each column

[1] +D = defoliation, -D = undefoliated.

Table 6.4 The interaction of nitrogen and water on the *F. campestris* focal plant changes in tiller numbers (first 2.5 months) during Experiment 1.

Water	Nitrogen	Tillers
+W[1]	+N	19.8(±2.29)a
	-N	8.4(±2.33)b
-W	+N	10.2(±2.36)b
	-N	7.3(±2.29)b

Letters denote differences significant at <0.05 in each column

[1] +W = field capacity, -W = low water, +N = ambient nitrogen, -N = low nitrogen,

Table 6.5 The effect of plant neighbor and nitrogen on change in tiller counts after 1 and 3 months of growth in Experiment 2.

Nitrogen	Plant Neighbor	1 Month Change in Tillers	2.5 Month Change in Tillers
+N[1]	*Festuca+Poa*	3.4(±1.12)d	7.9(±3.43)c
	Festuca+Festuca	12.5(±1.15)a	53.0(±3.53)a
-N	*Festuca+Poa*	5.9(±1.13)c	9.3(±3.48)c
	Festuca+Festuca	8.5(±1.13)b	36.2(±3.48)b

Letters denote differences significant at <0.05 in each column

[1] +N = ambient nitrogen, -N = low nitrogen,

Table 6.6 Summary of F and P values for the final change in tillers, root biomass, shoot biomass and R:S ratio's in Experiment 2 on water addition, sucrose addition, defoliation and plant neighbor treatments.

	Change in Tillers		Shoot Biomass		Root Biomass		R:S Ratio	
	F Value	Pr > F	F Value	Pr > F	F Value	Pr > F	F Value	Pr > F
Water (W)	0.9	0.34	0.5	0.48	0.4	0.54	2.0	0.16
Neighbor (P)	169.4	<.0001**	206.7	<.0001**	33.6	<.0001**	27.1	<.0001**
W*P	2.6	0.11	0.5	0.50	4.1	0.04*	0.1	0.74
Defoliation (D)	15.1	0.0002**	1.3	0.26	12.1	0.0007**	4.6	0.03*
W*D	0.5	0.46	0.1	0.72	0.4	0.55	0.0	1.00
D*P	23.9	<.0001**	14.5	0.0002**	13.0	0.0004**	0.2	0.70
W*D*P	0.2	0.65	0.9	0.35	0.0	0.95	0.1	0.79
Covariate	-	-	14.2	0.0002**	5.5	0.02*	0.7	0.41

* , ** Indicate significance at $p<0.05$ and $p<0.01$, respectively.

Table 6.7 Summary of F and P values for interm change in tillers, final shoot biomass, root biomass, and R:S ratios of focal *F. campestris* plants undergoing defoliation, sucrose addition, water addition and plant neighbor treatments in Experiment 1. Initial tiller counts used as a covariate for all biomass data.

	Change in Tillers		Shoot Biomass		Root Biomass		R:S Ratio	
	F Value	Pr > F	F Value	Pr > F	F Value	Pr > F	F Value	Pr > F
Water (W)	5.45	0.02*	10.12	0.002**	1.01	0.32	3.62	0.059
Nitrogen (N)	9.5	0.003**	2.82	0.096	6.54	0.011*	23.07	<.0001**
W*N	3.39	0.068	2.73	0.10	1.28	0.26	4.97	0.03*
Neighbor (P)	0.18	0.67	20.52	<.0001**	4.59	0.03*	8.9	0.003**
W*P	0.5	0.48	3.97	0.049*	3.36	0.069	0.01	0.93
N*P	0.59	0.45	0.21	0.65	0.51	0.48	0.17	0.68
W*N*P	0	0.98	1.6	0.21	0.28	0.60	4.15	0.04**
Defoliation (D)	-	-	1.81	0.18	2.27	0.13	4.27	0.04*
W*D	-	-	1.72	0.19	0.75	0.39	6.44	0.01*
N*D	-	-	10.68	0.001**	0.67	0.41	6.06	0.02*
W*N*D	-	-	2.67	0.11	0.63	0.43	0.31	0.58
D*P	-	-	8.01	0.005**	5.3	0.02*	0.34	0.56
W*D*P	-	-	0.49	0.48	0.01	0.93	0.85	0.36
N*D*P	-	-	0.02	0.90	0.17	0.68	0.34	0.56
W*N*D*P	-	-	0.02	0.88	0.55	0.46	0.87	0.35
Covariate	-	-	66.96	<.0001**	41.95	<.0001**	1.7	0.20

*, ** Indicate significance at $p<0.05$ and $p<0.01$, respectively.

Table 6.1 Summary of F and P values for interim change in tillers on defoliation, sucrose addition, water addition and plant neighbor treatments after 1 and 3 months in Experiment 2.

	1 Month Change in Tillers		3 Month Change in Tillers	
	F Value	Pr > F	F Value	Pr > F
Water (W)	8.5	0.004**	6.4	0.01**
Neighbor (P)	26.2	<.0001**	137.1	<.0001**
W*P	0.1	0.75	0.2	0.65
N	0.5	0.49	2.5	0.11
W*N	0.7	0.41	0.4	0.54
N*P	8.4	0.004**	6.4	0.01**
W*N*P	6.5	0.01**	0.6	0.45

* , ** Indicate significance at $p<0.05$ and $p<0.01$, respectively.

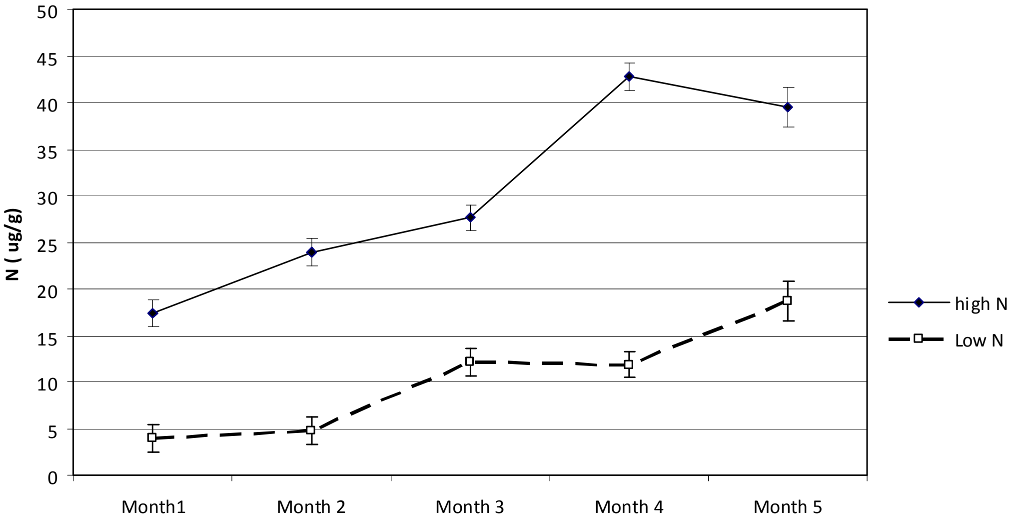

Figure 6.2 Concentration of available N (ug g-1) in soil exposed to sucrose addition (i.e. low N) and no sucrose addition (i.e. high N) in Experiment 1. Time = months since adding sucrose.

[1] +N = ambient nitrogen, -N = low nitrogen,

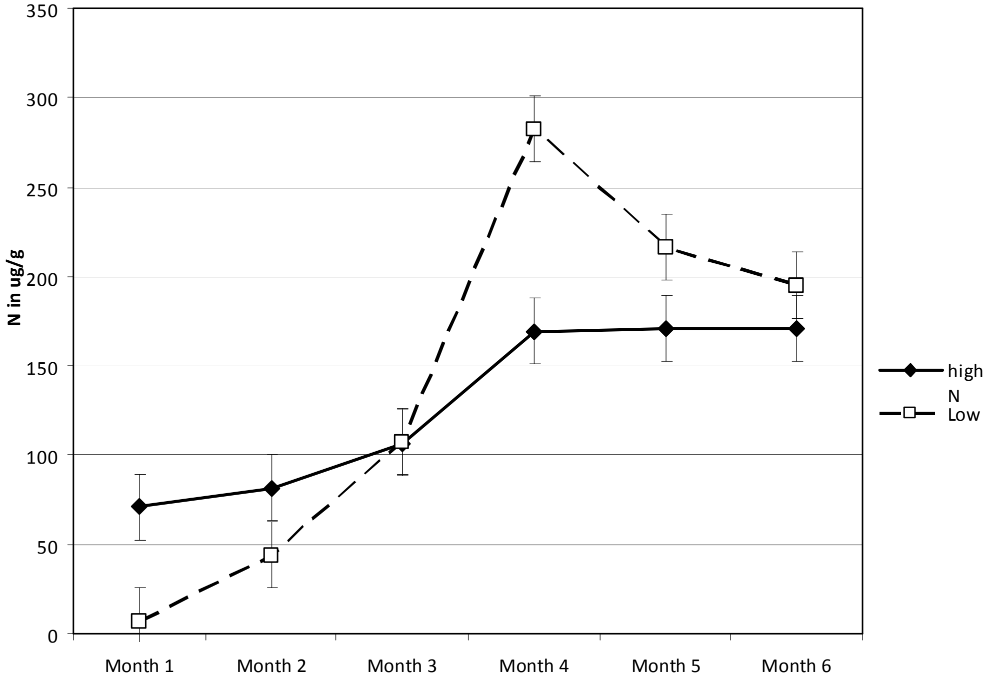

Figure 6.3 Concentration of available N (ug g-1) in soil exposed to sucrose addition (i.e. low N) and no sucrose addition (i.e. high N) in Experiment 2. Time = months since sucrose was added.

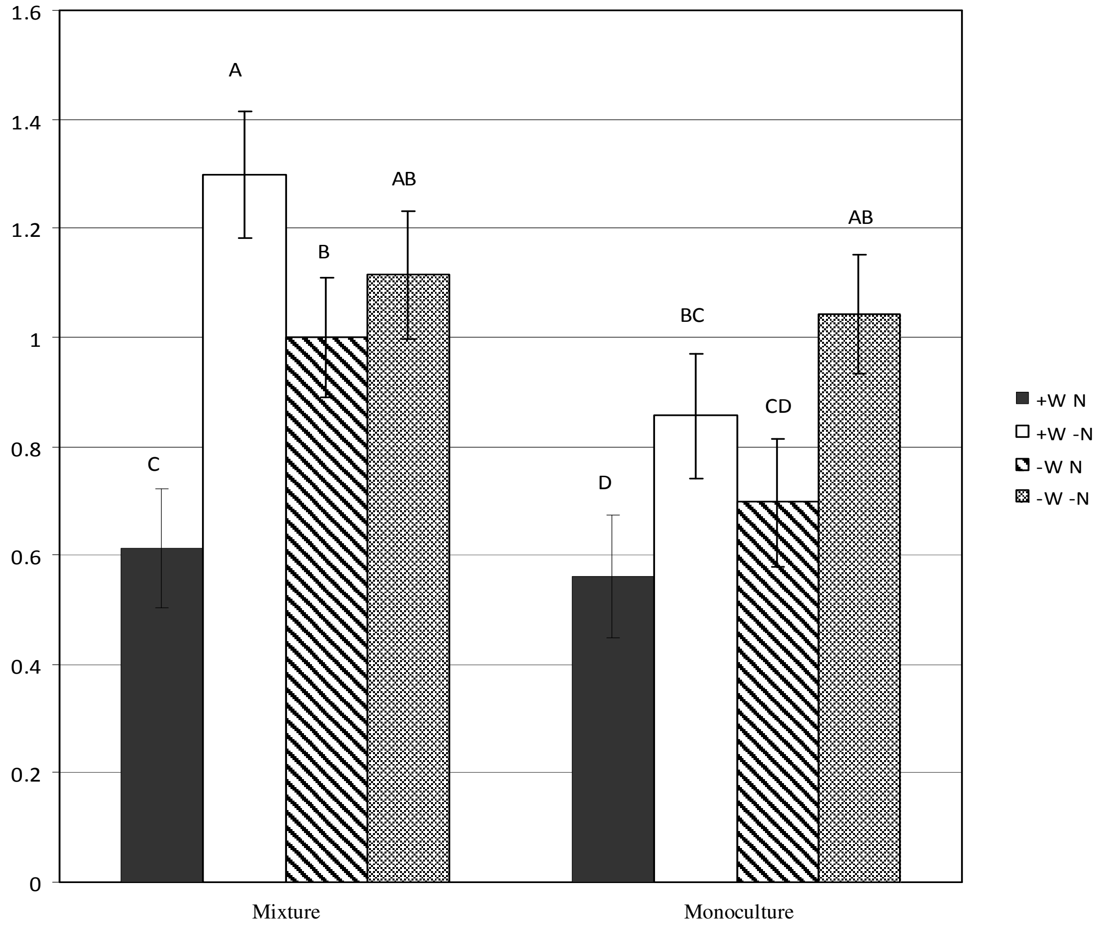

Figure 6.4 Changes in the R:S ratio of *F. campestris* when exposed to varying nitrogen, water and neighbor treatments in Experiment 1. Means with different letters differ. P<0.05. +N = ambient addition, -N = low nitrogen, +W = field capacity, -W = low water, Mixture = Festuca focal plant with Poa exterior plants, Monoculture = Festuca focal and exterior plants

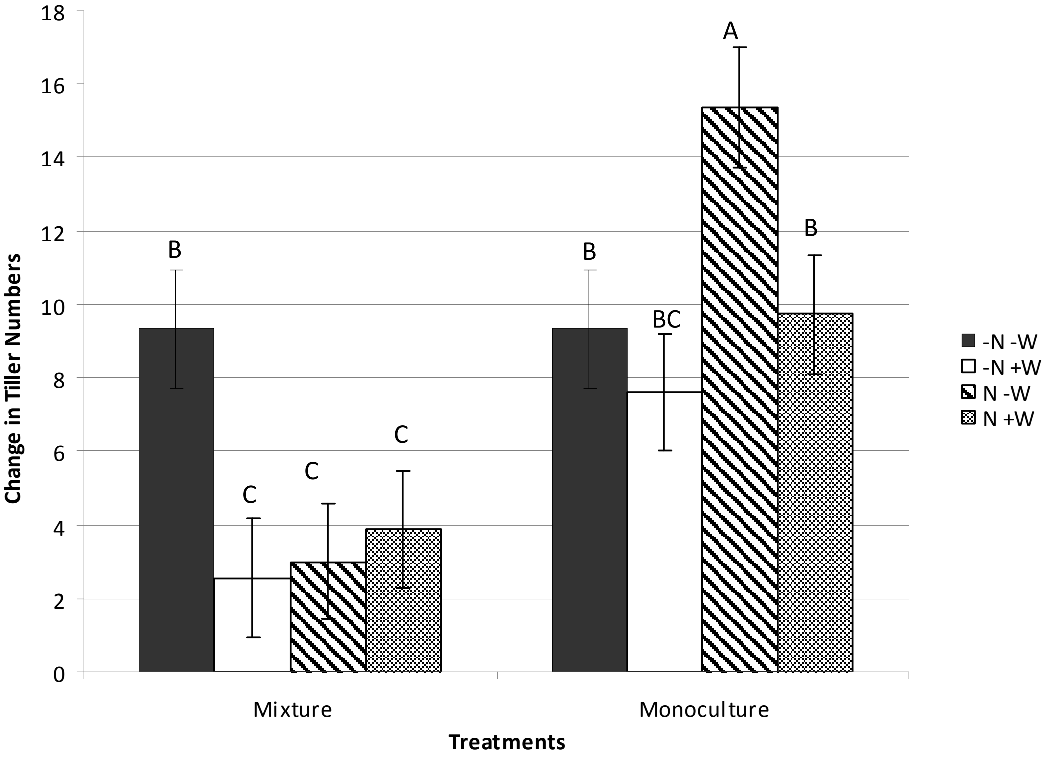

Figure 6.5 Change in tiller counts after 1 month of growth under sucrose addition and water addition treatments on *F. campestris* plants with *F. campestris* and *P. pratensis* neighbors during Experiment 2. Means with different letters differ. P<0.05. +N = ambient addition, -N = low nitrogen, +W = field capacity, -W = low water, Mixture = Festuca focal plant with Poa exterior plants, Monoculture = Festuca focal and exterior plants

Chapter 7 CAN SOIL PREPARATION AND PLANTING METHOD IMPROVE *FESTUCA CAMPESTRIS* (RYBD.) ESTABLISHMENT IN *POA PRATENSIS* (L.) DOMINATED GRASSLANDS?

7.2 Introduction

Industrial activities often remove native grassland communities. On public lands, where conservation of native vegetation is an important management objective, this necessitates community restoration with the goal of recreating the previous community or ecosystem (Ehrenfeld 2000). Natural recovery of plant communities depends on the composition of the seed bank, which may differ from the above ground composition of the previous vegetation (Thompson and Grime 1979), subsequently leading to a community unlike that of the original. Where seeding of native plant species is undertaken to augment the soil seed bank, the establishment of dominant native grassland species is often unsuccessful (Sheley et al. 2006). Two factors in particular may have a significant influence on restoration success including: the presence of invasive species and the poor reproductive capability of dominant species (Sheley et al. 2006).

Invasive species are considered a world wide problem causing a loss of native biodiversity (Didham et al. 2005), particularly within bunchgrass communities (Mack 1986; Tyser 1992). Invasive species, especially those already present in the pre-disturbance plant community, pose serious challenge to reclamation and restoration efforts because of their aggressive growth habit (Mack 1981; Tyser 1992; D'Antonio 1993;). Even small invasions pre-disturbance may lead to a disproportionately large representation of these species in the soil seed bank, especially where past management such as grazing favors their presence (Willms and Quinton 1995) or increases their sexual reproduction. Additionally, rhizomes can give a disproportionate advantage to some invasive species by leaving root propagules with large carbohydrate reserves capable of quickly colonizing the soil surface after disturbance (James 1984; Suzuki and Stuefer 1999;).

Many dominant grasses associated with late seral or climax communities in native grasslands are often slow to establish on bare ground. The reason that climax species are slow to establish may be because during succession the community tends to change in herbaceous composition towards plants that have decreased sexual reproduction, increased root biomass for resource capture or vegetative reproduction, and extended life spans (Newell and Tramer 1978). These changes favor plant species in late seral communities that are stable and persistent. The opposite is also true, however, as these dominant grasses are typically poorly adapted to colonization, especially after the removal of all above ground biomass from the environment to which they are adapted.

In the foothills fescue (*Festuca campestris* Rybd) grasslands of SW Alberta, *Poa pratensis* (L) is widely recognized as an opportunistic invader. These invasions have been aided by factors such as increased grazing pressure (Looman 1969) and an aggressive rhizomatous growth habit. Reclaiming these grasslands following disturbance has historically been difficult because of poor establishment (Sheley et al. 2006) and planting failures (Desserud 2006). *Festuca campestris* is a long-lived species, making seed production relatively infrequent and leading to limited propagation from seed (Willms and Quinton 1995). Moreover, problems associated with restoration of *F. campestris* are not limited to poor seed production, but also lie in its inherently small seed and poor germination (Wilson and Johnston 1969; Sheley et al. 2006).

Festuca hallii, a closely related species to *F. campestris*, has a narrower tolerance for water stress and temperature change during germination than introduced forage grasses (Grilz et al. 1994), with lower temperatures and increased moisture favoring its establishment (Qiu et al. 2010). Once germination occurs, the slow growth rate of *F. campestris* (Wilson and Johnston 1969) (slower than *P. pratensis*) leaves the native grasses poorly adapted to adverse environmental conditions and competition (Bailey 1972). Ultimately, the life strategy of *F. campestris* places this species at considerable disadvantage following disturbance where speed of colonization is a significant competitive advantage (Miller 1982). To avoid poor vigor of *F. campestris* during establishment, cuttings from mature plants (i.e. cuttings) and seedlings started in a greenhouse (i.e. plugs) have been utilized to increase the vigor of long lived native bunch grasses like *F. campestris.* The advantage of establishing more mature plants is in the ability to skip the most vulnerable periods of growth for this species (Petherbridge 2000; Page and Bork 2005).

Native grassland soils typically have low available N compared to soils on disturbed sites (Craine et al. 2001), which are characterized by high bare ground, warm soil temperatures, favorable aeration, and high mineralization. Instead, these conditions likely favor fast growing, opportunistic species such as *P.*

pratensis that are adapted to rapid capture and use of excess N, with subsequent benefits over slower growing species (Corbin and D'Antonio 2004) such as *F. campestris*. Consequently, disturbed sites may be more susceptible to invasion by *P. pratensis* under abundant soil N (Alpert et al. 2000; Wilson and Tilman 1991). In contrast, reduced N may inhibit *P. pratensis* growth and favor species adapted to low N, including *F. campestris* (Martin and Chambers 2001; Chapter 6). Successful restoration of habitats high in N may therefore be aided by reducing N concentrations to restore the competitive balance between native and invasive plants (Corbin and D'Antonio 2004).

Plant available soil N has been reduced by adding carbon (sucrose) to soil (Alpert and Maron 2000), while maintaining the complex trophic relationships. In theory, carbon addition allows native species to become more competitive against adaptable invasive grasses (Alpert and Maron 2000; Paschke et al. 2000; Blumenthal et al. 2003). This is accomplished by decreasing the growth rate of invaders relative to the growth rate of slower growing native species, thereby enabling the latter to re-establish an advantage over invasive species (Corbin and D'Antonio 2004).

Litter addition or accumulation may enhance the ability of establishing *F. campestris* plants to survive by increasing soil moisture and reducing associated water stress (Weaver and Rowland 1952; Fowler 1986; Facelli and Pickett 1991). Additionally, litter may maintain temperatures closer to the narrow tolerance optimum for this species (Grilz et al. 1994; Qiu et al. 2010). The disadvantage of added litter is that it may contain contaminant (i.e. non-native) seed with little to minimal contributions of seed from late seral grasses such as *F. campestris* because of the latter's sporadic and poor seed production (Wilson and Johnston 1969; Sheley et al. 2006).

7.2 Objectives

The goal of this study was to evaluate the effects of site preparation, including tillage, carbon addition, and litter presence, on the survival and growth of *F. campestris* established using 3 planting techniques in a *P. pratensis* dominated grassland. Specifically, the following questions were addressed:

1) How does carbon addition, tilling, and litter removal impact seedling emergence and survival of *F. campestris*?
2) How does carbon addition, tilling, and litter removal impact the survival and growth of transplanted cuttings from mature *F. campestris*?
3) How does carbon addition, tilling, and litter removal impact the survival and growth of *F. campestris* plugs started in a greenhouse?
4) Does carbon addition, tilling, and litter removal alter the establishment of *P. pratensis*?

7.3 Methods

7.3.1 Research Site

This study was conducted on a proposed well site that was stripped and abandoned without drilling near Stavely, Alberta (4-12-30-1 W4M). The ecosite was a well-drained, south facing terrace with a history of moderate to heavy grazing by cattle. Plant community composition before the well site disturbance was comprised primarily of *P. pratensis* (49% cover), although *F. campestris* remained part of the pre-disturbance community (<5%). After topsoil was replaced, the site was left for 1 year and *P. pratensis* increased to 70% cover. Soil on the site was an Orthic Black Chernozem, with a pH of 6.6, 12.7% organic matter, CEC of 26.4 meq/100g, and a clay loam texture (37% sand, 28% silt, and 35% clay).

All vegetation on the site was initially removed through two treatments of glyphosate (2.5L/ha) prior to the initiation of the experiments described here. After all plots had been established an additional application of Grazon (65g picloram/L and 240g 2,4-D Amine/L) was applied at 3.7 L/ha in July 2006 to help suppress broad leaf weeds for the duration of the experiment.

7.3.2 Experimental Design

Festuca campestris planting methods were assessed using 3 separate experiments on the same well site, with all experiments using a similar design, but conducted at different times between 2005 and 2008 (Table 7.1). Within each experiment on planting method, four soil preparation methods were tested, with four replications of each soil treatment for a total of 16 plots. Each plot was 2 m wide by 2 m long, with a 0.5 m buffer between plots.

Soil preparation treatments were designed to facilitate three comparisons (Table 7.1): 1) litter effects on untilled ground (+L vs. –L, respectively), 2) the presence or absence of tillage to achieve weed control and improve seedbed quality (+T vs. –T, respectively), and 3) the presence or 4) absence of carbon addition under tillage to suppress N (+C vs. –C, respectively). Treatment 1 utilized litter naturally accumulated on the site (approximately 350 g/m^2) for the litter added treatment (+L). Treatment 2 and the remaining treatments had litter removed through mowing and the removal of detached material. Tillage was completed to a depth of 5 cm soil depth using 3 passes with a rototiller on treatments 3 and 4. Treatment 3 also received the addition of carbon in the form of fresh pine sawdust (907 g/m^2). Three different *F. campestris* establishment techniques were examined in combination with the 4 soil preparation techniques. The first was the use of transplanted cuttings of mature *F. campestris* plants (MC), where transplants consisted of 5 cm diameter cuttings taken from *F. campestris* plants found within 0.3 km of the well site and planted in a 4 x 5 grid with 30 cm spacing during the first week of September 2005. The second establishment technique involved growing *F. campestris* plugs in a greenhouse for 2 months and planting them in July 2006 (GP). Seed was collected from a climaxgrassland 50 km south of the research site. The final technique was seeding of *F. campestris* at 17.2 kg ha^{-1} (PLS) in June 2006 (SE). For both the MC and GP experiments, 20 plants were installed in a 4 x 5 grid spaced 0.3 m apart in the center of each plot with the remainder of the space as a buffer.

7.3.3 Measurements

7.3.3.1 Environmental Monitoring

Volumetric soil moisture in the upper 15 cm of soil was recorded each month from May to August in 2006 and 2007 using a Delta-T ML2X moisture probe. Measurements were also taken until July 2008 up to final biomass was sampled. All soil moisture measures were taken a minimum of 24 hr after precipitation, with moisture values sampled non-destructively in each plot at 4 random locations. A rain gauge was used to record rainfall throughout the growing season, and compared to regional temperature and rainfall data from the Stavely weather station, approximately 30 km east of the study site.

Photsynthetically active radiation (PAR) in the 400 to 700 nm wavebands were measured using a Decagon AccuPAR^{TM} ceptometer. PAR was recorded over a 3 hr period around solar noon on uniformly overcast days using the average of 10 readings above each plot, and 15 at the soil surface under all standing plant biomass and litter. An equal number of readings were taken in 3 random locations within each plot. PAR readings were repeated monthly for each plot between 1 May and 31 August in 2006 and 2007, and from 1 May to 30 July 2008.

Soil samples were collected in each plot during the last week of August of each year, using three, 2.5 cm diameter cores to a depth of 15 cm. Sub-sample cores from each plot were combined, frozen, and later analyzed for available NO_3-N and NH_4-N by spectral absorption after extraction from soil using a 5:1 mixture of 2*M* KCl (Maynard and Kalre 1993).

7.3.3.2 Vegetation Measures

Vegetation was sampled using non-destructive, crown cover assessments, or the percent of plot occupied,in one 0.5 x 0.5 m permanent sampling quadrat located within each plot. Cover was assessed in August from 2005-2008 for the GP and MC experiments. Seedling counts and crown cover assessments were conducted monthly in seeded plots during 2006, and yearly crown cover in 2007 and 2008. Estimates of bare ground, moss and lichen combined, and litter cover, were also obtained for each plot. Additionally, tillers were counted annually on all *F. campestris* plants in the GP and MC experiments in August of 2006, 2007, and 2008.

Above ground net primary production (ANPP) of *F. campestris, P. pratensis*, grasses, forbs, shrubs and litter were assessed within each permanent sample plot at the beginning of August 2008 at final sampling. All material was removed at 2 cm height, sorted to components, dried at 50°C to constant mass, and weighed.

7.3.4 Analysis

All plant vigor measures together with environmental measures (PAR, SM, available N) were assessed for normality and homogeneity of variances prior to analysis. Assumptions of normality were met for most variables except tiller numbers in 2007 and 2008 in the MC experiment, and tiller numbers in the GP experiment in 2007, for which a square root transformation was completed to satisfy assumptions of normality.

Plant responses to the soil preparation treatments were analyzed using pre-planned pairwise comparisons in Proc Mixed using contrasts in SAS software v9.2 (SAS Institute Inc 2008), with minimum significance set at $P<0.1$. Data from each experiment (i.e. the MC, GP and SE experiments) were analyzed separately due to differences in the timing of soil preparation treatments (e.g. August 2005 to May 2006) and specific establishment times of *F. campestris* (e.g. July 2006 to September 2005). Block was considered random in all assessments, and all analyses used LS means. Separate contrasts were conducted for each year to assess temporal changes in responses. Within each year, three preplanned soil preparation comparisons were analyzed (Table 7.1), including litter effects on untilled ground (+L vs. –L, respectively), the presence and absence of carbon addition to suppress N (+C vs. –C, respectively), and the presence and absence of initial tillage (+T vs. –T, respectively).

Near complete failure of *F. campestris* establishment within the seeding treatments limited the extent of analysis of these data. Within each of the MC and GP experiments, *F. campestris* vigor (biomass, tiller numbers, and foliar cover), *P. pratensis* vigor (cover and biomass), *Hordeum jubatum* cover, and environmental measures (SM, PAR, and available N) were analyzed in 2006, 2007 and 2008 for the mature cuttings, and 2007 and 2008 for the greenhouse started plugs.

The impacts of soil preparation treatments on microenvironmental conditions, specifically soil N, available PAR and soil moisture, were examined using a similar method as used for plant vigor. However, data were pooled for the

MC and SE experiments because soil preparation occurred at the same time in those studies, with year of measurement considered random together with block in the analysis using Proc Mixed.

Finally, stepwise regression using Proc Reg in SAS v9.2 (SAS Institute Inc 2008) was utilized on data collected in 2006, 2007 and 2008 (mature cuttings), and in 2007 and 2008 (greenhouse plugs) to relate plant vigor responses to environmental conditions. Specifically, *F. campestris* cover, biomass, tiller numbers, and survival were analyzed. Response variables for *P. pratensis* included final biomass and cover, with *H. jubatum* cover done as well. Independent variables included mean monthly soil moisture (SM), photosynthetically active radiation (PAR) over the 3 years of data collection, and annual available soil N measured in August of each year.

7.4 Results

A complete summary of the statistical results generated by the analysis of data in this chapter are provided in Appendix F, including significance (P) values.

7.4.1 Effects of Soil Preparation on the Environment

Soil preparation methods had no effect (P=0.22 to P=0.67) on available soil N by the end of the growing season (August) within either the MC/SE, or GP experiments (Appendix F and Table 7.2). Although available N appeared to decline with carbon addition in the GP treatment, this response remained non-significant (P=0.47).

Photosynthetically active radiation was affected by soil preparation methods within the MC/SE experiments: litter removal increased average PAR transmittance in May and June (P<0.0001), yet in July (P=0.06) PAR remained lower under litter removal (Table 7.2). Notably, a reduction in light under litter removal (P=0.05) was also observed in the GP experiment, but only during June (Table 7.2). Effects of tilling on light were similar in all experiments: tilling increased PAR during June in the MC/SE experiments (P=0.08) and during July in the GP experiment (P=0.02). Carbon addition increased light availability within the MC/SE and GP experiments during June (P=0.01) and July (P=0.06), respectively (Table 7.2). Finally, tilling also increased (P=0.02) PAR within the GP experiment in July (Table 7.2).

Soil moisture was unaffected by soil treatments within the MC experiment (Table 7.2). Soil moisture was also relatively similar among treatments in the GP experiment, although tilling reduced average soil moisture content (P<0.0001) late in the growing season (i.e. August) (Table 7.2).

7.4.2 Effects of Soil Preparation on *F. campestris*

Emergence of *F. campestris* in seeded plots was poor regardless of soil preparation treatment. Seedlings were not detected until 2007, at which time a total of only 5, 1, and 1 seedlings were detected in the total area sampled (1m^2) of the carbon addition, tilled, and *in-situ* (i.e. with litter) plots, respectively. By 2008 no live *F. campestris* seedlings remained in any seeded plots, precluding further analysis of emergence in relation to the soil preparation.

All vigor measures of *F. campestris* in the MC experiment were influenced by soil preparation methods with the exception of tillers (Appendix F). Litter removal increased the cover of *F. campestris* transplants, a trend that became more apparent through 2007 (P=0.05) and 2008 (P=0.02) (Table 7.3). This was further supported by associated increases in survival (P=0.04) and a non significant (P=0.101) increase in the final biomass of *F. campestris* transplants in 2008 (Table 7.3). Unlike litter removal, tilling led to a weak reduction in the cover of *F. campestris* in the MC experiment during 2007 (P=0.102), with a stronger effect in 2008 (P=0.01) (Table 7.3). Although the final biomass and survival of *F. campestris* also trended lower with tilling, these measures were statistically non-significant (P=0.66 to 0.24) (Appendix F and Table 7.3). Carbon addition before planting cuttings increased the cover of *F. campestris*, in 2007 (P=0.002).

The vigor of *F. campestris* plants in the GP experiment was affected by all soil preparation methods. Litter removal increased tiller densities by the end of the study in 2008 (P=0.09) (Table 7.3). Tilling increased tiller densities (P=0.10) and cover (P=0.008) of *F. campestris* in 2007 within the GP experiment, with differential tiller densities persisting into 2008 (P=0.06). While final biomass and survival of *F. campestris* tended to be increased by tilling at the end of the study, these responses remained statistically non-significant (Appendix F, Table 7.3).

The lone effect of carbon addition in the GP experiment was an increase in *F. campestris* cover (P=0.04) during 2007 (Table 7.3).

Strong associations between *F. campestris* vigor and environmental variables were found from 2006 through 2008. Within the GP experiment, *F. campestris* tiller densities were negatively associated with SM in August 2007, while biomass and tiller densities were positively associated with SM in May 2008 (Table 7.4). Within the MC experiment, *F. campestris* cover and survival in 2006 were negatively associated with May SM. By 2007 *F. campestris* cover was positively associated with June PAR, but tiller densities were negatively correlated with August SM and available soil N (Table 7.5).

7.4.3 Effects of Soil Preparation on Introduced Species

7.4.3.1 Poa pratensis

The abundance of *Poa pratensis* varied little among the soil preparation treatments in the MC and GP experiment. Within the MC experiment, litter removal reduced cover of *P. pratensis*, but only in 2007 (P=0.097) (Table 7.6). Carbon addition and tilling had no significant affect on *P. pratensis* within the MC experiment. Similarly, in the GP experiment litter removal and carbon addition did not significantly alter the cover or biomass of *P. pratensis* (Table 7.6). Tilling of GP plots sharply reduced the cover of *P. pratensis* in 2007 (P=0.02) and 2008 (P<0.0001), and final biomass of this species (P=0.0002) (Table 7.6).

Poa pratensis biomass and cover were negatively correlated with May SM and May PAR during 2008 within GP plots (Table 7.4). Similar responses were observed in the MC experiment, with *P. pratensis* cover and biomass negatively correlated with June PAR in 2006 and July SM in 2008, respectively (Table 7.5).

7.5 Discussion

7.5.3 Establishment Success

This study confirmed responses seen elsewhere whereby *F. campestris* is difficult to establish (Wilson and Johnston 1969; Petherbridge 2000; Page and Bork 2005; Sheley et al. 2006;). This response suggests that *F. campestris* may have a very narrow window in which it can successfully establish from seed. Such a response is likely similar to *Festuca hallii,* a closely related species, which has a narrow tolerance for water stress and temperature change relative to introduced grasses during germination (Grilz et al. 1994). This is common for many long-lived bunchgrasses that do not require frequent sexual propagation to maintain their dominance within plant communities (Sheley et al. 2006). Mortality of the seedlings that did emerge may be related to the slow growth rate of *F. campestris* seedlings (Wilson and Johnston 1969) as compared with *P. pratensis*, which quickly dominated plots from volunteer seed in the seedbank.

Establishment of long-lived bunch grasses through cuttings and greenhouse grown plugs has previously been used for establishing grasses (Petherbridge 2000; Page and Bork 2005). Improved establishment of *F. campestris* was observed within the two live planting experiments as compared to the SE experiment. This suggests that plant age and size (SE, vs MC/GP) may differentially affect establishment of *F. campestris*, and the competitive ability of this species, as observed in Chapter 6. This relationship may be related to the slow growth of *F. campestris* (Wilson and Johnston 1969) and as such these plants are unable to react to adverse environmental conditions or competition from faster growing species (Bailey 1972).

While methods of soil preparation generally affected both environmental variables and the subsequent vigor of *F. campestris* plants (GP vs MC), soil moisture appeared to act independent of soil preparation method. However, soil nutrient content was the environmental variable most positively correlated with the vigor of *F. campestris*. The positive response of *F. campestris* plugs grown in the greenhouse and moved into the field to May SM appears to support experimental responses in the greenhouse (Chapter 4) where this grass benefited from high soil moisture content. In contrast, the larger cuttings used in the MC experiment were negatively correlated with SM, which may be related to their ability to utilize more water, thereby reducing this resource (see Chapter 5).

7.5.4 Litter Removal

Litter removal has multiple effects on plant communities including increased light availability (Facelli and Pickett 1991; Facelli and Facelli 1993), increased soil moisture (Facelli and Pickett 1991) and the removal of seeds within the litter. The main effect that litter removal had in this study was to increase PAR at the soil surface, although the removal of *P. pratensis* seeds trapped within the litter may also have had an impact. Litter removal appeared to be the most important soil preparation method increasing the vigor of mature *F. campestris* cuttings. A similar, but weaker positive effect of litter removal was also observed for the greenhouse plugs.

Positive responses in MC cover during 2008 may be linked to increased PAR after litter removal. However, the lack of an association with PAR in the GP experiment suggests that other factors such as the smaller size of 2 month old *F. campestris* plants may have contributed (see Chapter 6). More specifically, smaller *F. campestris* plants could have had lower competitive ability with *P. pratensis* (Chapter 6). Further evidence for this differential response by age was apparent in comparing mature *F. campestris* plants in Chapters 3, 4, and 5, whose increasing presence was associated with a reduction in *P. pratensis*. These results reinforce the notion that the abundance of *P. pratensis* is a function of the dominant bunchgrass rather than the opposite (MacDougall and Turkington 2005). This marked shift in competitive ability with plant age at establishment may explain many of the historic difficulties in establishing *F. campestris* (Petherbridge 2000; Wilson and Johnston 1969; Page and Bork 2005; Sheley et al. 2006;). This may be especially true of reclamation sites where *P. pratensis*, particularly that already present in the pre-disturbance plant community (i.e. *P. pratensis* in this study), have been found to pose a threat to reclamation and restoration efforts due to their aggressive growth habits (Mack 1981; Tyser 1992; D'Antonio 1993).

Notably, the only soil treatment that improved *P. pratensis* vigor in the MC experiment was ambient litter. This may explain why litter, which was previously found to enhance the growth of *F. campestris* in other studies (Chapter 3 and 4), may have reduced *F. campestris* vigor in the current investigation. Increases in *P. pratensis* may have been related to litter composition, which was largely made up primarily of *P. pratensis* (i.e. 98% of vegetative cover), and although most plants appeared dead, the litter likely contained viable seed. In contrast, the lack of a relationship between *P. pratensis* and litter removal in the GP experiment may have been caused by the longer period of control that occurred prior to the experiment being initiated.

Increases in *H. jubatum,* which were strongly associated with litter removal and increased PAR, may also have had a suppressive effect on *F. campestris*. Cover of *H. jubatum* was particularly associated with litter removal in the MC experiment. This did not occur in the GP experiment possibly due to similar circumstances that affected *P. pratensis* (i.e. longer period of control before experiment initiation). The disappearance of *H. jubatum* by the end of the study is consistent with the short lived nature observed in other studies (Best et al. 1978). Such results suggest that this species is not a long-term threat to reclamation, but instead will hinder initial establishment of *F. campestris*. Additionally the decline in cover of *H. jubatum* may have resulted from suppression by *P. pratensis* as has been seen previously (Best et al. 1978).

7.5.5 Tilling

Tilling was the most important soil treatment responsible for increasing the vigor of *F. campestris* plugs, and decreasing the vigor of *P. pratensis*. Reduction of *P. pratensis* by tilling is not surprising given that physical disturbance of the soil reduced the survival and cover of existing *P. pratensis* plants, forcing this species to re-establish from the soil seed bank, remaining root fragments or seed rain. Reduced *P. pratensis* may also explain the associated increase in *F. campestris* under tillage. Suppression of *P. pratensis* cover may have allowed for increased access to resources for *F. campestris* plugs, thereby favoring their survival and growth. Moreover, this positive response would have remained greater for plugs rather than the larger transplants that would have been capable of withstanding greater competition from *P. pratensis* within untilled plots. Therefore, these responses suggest that older *F. campestris* plants are superior for restoring fescue grasslands. In addition, initial treatments to achieve *P. pratensis* control are only likely to benefit reclamation when smaller plants are used. Plug size was positively correlated with growth of *F. campestris* (Page and Bork 2005) and supports the results found in the greenhouse study of Chapter 6.

A clear explanation for the differential response of *P. pratensis* to tilling within the MC and GP plots remains unknown. However, differences in timing of tillage, together with post treatment growing conditions, may have aided *P. pratensis* recovery. Additionally, tillage increased *H. jubatum* in both the GP and MC experiments and may account for some of the observed differences among treatments. Finally, the suppressive effects of *P. pratensis*, as noted in the litter removal treatment, may also have played an important role.

7.5.6 Carbon Addition

Carbon addition can aid in community restoration by reducing soil N and allowing for the preferential establishment of native species over invaders (Corbin and D'Antonio 2004). In this study, carbon addition did not reduce N significantly and may thus account for the limited effectiveness of this treatment. The use of sawdust, which is slower to break down than sucrose, may have reduced N immobilization rates (Torok et al. 2000). Additionally, the end of the year N sampling may also have reflected growing season uptake rather than net immobilization, where available N in untreated soil could easily have had its available N drawn down by plant growth.

Nevertheless, carbon addition suppresed *H. jubatum*, whose abundance in turn, was positively associated with available soil N. This response suggests that N depletion may have occurred earlier in the growing season prior to soil sampling and is consistent with similar results seen in short lived invasive grasses (Blumenthal et al. 2003) within other studies. Corroborating this was the fact that *H. jubatum*, which is positively associated with PAR, was suppressed even though PAR increased during carbon addition.

Unlike *H. jubatum*, carbon addition was not effective in suppressing *P. pratensis*, a species known for preferring high N (Ebdon et al. 1999). These findings may be related to the observation that carbon addition did not reduce N by the end of the growing season, and greater carbon additions may have been necessary to immobilize soil N in this grassland throughout the growing season to levels capable of impacting *P. pratensis*. The contrasting responses by *F. campestris* to carbon addition may be explained through the noted ability of older *F. campestris* plants to better withstand adverse conditions (see Chapter 6). Such a response would allow cuttings to expand in low N conditions as they did in the greenhouse (Chapter 6) while the younger plants were temporarily suppressed by a lack of nutrients.

7.6 Conclusions

While all three soil preparation methods affected vigor of *F. campestris* and *P. pratensis*, tilling and litter removal were the most effective methods at suppressing *P. pratensis* and increasing *F. campestris* vigor. The differential response of SE, GP and MC plants may be related to initial plant size (SE > GP > MC) or different planting dates (SE: May 2006, GP: July 2006 vs MC: September 2005). Such differences appear important in determining both resistance to invasive species and responses to soil preparation methods. This was best noted wherein tilling and litter removal together aided GP plants the most while litter removal alone was most beneficial to MC plants. The best method to suppress *P. pratensis* after it has been initially removed was to remove litter that possibly contained seeds, and then till the ground to kill seedlings and root propagates before establishing the new plant community. *Hordeum jubatum* in contrast benefitted the most from tilling and litter removal, but was suppressed by carbon addition, suggesting that soil preparation methods should be customized for each invasive species of concern on a specific site.

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Table 7.1 Summary of soil preparation treatments used where (-) represents the absence of the treatment and (+) represents the presence of the treatment.

	Soil Preparation Treatment		
Treatment Label	Tilling	Carbon Addition	Litter
In-situ (+L)*	-	-	+
Litter Removal (-L or –T)	-	-	-
Tilled (+T or -C)	+	-	-
Carbon Addition (+C)	+	+	-

* Letters represent the three comparisons completed on the four treatments (i.e. +L vs –L, +T vs –T, and +C vs –C)

Table 7.2 Mean comparisons of tilling, litter removal, and carbon addition effects within planting method, on environmental conditions, including available soil N, monthly photosynthetically active radiation (PAR), and monthly soil moisture. Data are averaged among years 2006 to 2008.

		Available N	Light (% PAR)			Soil Moisture (%)			
Planting Method	Soil Preparation	(ug/g)	May	June	July	May	June	July	August
Mature Cuttings & Seeding	*In-situ*	18.8	60.2**	63.4	42.8	29.0	33.2	15.2	13.1
	Carbon addition	21.2	67.5	63.1	46.7	28.0	32.3	13.7	13.4
	Litter removal	19.6	63.7***	54.9***	34.3*	27.9	32.7	13.3	13.8
	Litter	19.6	37.2	23.1	45.6	27.5	32.2	13.8	13.2
	Tilled	18.8	60.2	63.4*	42.8	29.0	33.2	15.2	13.1
	Untilled	19.6	63.7	54.9	34.3	27.9	32.7	13.3	13.8
	SE	3.8	2.2	3.3	4.2	0.9	0.8	0.8	0.9
Greenhouse Plugs	*In-situ*	52.1	64.9	32.1**	18.0*	26.1	21.1	12.3	8.6
	Carbon addition	41.3	45.8	68.6	6.8	26.7	19.7	13.2	8.8
	Litter removal	58.4	42.6	30.2**	3.8	24.1	19.2	14.9	15.0
	Litter	39.9	32.6	56.1	8.6	24.8	19.5	12.4	14.7
	Tilled	52.1	64.9	32.1	18.0**	26.1	21.1	12.6	8.6***
	Untilled	58.4	42.6	30.2	3.8	24.1	19.2	14.9	15.0
	SE	10.4	11.3	8.4	3.8	0.9	1.6	1.4	0.8

Pairwise means within a column differ at p<0.1 (*), p<0.05 (**), and p<0.01 (***).

Table 7.3 Mean (± SE) vigor of mature cuttings and greenhouse plugs of *F. campestris*, including tiller counts, cover, final biomass, and survival from 2006 through 2008.

		Tillers Counts (#/plant)		Cover (%)			Biomass (g)	Survival (%)		
Planting Method	Soil Preparation	2007	2008	2006	2007	2008	2008	2006	2007	2008
Mature Cuttings	*In-situ*	11.5(±2.2)	27.7(±5.5)	4.3	7.3***	2.3	33.0	57.5	53.8	22.5
	Carbon addition	14.2(±1.9)	29.6(±4.4)	7.3	22.0	11.0	68.5	56.3	56.3	35.0
	Litter removal	9.4(±2.2)	29.4(±4.5)	8.9	14*	17.3**	55.8*	60.0	57.5	31.3**
	Litter	10.2(±1.9)	31.9(±8.0)	4.5	5.8	3.0	18.0	50.0	52.5	10.0
	Tilled	11.5(±2.2)	27.7(±5.5)	4.3	7.3*	2.3**	33.0	57.5	53.8	22.5
	Untilled	9.4(±2.2)	29.4(±4.5)	8.9	14.0	17.3	55.8	60.0	57.5	31.3
	SE			2.5	2.7	3.6	15.0	9.0	5.9	5.1
Greenhouse Plugs	*In-situ*	27.8(±2.4)	61.3(±5.4)		20.0**	11.5	71.1		82.5	63.8
	Carbon addition	31.9(±2.4)	60.6(±5.8)		11.5	9.3	70.3		78.8	55.0
	Litter removal	21.8(±2.5)	45.6(±6.2)*		8.3	5.3	47.2		80.0	48.8
	Litter	21.1(±2.5)	30.9(±6.0)		10.8	3.5	27.5		88.8	51.3
	Tilled	27.8(±2.4)*	61.3(±5.4)**		20.0***	11.5	71.1		82.5	63.8
	Untilled	21.8(±2.5)	45.6(±6.2)		8.3	5.3	47.2		80.0	48.8
	SE				2.6	3.8	13.6		7.3	8.4

Pairwise means within a column differ at $p<0.1$ (*), $p<0.05$ (**), and $p<0.01$ (***).

Table 7.4 Results of the multiple regression analysis within the greenhouse plug planting method between *F. campestris, H. jubatum*, and *P. pratensis* vigor measures (cover, survival, tillers, and biomass) and environment [soil moisture (SM), photosynthetically active radiation (PAR), and available soil N], in each of 2006, 2007 and 2008. Responses are averaged across all soil preparation treatments.

Species	Year	Response	Environmental Variable	Model R^2	Partial R^2	*B*-coefficient	F Value	P Value
Festuca campestris	2007	Tillers	SM August	0.41	0.41	-0.64	9.7	0.008
	2008	Biomass	SM May	0.25	0.25	0.50	4.8	0.05
		Tillers	SM May	0.34	0.34	0.58	7.2	0.02
Poa pratensis	2008	Biomass	SM May	0.79	0.57	-0.77	18.5	0.001
			PAR May		0.18	-0.30	9.0	0.01
		Cover	SM May	0.64	0.54	-0.76	16.2	0.001
			PAR May		0.11	-0.33	3.9	0.07

Table 7.5 Results of the multiple regression analysis within the mature cutting planting method between *F. campestris, H. jubatum*, and *P. pratensis* vigor measures (cover, survival, tillers, and biomass) and environment [soil moisture (SM), photosynthetically active radiation (PAR), and available soil N] in each of 2006, 2007 and 2008. Responses were combined across all soil treatments.

Species	Year	Response	Environmental Variable	Model R^2	Partial R^2	*B*-coefficient	F Value	P Value
Festuca campestris	2006	Cover	SM May	0.18	0.18	-0.42	3.1	0.10
		Survival	SM May	0.33	0.33	-0.58	6.9	0.02
	2007	Cover	PAR June	0.21	0.21	0.46	3.7	0.07
		Tillers	SM August	0.67	51.93	-0.76	15.1	0.002
			Available N		0.16	-0.40	6.2	0.03
Poa pratensis	2006	Cover	PAR June	0.30	0.30	-0.55	6.0	0.03
	2008	Biomass	SM July	0.31	0.31	-0.56	6.4	0.02

Table 7.6 Effects of soil preparation techniques (carbon addition, litter removal, and tilling) on the mean (±SE) cover and biomass of *P. pratensis* within each of the experiments using mature cuttings and greenhouse plugs of *F. campestris*.

F. campestris Establishment Method	Soil Preparation	*P. pratensis* Cover (%)			Biomass (g/m^2)
		2006	2007	2008	2008
Mature Cuttings	*In-situ*	0.9	35.5	73.8	223.2
	Carbon addition	0.6	26.3	75.0	274.3
	Litter removal	4.0	57.5*	92.5	308.4
	Litter	7.8	83.8	97.5	364
	Tilled	0.9	35.5	73.8	223.2
	Untilled	4.0	57.5	92.5	308.4
	SE	2.9	10.3	8.4	44.4
Greenhouse Plugs	*In-situ*		4.0	14.3	57.9
	Carbon addition		2.5	5.0	0.0
	Litter removal		43.8	95.0	372.2
	Litter		45.0	85.0	267.9
	Tilled		4.0**	14.3***	57.9***
	Untilled		43.8	95.0	372.2
	SE		10.9	8.2	42.4

Pairwise means within a column differ at p<0.1 (*), p<0.05 (**), and p<0.01 (***).

Chapter 8 SYNTHESIS AND MANAGEMENT IMPLICATIONS

Invasion of *P. pratensis* into foothills fescue grasslands is well documented (Willms et al. 1985; Willoughby 2001; Alexander and Willoughby 2005), yet mechanisms by which invasion proceeds remains poorly understood. Established mechanisms such as summer grazing (Willms et al. 1985) do not explain all invasion events (e.g. benchmark exclosures where long term exclusion from grazing has occurred (Alexander and Willoughby 2005)). Other mechanisms such as changes in the environment (soil moisture (SM), available nitrogen (N) and photosynthetically active radiation (PAR)) and competition from native species (i.e. *F. campestris*) may, alone or together with disturbances such as grazing, help explain the process by which *P. pratensis* invasion occurs.

The purpose of this research was to examine the interactive effects of biotic and abiotic factors on the vigor of *P. pratensis*, including its abundance and invasion dynamics within foothills fescue grasslands. This was accomplished using a combination of greenhouse studies, microcosm studies conducted in fallow fields, experimental manipulation of intact foothills fescue grassland, and areas undergoing reclamation following intensive disturbance. Abiotic factors examined included soil moisture content, available N in the soil, and the presence of litter. Biotic factors tested included summer and winter defoliation as a surrogate for grazing. Primary response factors included the vigor and abundance of *P. pratensis* and *F. campestris*.

8.1 Key Results

Responses reported in Chapter 3 demonstrated that an experimental foothills fescue community responded to increases in PAR (litter removal), SM (water addition and litter accumulation), and available soil N (N addition), but these responses varied in time and effect on individual species. This community responded quickly to increases in SM and litter removal (i.e. +SM and +PAR), but was also relatively resilient, demonstrating recovery by the third year of the study. Effects of N addition took longer to manifest in changes to community composition (i.e. not until the 3rd and final year), most of which was attributed to expansion of the shrub *Symphoricarpos occidentalis*. Responses reported in Chapter 3 also showed that summer defoliation had a more significant impact on plant community composition than winter defoliation as compared with undefoliated conditions.*F. campestris* vigor also appeared to be a prominent factor influencing plant community composition. In contrast, *P. pratensis* was associated with environmental conditions that hindered *F. campestris* vigor including low soil moisture content, which typically limits *P. pratensis* growth (Chapter 6) (Ebdon et al. 1999).

Closer assessment of the individual responses of *P. pratensis* and *F. campestris* (Chapter 4) showed that *P. pratensis*, a normally W and N-loving species (Ebdon et al. 1999), was suppressed by adding W and N. This suggested that *P. pratensis* was acting as a ‘passenger’ in the invasion process, preferentially occurring where more competitive species such as *F. campestris* were suppressed. Specifically, *P. pratensis* was more abundant under ambient W and N conditions, particularly when litter was removed and light increased. Defoliation during the summer also allowed expansion of *P. pratensis* at the expense of the native plant community (Johnston et al. 1971), although this response was not observed under winter defoliation where *F. campestris* vigor was enhanced.

Contrasting the responses for *P. pratensis* were those of *F. campestris* (dominant species), which responded favorably to increased W, ambient litter, ambient N, and either winter defoliation or the absence of defoliation. These responses were unexpected because *F. campestris,* a drought tolerant species (Chapter 6), also appeared to be a strong competitor for increased soil moisture. In the absence of disturbance, *F. campestris* dominated this community regardless of drought (Chapter 6) or abundant soil water content (Chapters 3 & 4). The tolerance demonstrated by this species to winter defoliation and the contrasting negative response to summer defoliation was expected because of previous documentation (Johnston et al. 1971). Furthermore, the negative effects of summer defoliation were not altered by environmental conditions, making this disturbance the most important determinant (i.e. driver) of *F. campestris* abundance.

Notably, responses in *F. campestris* were for the most part directly opposed to those of *P. pratensis*; abundance of these two species was negatively associated (Chapters 3 & 4). Suppressive effects during normally advantageous growing conditions for *P. pratensis* (i.e. +W) (Figure 8.1), combined with the positive response of *F. campestris*, suggest that *F. campestris* was responsible for driving the invasion process. *Poa pratensis* on the other hand appeared dependent on conditions that suppress *F. campestris* such as litter removal and summer defoliation (Figure 8.1) to allow invasion. Overall, these responses suggest that *P. pratensis* is a passenger species whose abundance and invasion depends on the vigor of other species and the availability of empty niches (MacDougall and Turkington 2005).

To further understand the competitive interactions between these two species with changes in environmental conditions and disturbance regimes, a fallow field study (Chapter 5) and controlled greenhouse study were undertaken (Chapter 6). Rates of *P. pratensis* invasion into monocultures of mature *F. campestris* plants planted under fallow conditions (Chapter 5) suggested that the non-native species could impact *F. campestris* vigor negatively under summer defoliation (Figure 8.1) when the vigour of *F. campestris* is reduced (Willms et al. 1998). Moreover, *P. pratensis* impacts were limited to exterior *F. campestris* plants where intraspecific competition was reduced. At high densities, *F. campestris* exhibited a strongly competitive nature whereby it suppressed the vigor of other *F. campestris* plants and invading *P. pratensis*. These responses again support the theory that *P. pratensis* is relatively opportunistic in its growth pattern and invades here *F. campestris* plants (i.e. as the community driver) are either absent (i.e. at low density, or adjacent to exterior plants) or suppressed (i.e. under summer defoliation).

In contrast to the field study, immature *F. campestris* plants grown in competition with *P. pratensis* (Chapter 6 & 7) revealed that the most important factor determining the vigor of immature *F. campestris* plants was the presence or absence of *P. pratensis*. The presence of *P. pratensis* (Chapter 6) reduced above and below ground growth of *F. campestris*, although these responses were further tempered by the environment, with low moisture and reduced soil N able to mitigate or eliminate the suppressive effects of *P. pratensis* on immature *F. campestris* plants. In contrast, defoliation reduced the ability of *F. campestris* to compete with *P. pratensis*, thereby corroborating observations in Chapters 3, 4 and 5. Finally, plant age and size appeared to be an important factor, with older *F. campestris* plants better adapted to withstand competition than younger plants. Slow growth of *F. campestris* (Wilson and Johnston 1969) may be related to the differential response between *F. campestris* seedlings and mature plants in competitive interactions with *P. pratensis* (Chapter 7).

In Chapter 7 the seeding of *F. campestris* was unsuccessful in establishing this species, regardless of soil amendment treatments (i.e. carbon addition, litter removal and tillage). This failure may have been attributed to competition with *P. pratensis*, which dominated the site (similar to Chapter 6) and could have limited soil moisture content in July and August (Qiu et al. 2010), slowed growth rates (Wilson and Johnston 1969), or led to a combination of these with other unknown factors. In contrast, mature cuttings and greenhouse grown plugs demonstrated greater establishment. Soil treatments had mixed effects on the vigor of *F. campestris* plants with litter removal being the most important for improving the performance of cuttings, while tillage aided the establishment of *F. campestris* plugs. Suppression of *P. pratensis* was most effective through soil tillage before planting. These responses supported those observations in the greenhouse where age and size of *F. campestris* plants are clearly linked to its competitive ability with *P. pratensis*. This mechanism partly explains the differing responses between *in-situ* grasslands (Chapters 3 & 4) and highly disturbed lands (Chapter 7).

8.2 Implications

Management of foothills fescue grasslands to prevent *P. pratensis* invasion can be best achieved by optimizing the health of *F. campestris* in these grasslands. Land managers should avoid using N fertilizer, which can either aid shrub encroachment (Chapter 3) or *P. pratensis* invasion (Chapter 6), as well as minimize summer grazing in these grasslands. In addition, where and when grazing does occur, animal use patterns should remain uniform to minimize soil nutrient accumulation. For example, widespread conversion of lowlands to introduced species in the Fescue Prairie may be attributed to the preferential use of lowlands by cattle (Willms et al. 1998), which aside from impacting vegetation directly, may increase soil nutrients and thereby favor species such as *P. pratensis*. In contrast, soil moisture conservation by allowing litter accumulation and snow retention along with dormant season grazing, appear to be practical and effective tools increasing the vigor of *F. campestris* within these grasslands, while suppressing *P. pratensis*. Winter grazing, which has historically been recommended in these grasslands (Willms et al. 1998), appeared to be the most practical mechanism for land managers to reduce the abundance of *P. pratensis*.

In highly disturbed sites requiring reclamation, control of *P. pratensis* before establishing *F. campestris* appears necessary because immature *F. campestris* plants are vulnerable to competition from *P. pratensis* (Chapters 6 and 7). Tillage was the most effective method of reducing seedling abundance of *P. pratensis* during revegetation. While carbon addition was not effective in reducing *P. pratensis* in the field, it had a negative effect on this species in the greenhouse and suppressed *Hordeum jubatum* during the first two years of establishment.

Seeding of *F. campestris* should be done with the understanding that seedling establishment is difficult (Sheley et al. 2006) and that reasons for failure are not fully understood. Use of other planting techniques such as greenhouse-started plugs and mature cuttings of late seral grasses (Petherbridge 2000; Page and Bork 2005) appear to be more successful than seeding regardless of soil preparation. Thus, weed control should be a priority in any attempt to establish *F. campestris* because young plants are more susceptible to competitive suppression than mature plants.

8.3 Future Research

Our current understanding of invasion within foothills fescue grasslands by *P. pratensis,* while greatly enhanced by this research, would benefit from further study within native plant communities (*in-situ*) located in intact grasslands and in reclamation situations.

Further research should examine the mechanisms limiting *F. campestris* establishment and *P. pratensis* abundance across a wider range of environmental conditions in foothills fescue grasslands (i.e. drier grasslands). The current grasslands studied were at the higher end of the moisture gradient within the Foothills Fescue Natural Subregion of Alberta. Further study into other environmental variables may also lead to a greater understanding of how these two species interact across these grasslands.

Human impacts on fescue grasslands are not limited to minor modifications of the ecosystem, but also increasingly by intensified industrial land use. Further research within reclamation situations is needed, more specifically to identify the underlying constraints behind why seeding of *F. campestris* his generally unsuccessful (Sheley et al. 2006). Additionally, research into new methods of establishing *F. campestris* are needed. This research must take into account the competitive characteristics of common invaders in areas requiring reclamation as well as the changing competitive ability of *F. campestris*.

8.4 References

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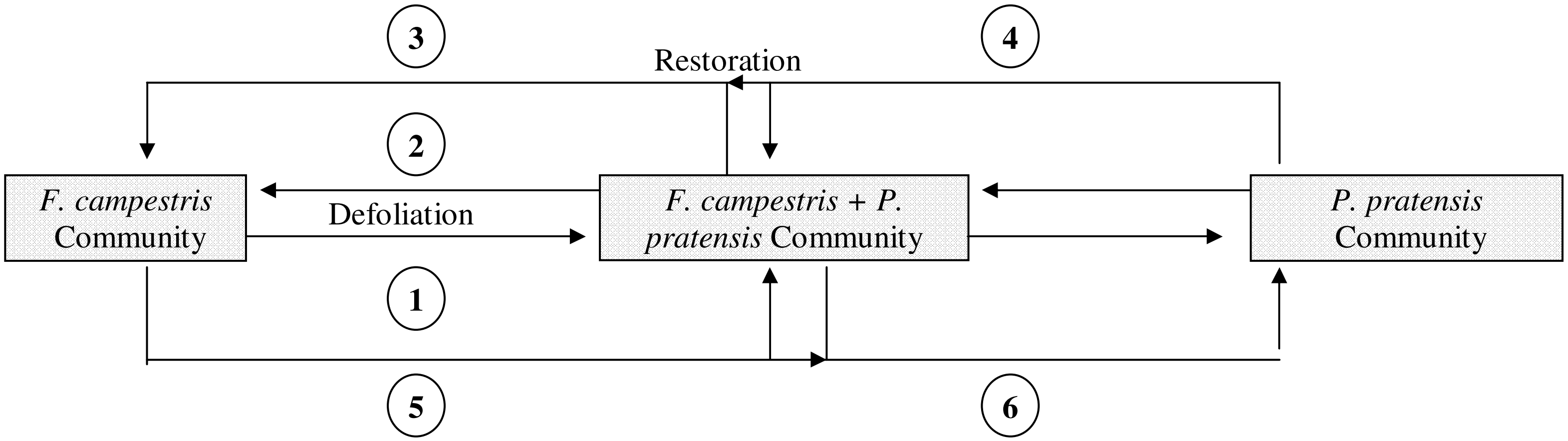

Figure 8.1 Plant community invasion dynamics between *Festuca campestris* and *Poa pratensis*

Note: Numbers are associated with specific mechanisms.

1) Summer defoliation
2) Winter defoliation and undefoliated conditions
3) Mature Plants: Increased soil moisture and increased litter
4) Immature plants: Drought conditions, low nitrogen conditions, no defoliation, older plants and soil preparation before planting that includes litter removal and tilling.
5) Mature Plants: Ambient soil moisture and litter removal
6) Immature plants: High water, nitrogen additions, defoliation, young plants and soil preparation treatments that include no tillage and no litter removal.

Appendix A Supplemental Information for Chapter 3

Change in Species Composition in Environmental Treatments from 2006 to 2008

The indicator species analysis of the change in cover from 2006 to 2008 revealed that litter was associated with *Agropyron riparium* (+L, +W+L, +L+N). Nitrogen application was associated with *Symphoricarpos occidentalis* while ambient N was associated with *Agroelymus bowdenii, Artemisia ludoviciana*, and *Galium boreal* (-N, -L-N). Water addition was associated with *Agropyron riparium* (+W, +W+L, +W+N) and *Viola adunca* while ambient W favored *Agroelymus bowdenii* growth. *Taraxacum officinale* also responded to low litter conditions with increased N (Table 3.6).

Analysis with NMS of the change in species composition from 2006 to 2008 data indicated a 3-dimensional solution (P=0.03). Axis 1, 2 and 3 represented 22.7, 12.6, and 54.6% of species variance, respectively. Axis 1 was associated with N (r^2=0.03) treatments which correlated increased diversity with *P. pratensis*, and reductions in soil moisture (June, August) with *F. campestris*. Axis 3 was associated with L (r^2=0.02) and W (r^2=0.02) treatments which correlated with increases in *Bromus pumpellianus,* evenness and diversity and decreases in species richness and *Bromus inermis*. Axis 2 was associated with N (r^2=0.05) treatments which correlated with increased diversity, reductions in *F. campestris* and litter (Fig 3.4-3.5).

Table A1: Summary significance (P & F) values of mean evenness, richness, and Shannon's diversity after the initial year of treatments (2006) and after the final treatments (2008), relative to W, N, and W*N treatments within the defoliation treatments (1,3,5,7,9-16). P values < 0.1 were considered significant for all main effects.

Diversity		2006		2008	
Measure	Treatment	F Value	P Value	F Value	P Value
Evenness	W	**4.46**	**0.04**	0.12	0.74
	N	**5.56**	**0.02**	**4.61**	**0.03**
	W*N	**6.14**	**0.02**	1.09	0.30
Richness	W	0.61	0.44	0.24	0.62
	N	0.75	0.39	0.73	0.40
	W*N	0.61	0.44	1.47	0.23
Shannon	W	**5.14**	**0.03**	0.01	0.93
	N	**4.87**	**0.03**	1.47	0.23
	W*N	**5.44**	**0.02**	0.02	0.88

[1] Treatments labels are as follows: W indicates water treatments; N indicates nitrogen treatments,

Table A2: The response of evenness to the change in cover of *F. campestr*is in the environmental treatments during 2006.

Factor	Factor	X	Intercept	R^2	Adj R^2	P Value
None	-	-0.002	0.62	0.15	0.14	0.002
W	+W	-0.003	0.59	0.18	0.16	0.01
	-W	-0.002	0.65	0.10	0.07	0.08
N	+N	-0.007	0.63	0.15	0.12	0.03
	-N	-0.002	0.60	0.17	0.14	0.02
L	+L	-0.002	0.61	0.10	0.07	0.08
	-L	-0.003	0.62	0.20	0.17	0.01

[1] Treatments labels are as follows: W indicates water treatments; L indicates litter treatments; N indicates nitrogen treatments; +W indicates water addition, -W ambient water; + L indicates litter remained intact, -L litter removed; +N indicates nitrogen addition, -N indicates no nitrogen addition.

Table A3: Summary significance (P & F) values of mean evenness, richness, and Shannon's diversity after the initial year of treatments (2006) and after the final treatments (2008), relative to W, N, L and interactions within the environmental treatments (1-8). P values < 0.1 were considered significant for all main effects.

Diversity Measure	Treatment	2006 F Value	2006 P Value	2008 F Value	2008 P Value
Evenness	L	0.32	0.57	1.23	0.27
	W*L	**2.84**	**0.10**	0.23	0.64
	N*L	2.48	0.12	0.07	0.79
	W*N*L	1.35	0.25	0.09	0.76
Richness	L	0.26	0.61	0.05	0.82
	W*L	0.01	0.92	0.01	0.91
	N*L	**4.12**	**0.05**	0.65	0.43
	W*N*L	0.66	0.42	0.47	0.49
Shannon	L	0.52	0.47	0.97	0.33
	W*L	2.27	0.14	0.12	0.73
	N*L	**4.06**	**0.05**	0.29	0.59
	W*N*L	1.74	0.19	0.00	0.97

[1] Treatments labels are as follows: W indicates water treatments; L indicates litter treatments; N indicates nitrogen treatments.

Table A4: Summary significance (P & F) values of mean evenness, richness, and Shannon's diversity after the initial year of treatments (2006) and after the final treatments (2008), relative to W, N,D and interactions within the defoliation treatments (1,3,5,7,9-16). P values < 0.1 were considered significant for all main effects.

Diversity		2006		2007		2008	
Measure	Treatment	F-stat	P-Value	F-stat	P-Value	F-stat	P-Value
Evenness	D	**3.85**	**0.03**	**8.17**	**0.001**	**3.39**	**0.04**
	W*D	1.56	0.22	0.10	0.90	1.18	0.31
	N*D	0.10	0.90	0.33	0.72	0.07	0.93
	W*N*D	1.19	0.31	0.55	0.58	0.22	0.80
Richness	D	**9.98**	**0.0001**	**4.66**	**0.01**	1.80	0.17
	W*D	0.02	0.98	2.21	0.116	1.58	0.21
	N*D	1.30	0.28	1.42	0.25	1.46	0.24
	W*N*D	0.29	0.75	0.40	0.67	0.17	0.84
Shannon	D	**9.15**	**0.0003**	**9.01**	**0.0003**	**2.48**	**0.09**
	W*D	1.36	0.26	0.77	0.47	0.12	0.89
	N*D	0.44	0.64	0.51	0.60	0.39	0.68
	W*N*D	0.88	0.42	0.13	0.88	0.27	0.76

[1] Treatments labels are as follows: W indicates water treatments; D indicates defoliation treatments; N indicates nitrogen treatments.

Table A5: The interaction of water addition (+W) with litter removal (-L) treatments on evenness during 2006 and richness during 2007.

Water	Litter	Evenness 2006	Richness 2007
+W	+L	0.57(±0.03)b	9.9(±0.6)b
	-L	0.64(±0.03)ab	11.0(±0.6)ab
-W	+L	0.69(±0.03)a	11.4(±0.6)a
	-L	0.65(±0.03)a	10.4(±0.6)ab

*Letters differing within columns represent significant differences (P<0.05).

[1] Treatments labels are as follows: +W indicates water addition, -W ambient water; + L indicates litter remained intact, -L litter removed;

Table A6: Indicator species analysis of the 2006-2008 environmental experiment. P values are considered significant at 0.1 for provincially important species (*P. pratensis, F. campestris, S. occidentalis, B. inermis*) and 0.05 for all other species.

Category	Treatment 1	Treatment 2	Species	Observed	Random	S. Dev	P value
Litter							
	Elym rip	+L[1]		50.8	50.2	2.26	0.04
Nitrogen							
	Agro Elym	-N		50.3	50	2.24	0.04
	Symp occ	+N		52.9	50.9	2.42	0.03
Water							
	Agro Elym	-W		50.3	50	2.24	0.04
		+W		50.6	50.2	2.26	0.06
Water*Litter							
	Elym rip	+W	+L	25.8	25.4	1.15	0.02
Water*Nitrogen							
	Elym rip	+W	+N	25.8	25.3	1.15	0.03
Nitrogen*Litter							
	Elym rip	+L	+N	25.7	25.4	1.15	0.05
	Gali bor	-L	-N	25.8	25.4	1.15	0.05

[1] Treatments labels are as follows: +W indicates water addition, -W ambient water; + L indicates litter remained intact, -L litter removed; +N indicates nitrogen addition, -N indicates no nitrogen addition.

Table A7: Indicator species analysis of the 2006 environmental experiment. P values are considered significant at 0.1 for provincially important species (*P. pratensis, F. campestris, S. occidentalis, B. inermis*) and 0.05 for all other species.

Category	Treatment 1	Treatment 2	Species	Observed	Random	S. Dev	P value
Litter							
	Elym lan	-L[1]		48	36	5.3	0.03
Nitrogen							
	Geum tri	+N		20	10.8	3.7	0.04
	Tara off	-N		17	9.3	3.0	0.04
Water							
	Agro Elym	+W		15.6	7.3	2.8	0.04
	Fest cam	+W		54.9	51.2	2.5	0.004
	Soli mis	+W		54.4	44.3	4.7	0.02
	Poa prat	-W		42.6	32.4	5.5	0.07
	Ther rho	-W		53	42.4	4.5	0.01
Water*Litter							
	Agro Elym	+W	+L	19.2	8.2	3.9	0.03
	Fest cam	+W	+L	28.7	26.5	1.4	0.01
	Soli mis	+W	-L	37.9	26.4	3.8	0.004
Water*Nitrogen							
	Agro Elym	+W	+N	23.1	8.3	3.9	0.01
	Fest cam	+W	+N	28.8	26.5	1.4	0.01
	Soli mis	+W	+N	38.1	26.4	3.5	0.01
	Tar aoff	+W	-N	22.7	9.4	4.7	0.04

[1] Treatments labels are as follows: +W indicates water addition, -W ambient water; + L indicates litter remained intact, -L litter removed; +N indicates nitrogen addition, -N indicates no nitrogen addition.

Table A8: Indicator species analysis of the 2008 environmental experiment. P values are considered significant at 0.1 for provincially important species (*P. pratensis, F. campestris, S. occidentalis, B. inermis*) and 0.05 for all other species.

Category	Treatment1	Treatment2	Species	Observed	Random	S. Dev	P value
Litter							
	Elym lan	-L[1]		53.6	39	5.54	0.02
	Agro rip	+L		35.1	19.1	4.92	0.004
Nitrogen							
	Elym rip	+N		31.2	19.6	5.23	0.05
	Symp occ	+N		59.9	52.9	4	0.04
Water							
	Achi mil	+W		58.5	46.8	5.51	0.02
	Fest cam	+W		55.6	51.9	2.8	0.04
	Rosa woo	-W		35.4	16	4.75	0.002
Water*Litter							
	Achi mil	+W	+L	43.2	29.4	5.04	0.01
	Elym rip	+W	+L	31.8	16.1	5.83	0.02
	Arte lud	+W	-L	26.7	16.6	5.34	0.05
	Rosa woo	-W	-L	31.4	14.1	6.21	0.03
Water*Nitrogen							
	Rosa woo	-W	+N	33	14.7	6.17	0.02
	Soli mis	+W	+N	37.7	29.3	4.17	0.04
Nitrogen*Litter							
	Elym rip	+L	+N	40.1	15.9	5.63	0.002
	Elym tra	-L	+N	19.4	8.7	4.54	0.04

[1] Treatments labels are as follows: +W indicates water addition, -W ambient water; + L indicates litter remained intact, -L litter removed; +N indicates nitrogen addition, -N indicates no nitrogen addition.

Table A9: Indicator species analysis of the 2007 defoliation experiment. P values are considered significant at 0.1 for provincially important species (*P. pratensis, F. campestris, S. occidentalis, B. inermis*) and 0.05 for all other species.

Category	Treatment 1	Treatment 2	Species	Observed	Random	S. Dev	P value
Defoliation							
	Fest cam	WD[1]		37	34.9	1.81	0.03
	Agro Elym	SD		37.7	9.9	3.34	0.002
	Elym tra	SD		24.6	17.5	3.76	0.05
	Care pen	SD		45.3	33.1	3.44	0.004
	Stip cur	SD		47.4	14.4	3.73	0.002
Water*Defoliation							
	Achi mil	SD	+W	26.3	18.8	2.97	0.02
	Elym lan	SD	+W	27	18.7	3.3	0.02
	Agro Elym	SD	+W	27.3	9	3.75	0.002
	Care pen	SD	+W	25.3	19.6	2.56	0.02
	Stip cur	SD	-W	26.5	11.2	3.83	0.006
	Gera vis	WD	-W	14.4	7.4	3.45	0.05
Nitrogen*Defoliation							
	Fest cam	UD	-N	19.6	18.4	1.07	0.06
	Achi mil	SD	+N	26.3	18.8	2.85	0.02
	Elym lan	SD	+N	27.7	18.4	3.46	0.02
	Agro Elym	SD	+N	31.4	9.3	3.73	0.002
	Care pen	SD	-N	27.1	19.5	2.46	0.004
	Stip cur	SD	-N	26.4	11.5	3.92	0.008

[1] Treatments labels are as follows: +W indicates water addition, -W ambient water; + L indicates litter remained intact, -L litter removed; +N indicates nitrogen addition, -N indicates no nitrogen addition.

Table A10: Indicator species analysis of the 2008 defoliation experiment. P values are considered significant at 0.1 for provincially important species (*P. pratensis, F. campestris, S. occidentalis, B. inermis*) and 0.05 for all other species.

Category	Species	Treatment 1	Treatment 2	Observed	Random	S.Dev	P value
Defoliation							
	Agro Elym	SD[1]		12.5	4.7	2.26	0.03
	Brom pum	UD		12.5	4.6	2.24	0.03
Water*Defoliation							
	Pascs mi	SD	+W	15.2	7.3	3.32	0.03
	Care pen	SD	-W	26.9	20.3	2.98	0.03
Nitrogen*Defoliation							
	Fest cam	UD	-N	20	18.7	1.11	0.07

[1] Treatments labels are as follows: SD indicates summer defoliation; UD indicates undefoliated conditions.

Table A11: Summary correlations (minimum r=|0.12|, |0.22|, |0.38|) between treatments, environmental factors, and key species, with each of the 3 axes arising from the NMS ordination of 2006-2008 vegetation responses and environmental treatments. Species shown include all those with a P value <0.1 based on the indicator species analysis.

		2006-08 Ordination Axes (% Variance Represented)		
		1 (22.7%)	2 (12.6%)	3 (54.6%)
Factor & Description		r	r	r
Treatment Vectors[2]				
Light		-0.03	0.02	**-0.13**
Nitrogen		**0.17**	**-0.23**	0.10
Water		0.06	-0.10	**-0.16**
Environmental factors[2]				
Mjun	June soil moisture	**-0.31**	-0.1	0.0
Diversity Measures[2]				
Ri	Species richness	0.0	0.0	**0.28**
Ev	Evenness	0.0	0.0	**-0.23**
Sh	Shannon's diversity index	**0.38**	**-0.31**	**-0.24**
SB	Shrub biomass	**0.25**	-0.3	0.0
GB	Other grass biomass	-0.1	-0.1	**0.73**
PPB	Poa pratensis biomass	**0.27**	0.0	-0.2
FCB	Festuca campestris biomass	**-0.28**	0.2	**-0.27**
Key species[1]				
Bromine	*Bromus inermis*	0.0	-0.1	**0.85**
Festcam	*Festuca campestris*	**-0.81**	**0.51**	0.0
Poaprat	*Poa pratensis*	**0.73**	-0.2	-0.2
Sympocc	*Symphoricarpos occidentalis*	0.2	**-0.63**	0.3

[1] Treatment vectors show trends in overlays of the ordinations at a cutoff r value of |0.12|

[2] Key variables show trends in overlays of the ordinations at a cutoff r value of |0.22|

[3] Key species show trends in overlays of the ordinations at a cutoff r value of |0.38|

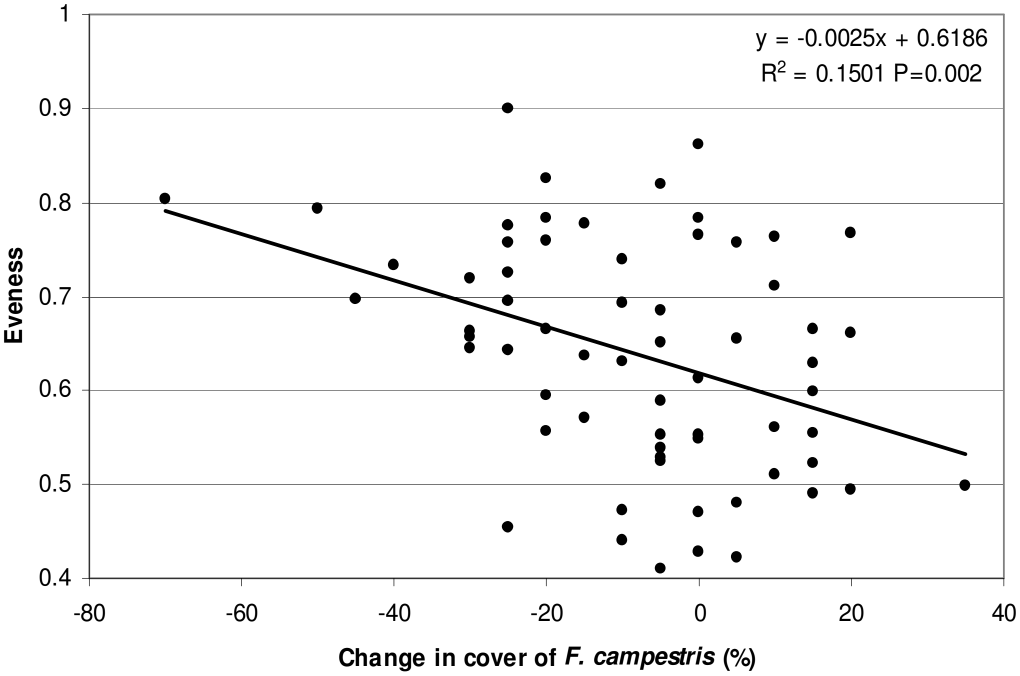

Figure A1: The response of evenness to changes in *F. campestris* cover during the 2006 growing season within the environmental analysis.

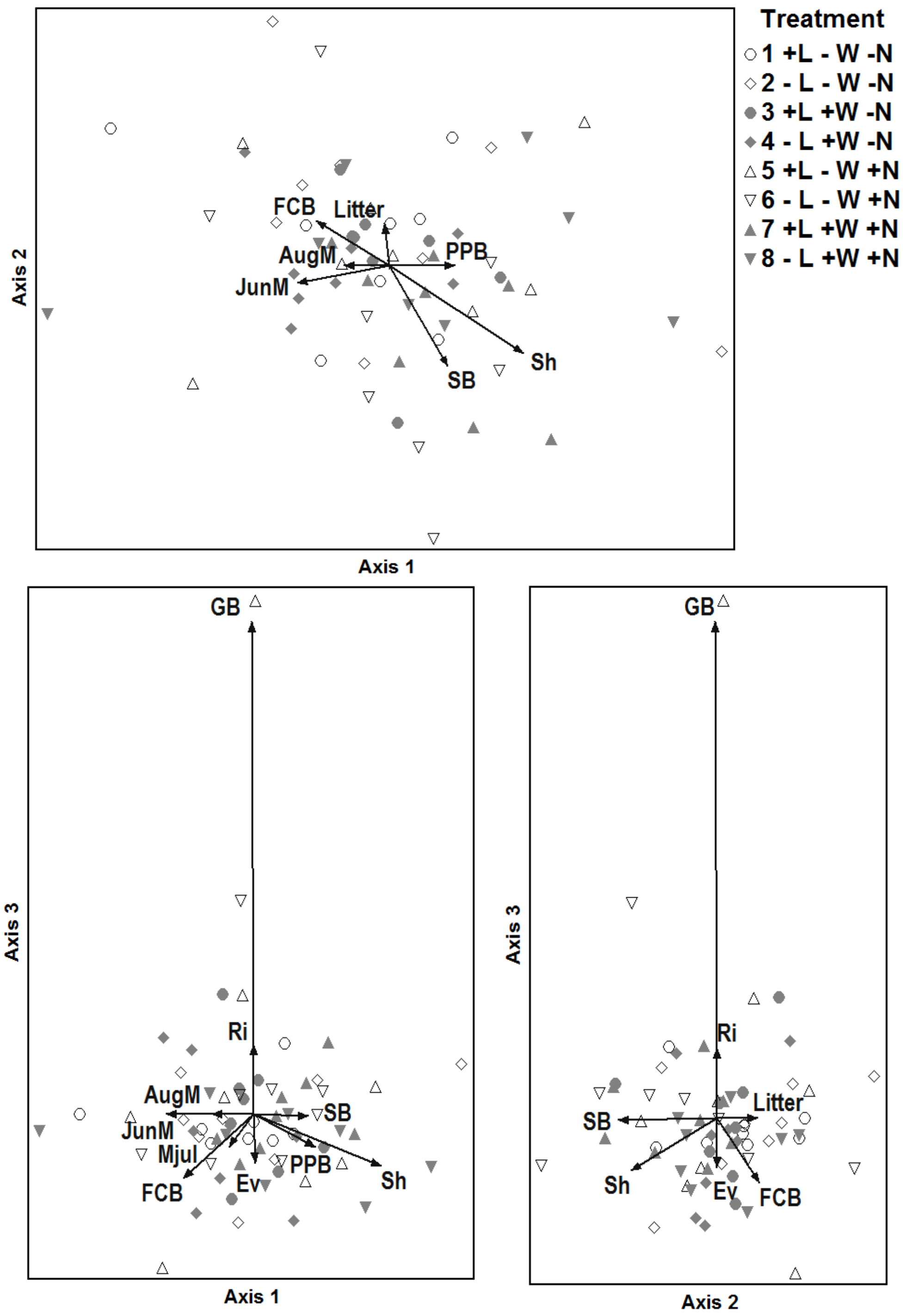

Figure A2: Non-metric multi-dimensional scaling ordination of the environmental analysis of plant available nitrogen, soil moisture, and PAR, categorized by water addition and nitrogen addition treatments in 2006-2008. Moss=Moss cover, Litter=Litter cover, Richness=Species richness Ev=Evenness Sh=Shannon's diversity index, Ri=Species Richness, MayL= May %PAR, JunM=June soil moisture, AugM=August soil moisture, FCB=*F. campestris* biomass, GB=other grass biomass, PPB=*P. pratensis* biomass, SB=Shrub biomass, LB=Litter biomass. Key environmental factors show trends in overlays of the ordinations at a cut off r^2 value of 0.045..[1]Treatments labels are as follows: +W indicates water addition, -W ambient water; + L indicates litter remained intact, -L litter removed; +N

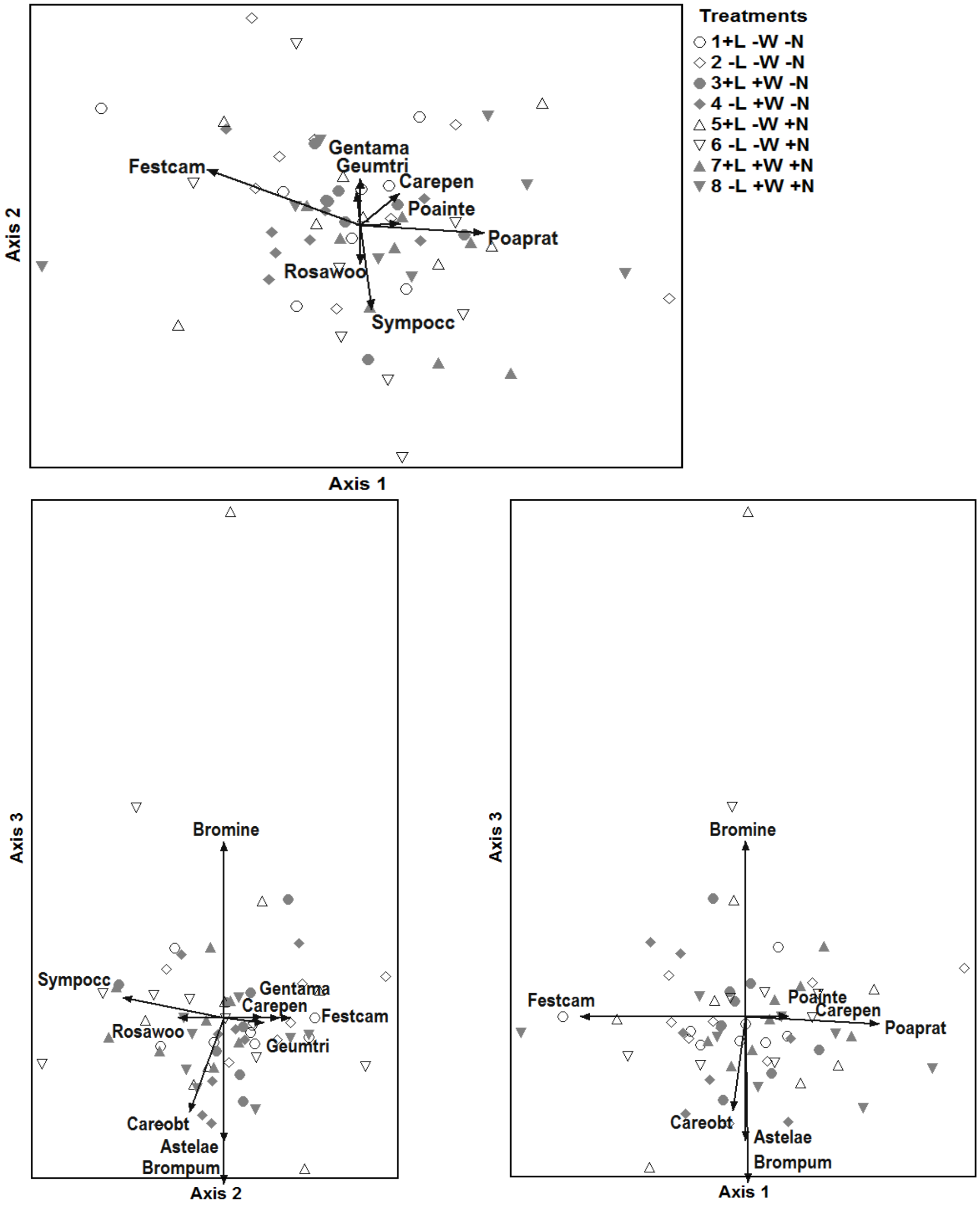

Figure A3: Non-metric multi-dimensional scaling ordination of the environmental analysis with plant cover overlays and categorized by water addition and nitrogen addition treatments in 2006-2008. Festcam=*F. campestris,* Sympocc=*Symphoricarpos occidentalis,* Geumtri= *Geum triflorum,* Careobt=*Carex obtusata,* Astelae=*Aster laevis,* Bromine=*Bromus inermis,* Brompum=*Bromus pumpellianus* Poaprat=*P. pratensis.* Key species show trends in overlays of the ordinations at a cut off r^2 value of 0.15. Treatments labels are as follows: +W indicates water addition, -W ambient water; + L indicates litter remained intact, -L litter removed; +N indicates nitrogen addition, -N indicates no nitrogen addition.

Appendix B Supplemental Information for Chapter 4

Temporal Variation in *P. pratensis* and *F. campestris* Vigor

Following is a summary of the temporal variation in vigor of both focal species examined. *Poa pratensis* varied across years in reproductive tiller densities (P=0.009; 2006: 2.7±3.7m^2, 2007: 5.4±3.0m^2, 2008: 17.2±2.9m^2), vegetative tiller heights (P<0.0001; 2007: 25.6±2cm 2008: 45.2±1.9cm) and cover (P=0.03; 2006: 8.0±2% , 2007: 7.1±2%, 2008: 12.6±2%), with all data demonstrating increased vigor over time, peaking in the final year of sampling (2008) (Table B1).

Measures of *Festuca campestris* cover (P<0.0001), basal diameter (P=0.02), reproductive tiller counts? (P<0.0001), total tiller densities? (P<0.0001), and tiller heights (P<0.0001), also varied among years, although trends demonstrated mixed results. For example, the cover of *F. campestris* was greater in 2006 (70.6±2.3%) than 2007 (60.6±2.3%) and 2008 (55.3± 2.3%). In contrast, total tiller densities were lower in 2006 (125.6±13.7/plant) and 2007 (105.6±13.7/plant) compared to 2008 (220.6±13.7/plant). Other measures of vigor (e.g. basal diameter, proportion of tillers with inflorescences, and vegetative tiller heights) had a variable trend, whereby 2006 levels (13.6±0.67cm, 0.4±0.7%, and 51±1.3cm, respectively) were significantly lower than 2007 (15.8±0.73cm, 6.0±0.7%, 59.2±1.3cm), with 2008 levels (15.3±0.7cm, 1.25±0.7%, 53.6±1.3cm) intermediate between the two (Table B1).

Table B1: Temporal variation in the vigor of *F. campestris* and *P. pratensis* plants during each year of sampling (2006, 2007 and 2008). Data are from plants sampled within the environmental treatments (1-8) only.

Species	Year	Cover (%)	Basal Diameter (cm)	Inflorescences[2] (% or #/m2)	Tiller Density (#/plant)	Vegetative Tiller Heights (cm)
F. campestris	2006	70.6(±2.3)a[1]	13.6(±0.7)b	0.4(±0.7)b	125.6(±13.6)b	51(±1.3)b
	2007	60.6(±2.3)b	15.8(±0.7)a	6(±0.7)a	105.6(±13.6)b	59.2(±1.3)a
	2008	55.3(±2.3)c	15.3(±0.7)a	1.3(±0.7)b	220.6(±13.6)a	53.6(±1.3)b
P. pratensis	2006	8(±2)b	-	0.7(±0.9)b	-	-
	2007	7.1(±2)b	-	1.4(±0.8)b	-	25.6(±2)b
	2008	12.6(±2)a	-	4.3(±0.7)a	-	45.2(±1.9)a

[1] Within a column and species, means with different letters differ (P<0.05).

[2] Inflorescence data are provided either as a proportion of tillers (*F. campestris*) or as a density (*P. pratensis*).

Table B2: Mean *F. campestris* basal diameter associated with N addition for each of the 3 years of sampling. Data are from the environmental treatments (1-8) only.

Year	Nitrogen	Basal Diameter (cm)
2006	+N	13.4(±0.9)a
	-N	13.8(±0.9)a
2007	+N	15.2(±0.9)a
	-N	16.4(±0.9)a
2008	+N	13.3(±0.9)b
	-N	17.3(±0.9)a

[1] Within a year, means with different letters differ, P<0.05.

[2] Treatments labels are as follows: +N indicates nitrogen addition, -N indicates no nitrogen addition.

Table B3: Mean proportion of tillers with inflorescences within *F. campestris* focal plants following water addition during each of the 3 years of sampling. Data are the environmental treatments (1-8) only.

Year	Water	Proportion of Tillers with Inflorescences (%)
2006	+W	0.3(±1.0??)a
	-W	0.6(±0.99)a
2007	+W	7.6(±0.99)a
	-W	4.4(±0.99)b
2008	+W	0.7(±0.99)a
	-W	1.8(±0.99)a

[1] Within a year, means with different letters differ, $P<0.05$.

[1] Treatments labels are as follows: +W indicates water addition, -W ambient water.

Table B4: Mean basal diameter of *F. campestris* plants under various combinations of water addition, N addition and litter removal (-L). Data are from the environmental treatments (1-8) only.

Water	Nitrogen	Litter	Basal Diameter (cm)
+W	+N	+L	12.5(±1.1)d[1]
		-L	16.9(±1.1)ab
	-N	+L	18.5(±1.1)a
		-L	16.2(±1.1)ab
-W	+N	+L	13.6(±1.1)dc
		-L	12.9(±1.1)d
	-N	+L	15(±1.1)bc
		-L	13.6(±1.1)dc

[1] Means with different letters differ, P<0.05.

[2] Treatments labels are as follows: +W indicates water addition, -W ambient water; + L indicates litter remained intact, -L litter removed; +N indicates nitrogen addition, -N indicates no nitrogen addition.

Table B5: Summary significance (P & F) values of mean *F. campestris* cover, basal diameter, proportion of tillers with inflorescences, total tillers counts, and biomass, from 2006 through 2008, relative to the environmental treatments (1-8). Biomass data were only available from 2008. Analyses of data (except biomass) used 2005 tiller counts as a covariate. P values were considered significant at $P<0.1$ for all main effects.

	Cover		Basal Diameter		Proportion of Tillers with Inflorescences		Total Tiller Counts		Final Biomass	
	F Value	P Value	F Value	P Value	F Value	P Value	F Value	P Value	F Value	P Value
Y	**11.5**	**<0.0001**	**3.9**	**0.02**	**33.2**	**<.0001**	**17.5**	**<0.0001**		
W	**9.5**	**<0.001**	**9.9**	**<0.01**	0.1	0.8	**10.3**	**<0.01**	**9.8**	**<0.01**
Y*W	0.4	0.7	1.7	0.2	**3.3**	**0.04**	2.0	0.1		
N	1.2	0.3	**9.3**	**<0.01**	0.0	1.0	**8.5**	**<0.01**	**8.7**	**<0.01**
Y*N	0.7	0.5	**3.7**	**0.03**	0.2	0.8	2.1	0.1		
W*N	0.1	0.7	1.5	0.2	1.0	0.3	0.1	0.7	0.1	0.7
Y*W*N	1.2	0.3	0.01	1.0	0.8	0.5	0.3	0.7		
L	1.1	0.3	0.0	1.0	0.01	0.9	0.1	0.8	0.1	0.8
Y*L	0.9	0.4	1.1	0.3	1.6	0.21	0.4	0.6		
W*L	0.01	0.9	**2.9**	**0.09**	**6.0**	**0.02**	**3.2**	**0.08**	0.0	0.8
Y*W*L	0.6	0.6	1.9	0.2	1.7	0.2	1.2	0.3		
N*L	**12.0**	**0.001**	**6.4**	**0.01**	0.1	0.79	**16.7**	**<.0001**	2.1	0.2
Y*N*L	1.0	0.4	0.9	0.4	2.4	0.10	0.7	0.5		
W*N*L	0.4	0.5	**4.9**	**0.03**	0.0	0.9	0.1	0.8	0.4	0.6
Y*W*N*L	0.3	0.8	**2.8**	**0.06**	0.1	0.90	0.6	0.6		
Covariate	**14.6**	**<0.001**	**51.9**	**<.0001**	0.4	0.54	**45.0**	**<.0001**		

[1] Treatments labels are as follows: W indicates water treatments; L indicates litter treatments; N indicates nitrogen treatments, Y indicates year effect.

Table B6: Summary significance (P & F) values of mean *F. campestris* cover, basal diameter, proportion of tillers with inflorescences, and total tiller counts in each of 2006, 2007, and 2008, relative to the defoliation treatments. Biomass data were only available for 2008. Analyses of all data (except biomass) use 2005 tiller counts as a covariate. P values were considered significant at P<0.1 for all main effects.

	Cover		Basal Diameter		Proportion of Tillers with Inflorescences		Total Tiller Counts		Final Biomass	
	F Value	P Value	F Value	P Value	F Value	P Value	F Value	P Value	F Value	P Value
D	**15.6**	**<.0001**	1.0	0.4	0.6	0.5	**4.1**	**0.02**	0.7	0.48
Y*D	**5.1**	**0.001**	1.4	0.2	1.2	0.3	0.1	1.0		
W*D	1.1	0.3	1.8	0.2	1.6	0.2	**5.4**	**0.01**	2.0	0.14
Y*W*D	0.3	0.9	0.4	0.8	0.7	0.6	1.4	0.2		
N*D	**3.8**	**0.02**	**6.9**	**0.001**	0.3	0.76	**10.1**	**<.0001**	**3.4**	**0.04**
Y*N*D	0.8	0.5	1.8	0.1	0.7	0.6	**2.5**	**0.05**		
W*N*D	0.6	0.5	2.3	0.1	0.8	0.4	0.7	0.5	0.5	0.63
Y*W*N*D	0.3	0.9	1.9	0.1	0.1	1.0	1.1	0.3		
Covariate	**25.5**	**<.0001**	**40.0**	**<.0001**	2.5	0.11	**8.1**	**0.005**		

[1] Treatments labels are as follows: W indicates water treatments; D indicates deffoliation treatments; N indicates nitrogen treatments, Y indicates year effect.

Table B7: Summary significance (P & F) values of mean *P. pratensis* cover, inflorescences density, vegetative tiller heights, and final biomass in relation to the environmental treatments in each of 2006, 2007 and 2008. Biomass data were available only for 2008. For all analyses but that of biomass, cover from 2005 was used as a covariate for all vigor measures. P values were considered significant at P<0.1 for all main effects.

	Cover		Inflorescences		Vegetative Tiller Heights		Final Biomass	
	F Value	P Value	F Value	P Value	F Value	P Value	F Value	P-Value
Y	**3.7**	**0.03**	**5.0**	**0.009**	**60.2**	**<.0001**		
N	**5.7**	**0.02**	1.5	0.2	0.1	0.8	**4.0**	**0.05**
Y*N	0.3	0.7	0.3	0.7	**3.4**	**0.07**		
L	1.6	0.2	**3.2**	**0.08**	0.0	0.9	0.0	0.9
Y*L	0.0	1.0	0.6	0.6	0.4	0.5		
N*L	1.7	0.2	0.2	0.7	0.3	0.6	0.0	1.0
Y*N*L	0.1	0.9	0.4	0.7	0.4	0.5		
W	0.5	0.5	0.2	0.7	**5.4**	**0.02**	**4.4**	**0.04**
Y*W	0.8	0.4	0.4	0.7	0.3	0.6		
N*W	1.1	0.3	1.3	0.3	0.0	0.9	0.0	1.0
Y*N*W	0.0	1.0	0.1	0.9	0.1	0.7		
L*W	1.5	0.2	0.4	0.5	1.9	0.2	0.2	0.7
Y*L*W	0.0	1.0	0.1	0.9	1.7	0.2		
N*L*W	**5.0**	**0.03**	0.4	0.5	0.0	0.9	**3.2**	**0.08**
Y*N*L*W	0.5	0.6	0.5	0.6	0.2	0.7		
Covariate	**56.4**	**<.0001**	**23.4**	**<.0001**	**5.4**	**0.04**		

[1] Treatments labels are as follows: W indicates water treatments; L indicates litter treatments; N indicates nitrogen treatments, Y indicates year effect.

Table B8: Summary significance (P & F) values of mean *P. pratensis* cover, inflorescence density, vegetative tiller heights, and final biomass within the defoliation treatments in 2006, 2007 and 2008, with initial cover from 2005 used as a covariate. Biomass data were available only for 2008. Values were considered significant at P<0.1 for all main effects.

	Cover		Inflorescence Density		Vegetative Tiller Height		Final Biomass	
	F Value	P Value	F Value	P Value	F Value	P Value	F Value	P Value
D	0.6	0.5	0.9	0.43	0.2	0.9	**2.4**	**0.09**
Y*D	1.2	0.3	**3.0**	**0.02**	**2.9**	**0.06**		
N*D	**5.1**	**0.007**	0.6	0.6	**4.2**	**0.02**	2.2	0.1
Y*N*D	0.2	0.9	0.9	0.5	0.1	1.0		
Y*D*W	0.1	1.0	1.0	0.4	1.3	0.3		
N*D*W	0.3	0.7	0.2	0.8	0.3	0.8	2.0	0.1
Y*N*D*W	0.6	0.7	0.0	1.0	1.9	0.2		
Covariate	**55.9**	**<.0001**	**9.2**	**0.004**	**19.0**	**0.0001**		

[1] Treatments labels are as follows: W indicates water treatments; D indicates deffoliation treatments; N indicates nitrogen treatments, Y indicates year effect.

Appendix C Supplemental information for Chapter 5

Table C1: Effect of distance from the focal *F. campestris* plant and its interaction with planting density and defoliation, on *P. pratensis* and *F. campestris* cover.

	F. campestris Cover		*P. pratensis* Cover	
	F Value	P Value	F Value	P Value
Covariate	2.0	0.2	**5.2**	**0.02**
Distance	1.7	0.2	**81.9**	**<.0001**
Density*Distance	**2.6**	**0.03**	1.7	0.11
Defoliation*Distance	0.5	0.7	0.8	0.5
Density*Defoliation*Distance	0.2	1.0	**3.4**	**0.002**

Table C2: Effect of variable planting density and defoliation on the cover of *F. campestris*, and the distance *P. pratensis* invaded towards the focal *F. campestris* plant.

	Cover				Distance to *P. pratensis* from			
	F. campestris		*P. pratensis*		Exterior Plants		Focal Plants	
	F Value	P Value	F Value	P Value	F Value	P Value	F Value	P Value
Covariate	1.9	0.2	**3.9**	**0.05**	**27.6**	**<0.0001**	**6.4**	**0.01**
Density	**7.2**	**0.001**	2.0	0.2	**3.2**	**0.04**	**36.8**	**<.0001**
Defoliation	**3.5**	**0.06**	3.2	0.08	**6.0**	**0.02**	0.1	0.7
Density*Defoliation	1.5	0.2	**3.9**	**0.02**	3.0	0.05	0.8	0.5

Table C3: Effect of sampling year, planting density, defoliation and *P. pratensis* introduction, on total number of tillers and the proportion of tillers with inflorescences within focal and exterior *F. campestris* plants.

	Focal *F. campestris* Plants				Exterior *F. campestris* Plants			
	Total Tiller counts		Proportion With Seed Heads		Total Tiller counts		Proportion With Seed Heads	
	F Value	P Value	F Value	P Value	F Value	P Value	F Value	P Value
covariate	2.3	0.1			2.3	0.1		
Year	**35.8**	**<0.0001**	**25.1**	**<.0001**	**176.7**	**<0.0001**	**186.8**	**<.0001**
Density	**14.8**	**<0.0001**	1.3	0.3	13.1	**<0.0001**	0.5	0.6
Year*Density	**6.4**	**0.002**	**4.5**	**0.01**	**9.1**	**0.0002**	0.3	0.8
Defoliation	**17.2**	**<0.0001**	0.8	0.4	13.4	**0.0003**	**6.3**	**0.01**
Year*Defoliation	1.5	0.2	2.3	0.1	6.8	**0.01**	0.3	0.6
Density*Defoliation	2.4	0.09	1.9	0.1	0.8	0.5	0.6	0.6
Year*Density*Defoliation	0.2	0.8	0.07	0.9	0.5	0.6	1.2	0.3
P. pratensis	0.8	0.4	0.6	0.4	0.3	0.6	0	1.0
Year**P. pratensis*	0.3	0.6	1.1	0.3	0.0	0.9	0	1.0
Density**P. pratensis*	1.1	0.3	2.0	0.1	0.1	0.9	0.8	0.4
Year*Density**P. pratensis*	0.9	0.4	0.8	0.5	0.1	1.0	1.6	0.2
Defoliation**P. pratensis*	0.6	0.4	0.7	0.4	**2.9**	**0.1**	2.8	0.1
Year*Density**P. pratensis*	0.3	0.6	0.6	0.5	0.4	0.5	1.3	0.2
Density*Defoliation**P. pratensis*	**3.8**	**0.02**	1.8	0.2	1.0	0.4	1.3	0.3
Year*Density*Defoliation**P. pratensis*	1.1	0.4	0.7	0.5	0.9	0.4	0.4	0.7

Table C4: Effect of plant density, defoliation, and *P. pratensis* introduction on the total biomass and biomass/tiller of *F. campestris* focal and exterior plants, and the effects of density and defoliation on *P. pratensis* biomass.

	F. campestris Focal Plant Biomass				*F. campestris* Exterior Plant Biomass					
	Whole Plant		Tiller		Whole Plant		Tiller		*P. pratensis* Biomass (g/m^2)	
	F Value	P Value	F Value	P Value	F Value	P Value	F Value	P Value	F Value	P Value
Density	**11.3**	**<0.0001**	**3.4**	**0.04**	**20.7**	**<0.0001**	2.8	0.07	1.8	0.2
Defoliation	**8.0**	**0.006**	2.5	0.12	3.1	0.08	**4.0**	**0.05**	0.2	0.7
Density*Defoliation	**3.3**	**0.04**	1.1	0.4	0.2	0.8	0.6	0.6	**3.2**	**0.05**
P. pratensis	**3.9**	**0.05**	**5.5**	**0.02**	3.5	0.07	2.3	0.1	-	-
Density**P. pratensis*	2.8	0.07	2.1	0.1	0.3	0.8	0.01	1.0	-	-
Defoliation*Density	0.1	0.7	0.8	0.4	1.3	0.3	0.5	0.5	-	-
Density*Defoliation* *P. pratensis*	1.0	0.4	0.3	0.7	1.1	0.3	0.6	0.5	-	-

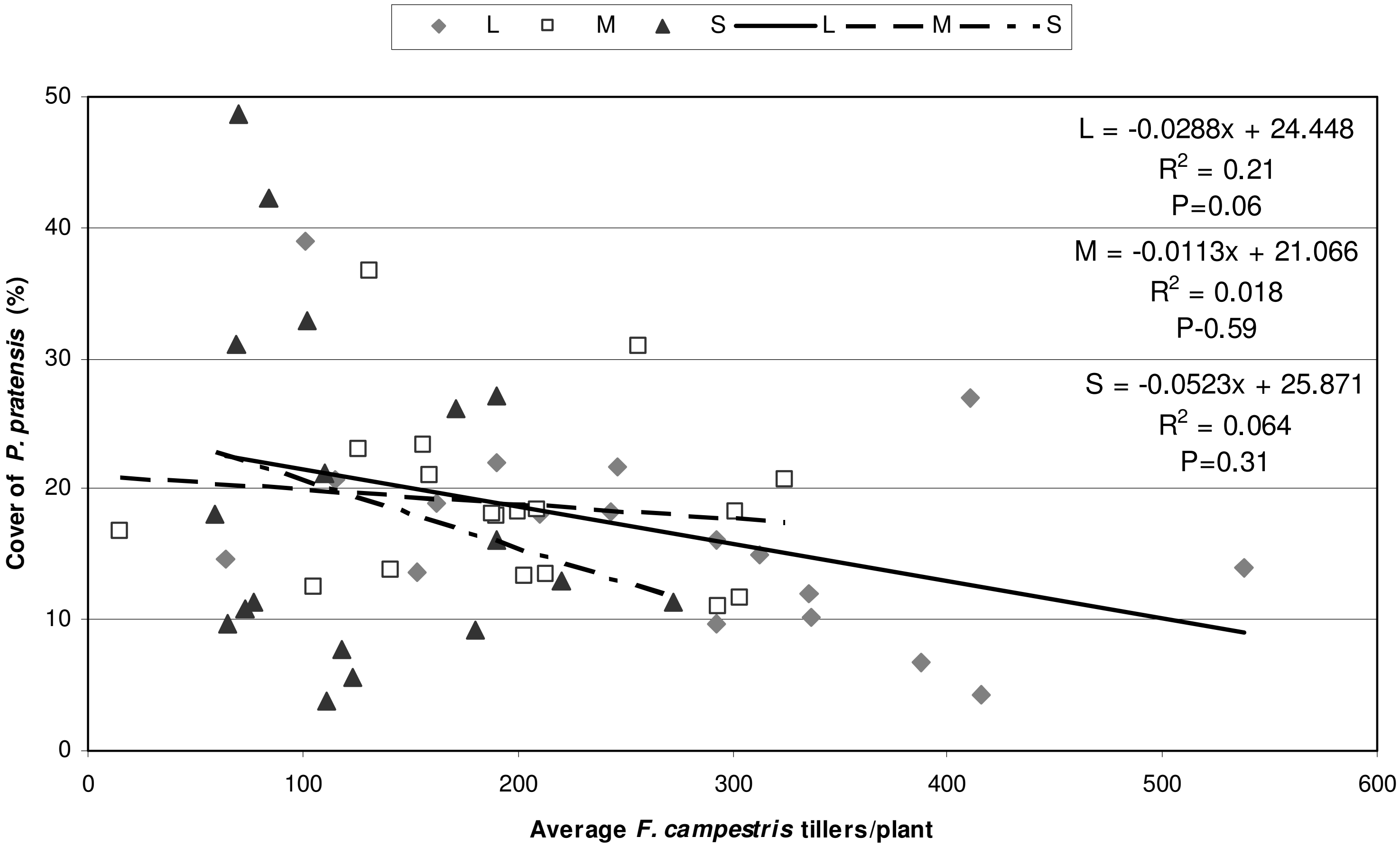

Figure C1: The relationship between mean *P. pratensis* cover in the outer 30 cm of each plot and *F. campestris* tiller counts per plant in each planting density.

Appendix D Supplemenatal Information for Chapter 6

Tiller Heights from Chapter 6

Defoliation had a clear effect on the growth of *F. campestris* through tiller heights after 4 (P=<0.0001) and 6 months (P=<0.0001) in Experiment 1. Defoliation reduced tiller heights after 3 months (–D: 22.10 cm ± 0.40 cm, +D: 15.29 cm ± 0.40 cm), and after 6 months from 24.77 cm to 20.77 cm (±0.49 cm). In Experiment 2 tiller heights were suppressed (P=0.0001) from 21.78cm (±0.69cm) to 17.88cm (±0.7cm). This shows a clear suppression of *F. campestris* growth under defoliated conditions.

In Experiment 1 drought reduced tiller heights after 4 months (P=0.004) (+W: 19.75 cm ± 0.46cm, -W: 17.64 cm ± 0.46 cm) and after 6 months (P=<0.0001) from 24.94 cm (±0.56 cm) to 20.59 cm (±0.56 cm). In Experiment 2 high water conditions had the opposite although weaker effect on tiller heights (P=0.9). *F. campestris* plants under high water conditions were shorter (18.98cm ±0.7cm) than those under low water conditions (20.69cm ±0.7cm).

Sucrose addition had a significant impact on tiller heights in Experiment 1. Tiller heights were increased after 4 months (P=0.0005, N=17.56 cm ±0.44 cm, -N=19.75 cm ±0.44 cm) and after 6 months (P=0.006, N=21.61 cm ±0.54 cm, -N=23.93 cm ±0.55 cm) as a result of sucrose addition. In Experiment 2 there was no effect of sucrose addition in the first 4 months before sucrose additions became ineffective in suppressing N levels.

Sucrose addition interacted with water addition treatments on tiller heights after 4 months (P=0.02) in Experiment 1. Tiller heights of *F. campestris* plants increased as a result of sucrose addition, however drought conditions eliminated the significance of this relationship (Appendix D1).

Plant Neighbor

Tiller heights responded much in the same way as biomass with taller *F. campestris* plants found in monocultures after 4 months (P=0.0009, FC+FC=19.63 cm ±0.4 cm, FC+PP=17.76 cm ±0.4 cm) and after 6 months (P=<0.0001, FC+FC=25.03 cm ±0.5 cm, FC+PP=20.51 cm ±0.5 cm) in Experiment 1 The same effect was observed in Experiment 2 (P=<0.0001) where interspecific competition from *P. pratensis* resulted in smaller *F. campestris* plants (15.01cm ±0.7cm) than under intraspecific competition (24.65cm ±0.7cm).

Plant neighbor interacted with water and sucrose additions to affect tiller heights (P=0.03) in Experiment 2. *F. campestris* plants with *P. pratensis* as neighbors were significantly shorter except under –W+N conditions. Under +W+N and -W-N conditions the effects of intraspecific competition on *F. campestris* by *P. pratensis* increased,(Fig D4) suggesting intraspecific competition has the greatest effects under these conditions.

Plant neighbor interacted with defoliation on tiller heights (P=0.006). Plant tiller height showed similar results to biomass in that there was an additive effect of defoliation. Interspecific competition reduced plant height more than intraspecific competition and defoliation reduced plant height compared to undefoliated plants (Table D2).

Water also interacted with plant neighbor and defoliation (P=0.0001) on the final plant heights (Fig D3). In monocultures of *F. campestris,* high water conditions eliminated the negative effects of defoliation on tiller height, however the same effect did not occur under low water conditions. In interspecific competition, drought decreased the tiller height of *P. pratensis* under undefoliated conditions but not under defoliated conditions. Defoliation also significantly reduced height of *F. campestris* under high water conditions but not under low water conditions.

Nitrogen interacted with defoliation and plant neighbor after 4 months of growth on tiller heights (P=0.03) but not on the final tiller heights (Fig D4). In monocultures, *F. campestris* that is defoliated is taller when sucrose is added. This does not occur if *P. pratensis* is the neighbor. Defoliation significantly reduced tiller heights regardless of sucrose treatment.

Table D1: The interaction of nitrogen and water on the *F. campestris* focal plant tiller heights (3.5 months) and tillers numbers (2.5 months) during Experiment 1. Letters that differ denote differences significant at <0.05 in each column.

Water	Nitrogen	Tiller Heights	Tillers
+W	+N	18(±0.76)b	19.8(±2.29)a
	-N	21.5(±0.57)a	8.4(±2.33)b
-W	+N	17.1(±0.59)b	10.2(±2.36)b
	-N	18.1(±0.64)b	7.3(±2.29)b

[1] Treatments labels are as follows: +W indicates water addition, -W ambient water; +N indicates nitrogen addition, -N indicates no nitrogen addition.

Table D2: Plant neighbor interactions with defoliation on the final *F. campestris* focal plant tiller heights during Experiment 1. Letters that differ within a column and abiotic factor denote differences significant at <0.05.

Abiotic Factor	Level	Neighbor	Tiller Heights	Shoot Biomass	Root Biomass
Defoliation	+D	Fescue+Bluegrass	17.5(±0.7)c	2.99(±0.18)c	1.86(±0.35)b
		Fescue+Fescue	24(±0.7)b	4.52(±0.19)a	3.03(±0.37)a
	-D	Fescue+Bluegrass	23.5(±0.7)b	3.72(±0.18)b	2.53(±0.35)a
		Fescue+Fescue	26(±0.7)a	4.33(±0.19)ab	3.2(±0.35)a
Water	+W	Fescue+Bluegrass		3.04(±0.33)b	2.03(±0.36)b
		Fescue+Fescue		5.38(±0.33)a	3.53(±0.36)a
	-W	Fescue+Bluegrass		2.51(±0.33)b	2.35(±0.35)b
		Fescue+Fescue		3.26(±0.32)b	2.7(±0.35)b

[1] Treatments labels are as follows: +W indicates water addition, -W ambient water; + D indicates defoliated conditions, -D undefoliated conditions .

Table D3: The effects of plant neighbor interactions with presence or absence of defoliation on final root and shoot biomass, tiller counts and tiller heights. Letters that differ within a column denote differences significant at <0.05.

Neighbor	Neighbor	Shoot Biomass	Root Biomass	Final Tiller Counts	Tiller Heights
+D	Fescue +Bluegrass	1.15(±0.29)c	0.64(±0.13)b	-0.01754(±3.57)c	14.14(±0.98)c
	Fescue +Fescue	3.28(±0.3)b	0.82(±0.13)b	29.3775(±3.67)b	21.62(±1.01)b
-D	Fescue +Bluegrass	0.74(±0.3)c	0.65(±0.13)b	-3.6389(±3.62)c	15.88(±0.99)c
	Fescue +Fescue	5.12(±0.3)a	1.86(±0.13)a	61.1111(±3.62)a	27.68(±0.97)a

[1] Treatments labels are as follows: + D indicates defoliated conditions, -D undefoliated conditions.

Table D4: Summary of the F and P values for Tiller heights on defoliation, sucrose addition, water addition and plant neighbor treatments after one and thee months in Experiment 2.

	Interm Tiller Heights		Final Tiller Heights	
	F Value	P Value	F Value	P Value
Water (W)	0.8	0.37	**2.9**	**0.09**
Neighbor (P)	**62**	**<.0001**	**94.9**	**<.0001**
W*P	0.5	0.49	0.4	0.6
Defoliation (D)			**15.5**	**0.0001**
W*D			0	0.93
D*P			**4.8**	**0.03**
W*D*P			0	0.9
Covariate	**14.6**	**0.0002**	**13.1**	**0.0004**

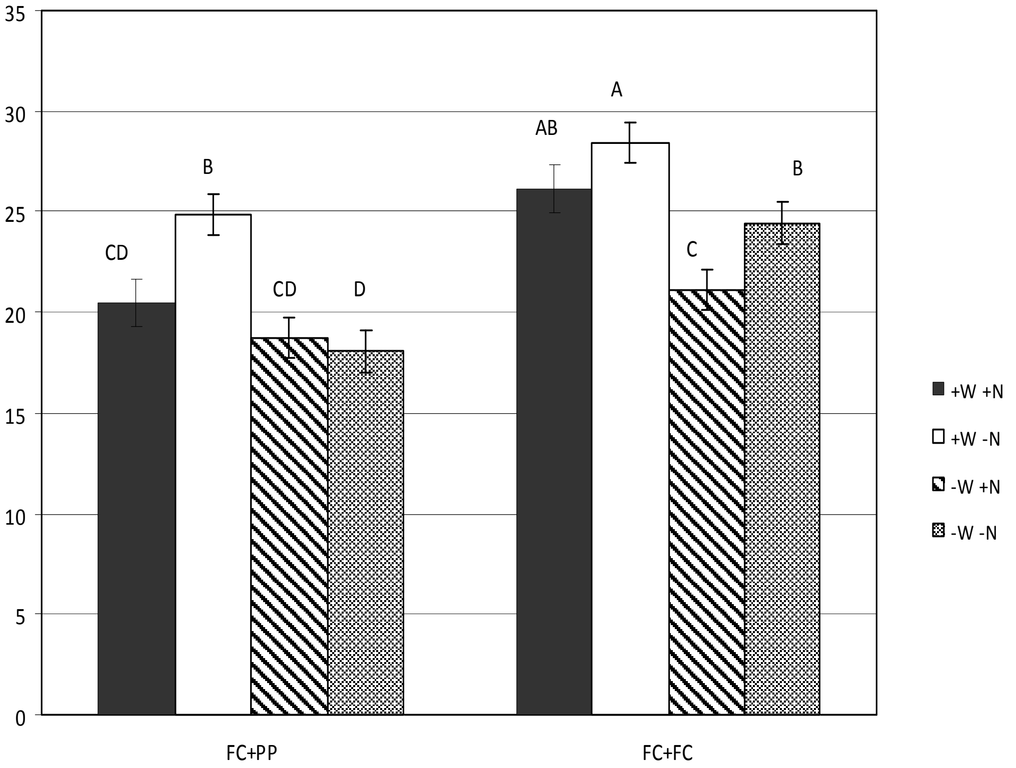

Figure D1: Changes in final tiller heights of *F. campestris* when exposed to varying nitrogen, water, and neighbor treatments in Experiment 1. Means with different letters differ. P<0.05

[1] Treatments labels are as follows: +W indicates water addition, -W ambient water; +N indicates nitrogen addition, -N indicates no nitrogen addition.

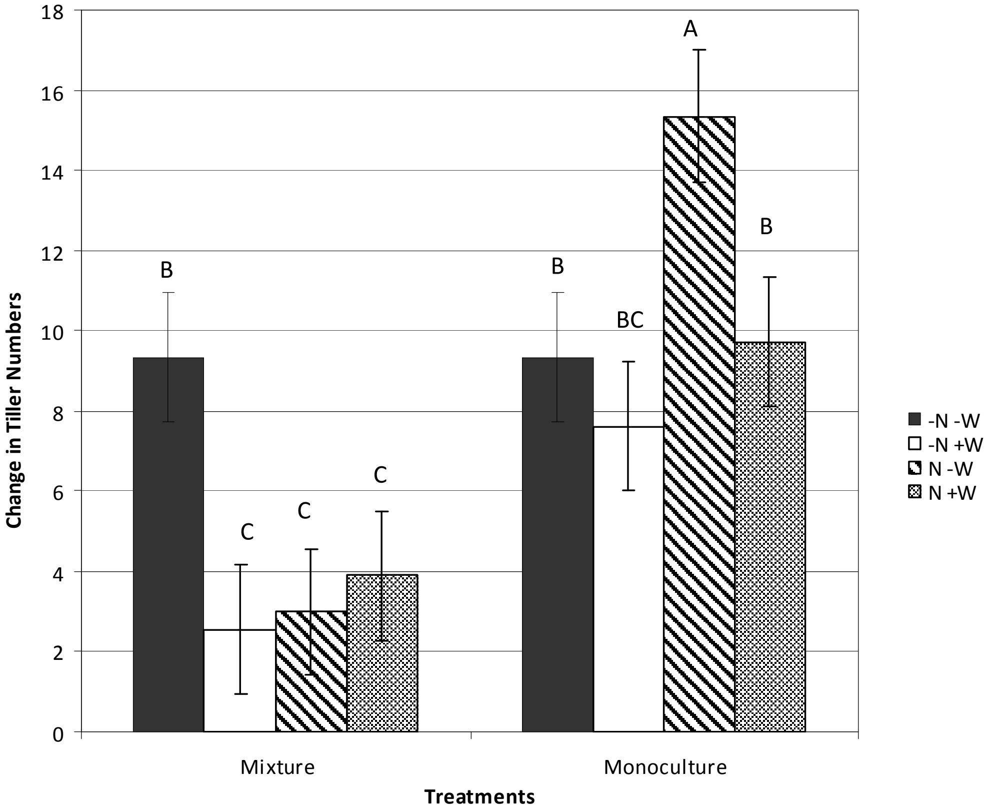

Figure D2: Change in tiller counts after 1month of growth under sucrose addition and water addition treatments on *F. campestris* plants with *F. campestris* and *P. pratensis* neighbors.

[1]Treatments labels are as follows: +W indicates water addition, -W ambient water; +N indicates nitrogen addition, -N indicates no nitrogen addition.

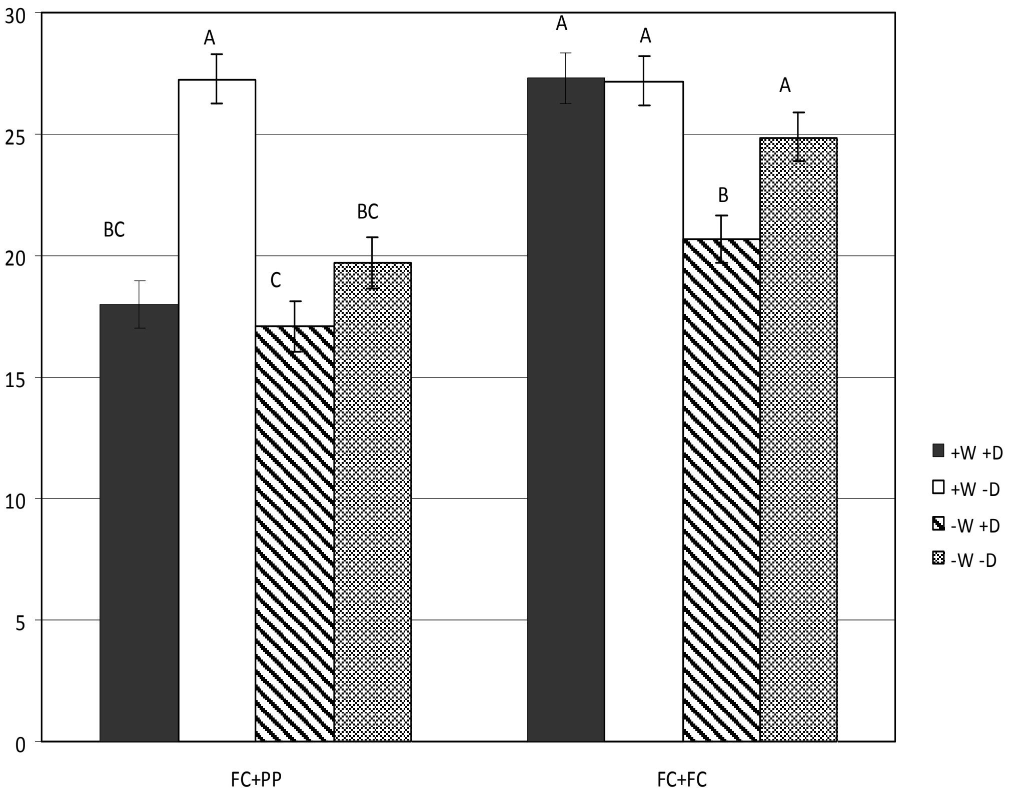

Figure D3: Changes in final tiller heights of *F. campestris* when exposed to varying water, defoliation and neighbor treatments in Experiment 1. Means with different letters differ. P<0.05

[1] Treatments labels are as follows: +W indicates water addition, -W ambient water; + D indicates defoliated conditions, -D undefoliated conditions.

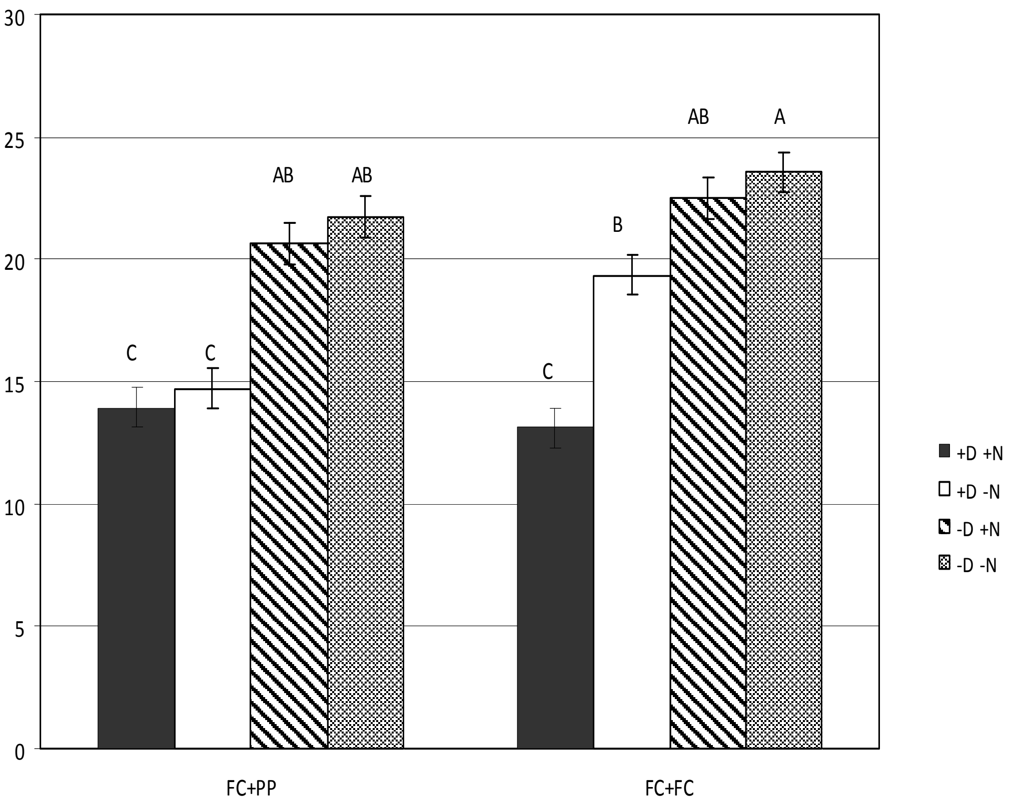

Figure D4: Changes in tiller heights (3.5 months) of *F. campestris* when exposed to varying nitrogen, defoliation and neighbor treatments in Experiment 1. Means with different letters differ. $P<0.05$

[1] Treatments labels are as follows: +N indicates nitrogen addition, -N indicates no nitrogen addition; + D indicates defoliated conditions, -D undefoliated conditions.

Appendix E Supplemental Information on the Environment for Chapters 3 & 4

Treatment Induced Changes to the Environment

Litter removal increased light transmittance from May through August of 2006 ($P<0.05$), although this effect declined over the growing season (May +L = 25.7±0.7%, May –L = 48.4±0.7%; Aug +L = 14.1±0.3%, Aug –L = 15.2±0.3%). The following year, light transmittance remained greater in –L plots (18.2±1.5%) than +L plots (13.6±1.5%), but only in May (Table E.1). Levels of PAR during May remained negatively correlated with final litter biomass ($r^2=0.15$ $p=0.002$). Litter removal also tended to alter soil moisture, as these plots were up to 2.8% lower in May and June of 2006 compared to plots with litter intact (Table E1). However, this pattern reversed in July 2007 and June 2008, when -L plots had up to 1.5% more soil moisture.

As expected, plots with water addition had greater soil moisture, although the timing of sampling (2 weeks after application) led to small differences between treatments (≤4.4%). Additionally, soil moisture varied widely over time. For example, in 2006, +W plots had greater moisture in May and August, but not June (Table E1). During 2007, +W plots had greater moisture than –W plots, but only during the second half of the growing season (July and August). In contrast, soil moisture remained greater within +W plots during May and June of 2008 (Table E1).

Soil moisture was also affected by N application in August 2006 ($P = 0.04$), July 2007 ($P = 0.04$) and June 2008 ($P =0.03$), during which N addition reduced monthly soil moisture values relative to ambient plots by 0.7% (12.5±0.2% to 11.9±0.2%), 1.1% (13.0±0.4% to 11.9±0.4%), and 1.4% (25.8±0.5% to 24.44±0.5%), respectively. Soil moisture was also lower in May 2006 (P <0.0001) within winter defoliated plots (18.2±0.6%) compared to those non-defoliated (22.3±0.6%), with this pattern reversing in August of that year (WD = 13.3±0.3%; ND = 11.9±0.3%).

Not surprisingly, fertilization led to greater (min P<0.02) detectable soil N in the environmental study at the end of the growing season in both 2007 (+N = 1.99±0.11ug/g; -N = 1.31±0.11ug/g) and 2008 (+N = 5.53±0.55ug/g; -N = 3.4±0.55ug/g). The same pattern occurred within the defoliation study during 2007 (+N = 1.7± 0.077ug/g; -N = 1.06± 0.077ug/g) and 2008 (+N = 5.12± 0.27ug/g; -N = 2.67± 0.27ug/g).

During the analysis of defoliation in 2007 there was an interaction of N and W addition (P =0.005) on observed soil N, together with an effect of defoliation (P =0.03). Undefoliated plots (1.62±0.09ug/g) had greater (P<0.05) soil N than those summer defoliated (1.29±0.09ug/g) or winter defoliated (1.23±0.09ug/g). The interaction of N and W arose from the finding that N depletion occurred within the +N treatment, but only under high water conditions (+W+N 1.49±0.11ug/g; +W-N 1.22±0.11ug/g) rather than ambient moisture (-W+N 1.91±0.11ug/g; -W-N 0.91±0.11ug/g).

Figure E1: The effects of water addition and one time litter removal (-L) on measured soil moisture (%) and light transmittance (% PAR) during each of the 2006, 2007 and 2008 growing seasons.

Year	Factor	Treatment[1]	May	June	July	August
2006	Soil Moisture	+W	22.0 (0.5) *[2]	36.1(0.4)	---	12.6(0.2)*
		-W	19.7(0.5)	35.5(0.4)	---	11.8(0.2)
	Soil Moisture	+L	22.3(0.7)*	25.8(0.5)*	---	11.9(0.3)
		-L	19.5(0.7)	23.4(0.5)	---	11.6(0.3)
	Light	+L	25.7(2.3)*	11.2(1.3)*	13.0(2.2)*	14.1(2.0)*
		-L	48.4(2.3)	23.4(1.3)	15.9(2.2)	15.2(2.0)
2007	Soil Moisture	+W	34.6(0.4)	28.1(0.4)	14.0(0.4)*	28.9(0.4)*
		-W	34.2(0.4)	28.6(0.4)	10.9(0.4)	24.5(0.4)
	Soil Moisture	+L	34.3(0.4)	25.2(0.4)	11.3(0.3)*	26.8(0.6)
		-L	34.4(0.4)	25.7(0.4)	12.1(0.3)	26.7(0.6)
	Light	+L	13.6(1.5)*	11.1(1.9)	14.9(1.2)	---
		-L	18.2 (1.5)	13.8(1.9)	14.1(1.2)	--
2008	Soil Moisture	+W	28.9(0.4)*	25.7(0.5)*	---	---
		-W	24.5(0.4)	24.4(0.5)	--	--
	Soil Moisture	+L	26.8(0.4)	24.2(0.4)*	---	---
		-L	26.7(0.4)	25.7(0.4)	--	--
	Light	+L	10.4(1.2)	---	---	---
		-L	10.7(1.2)	--	--	--

[1] +W and –W indicate plots with and without supplemental water; +L and –L indicate plots that retained litter and had litter removed, respectively.

[2] Within a column, paired treatment means with an asterisk differ, P<0.05.

[1]Treatments labels are as follows: +W indicates water addition, -W ambient water; + L indicates litter remained intact, -L litter removed; +N indicates nitrogen addition, -N indicates no nitrogen addition.

Table E2: Precipitation at the Cochrane weather station including 2006, 2007, 2008, 30 year normal and percentage of the 30 year normal precipitation experienced in each month. 2008 data is underestimated as data points were missing from the weather station.

	Precipitation (mm)						
	2006	2007	2008	30 year Normal	2006 % of Normal	2007 % of Normal	
May	59.2	117.3	158	72.2	82%	162%	219%
June	104	138.6	134.2	78.4	133%	177%	171%
July	39.1	42		57.8	68%	73%	
August	98	97.8		51.2	191%	191%	
Total	300.3	395.7		259.6	116%	152%	

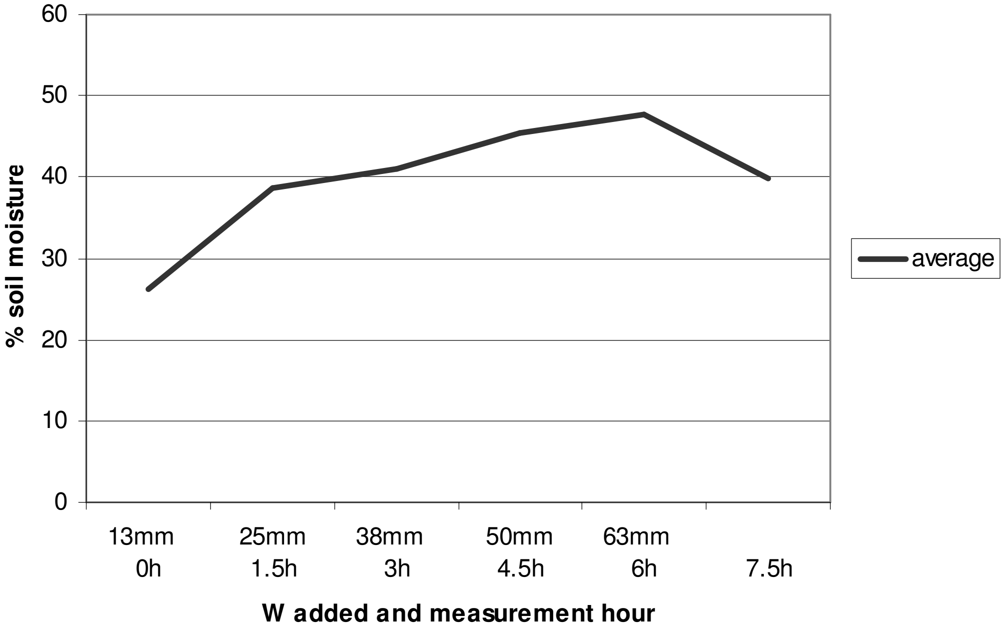

Figure E1: Average soil moisture levels 1.5 hrs after addition of 12.7 mm of water to each of 4 plots repeated six consecutive times.

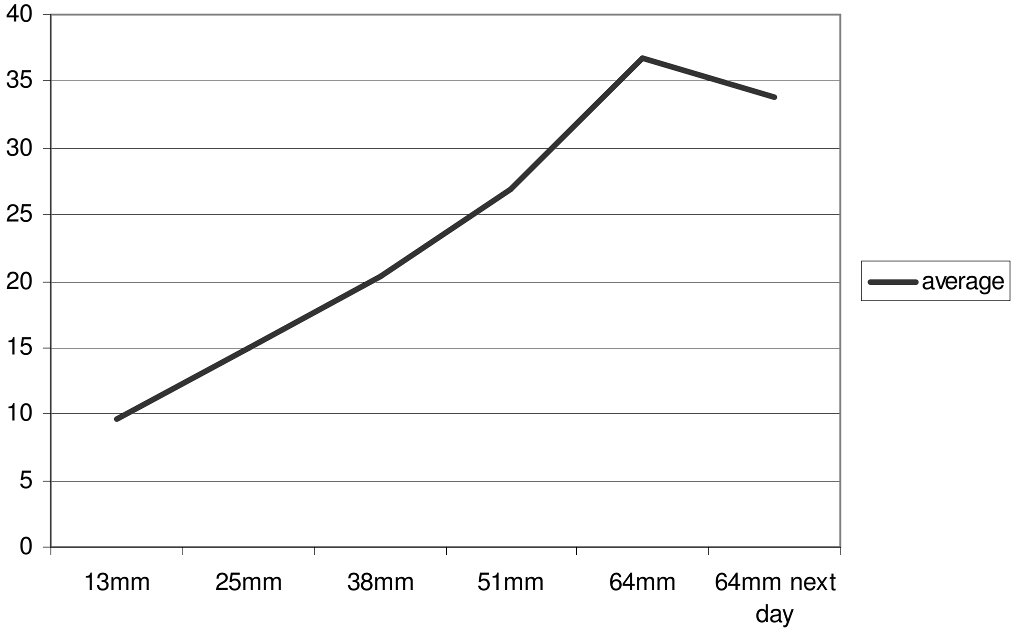

Figure E2: Mean soil moisture values 2 hrs after water addition at each of five separate levels (n=4). The 64 mm treatment was also assessed 24 hrs after water addition.

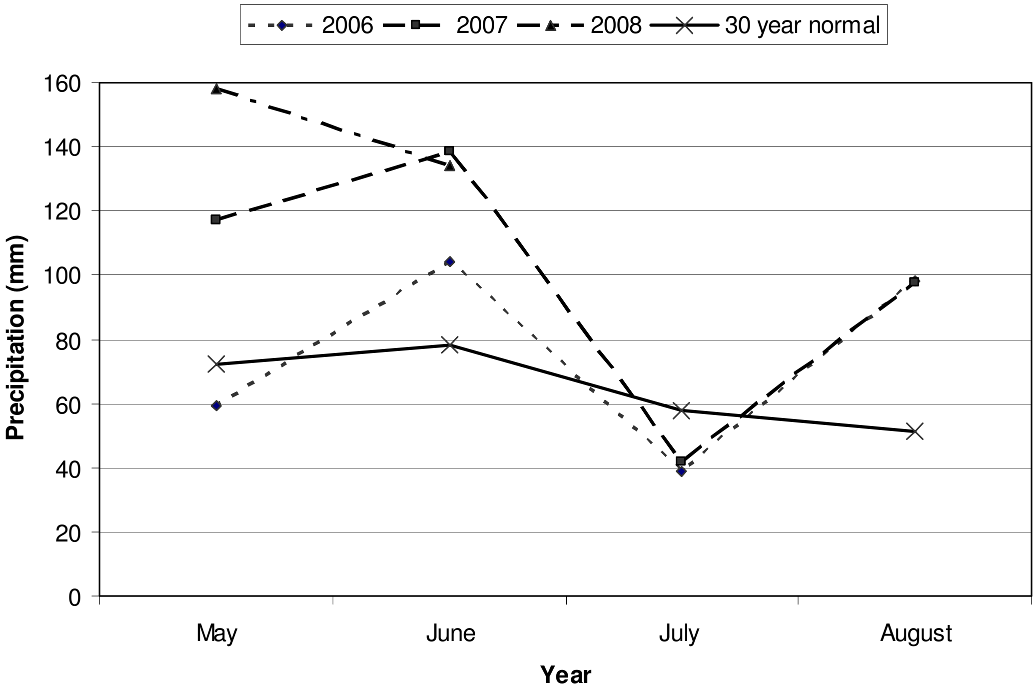

Figure E3: Precipitation data for the Cochrane weather station for 2006, 2007, 2008, and 30 year climate normals. The 2008 data was missing data points and is likely an underestimate of precipitation levels in the area.

Appendix F Supplemental Information for Chapter 7

Hordeum jubatum

Hordeum jubatum cover increased within litter removal in the MC experiment. While this relationship was particularly strong in 2006 (P=0.02), it weakened in 2007 (P=0.07) and 2008 (P=0.09) due to a marked decline in *H. jubatum* across all plots (Tale F6). In contrast, litter removal had no detectable effect on *H. jubatum* cover in GP plots during all 3 years (Appendix F and Table F6). Divergent responses were also observed in *H. jubatum* response to tilling, depending on the establishment method. Tilling of plots in the MC experiment reduced *H. jubatum* cover, primarily during 2006 (P=0.06) and 2008 (P=0.0005) (Table F6). Carbon addition reduced *H. jubatum* cover in the MC experiment but only in 2007 (P=0.04) (Table F6, Appendix F). This was contrasted by increases in *H. jubatum* within the GP plots (P=0.08) during the same year (Table F6).

Cover of *H. jubatum* positively correlated with available soil N and June PAR during 2007, and again with May SM and May PAR during 2008 within the GP plots (Table F5). In contrast, *H. jubatum* cover within the MC experiment was negatively associated with July PAR and August SM in 2006, but was positively associated with available N during 2008 (Table F5.1).

Table F1: Summary of significance tests for available soil N, as well as May, June and July photosynthetically active radiation (PAR), within the soil preparation treatments (carbon addition, litter removal and tilling treatments) and planting methods (mature cuttings and greenhouse plugs). P values <0.1 are considered significant.

		Available N		PAR May		PAR June		PAR July	
Planting Method	Soil Treatment	F value	P value	F value	P value	F value	P value	F value	P value
Mature Cuttings	Carbon Addition	1.0	0.3	**5.5**	**0.02**	0.0	1.0	0.4	0.5
	Litter Removal	0.3	0.6	**73.2**	**<0.0001**	**45.4**	**<0.0001**	**3.6**	**0.06**
	Tilling	0.5	0.5	1.2	0.3	**3.3**	**0.08**	2.0	0.2
Greenhouse Plugs	Carbon Addition	0.5	0.5	1.4	0.3	**9.5**	**0.01**	**4.3**	**0.06**
	Litter Removal	1.6	0.2	0.4	0.5	**4.8**	**0.05**	0.8	0.4
	Tilling	0.2	0.7	2.0	0.2	0.0	0.9	**7.0**	**0.02**

Table F1.1: Summary of the P-values of Environmental measures (May, June, July and August soil moisture) within the soil preparation treatments (carbon addition, litter removal and tilling treatments) and planting methods (mature cuttings, and greenhouse plugs). P values <0.1 are considered significant.

		SM May		SM June		SM July		SM August	
Planting Method	Soil Treatment	F value	P value	F value	P value	F value	P value	F value	P value
Mature Cuttings	Carbon Addition	0.7	0.4	0.7	0.4	1.6	0.2	0.1	0.8
	Litter Removal	0.1	0.8	0.2	0.6	0.1	0.7	0.2	0.7
	Tilling	0.7	0.4	0.2	0.6	2.6	0.1	0.3	0.6
Greenhouse Plugs	Carbon Addition	0.2	1.0	0.4	0.5	0.2	0.6	0.04	0.8
	Litter Removal	0.3	0.6	0.0	0.9	1.6	0.2	0.09	0.8
	Tilling	2.5	0.12	0.7	0.4	1.8	0.2	**32.6**	**<0.0001**

Table F2: Summary of the P-values of *F. campestris* vigor measures including Tillers (2007, 2008, and total) and Cover (2007, 2008 and Total) within the soil preparation treatments (carbon addition, litter removal and tilling treatments) and planting methods (mature cuttings, and greenhouse plugs). P values <0.1 are considered significant.

		Tillers 2007		Tillers 2008		Total Tillers		Cover 2006		Cover 2007		Cover 2008		Total Cover	
Planting Method	Soil Treatment	F value	P value	F value	P value	F value	P value	F value	P value	F value	P value	F value	P value	F value	P value
Mature Cutting	Carbon addition	0.96	0.3	0.08	0.8	0.7	0.4	0.5	0.5	**12.3**	**0.001**	**4.3**	**0.04**	**13.2**	**0.0009**
	Litter Removal	0.00	1.0	0.38	0.5	0.3	0.6	1.1	0.3	**3.8**	**0.06**	**11.5**	**0.002**	**13.1**	**0.0009**
	Tilling	0.10	0.8	0.10	0.8	0.0	1.0	1.2	0.3	**2.6**	**0.12**	**12.7**	**0.001**	**13.6**	**0.0007**
Greenhouse Plugs	Carbon addition	0.53	0.5	0.00	1.0	1.3	0.6			**3.4**	**0.08**	0.2	0.6	2.7	0.11
	Litter Removal	0.09	0.8	**5.57**	**0.02**	**4.2**	**0.05**			0.3	0.6	0.0	0.7	0.0	0.9
	Tilling	1.66	0.2	**5.11**	**0.03**	**6.9**	**0.01**			**6.6**	**0.017**	1.8	0.2	**7.7**	**0.01**

Table F2.1: Summary of the P-values of *F. campestris* vigor measures including final biomass and survival (2006, 2007, 2008 and Total) within the soil preparation treatments (carbon addition, litter removal and tilling treatments) and planting methods (mature cuttings, and greenhouse plugs). P values <0.1 are considered significant.

		Biomass		Survival 2006		Survival 2007		Survival 2008		Total Survival	
Planting Method	Soil Treatment	F value	P value	F value	P value	F value	P value	F value	P value	F value	P value
Mature Cutting	Carbon addition	2.8	0.12	0.0	0.9	0.07	0.8	1.6	0.2	0.7	0.4
	Litter Removal	**3.2**	**0.10**	1.0	0.3	0.3	0.6	**4.7**	**0.04**	**4.6**	**0.04**
	Tilling	1.2	0.3	0.1	0.8	0.1	0.7	0.8	0.4	0.8	0.4
Greenhouse Plugs	Carbon addition	0.0	1.0			0.0	0.7	0.3	0.5	0.6	0.4
	Litter Removal	1.1	0.3			0.5	0.4	0.0	0.8	0.5	0.5
	Tilling	1.6	0.2			0.0	0.8	2.5	0.2	1.2	0.3

Table F3: Summary of the P-values of *P. pratensis* vigor measures including final biomass and Cover (2007, 2008 and Total) within the soil preparation treatments (carbon addition, litter removal and tilling treatments) and planting methods (mature cuttings, and greenhouse plugs). P values <0.1 are considered significant.

		Cover 2006		Cover 2007		Cover 2008		Total Cover		Biomass 2008	
Planting Method	Soil Treatment	F value	P value	F value	P value	F value	P value	F value	P value	F value	P value
Mature Cuttings	Carbon Addition	0.0	1.0	0.7	0.4	0.0	0.9	0.2	0.7	0.3	0.43
	Litter Removal	0.1	0.7	**5.6**	**0.02**	0.0	0.7	**3.3**	**0.08**	0.8	0.4
	Tilling	0.1	0.8	3.9	0.06	2.8	0.10	**5.2**	**0.03**	1.8	0.2
Greenhouse Plugs	Carbon Addition			0.01	0.9	0.4	0.5	0.3	0.6	0.9	0.4
	Litter Removal			0.008	0.9	0.5	0.5	0.2	0.7	3.0	0.11
	Tilling			**8.4**	**0.008**	**34.7**	**<0.0001**	**38.7**	**<0.0001**	**27.3**	**0.0002**

Table F4: Summary of the P-values of *H. jubatum* Cover (2006, 2007, 2008 and Total) within the soil preparation treatments (carbon addition, litter removal and tilling treatments) and planting methods (mature cuttings, and greenhouse plugs). P values <0.1 are considered significant.

		Cover 2006		Cover 2007		Cover 2008		Total Cover	
Planting Method	Soil Treatment	F value	P value	F value	P value	F value	P value	F value	P value
Mature Cuttings	Carbon Addition	3.1	0.08	**6.0**	**0.02**	0.0	0.9	**5.6**	**0.02**
	Litter Removal	13.4	**0.001**	**4.5**	**0.04**	**0.0**	**0.9**	**11.8**	**0.002**
	Tilling	7.8	**0.01**	1.8	0.2	**0.0**	**0.9**	0.9	0.4
Greenhouse Plugs	Carbon Addition			**2.0**	**0.17**	2.6	0.1	**4.5**	**0.04**
	Litter Removal			0.0676	0.8	2.0	0.2	0.7	0.4
	Tilling			**1.7**	**0.21**	**33.1**	**<0.0001**	**9.9**	**0.004**

Table F5: Results of the multiple regression analysis within the greenhouse plug planting method between, *H. jubatum*, vigor measures (cover, survival, tillers, and biomass) and environment [soil moisture (SM), photosynthetically active radiation (PAR), and available soil N], in each of 2006, 2007 and 2008. Responses are averaged across all soil preparation treatments.

Hordeum jubatum	2007	Cover	Available N	0.63	0.36	0.58	7.8	0.01
			PAR June		0.27	0.85	9.4	0.009
	2008	Cover	SM May	0.65	0.56	0.77	17.5	0.001
			PAR May		0.92	0.30	3.4	0.09

Table 5.1: Results of the multiple regression analysis within the mature cutting planting method between F. campestris, H. jubatum, and P. pratensis vigor measures (cover, survival, tillers, and biomass) and environment [soil moisture (SM), photosynthetically active radiation (PAR), and available soil N] in each of 2006, 2007 and 2008. Responses were combined across all soil treatments.

Species	Year	Response	Environmental Variable	Model R^2	Partial R^2	*B*-coefficient	F Value	P Value
Hordeum jubatum	2006	Cover	PAR July	0.82	0.75	-0.28	41.6	<0.0001
			SM August		0.75	-0.84	5.6	0.03
	2008	Cover	Available N	0.24	0.24	0.49	4.4	0.06

Table F6: Effect of soil preparation techniques (carbon addition, litter removal, and tilling) on the mean (±SE) cover of *H. jubatum* within each of the experiments using mature cuttings and greenhouse plugs of *F. campestris*.

Planting Method	Soil Preparation	2006 cover (%)	2007 cover (%)	2008 cover (%)
Mature Cuttings	*In-situ*	25.0	56.3**	0.0
	Carbon addition	0.8	22.5	1.0
	Litter removal	63.8**	37.5*	2.3*
	Litter	13.0	8.3	0.0
	Tilled	25.0*	56.3	0.0*
	Untilled	63.8	37.5	2.3
	SE	13.5	10.3	0.9
Greenhouse Plugs	*In-situ*		2.5*	72.5
	Carbon addition		18.8	91.3
	Litter removal		17.5	5.8
	Litter		14.5	22.3
	Tilled		2.5*	72.5***
	Untilled		17.5	5.8
	SE		6.0	9.9

Pairwise means within a column differ at p<0.1 (*), p<0.05 (**), and p<0.01 (***).