EFFECTS OF COMPETITION, SALINITY AND DISTURBANCE ON THE GROWTH OF *POA PRATENSIS* (KENTUCKY BLUEGRASS) AND *PUCCINELLIA NUTTALLIANA* (NUTTALL'S ALKALIGRASS)

by

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“The moment one gives close attention to anything, even a blade of grass it becomes a mysterious, awesome, indescribably magnificent world in itself.”

-Henry Miller

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ABSTRACT

Climate change may reduce water levels in the interior wetlands and ponds of British Columbia, Canada, potentially changing aquatic and soil salt concentrations. An increase in salinity can reduce plant growth and affect competitive interactions between plants. A field experiment and a greenhouse experiment tested the effects of salinity and competition on the growth of two wetland plants, *Poa pratensis* (a glycophyte) and *Puccinellia nuttalliana* (a halophyte). For the field experiment, seedlings of *Poa pratensis* and *Puccinellia nuttalliana* were transplanted to six sites (two highly saline, two moderate, and two at low salinity) with and without plant neighbours. All sites were affected by high mortality and poor growth of the transplants. Survivorship was greater for plants grown alone. Biomass of plants grown alone was greatest at one of the moderate saline sites. The greenhouse experiment tested the response of *P. nuttalliana* and *P. pratensis* in a factorial design with 70 combinations (2 species x 7 salinity x 5 competition) replicated 6 times. Both of the species' biomass was greatest when grown alone without salt. Species, salt type and competition had greatest effect on survivorship. *P.nuttalliana* displayed a greater degree of salt tolerance than *P. pratensis*. Re-growth after clipping was suppressed at higher salinities. I conclude that not only salt concentration but also ionic combinations can influence plant growth on interior saline wetland plant communities.

Keywords: *Poa pratensis, Puccinellia nuttalliana,* salinity gradient, climate change, competitive importance, cattle grazing

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CHAPTER 1

INTRODUCTION

Wetlands are important ecosystems, biologically, chemically and hydrologically. They provide a source of water, food, refuge and habitat for numerous organisms, including many endemic, endangered and threatened species (Poiani and Johnson 1991; Zedler 2003; Pyke and Marty 2005; Junk et al. 2006). Wetlands act as water stores, filters and nutrient sinks (Richardson 1994; Weller et al. 1996; Mitsch and Gosselink 2007). Many wetlands are areas for groundwater recharge, hydraulic stabilization and protection (Gren et al. 1994; La Baugh et al. 1998; Lotze et al. 2006; Mitsch and Gosselink 2007). When functioning properly, these features and processes greatly improve the quality of the wetlands themselves, their surrounding ecology and the world. The benefits of healthy wetlands are difficult to economically quantify, but are recognized for their ecosystem values and services (Gren et al. 1994; Richardson 1994; Costanza et al. 1997; Turner et al. 2000). Unfortunately, human interference has destroyed, damaged or irreversibly altered much of the world's wetland systems (Fraser and Keddy 2005; Lotze et al. 2006). The loss of many wetlands can be attributed to human engineering: draining, diking, damming and filling, and global climate change; while those that remain are under threat from poor land management practices and a rapidly changing environment.

Wetlands can be biologically rich arenas that boast numerous endemic and unique species (Murdock 1994; Fensham and Price 2003). Interspecific competition is an important factor controlling community structure and composition (Connell 1983; Schoener 1983). Plants compete for light above ground, and water and mineral nutrients below ground. There are two prevailing theories on plant competition, CSR theory (Grime 1977) and R* theory (Tilman 1982). Grime (1977) defined competition as an individual's ability to sequester an ion of mineral, a photon of light, and a molecule of water quicker and more efficiently than another individual. Tilman (1982) has defined competition as a species' or individual's ability to draw down resources to such a low level that the competing species or individual cannot survive.

Competitive exclusion occurs along environmental gradients, where the dominant competitor obtains or limits resources thereby inhibiting the establishment and growth of another plant and influencing species position along the gradient (Grosshans and Kenkel 1997). According to Grime, competition is a stronger factor in determining species zonation in less disturbed or less stressful environments (Grime 2001, Keddy 2002). In Keddy's centrifugal model the optimal (core) environment contains the strongest competitors but as you move into the increasingly disturbed or stressed (periphery) habitats the species composition shifts towards the less competitive stress-tolerant or ruderal species (Keddy 2002). A physiological trade-off between competitive ability and stress-tolerance has been proposed (Grime 1973, 1979; Grosshans and Kenkel 1997; Keddy 2002). However, there is controversy regarding the role of competition along a productivity gradient (Gough and Grace 1999; Craine 2005). While Grime suggests that competition increases with productivity, Tilman's view is that competition remains constant and only the competitive 'winners' change along the productivity gradient (Tilman 1982, 1988). Others have suggested that the impact of competition on individuals should be considered with and without the influence of abiotic stresses in order to understand and predict community dynamics (Greiner La Peyre et al. 2001).

Salt occurs naturally in many of the world's wetland systems, whether it is from the ocean in estuaries and tidal marshes or from the ground and atmosphere in inland potholes and playas. Coastal wetlands are dominated by NaCl salts derived from the oceans, whereas inland wetlands may contain various salt combinations leached from bedrock and surface material, deposited from atmospheric salts and agricultural run-off. In addition to salt composition, inland wetlands may vary in salt concentration (Topping and Scudder 1977), which is influenced by local climatic trends (McKinstry et al. 2004). Arid and semi-arid climates where evaporation is greater than precipitation can often lead to saline water bodies.

British Columbia's southern interior is a prime example of a semi-arid environment possessing numerous saline alkali lakes and wetlands. Salinity in this region can be attributed to the composition of underlying volcanic bedrock and overlying glacial till and a semi-arid climate. Interior depressional or intermountain wetlands, like those in the southern interior, are considered to be very susceptible to climate change (Winter 2000; Mitsch and Gosselink 2007). Small catchment areas and locations within semi-arid or arid regions make these systems sensitive to increasing temperatures and shifting precipitation patterns (Mitch and Gosselink 2007). Furthermore, even a slight increase in temperature may drastically alter the recharge and discharge rates of groundwater in the southern interior (Walker and Sydneysmith 2008). In some predicted climate change models, British Columbia's southern interior may experience warmer temperatures, drier summers and reduced snowpack which may lead to as high as a 65% of a reduction in the annual surface water supplies (Merritt et al. 2006; Spittlehouse 2008; Walker and Sydneysmith 2008). Less surface water and greater rates of evaporation may lead to reduced water volume in many of the southern interiors' lakes and wetlands; with less water, there will be a higher concentration of ions and salts. Higher salinities can generate more stress for vegetation and create toxic environments for many plants and animals. A shift in vegetation towards more salt-tolerant species will result.

My transplant experiment (Chapter 2) was to determine the growth (aboveground biomass) of two transplanted wet meadow species, *Poa pratensis* and *Puccinellia nuttalliana,* with and without neighbours in six wetland systems with varying salinities.

My greenhouse experiment (Chapter 3) was to determine the effects of two salt types (NaCl and Na_2SO_4) along an artificially manipulated salinity gradients, competition and clipping (to simulate grazing) on two wet meadow species *Poa nuttalliana* (Schult.) Hitchc. and *P. pratensis* L. grown for three months in a controlled greenhouse environment.

The transplant and greenhouse experiments are closely related and were designed to complement each other. *Poa pratensis* and *Puccinellia nuttalliana* were selected based on their presence in and around the study area and were used in both studies. The field provided a natural, realistic environment to conduct my study and enabled me to gather a better understanding of how the transplants interacted with their environment. The greenhouse experiment permitted me to isolate the desired variables and manipulate the environment within a controlled setting. Both studies provided valuable information regarding *P. pratensis* and *P. nuttalliana*, plant-plant interactions and the role of stress and disturbance on plant growth.

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CHAPTER 2

THE EFFECTS OF COMPETITION ON TWO GRASS SPECIES ALONG A SALINITY GRADIENT

Introduction

A species' competitive ability and adaptations to environmental stress will determine its range (Silvertown 2004; Brooker 2006). Wetlands are excellent arenas to study the effects of plant competition and environmental stress gradients in the field because of their rich biodiversity and wide range of topographical, hydrological and chemical characteristics (Keddy 2001; Mitsch and Gosselink 2007). The effects of environmental stresses can be observed in the field by manipulating a natural stress gradient (Wilson and Keddy 1988; Grosshans and Kenkel 1997) or utilizing a natural stress gradient (Craine et al. 2004; Sanderson et al. 2008). In wetlands, interactions between competition and sea inundation (Disraeli and Fonda; Ewing 1983; Bertness and Ellison 1987), competition and water level (Grosshans and Kenkel 1997; Fraser and Miletti 2008) and competition and soil-water chemistry (Sanderson et al. 2008) have been used to understand plant community composition.

In North America, saline wetlands can be found in arid and semi-arid regions of the prairies and mountain ranges where evaporation exceeds precipitation (Cumming and Smol 1993; Wilson et al. 1994; Chhabra 1996). Intermountain wetlands have a range of salinities dependant on bedrock and substrate composition, hydrologic regime and microclimate (Topping and Scudder 1977; Chhabra 1996). Differences in salinity can lead to a variety of plant communities by influencing plant-plant competitive interactions and restricting the range of salt-intolerant plants (Kenkel at al. 1991). Global climate change is predicted to increase warming and alter precipitation patterns which could lead to altered hydrology (Poiani and Johnson 1991). Such changes to intermountain hydrologic patterns might impact wetland salinity and therefore plant community composition.

Within the semi-arid grasslands of the southern interior of British Columbia, Canada, the rugged topography, limited precipitation and extreme temperatures have resulted in numerous, often isolated, wetlands and lakes. Forming in valleys and depressions, these water bodies are largely spring run-off and groundwater fed (Topping and Scudder 1977; Renaut 1990). Groundwater leaches minerals from the bedrock and overlain glacial till and accumulates in these wetlands and lakes causing many of them to be saline (Renaut 1990; Chhabra 1996), often characterized as athalassic alkaline wetlands (Topping and Scudder 1997). Throughout the growing season, water volume generally decreases due to evaporation and groundwater drawdown in many of the small or shallow wetlands. Declining water levels or complete loss of surface water can lead to a higher concentration of solutes and therefore salinity of the remaining water and soil (Topping and Scudder 1977; Wilson et al. 1994; Smith L., pers comm.). Intermountain wetlands are used as water sources and their vegetation provides forage for grazing cattle and wildlife.

In this study I focused on the effects of salinity on aboveground biomass and competitive abilities of two grass species, *Puccinellia nuttalliana* (Schult.) Hitchc. (Nuttall's alkaligrass) and *Poa pratensis* L. (Kentucky bluegrass). Both species are commonly found in the southern interior of British Columbia. *Puccinellia nuttalliana* is often limited to wetlands and areas with alkali soils in mid to low elevations (Kenkel et al. 1991; Tarasoff 2007). *Poa pratensis,* commonly used as lawn and pasture seed (Tarasoff et al. 2007), can be found in a wider range of habitats including meadows, open forests and areas of disturbance from low to high elevation (USDA 2004). The species differ in their salt tolerances; *P. nuttalliana* is a facultative halophyte and grows in and around alkali and saline wetlands, but can flourish in fresh water conditions (Kenkel et al. 1991; Tarasoff et al. 2007). *Poa pratensis* has a relatively low tolerance to salt (Kenkel et al. 1991). Both species are flood tolerant and can survive in saturated soils, but *P. nuttalliana* is better adapted to drought conditions (Tarasoff et al. 2009). While *P. pratensis* and *P. nuttalliana* may be restricted by different abiotic and biotic stresses they can overlap in their distribution (Tarasoff et al. 2007), making them good species for competition studies.

My study examined the effects of salinity and competition on these two grass species in intermountain ponds in British Columbia, Canada. I tested the following hypotheses: 1) Survivalship of *P. nuttalliana* and *P. pratensis* will be greatest at the freshwater sites and least at the saline sites, with *P. nuttalliana* being less affected by salinity than *P. pratensis*; 2) survivalship of *P. nuttalliana* and *P. pratensis* will be greater when neighbouring vegetation is removed than with neighbours present; 3) aboveground biomass of both species will be greater when neighbouring vegetation is removed; 4) aboveground biomass of *P. pratensis* will be less effected than *P. nuttalliana* when neighbours are present.

Materials and Methods

Study Site

Six intermountain ponds were selected within Lac du Bois Provincial Park, located approximately 10 km north of Kamloops, British Columbia, Canada (Fig 2.1). During May to October the upper grasslands received 145mm rain and had a mean temperature of 15.7 ºC in 2007, less than 145mm rain (uncertain value due to missing data) and had a mean temperature of 15.0 ºC in 2008 and 179mm of rain and a mean temperature of 14.4 ºC in 2009 (Carlyle pers comm.).The ponds are depressional wetlands surrounded by grasslands matrix. All ponds were athalassic alkaline, but differed in salinity concentration: two were relatively fresh (≤5 ppt or oligosaline), two moderately saline (5-18 ppt or mesosaline) and two saline (30-40 ppt or eusaline) (Cowardin et al. 1978). Water input is from precipitation, run-off and ground water inflow. Evapotranspiration and ground water outflow were the main processes for water output. Fresh 1, Fresh 2, Saline 1 and Saline 2 dried out during the course of the 2009 growing season. Each pond contained a wet meadow section where transplantation occurred. *Juncus balticus, Lactuca serriola* and *Poa compressa* dominated the wet meadow of the fresh sites and Mid 1 (moderately saline site). The wet meadow of Mid 2 (moderately saline site) was dominated by *P. nuttalliana* and *Suaeda depressa*, while *P. nuttalliana*, *Elymus elymoides* and *Distichlis stricta* were the dominant species at the saline sites. Upland grassland vegetation occupied the area surrounding the wet meadow.

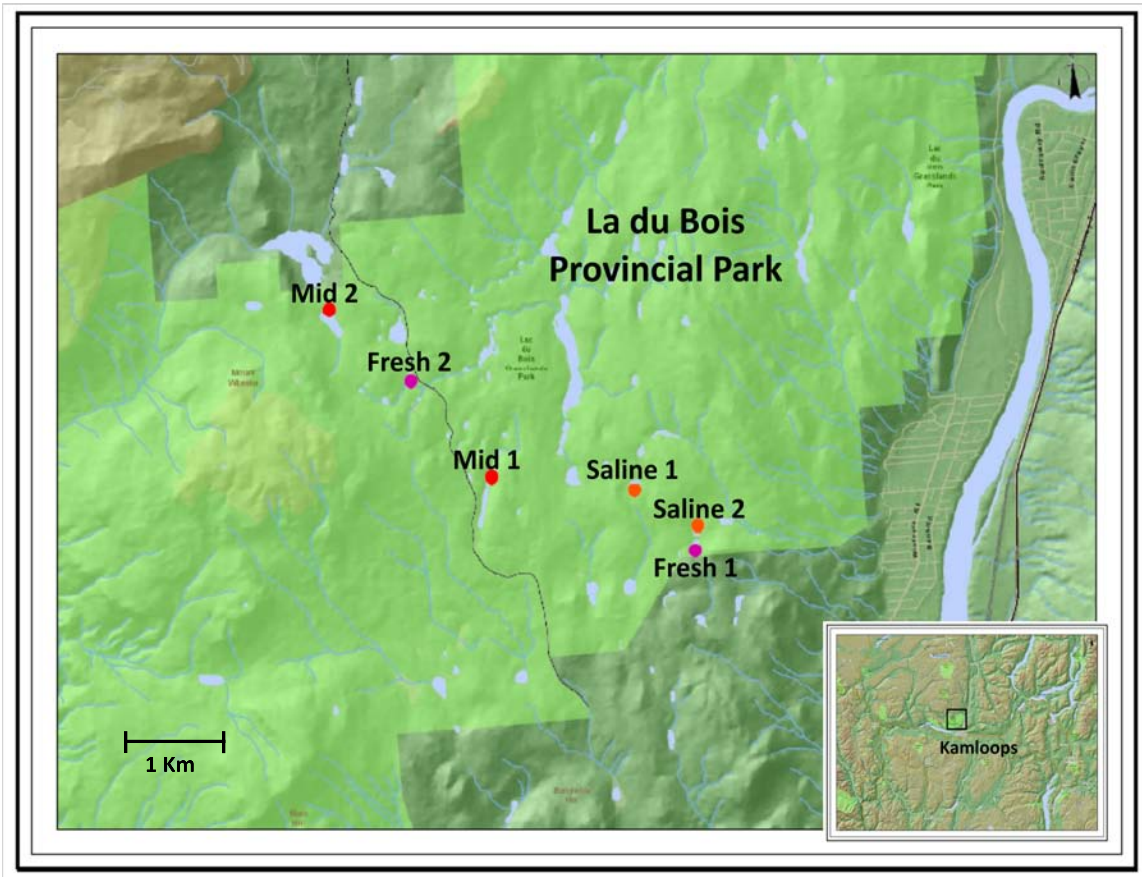


Figure 2.1. Map of study sites in Lac du Bois Provincial Park, British Columbia, Canada. Map scale 1: 73 858 (iMapBC 2010).

Experimental Design

I performed a factorial experiment that included two wet meadow species (*Puccinellia nuttalliana* and *Poa pratensis*), two levels of competition (with neighbours and neighbouring vegetation removed) at six sites varying in salinity. Treatment combinations contained only one transplant. Each treatment had six replicates at each pond for a total of 144 transplanted individuals.

Ponds were selected based on their salinity, presence of a wet meadow zone, and accessibility. Water conductivity readings were done using a Palintest waterproof 800 pH/conductivity/TDS meter on May 11, 2009, where a relative range was determined and each pond was designated its position along the respective salinity/conductivity gradient.

I established six 2.5 x 2.5 m blocks, each block contained four 50 x 50 cm quadrats that were randomly assigned one of the four treatment combinations (*P. nuttalliana* with neighbours, *P. nuttalliana* without neighbours, *P. pratensis* with neighbours or *P. pratensis* without neighbours) randomly assigned. Blocks and quadrats were orientated so that there was at least 50 cm separating each block and 50 cm between each quadrat within a block.

Transplants were cultivated in the greenhouse. Seeds of *P. nuttalliana* and *P. pratensis* were sown March 7, 2009 onto a distilled water saturated peat medium (peat pellet) placed in large trays. Distilled water was supplied as needed to the bottom of the trays to ensure the peat remained saturated during the germination and establishment process and to prevent seedling desiccation. On May 6, 2009 the transplants were moved outside to a protected area with high sun exposure to acclimate and test for temperature shock. Prior to transfer and planting in the field, a single dose of 200 ml of Rorison's nutrient solution was added to each tray containing the transplants to help reduce transplant shock.

The neighbouring vegetation was manually removed by clipping at the soil surface in half of the randomly selected quadrats. Quadrat selection and above ground biomass removal was conducted May 14 and 15, 2009 and transplanting occurred May 15, 2009. Transplanted individuals were planted in the centre of each 50 x 50 cm quadrat. Above ground biomass was continually removed by clipping and discarded throughout the season, weekly for the first 10 weeks then biweekly for the remaining 4 weeks.

Transplants were examined on Day 3, Day 6 and Day 13 following planting for signs of shock, herbivory and desiccation. Within this time period any individuals that had died were replaced. Individuals that died after Day 13 were not replaced and considered a mortality. Transplants severely damaged by herbivory were also removed from the analysis. In all plots that the transplant survived, the transplants aboveground biomass was harvested on August 3 and 4, 2009. Percent cover estimates of the other species in the 'with neighbours' plots were collected in addition to their aboveground biomass. Aboveground biomass was identified and separated to species in the field. Biomass was dried in a drying oven at 65ºC for 48 hours and weighed with a Fisher Scientific analytical balance accu-225D (d=0.01/0.1 mg) or Fisher Scientific analytical balance accu-4102 (d=0.01 g) on August 7-9, 2009.

Soil samples were collected on August 3 and 4, 2009. Small soil plugs were removed from the uppermost 6 cm of each plot by a 2.5 cm diameter soil corer. The individual plot soil samples were then combined by block within each site. Individual block soil samples were mixed for uniformity and sieved through a 0.2 mm mesh sieve for soil nutrient analysis. Block soil samples were combined into site samples for further analysis conducted outside of the lab. Site soil samples were sent to Bodycote Exova Testing Group, Edmonton, Alberta, Canada for soil nutrient and soil quality analysis.

Statistical Analysis

A 3-way ANOVA was conducted on the transplant biomass to test the effect of site, transplant species and presence/absence of neighbours. Biomass data were log transformed to satisfy assumptions of a normal distribution. Mortality among the transplants almost fifty percent; therefore, all transplants were analyzed for survivorship and only site Mid 2 was analyzed for the effects of neighbours on each species.

A 3-way Generalized Linear Model was conducted on the survivorship data of all the transplants by transplant species, neighbours presence or absence and site, with survivorship as a binomial response variable. Site Mid 2 surviving transplant biomass was transformed using a natural log function to satisfy assumptions of a normal distribution. A 2-way ANOVA was conducted by transplant species and presence/absence of neighbours. The transplants were separated and ANOVAs were conducted on both species individually by presence/absence of neighbours. Post-Hoc Tukey tests were run to determine statistical differences between sites or between treatments.

Total species community biomass was analyzed by using both biomass and percent cover value estimates. Results of both analyses were compared for consistency. Total species biomass values were selected to be used for further analysis including richness, diversity and total species biomass. A 1-way ANOVA was conducted on species richness, Shannon's diversity, Simpson's diversity, Inverse Simpson's diversity, community biomass and litter by site with a Post-Hoc Tukey test to determine statistical difference between sites. Shannon's diversity was selected and a Post-Hoc Tukey test was conducted to determine statistical difference between sites. Community biomass was transformed with a natural log function. All ANOVAs and the Post-Hoc Tukey tests were conducted using R version 2.9.1 (2009).

Results

Abiotic

All six study areas were identified as alkaline with soil pH values ranging from 9.2 to 7.8 (Table 2.1). The Saline sites had the highest soil and water electrical conductivity, substantially greater than the Mid and Fresh sites. Nitrogen levels were relatively low for all sites except Mid 2, while phosphorus levels were relatively low at both Fresh sites and Mid 1. Potassium, sulphate, calcium and magnesium levels were high and considered in excess for farm soil (farm soil is a standard the samples were compared to by Bodycote Exova Testing Group) (Table 2.1). Saline 1 showed extremely high levels of calcium. Chloride was present in all the ponds and its concentration increased with salinity. Sodium was present in all ponds with the greatest concentration in the Saline and Mid 2 sites. Calcium and magnesium accounted for the majority of cations present in the soil, 78.8-95.2% (Saline 1 and Fresh 1).

The size of the ponds ranged from just under a half hectare (Fresh 2) to just under 5 hectares (Mid 2). While slope did vary by block at each site the average values were greatest at the Fresh sites and least at the Saline sites.

Biotic

Species richness was greatest at Mid 1 and lowest at Saline 2 (Table 2.2). Mid 1 species richness was greater than all other sites. Species richness was very similar for both fresh sites and Mid 2. Saline 1 and Saline 2 recorded on average one less species than the Fresh and Mid 2 sites. Mid 1 had the highest Shannon's Diversity value, closely followed by Fresh 1. The Saline sites reported the lowest Shannon's Diversity values. Total species biomass was not significantly different. Fresh 1 and Mid 2 had the largest amount of total species biomass. Saline1 had the smallest amount of total species biomass, almost half of Fresh 1 and Mid 2. Litter biomass covered a large range of values. Fresh 1 contained a significantly larger amount of litter biomass than the other sites. The Mid sites and Saline 2 had significantly lower amounts of litter biomass with Mid 1 containing less than 2.5 g/m^2.

Site Mid 2 Transplants

Site Mid 2 had a significantly greater amount of transplant biomass than all the other sites (Table 2.3, Figure 2.2) because of re-growth. Therefore, further analysis was only conducted on the biomass of Mid 2. A Post-Hoc power analysis (α= 0.05) was conducted on the transplant data and showed that there was a 35% chance of committing a Type II error (Φ=1.130462). Power analysis results may be conservative due to the high number of treatment combinations. At Mid 2 the mean aboveground biomass of *P. nuttalliana* was significantly greater than the mean aboveground biomass of *P. pratensis* (p<0.1, Figure 2.3) and aboveground biomass was significantly less when transplants were grown with neighbours versus grown with neighbours (aboveground biomass) removed ($P<0.05$).

Table 2.1. Soil and water analysis for each transplant site. Soil analysis on samples collected August 3 and 4, 2009, provided pH, soil EC and ionic concentrations. Water EC values were measured on May 11, 2009.

Site	pH	Soil EC (ppm)	Water EC (ppm)	N (ppm)	P (ppm)	K (ppm)	S (ppm)	Ca (ppm)	Mg (ppm)	Cl (ppm)	Na (ppm)
Fresh 1	7.8	595	5070	<2	12	>600	58	3540	2050	12	40
Fresh 2	8.3	659	3110	4	34	>600	31	2610	2780	11	180
Mid 1	8.2	1421	9340	<2	10	>600	>200	2920	2260	18	180
Mid 2	9.2	1421	7550	28	>60	>600	139	2670	1960	20	1070
Saline 1	8.4	10560	35000	6	20	>600	>200	5400	2810	59.4	2830
Saline 2	8.2	7936	39700	10	29	>600	>200	26800	3120	26	1770

Table 2.2. Descriptive topographical and biological characteristics of each transplant site. Subscript letters represent significant differences based on a post-Hoc Tukey test (P>0.1). Standard error values are included for richness, diversity, and litter and biomass data.

Site	Location	Elevation (masl)	Area (ha)	Slope	Aspect	Richness	Shannon's Diversity	Total Biomass ($g/0.25m^2$)	Litter ($g/0.25m^2$)
Fresh 1	50º45'40"N 120º23'24"W	739	0.543	10.67º	N	$5.27 \pm 0.19_{ab}$	$1.11 \pm 0.05_{a}$	$28.60 \pm 5.25_{a}$	$27.11 \pm 0.96_{a}$
Fresh 2	50º46'58"N 120º26'22"W	861	0.432	10.08º	ENE	$5.60 \pm 0.24_{ab}$	$1.01 \pm 0.17_{abc}$	22.79±0.91a	$9.54 \pm 1.37_{bd}$
Mid 1	50º46'16"N 120º25'32"W	766	3.540	9.67º	SW	$7.33 \pm 0.33_{c}$	$1.17 \pm 0.15_{ac}$	19.00±2.47a	$0.62 \pm 0.03_{cd}$
Mid 2	50º47'28"N 120º27"15"W	895	4.934	7.58º	SE	$5.25 \pm 0.41_{ab}$	$1.07 \pm 0.11_{ac}$	28.39±2.14a	$2.89 \pm 0.67_{cd}$
Saline 1	50º46"06"N 120º23'60"W	778	1.190	5.50º	WNW	$4.17 \pm 0.31_{a}$	$0.58 \pm 0.13_{b}$	16.54±2.07a	$9.52 \pm 1.23_{bd}$
Saline 2	50º45'48"N 120º23'19"W	736	1.413	5.00º	SW	$4.00 \pm 0.42_{a}$	$0.64 \pm 0.19_{bc}$	23.25±2.12a	$3.68 \pm 0.25_{bcd}$

Table 2.3. Mean total aboveground biomass 3-way ANOVA results examining the effects of site, species and competition (with or without neighbours present). Significant values are in bold.

	df	Sum of Squares	F Value	P Value
Site	**5**	**42.356**	**27.648**	**<0.001**
Species	**1**	**1.336**	**4.361**	**0.041**
Competition	**1**	**2.525**	**8.242**	**0.006**
Site: Species	5	1.091	0.170	0.617
Site: Competition	5	2.608	1.703	0.149
Species: Competition	1	0.155	0.507	0.480
Site: Species: Competition	3	0.652	0.710	0.550
Residuals	57	17.464		

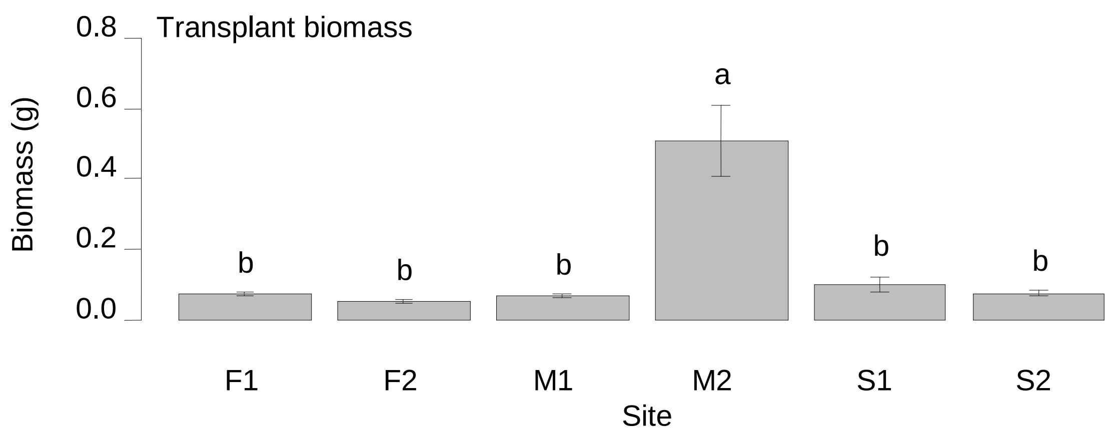
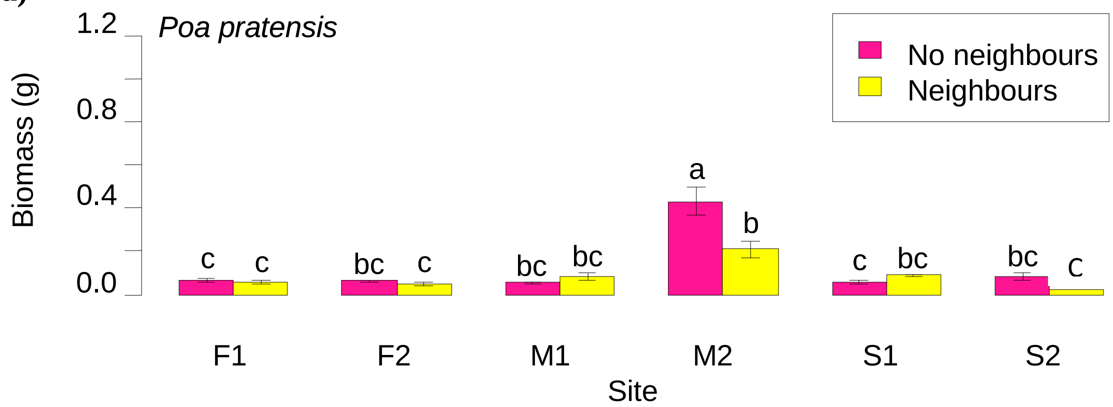


Figure 2.2. Mean (± 1 SE) total aboveground biomass of transplants combined at six sites in Lac du Bois Provincial Park. In figure, 'F' is Fresh, 'M' is Mid, and 'S' is Saline. Bars sharing the same letter are not significantly different using Tukey HSD (P>0.1).

a)



b)

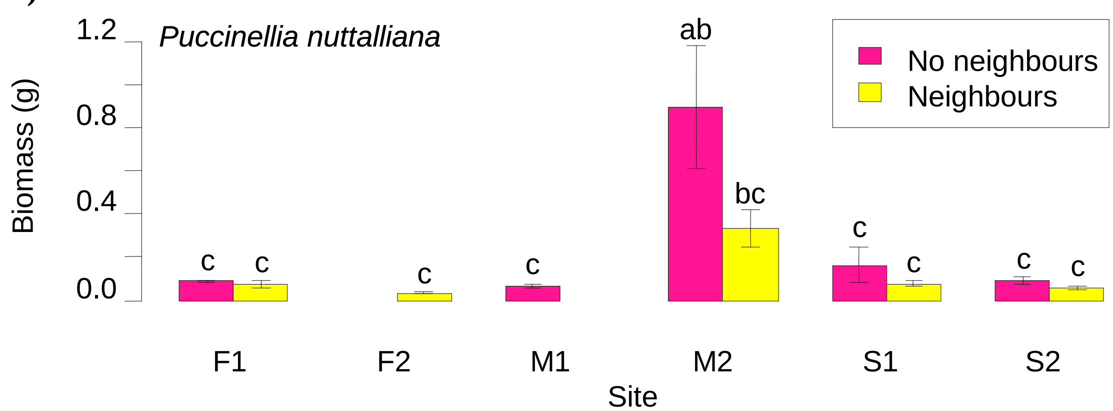


Figure 2.3. Mean total (± 1 SE) biomass of (a) *Poa pratensis* and (b) *Puccinellia nuttalliana* at six sites in Lac du Bois Provincial Park grown with neighbours and without neighbours present. 'F' is Fresh, 'M' is Mid, and 'S' is Saline. Bars sharing the same letter are not significantly different using Tukey HSD (P>0.1).

Transplants Survivorship

Transplant survivorship was just over half (79 out of 144), 40 *P. pratensis* and 39 *P. nuttalliana* (Table 2.4). The presence of neighbouring vegetation did not affect survivorship. A GLM (binomial response variable) found site to have a significant reduction in survivorship at Mid 1 only. Fresh 1, Fresh 2 and Mid 1 trended towards greater *P. pratensis* survival but were not significant. Mid 2 and Saline 1 survival was equal while Saline 2 trended, but was not significant, towards greater *P. nuttalliana* survival (Table 2.4).

Table 2.4. Number of transplants surviving for *Poa pratensis* and *Puccinellia nuttalliana*, with and without neighbours present, at Fresh 1, Fresh 2, Mid, 1, Mid 2, Saline 1 and Saline 2.

		Fresh 1	Fresh 2	Mid 1	Mid 2	Saline 1	Saline 2	Total
Poa pratensis	**No Neighbours**	6	3	2	4	4	2	21
	Neighbours	6	3	2	5	3	1	20
Puccinellia nuttalliana	**No Neighbours**	5	0	2	6	4	5	22
	Neighbours	5	2	0	3	3	3	16
Total		22	8	6	18	14	11	79

Discussion

I found that the biomass and survivorship of transplanted *P. nuttalliana* and *P. pratensis* seedlings were affected by site and by the presence of neighbours, but those responses depended on the transplanted species as well as site. All the sites were characterized by alkali soils with some having low or deficient levels of nitrogen and phosphorus and excesses of potassium, sulphur, calcium and magnesium. Species richness, diversity, total species biomass and litter varied among sites.

Survivorship

Survivorship results did not support the hypothesis that the survivorship of *P. nuttalliana* and *P. pratensis* would be greatest at the fresh sites and least at the saline sites, with *P. nuttalliana* being less affected by salinity than *P. pratensis*. While Fresh 1 did have the greatest number of surviving transplant, Fresh 2 had the lowest number of surviving transplants. Additionally, I cannot conclude from the survivorship data that *P. nuttalliana* was less affected by salinity than *P. pratensis.* Hypothesis 2 was also not supported because transplant survivorship was not significantly greater when neighbouring vegetation was removed. The low rate of survivorship and poor growth of most plants could be attributed to numerous factors such as climate, timing of transplantation, soil nutrient deficiency and herbivory.

The Kamloops growing season is generally characterized by spring rains and a hot and dry summer. Average temperature for May to August is 18.5º C with 29.6 mm per month of rain, However in 2009 the average temperature for May to August was 20.3º C with only 13.9 mm of rain monthly. Most of the rain fell in May (29.0 mm) and July (18.6mm) while June (6.1mm) and August (1.7mm) were extremely dry (Environment Canada 2010). This warmer and drier than normal growing season likely made the environment unfavorable for the transplants to establish and grow leading to high mortality and low biomass. Abiotic stresses, like drought, can cause plants to slow or cease growth, inhibit the production of new cells, enter a dormant stage or die (Grime 2001; Zhu 2001). Re-growth may have possibly occurred if the transplants had remained in the field until the fall when precipitation generally increases (Grime 2001; Environment Canada 2010).

Facilitation may have played a greater role in the plant-plant interactions than competition at some of the 'with neighbours' plots. Removing biomass and litter in a semi-arid climate would have exposed the soil and plants to more direct sunlight and wind which may have lead to greater rates of evaporation and thus drier soil (Facelli and Pickett 1991). Without the facilitative cover of other plants the transplants would be exposed to higher temperatures and stronger winds than the 'with neighbours' transplants. In alpine environments, Callaway et al. (2002) found that as abiotic stress increased, competition shifted to facilitation; in general more facilitation is observed at high elevation or high abiotic stress locations than at the low elevation or low abiotic stress locations. The increased stress of a hotter and drier than average summer may have assisted a transplant-neighbours interaction shift towards facilitation. The possible presence of facilitation among transplants with neighbours does not support hypothesis 2.

The timing of transplantation could help explain the low survivorship. Seedlings grew for 2 months in the greenhouse in small peat pellets that contained a limited amount of nutrients and space which could have lead the plants to become root bound. *Puccinellia nuttalliana* transplants began to flower in the greenhouse, which is a clear indication they were kept too long before transplantation. The advanced stage of the plants before transplantation may have been a contributing factor why there was limited growth and high mortality in the field. Furthermore, transplantation may have occurred after the spring rains which may be necessary for successful establishment.

Low levels of nutrients, especially nitrogen and phosphorus, could have contributed to the poor growth and low survivorship of the transplants. Nitrogen and phosphorus levels are consistently considered important variables when defining infertile soils (Grime 2001). According to the soil analysis, Mid 2 was the only site to have sufficient levels of nitrogen and phosphorus based on a farm soil standard (Bodycote Exova Testing Group); Mid 2 was the only site where the transplants successfully established and grew. Low levels of nitrogen and likely phosphorus, can lead to less aboveground biomass because energy thus biomass is reallocated to the belowground parts of the plant (Lambers et al. 1998). Because only aboveground transplant biomass was collected, biomass reallocation to roots and increased root growth cannot be verified.

Herbivory and animal disturbance is also a possible factor affecting survivorship observed at Mid 1, Mid 2 and Saline 2. Grazing from cattle, ungulates, small mammals and insects may have added an additional disturbance to plants that were already experiencing abiotic stress. The additional disturbance of herbivory may have contributed to high mortality at Mid 1 and Saline 2.

Abiotic and Biotic

Soil analysis of the transplant sites identified all sites as alkaline with calcium and magnesium the dominant ions. Alkali soils, ponds and lakes are common in the southern interior (Toppings and Scudder 1977). High levels of calcium and magnesium can be attributed to intrusions of greenstone and igneous bedrock material (Renaut 1990). Ionic difference between sites may be the result of unconformities in bedrock material, glacial deposits or individual basin characteristics (Renaut 1990).

Species richness followed a general trend with highest richness at the mid and fresh sites, Mid 1 having significantly higher richness, and lowest richness at the saline sites. Diversity followed a similar trend with the mid and fresh sites having highest diversity and the saline sites having the lowest. Both trends show the saline sites having the least amount of species richness and diversity which would be expected in these stressed environments (Grime 2001). Total biomass varied by site; however, no definitive trends could be deduced. Litter was significantly greater at site Fresh 1 than all the other sites. Litter tended to be greatest at the fresh sites, followed by the saline sites and finally by the mid sites. The large variation in litter could be due to selective herbivory by wildlife and insects or species composition.

Site Mid 2 Transplants

An analysis of the mean total biomass of both transplants at all sites did not support either hypothesis 3 or 4. However, if site Mid 2 is analyzed alone the results support hypothesis 3 that aboveground biomass of both species will be greater when neighbouring vegetation is removed. Site Mid 2 was considered moderately saline based on its initial water conductivity readings with those findings reinforced by the final soil conductivity readings. However, the plant communities present at Mid 2 are indicative of an alkali-saline ecosystem and more similar to Saline 1 and Saline 2 than Mid 1. The high pH value and sodium level of Mid 2 soil may have contributed to the site containing more alkali vegetation than the other moderate salinity site (Mid 1). Mid 2 reported the highest levels of nitrogen and phosphorus, limiting nutrients that are key for plant growth (Tilman 1988; Grime 2001), which may have improved the success of the transplants.

Aboveground biomass for *P. nuttalliana* was greater than *P. pratensis* at the Mid 2 site. The high pH and moderate soil conductivity would have created soil conditions that *P. nuttalliana* is better adapted to than *P. pratensis*. These finding are supported by field observation (Tarasoff et al. 2007) and greenhouse manipulation experiments (Kenkel et al. 1991) that have observed the salinity range of *P. nuttalliana* and *P. pratensis*. Tarasoff et al. (2009) found that in the first year of a competition study *P. nuttalliana* grew at a much faster rate, obtained more biomass and was more competitive than *P. pratensis* which may explain why the biomass of *P. nuttalliana* was that much greater than *P. pratensis*. The natural presence of *P. nuttalliana* and absence of *P. compressa* at Mid 2 further supports the findings that *P. nuttalliana* is better adapted to moderate salinities than *P. pratensis*.

Transplants grown in the presence of neighbours had less biomass than those grown without neighbours suggesting competition played an integral role in growth, at site Mid 2 only, supporting hypothesis 3. *Puccinellia nuttalliana* showed a trend in decreased aboveground biomass with neighbours which may be attributed to the limited number of *P. nuttalliana* with neighbours present survivors (n=3). *Poa pratensis* clearly followed the same trend but reported significant values. Intraspecific and interspecific competition occurred at Mid 2 because *P. nuttalliana* was found in every plot that contained a survivor. The hypothesis that the aboveground biomass of *P. pratensis* would be less affected by neighbours than *P. nuttalliana* was not supported. This may be due to the low number of transplants at this site leading to an insufficient number to conduct a proper analysis. Also the stress of the sites alkalinity and moderate salinity could have hindered the competitive ability of the salt-intolerant *P. pratensis*.

Conclusion

Low transplant survival and the poor performance of most of the surviving transplants caused the hypotheses focused on aboveground biomass to be applied strictly to site Mid 2 while the survivorship hypotheses were applied to all the transplants. Low transplant survival may be attributed to numerous factors or a combination of factors: climate, timing and herbivory. May to August 2009 was warmer (+1.8ºC) and drier (-15.7mm) than average for Kamloops, B.C., Canada which may have contributed additional stress to the already stressed transplants. Seedlings should have been transplanted earlier in the season to prevent becoming root bound, nutrient limited and flowering in the greenhouse. The transplantation date of May 15, 2009 occurred after the majority of the stunted spring rains, likely causing an establishment and growth disadvantage for the transplants. Herbivory and animal interference were not factors that this study set out to observe and therefore protect against; however, they occurred and caused notable damage to numerous plants. While mortalities were expected, and steps and precautions were taken to reduce their potential, they were ultimately too great for some of the hypothesized analyses to be conducted.

Mid 2 was classified as a mid-level salinity site based on water conductivity readings and that finding was supported by the soil conductivity analysis. However, the plant species present at Mid 2 shared more similarities to the saline sites than with the other mid-level salinity site (Mid 1), even though their water conductivity values were very similar. Based on the presence of salt-tolerant species, high pH value and the high level of sodium (Na) at Mid 2, we can consider Mid 2 more indicative of a saline site than Mid 1; therefore it is expected that *P. nuttalliana* should perform better at Mid 2 than *P. pratensis. Puccinellia nuttalliana* preformed better than *P. pratensis* at Mid 2 by producing a greater amount of aboveground biomass likely due to its high level of salt tolerance. Neighbours present was shown to reduce the aboveground biomass of both species as expected. *Puccinellia nuttalliana* preformed better than hypothesized with neighbours present but that can be attributed to low replication leading to statistical error.

More replicates may have lead to more survivorship of transplants thus increasing the power of the analyses.

My study experienced some problems and limitations that prevented me from gathering complete data and in some cases added to failure of transplant survival. I was unable to gather belowground biomass of the transplants for analysis because of the texture of the transplant medium, soil characteristic and destructive nature of removing delicate roots from neighbouring roots. This prohibited me from analyzing total transplant biomass and root:shoot ratios. *Poa compressa* was identified at the sites but *P. pratensis* was not; however, the identification of *P. compressa* for *P. pratensis* could have been incorrect due to human error and inexperience. The unpredictability of climate was a huge issue during the study. A cold winter and spring with a large snow pack limited reconnaissance trips to the sites, preparation of the sites and timing of transplantation. Dry, hot weather after transplantation lead to an extension of the hand watering period to prevent desiccation, thus manipulating climate which was something I had not planned on doing. My sample size for transplant biomass became limited to a single site due to mortalities, poor performance and herbivory. The small number of transplants and only one set of environmental variables, most specifically salinity, limited analysis.

My study, though incomplete in many ways, provides a base for future research. The failure of many of the transplants has identified key factors that may have to be considered when conducting a future transplant experiment in the Kamloops, BC region and likely elsewhere. While climate cannot be largely controlled in the field, issues such as germination and transplantation timing, transplant medium and nutrient levels in the greenhouse and site selection can be. A more extensive knowledge of the field site, climate of the southern interior and herbivore activity could aid in more successful survivorship. Furthermore, plant community composition should be considered, in addition to water and soil salinity, when attempting to categorize sites.

Climate change may have the potential to alter the hydrology of intermountain wetland systems, and in turn increase or alter their salinity. Increased salinity can lead to a shift towards salt tolerant vegetation or provide new habitat for salt tolerant species as water volume decreases and saline soils are exposed. Unfortunately the low survivorship and low success rate of the transplants along the salinity gradient could not provide me with much insight into future projections.

Management Implications

Only limited management recommendations for grassland ecosystems containing saline wetlands can be made from this study. Based on species richness, biomass and litter values collected from the sites fresh and mid-level salinity areas will provide the greatest amount of forage for grazing cattle and ungulates. Furthermore, the high levels of salt ions in the saline wetlands may prove to be too high and even toxic to many species that have to use them for a water source. Alternative water sources, such as rain buckets and tanks, should be provided for cattle in such environments. High levels of salts and other ions in the soil surrounding these wetlands may be toxic or too saline for many pasture or agronomic species, soil analyses are recommended in order to understand soil quality and thus the correct species to plant to provide the highest quality and quantity of forage for cattle. Understanding not just the vegetation and hydrology of a system but the chemistry is imperative for proper management and use.

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CHAPTER 3

COMPETITION BETWEEN TWO GRASS SPECIES WITH AND WITHOUT CLIPPING ALONG TWO SALINITY GRADIENTS

Introduction

Hydrology explains over fifty percent of the variation in the structure and composition of wetland plant communities (Keddy 2001; Mitsch and Gosselink 2007). Wetlands occupy a transition zone between aquatic and terrestrial environments where there is variation in the depth and duration of flooding. Wetland plants have adapted to these anaerobic or semi-anaerobic conditions caused by high water levels and flooding (Blom and Voesenek 1996; Vartapetian and Jackson 1997; Pezeshki 2001). Nevertheless, there is still a wide range of growth response between wetland plant species to flooding and to tolerance of different water levels (Fraser and Karnezis 2005; Mitsch and Gosselink 2007; Araya et al. 2010). One aspect of hydrology that is rarely considered in wetland plant studies is the indirect effects of hydrology on water chemistry. In intermountain freshwater ponds and prairie potholes, salinity has the potential to change as water levels fluctuate. In particular, as water levels subside through the summer months the concentration of salts in the water can increase (Topping and Scudder 1977; Wilson et al. 1994; Smith, L., personal communication), which may affect wetland plant growth. Global warming and changes in precipitation patterns caused by global climate change will likely affect hydrology (Poiani and Johnson 1991), and therefore salinity (Covich et al. 1997; Mitsch and Gosselink 2007), of intermountain freshwater ponds.

Intermountain freshwater ponds vary in their water chemistry (Topping and Scudder 1977; Renaut 1990; LaBaugh et al. 1998). Salinity can reduce plant performance, vigor, biomass, nutritional value and palatability (Younis and Hatata 1971; Parrondo et al. 1978; Cheeseman 1987; Kenkel et al. 1991; Covich et al. 1997). Increasing salt stress can cause a shift in biomass from below-ground to above-ground, especially in salt-intolerant species (Barbour 1978; Kenkel et al 1991). Highly saline areas support few species and are dominated by salt tolerant halophytes that posses mechanisms to maintain osmotic potential and maintain metabolic processes (Glenn 1987; Cheeseman 1988; Tarasoff et al. 2007b). The majority of salt tolerant species likely grow best in non-saline soils (Crawley 1997), but will often be displaced by competitively dominant salt-intolerant species under these conditions (Kenkel et al. 1991).

Competition has been shown to interact with hydrology to affect plant growth (Grosshans and Kenkel 1997; Fraser and Miletti 2008; Araya et al. 2010). There is also evidence that competition can interact with salinity to affect plant performance (Kenkel et al. 1991). The importance competition plays in determining plant community distribution along an environmental gradient is a debated topic in ecology (Tilman 1982; Grace 1991; Gough and Grace 1999; Grime 2001; Craine 2005). One view is that competition is stronger in less stressful, more productive environments and as stress increases, the role of competition decreases (Grime 2001; Keddy 2002). The other view is that competition remains constant along an environmental stress or productivity gradient, with a shift from below-ground competition in low productivity environments to above-ground in high productivity environments (Tilman 1982, 1988). Disturbance, especially herbivory, has also been shown to influence plant-plant interactions (Campbell and Grime 1992; Turkington et al. 1993; Gough and Grace 1998). Herbivores are often selective, feeding preferentially on competitive dominants (Fraser and Grime 1999). The removal of aboveground biomass by herbivores can cause a shift in root: shoot ratio; plants that invest more energy in leaf production after herbivore disturbance may experience a reduction in their root: shoot ratio (Kuijper et al. 2005). I studied the interactions between stress (productivity) and disturbance (clipping) on plant growth and plant community composition.

My study investigates the main and interacting effects of salt concentration, salt type, competition and clipping, as a surrogate of grazing, on two grass species, *Poa* *pratensis* L. and *Puccinellia nuttalliana* (Schult.) Hitchc. in a greenhouse environment. The species were selected based on salt-tolerance and recorded presence in the intermountain freshwater ponds and wetlands of the southern interior of British Columbia, Canada. *Poa pratensis* is a perennial glycophyte commonly used as a lawn and pasture species that represents a salt intolerant forage grass in this study (Kenkel et al.1991; Tarasoff 2007). *Puccinellia nuttalliana*, a perennial halophyte associated with saline and alkaline wetlands (Tarasoff et al. 2007a), represents a salt tolerant forage grass. Although a wide range of ions and salt complexes are found throughout British Columbia's lakes, ponds and wetlands, NaCl and Na_2SO_4 were chosen based on their common cation and presence in water bodies of Lac du Bois Provincial Park, Kamloops, B.C., Canada (Topping and Scudder 1977). A salt concentration gradient was used to simulate the natural range (Topping and Scudder 1977; Kenkel et al. 1991). Clipping, a disturbance, was chosen to simulate cattle grazing, a prevalent land-use practice in the southern interior of B.C. The competition treatment included plants grown alone (the control), two of the same species grown together (intraspecific competition) and one of each species grown together (interspecific competition). While numerous competition indices have been developed to better understand the role of competition in plant community structure (Weigelt and Jolliffe 2003), this study focuses on competitive importance (Brooker et al. 2005). Competitive importance indices have been identified as the best solution to determine the role of competition along a gradient (Brooker at al 2005; Carlyle et al. 2010), but not without criticism (Freckleton et al. 2009). The inclusion of the plant's maximum biomass on the entire gradient in the equation enables the index to show the relative role of competition in different environments (or along the gradient). It must be acknowledged that the competitive importance index is thought to be biased towards supporting Grime's theory on competition along a gradient (Carlyle et al. 2010).

My study examines not only the role of competition, in the form of competitive importance, along a salt stress gradient but how competitive importance may be affected changes in a gradient's composition or the incorporation of an additional stress. Is competition affected differently by different salt complexes? How does the addition of clipping affect biomass and competitive ability along a salt stress gradient? Do different salt complexes interact with disturbance differently?

My study tested the following hypotheses: 1) Biomass will decrease with increasing concentration of salt, with *Poa pratensis* experiencing a greater reduction in relative biomass than *Puccinellia nuttalliana* when subjected to the salt treatments; 2) There will be no difference in plant biomass between plants grown in NaCl and Na_2SO_4; 3) R:S ratio of *P. pratensis* will decrease with increasing salt concentration while R:S ratio of *P. pratensis* and *P. nuttalliana* will increase with clipping; 4) Competitive importance will decrease for *P. pratensis* and *P. nuttalliana* with increasing salt concentration.

Materials and Methods

My experiment tested the interacting effects of salt concentration, salt type, competition and clipping on *Puccinellia nuttalliana* and *Poa pratensis*. The factorial combination included the 2 wet meadow grass species (*P. nuttalliana* and *P. pratensis*) at 7 salt type-concentration combinations (3 levels of Na_2SO_4, 3 levels of NaCl and 1 control) x 5 competition (*P. nuttalliana* alone, *P. pratensis* alone, and three pair wise interactions) x 2 clipping (clipped or not) x 6 replicates for a total of 672 plants in 420 pots. The factorial design was unbalanced due to the seven salinity levels.

Greenhouse Conditions

The greenhouse climate was set with a 16:8 hr day:night cycle with light in each greenhouse room supplemented with three 1000W halogen sulfide lamps, temperature was maintained at 22:15 C and relative humidity at 65:80 day: night cycle for 90 days. Pots were evenly divided between two greenhouse rooms containing three blocks each. Each block contained 70 pots, one of each treatment combination. Pots were randomly arranged within each block. Due to the large number of pots, experiment room 1 was planted a day later than room 2 allowing staggered treatment applications.

Germination

Approximately 400 seeds of *P. nuttalliana* and *P. pratensis* were placed in separate plastic Petri dishes filled with a sand medium saturated in distilled water. An initial germination experiment indicated that the *P. nuttalliana* seeds required approximately 12 days to germinate, whereas *P. pratensis* germinated in approximately 7 days; therefore seed sowing was staggered. *Puccinellia nuttalliana* seeds were sown on September 11 and 14, 2009 and *P. pratensis* seeds were sown on September 16 and 18, 2009 to ensure germination of both species occurred within days of each other. Seeds received distilled water while in the Petri dishes because germination results are best when initially grown under freshwater conditions (Flowers et al. 1986; Kenkel et al. 1991). Seedlings were covered with the Petri dish lids to increase humidity, and received 16 hrs of light in the greenhouse to stimulate germination.

Treatments

Seedlings were removed from Petri dishes on September 30 and October 1 2009 (Week 1) and transplanted into 900 ml plastic pots (12.5 cm tall, 7.5 x 7.5 cm base and 11 x11 cm top) containing a sand medium. Holes in the bottoms of the pots were covered with 0.5 mm perforated plastic landscaping fabric to allow passing of water but not sand and roots. Pots were placed in 350 ml styrofoam dishes (4.5 cm tall, 9 x 9 cm base and 13 x 13 cm top). Each pot received one or two transplants: *Puccinellia nuttalliana alone, P. pratensis alone, P. nuttalliana* with *P. nuttalliana, P. pratensis* with *P. pratensis* or *P. nuttalliana* with *P. nuttalliana*.

The sand medium was saturated with 270 ml of Rorison's nutrient solution (see Hendry and Grime 1993) immediately prior to transplantation. One week after planting (Day 7) the pots were flushed by adding 270 ml of Rorison's nutrient solution (270 ml was found to be sufficient in flushing old salt-nutrient medium from the pots) to the top of the pots (Kenkel et al. 1991). By Week 2, Na_2SO_4 or NaCl was added to the Rorison's solution at low levels (0 for the control or 2.5 g/L for all the others) and flushed through the pots. Salt concentrations were gradually increased by 2.5 g/L per week until the desired final concentrations were achieved (5, 10, 15 g/L Na_2SO_4 and 5, 10, 15 g/L NaCl). Flushing occurred once a week. The control of no salt addition remained at 0 g/L and only received Rorison's nutrient solution. Distilled water was added to the pots from the bottom to keep the sand medium saturated and reduce the potential of flushing the salts and nutrients. Plants that had died within two weeks were replaced. Mortalities consisted of only those plants that had died after the two week replacement period. If only one plant had died within a pot of 2 plants, a single mortality was recorded and the other plant was removed from all analyses.

To simulate cattle grazing, half of all treatment combinations were clipped. Pots were randomly selected so their plants underwent manual clipping on Day 44. Clipping removed 75% of the plants' photosynthetic material, so that only 25% remained; this process was repeated on Day 63 (Hendry and Grime 1993).

Harvesting

Harvesting occurred on day 90 (December 29 and 30, 2009). Individuals were separated to species and then into above-ground and below-ground biomass. Biomass was dried in the drying oven at 65ºC for 10 days and weighed with Fisher Scientific analytical balance accu-225D (d=0.01/0.1 mg).

Statistical Analysis

To analyze mean total biomass I used only the plant grown alone data. All biomass data were log transformed and R:S rations were arcsine transformed to meet the assumptions of normality. A 4-way unbalanced ANOVA with a blocking factor was conducted to test the effects of species, salt concentration, salt type and clipping on the total plant biomass, above ground biomass, below ground biomass and R:S ratio. Competitive importance was calculated using the equation:

$$C_{imp}= (P_{-N}-P_{+N})/ (MaxP_{-N}-y)$$

where P_{-N} is plant grown without neighbours (alone) and P_{+N} is plant grown with neighbours (both inter and intraspecific competition), and $MaxP_{-N}$ is the maximum value of P_{-N} and y is the lesser of P_{-N} or P_{+N} (Brooker et al. 2005). The equation was slightly modified from the original used by Brooker et al. (2005) to show C_{imp} as a positive value instead of a negative. A 5-way unbalanced ANOVA with a blocking factor was conducted to test the effects of species, salt concentration, salt type, competition type and clipping. P values <0.05 were considered significant. All ANOVA's and the Post-Hoc Tukey test were done using R version 2.9.1 (2009).

Results

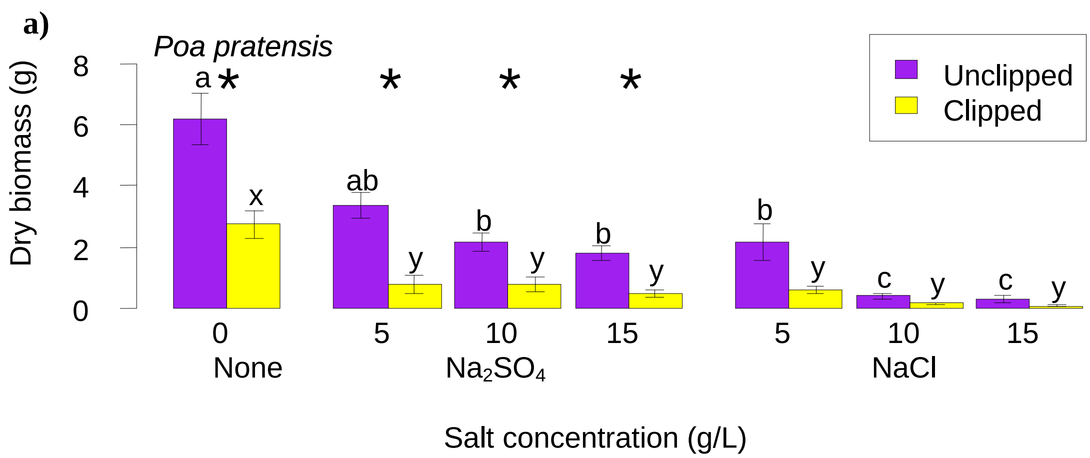
Total Biomass

The mean total biomass of both *P. pratensis* and *P. nuttalliana* when grown alone (without competition) was significantly reduced by all the main effects (Table 3.1; Fig. 3.1). The mean total biomass of *P. pratensis* was greater than *P. nuttalliana* at the control (Table 3.1; Fig. 3.1). Salt concentration and salt type reduced the mean total biomass of both species, but the reduction was larger for *P. pratensis* (Table 3.1; Fig. 3.1). Mean total biomass of *P. pratensis* and *P. nuttalliana* was highest at 0 g/L salt (control) and lowest at 15 g/L NaCl. The NaCl treatment reduced the mean total biomass of both species to a greater degree than the Na_2SO_4 treatment. Salt concentration reduced the mean total biomass of both species. This trend was most evident in the NaCl treatment of both species and the Na_2SO_4 treatment of *P. pratensis*.

The two-way interaction between species and salt type was shown to be significant indicating that the two species are affected by salt type and concentration differently. Post-Hoc Tukey results showed a reduction in biomass in species and salt type interactions combinations involving *P. pratensis* and that 'no salt' controls for both species have greater biomass than the salt treatments (Fig. 3.1). The two-way interaction between salt and clipping was significant; Post-Hoc Tukey test indicates clipping with both salt treatments reduced the biomass of both species (Fig. 3.1). The two-way interaction between concentration and clipping was significant. Post-Hoc Tukey results show that biomass was greatest for both species at the control of 0 g/L salt with no clipping and in general showed greater reductions in biomass with clipping and increasing salt concentrations (Fig. 3.1).

Table 3.1. Results of 4-way ANOVA with blocking factor (Block) examining the effects of species, salt type (Salt), salt concentration (Conc) and clipping (Clip) on the mean total biomass of *Poa pratensis* and *Puccinellia nuttalliana*. Significant values are in bold.

Treatment	Df	Sum of Sq.	F Value	P Value
Block	**5**	**1.682**	**6.774**	**<0.001**
Species	**1**	**0.203**	**4.079**	**0.045**
Salt	**2**	**14.284**	**143.808**	**<0.001**
Conc	**2**	**1.928**	**19.407**	**<0.001**
Clip	**1**	**14.800**	**298.010**	**<0.001**
Species: Salt	**2**	**2.244**	**22.588**	**<0.001**
Species: Conc	2	0.304	3.062	0.050
Salt: Conc	2	0.301	3.027	0.052
Species: Clip	1	0.117	2.358	0.127
Salt: Clip	**2**	**0.852**	**8.580**	**<0.001**
Conc: Clip	**2**	**0.400**	**4.030**	**0.020**
Species: Salt: Conc	2	0.223	2.245	0.110
Species: Salt: Clip	2	0.065	0.659	0.519
Species: Conc: Clip	2	0.044	0.447	0.640
Salt: Conc: Clip	2	0.114	1.152	0.319
Species: Salt: Conc: Clip	2	0.088	0.886	0.414
Residuals	**120**	**5.960**		



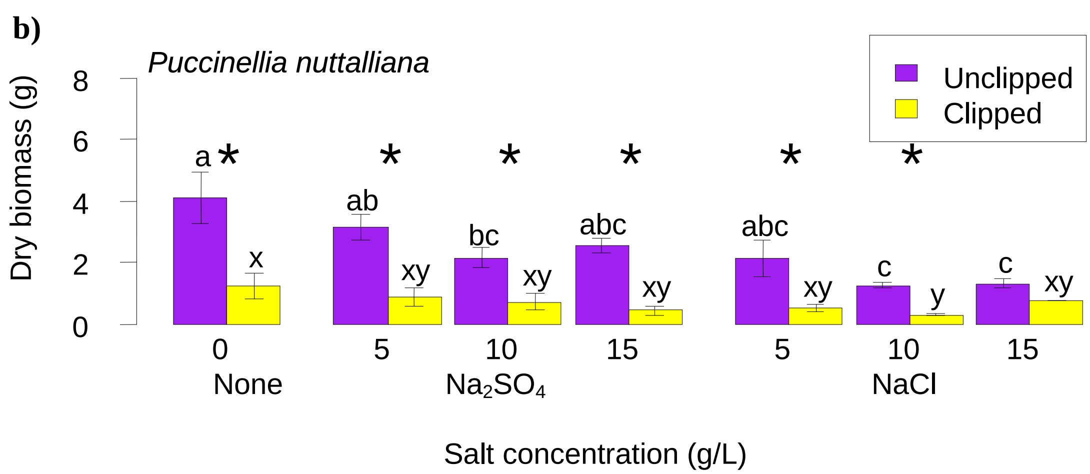


Figure 3.1. Mean total biomass (± 1 SE) of (a) *Poa pratensis* and (b) *Puccinellia nuttalliana* grown alone: clipped and unclipped at six salinities and the control. For clarity of interpretation, Tukey results have been assigned by sub-set (P>0.05). The asterisks indicate a significant difference between the clipped and unclipped paired bars within a salt-concentration treatment. Letters a,b,c were used for the unclipped treatments and letters x,y,z were used for the clipped treatments. Bars sharing the same letter are not significantly different using Tukey HSD.

Aboveground Biomass

Blocking and all main effects significantly affected the aboveground biomass of both species. The aboveground biomass of *P. pratensis* was greater than *P. nuttalliana* (results comparable to total biomass thus refer back to Fig. 3.1). Salt type reduced the aboveground biomass of *P. pratensis* and *P. nuttalliana* (Fig. 3.1, Table 3.2). Salt concentration reduced the aboveground biomass for both species, with the strongest trend occurring in the NaCl treatment for *P. pratensis*. Clipping reduced the aboveground biomass of both species. The significant two-way interactions for aboveground biomass are the same as the result for the two-way interactions for biomass.

Table 3.2. Results of 4-way ANOVA with blocking factor (Block) examining the effects of species, salt type (Salt), salt concentration (Conc) and clipping (Clip) on mean total aboveground biomass *Poa pratensis* and *Puccinellia nuttalliana*. Significant values are in bold.

Treatment	Df	Sum of Sq.	F Value	P Value
Block	**5**	**1.331**	**6.759**	**<0.001**
Species	**1**	**0.766**	**19.440**	**<0.001**
Salt	**2**	**8.763**	**111.256**	**<0.001**
Conc	**2**	**1.506**	**19.123**	**<0.001**
Clip	**1**	**11.271**	**286.201**	**<0.001**
Species: Salt	**2**	**0.869**	**11.034**	**<0.001**
Species: Conc	2	0.158	2.010	0.138
Salt: Conc	2	0.194	2.465	0.089
Species: Clip	1	0.146	3.711	0.056
Salt: Clip	**2**	**0.561**	**7.121**	**0.001**
Conc: Clip	**2**	**0.310**	**3.930**	**0.022**
Species: Salt: Conc	2	0.139	1.761	0.176
Species: Salt: Clip	2	0.115	1.459	0.236

Species: Conc: Clip	2	0.019	0.242	0.785
Salt: Conc: Clip	2	0.144	1.824	0.165
Species: Salt: Conc: Clip	2	0.037	0.474	0.623
Residuals	**120**	**4.726**		

Belowground Biomass

Blocking was shown to have a significant effect on the belowground biomass. Belowground biomass was not significantly different between *P. pratensis* and *P. nuttalliana* for the main effects (Table 3.3). Salt type reduced belowground biomass for both species with the strongest trend occurring with the NaCl treatment for both species and the Na_2SO_4 treatment for *P. pratensis* (Fig. 3.2, Table 3.3). Concentration significantly reduced the belowground biomass of *P. pratensis* and *P. nuttalliana*. Clipping significantly reduced the belowground biomass of both species (Fig. 3.2). The two-way interaction involving species and salt type was significant. Post-Hoc Tukey results show the greatest differences in the belowground biomass of both species at the control, 0 g/L salt. The NaCl treatments showed less belowground biomass for both species and the Na_2SO_4 treatment significantly reducing the biomass of *P. pratensis* but not *P. nuttalliana*. The two-way interaction between salt type and clipping was significant; Post-Hoc Tukey results indicate that the combination of NaCl and clipping reduced belowground more than any other interaction (Fig. 3.2). The two-way interaction between salt concentration and clipping was significant; Post-Hoc Tukey results do not show any clear trends except that belowground biomass is greatest at 0 g/L salt with clipping than any other salt concentration with clipping (Fig. 3.2).

Table 3.3. Results of 4-way ANOVA with blocking factor (Block) examining the effects of species, salt type (Salt), salt concentration (Conc) and clipping (Clip) on mean total belowground biomass. Significant values are in bold.

Treatment	Df	Sum of Sq.	F Value	P Value
Block	**5**	**0.347**	**2.728**	**0.022**
Species	**1**	**0.601**	**23.608**	**<0.001**
Salt	**2**	**5.054**	**99.335**	**<0.001**
Conc	**2**	**0.293**	**5.760**	**0.004**
Clip	**1**	**2.694**	**105.887**	**<0.001**
Species: Salt	**2**	**2.111**	**41.494**	**<0.001**
Species: Conc	2	0.155	3.042	0.051
Salt: Conc	2	0.034	0.665	0.516
Species: Clip	1	0.014	0.559	0.456
Salt: Clip	**2**	**0.639**	**12.551**	**<0.001**
Conc: Clip	**2**	**0.169**	**3.307**	**0.039**
Species: Salt: Conc	2	0.025	0.488	0.615
Species: Salt: Clip	2	0.113	2.228	0.112
Species: Conc: Clip	2	0.063	1.244	0.292
Salt: Conc: Clip	2	0.001	0.019	0.981
Species: Salt: Conc: Clip	2	0.052	1.020	0.363
Residuals	**120**	**3.053**		

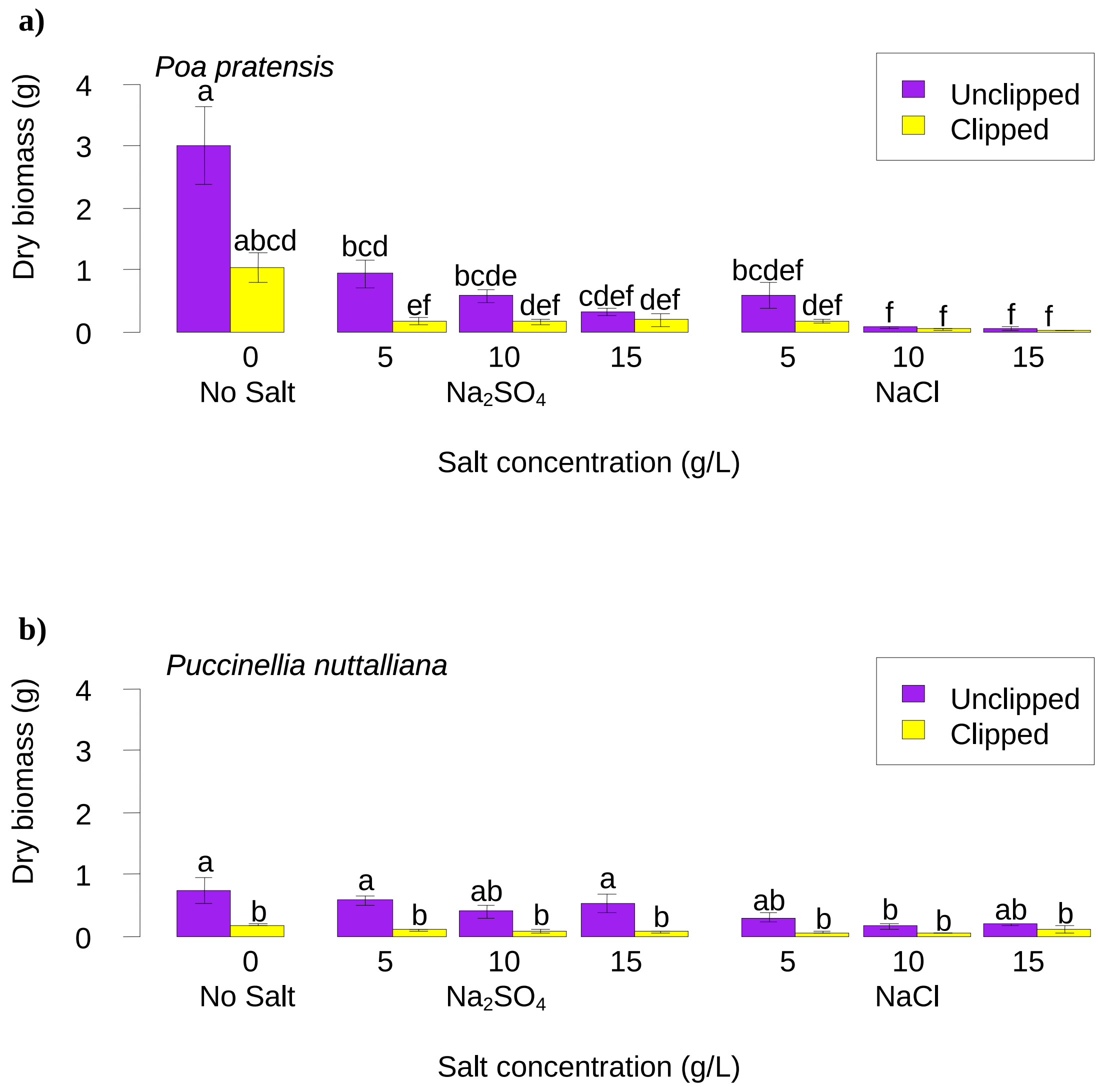


Figure 3.2. Belowground biomass (± 1 SE) of (a) *Poa pratensis* and (b) *Puccinellia nuttalliana* grown alone: clipped and unclipped at six salinities and the control. Bars sharing the same letter are not significantly different using Tukey HSD (P>0.05).

Root to Shoot Ratio

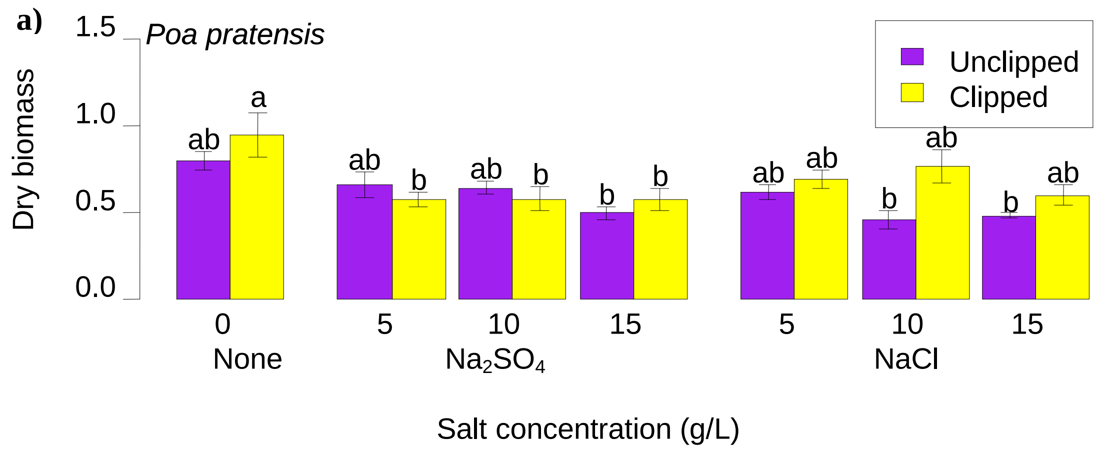
Blocking had no effect on root to shoot ratio (R: S ratio) and was not included in the analysis. *Poa pratensis* had a greater R:S ratio than *P. nuttalliana* (Table 3.4; Fig. 3.3). Salt type significantly affected the R:S ratio; however, it is difficult to conclude a general trend. The other two main effects, salt concentration and clipping, had no effect on R:S ratio (Table 3.4).

The two-way interaction between species and salt is significant (P>0.001); Post-Hoc Tukey analysis show that the R:S ratio of *P. pratensis* and *P. nuttalliana* shift differently for each species at the control and when exposed to the salt treatments. The two-way interaction between species and concentration was significant; the R:S ratio of *P. pratensis* is reduced with increased concentration while *P. nuttalliana* remains relatively constant (Fig. 3.3). The two-way interaction between species and clipping was significant; Post-Hoc Tukey analysis indicate that clipping caused a shift in the R:S ratio for *P. pratensis* more than *P. nuttalliana*. The two-way interaction of salt type and clipping was significant; clipping in combination with the Na_2SO_4 salt treatment lowered the R:S ratio while clipping and NaCl increased or did not change the R:S ratio (Fig. 3.3).

Table 3.4. Results of 4-way ANOVA results examining the effects of species, salt type (Salt), salt concentration (Conc) and clipping (Clip) on root to shoot ratio. Significant values are in bold.

Treatment	Df	Sum of Sq.	F Value	P Value
Species	**1**	**1.413**	**77.095**	**<0.001**
Salt	**2**	**0.386**	**10.538**	**<0.001**
Conc	2	0.006	0.168	0.845
Clip	1	0.001	0.044	0.834
Species: Salt	**2**	**0.397**	**10.843**	**<0.001**
Species: Conc	**2**	**0.149**	**4.077**	**0.019**
Salt: Conc	2	0.005	0.144	0.865
Species: Clip	**1**	**0.177**	**9.685**	**0.002**
Salt: Clip	**2**	**0.189**	**5.163**	**0.007**
Conc: Clip	2	0.033	0.912	0.404
Species: Salt: Conc	2	0.004	0.103	0.902

Species: Salt: Clip	2	0.020	0.534	0.587
Species: Conc: Clip	2	0.010	0.277	0.758
Salt: Conc: Clip	2	0.043	1.179	0.311
Species: Salt: Conc: Clip	2	0.031	0.849	0.431
Residuals	**121**	**2.217**		



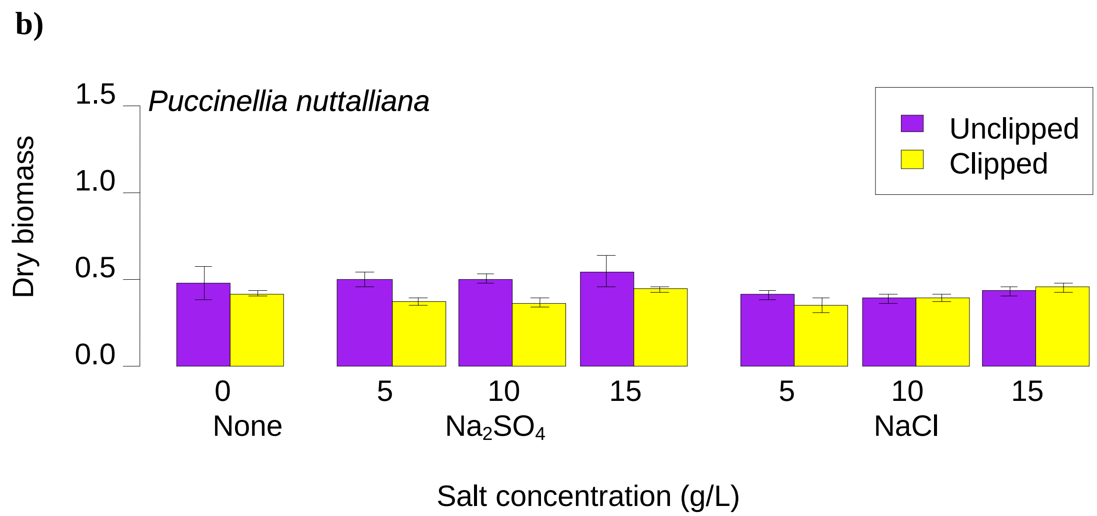


Figure 3.3. Root to shoot ratio (± 1 SE) of (a) *Poa pratensis* and (b) *Puccinellia nuttalliana* grown alone: clipped and unclipped at six salinities and the control. Bars sharing the same letter are not significantly different using Tukey HSD (P>0.05), no letters in figure 3.2 b indicate no significant differences between bars.

Competitive Importance

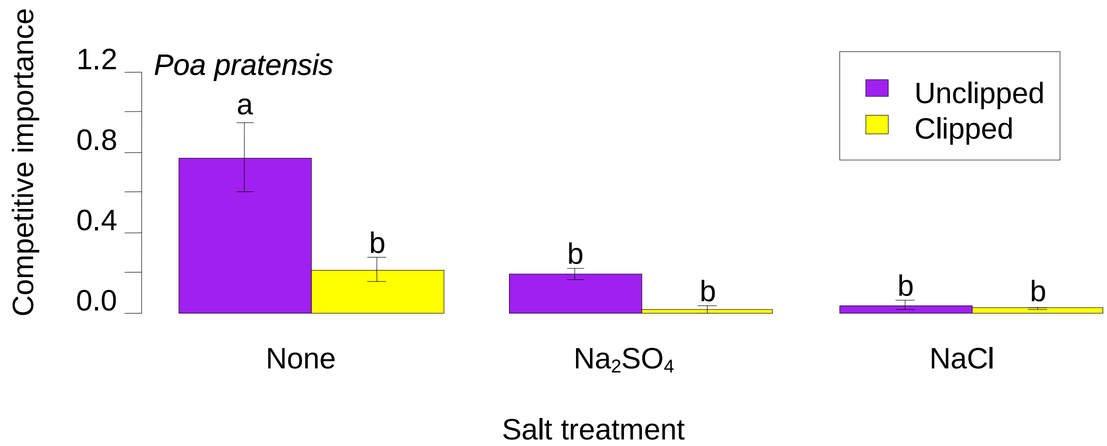
Blocking had a significant effect on competitive importance (C_{imp}) (Table 3.5). The degree of C_{imp} between species was not significantly different (Table 3.5). Salt type reduced the degree of C_{imp} of *P. pratensis* and *P. nuttalliana*. Salt concentration did not differ by treatment. Clipping was shown to significantly reduce C_{imp} of both species (Table 3.5, Fig 3.4). The presence of competition (interspecific and intraspecific) did not have a significant effect. The 2-way interaction between salt and clipping was significant; the addition of salt and clipping always reduced C_{imp} (Fig 3.4). The two-way interaction between clipping and competition type was significant; clipping and intraspecific competition reduced C_{imp} more than clipping and interspecific competition. When examined closer, the C_{imp} of *P. nuttalliana* was shown to be significantly affected by competition type and clipping, with intraspecific competition and clipping reducing the C_{imp} to a greater degree than interspecific competition and clipping (Fig 3.5).

Table 3.5. Results of 5-way ANOVA with blocking factor examining the effects of species, salt type (Salt), salt concentration (Conc), clipping (Clip) and competition (Comp) on competitive importance. Significant values are in bold.

Treatment	Df	Sum of Sq.	F Value	P Value
Block	**5**	**1.506**	**3.248**	**0.008**
Species	1	0.031	0.332	0.565
Salt	**2**	**5.700**	**30.725**	**<0.001**
Conc	2	0.075	0.406	0.667
Clip	**1**	**3.006**	**32.407**	**<0.001**
Comp	1	0.108	1.162	0.282
Species: Salt	2	0.146	0.789	0.456
Species: Conc	2	0.192	1.037	0.357
Salt: Conc	2	0.200	1.078	0.342
Species: Clip	1	0.007	0.074	0.786

Salt: Clip	**2**	**2.666**	**14.372**	**<0.001**
Conc: Clip	2	0.203	1.092	0.338
Species: Comp	1	0.067	0.727	0.395
Salt: Comp	2	0.160	0.863	0.423
Conc: Comp	2	0.162	0.876	0.418
Clip: Comp	**1**	**0.363**	**3.913**	**0.049**
Species: Salt: Conc	2	0.098	0.527	0.591
Species: Salt: Clip	2	0.073	0.394	0.675
Species: Conc: Clip	2	0.078	0.420	0.657
Salt: Conc: Clip	2	0.015	0.079	0.925
Species: Salt: Comp	2	0.081	0.434	0.649
Species: Conc: Comp	2	0.172	0.927	0.398
Salt: Conc: Comp	2	0.018	0.095	0.910
Species: Clip: Comp	2	0.167	1.800	0.181
Salt: Clip: Comp	2	0.047	0.254	0.776
Conc: Clip: Comp	1	0.081	0.439	0.646
Species: Salt: Conc: Clip	2	0.038	0.204	0.816
Species: Salt: Conc: Comp	2	0.034	0.182	0.834
Species: Salt: Clip: Comp	2	0.010	0.053	0.949
Species: Conc: Clip: Comp	2	0.062	0.334	0.716
Salt: Conc: Clip: Comp	2	0.096	0.518	0.597
Species: Salt: Conc: Clip: Comp	1	0.068	0.734	0.393
Residuals	**197**	**18.275**		

a)



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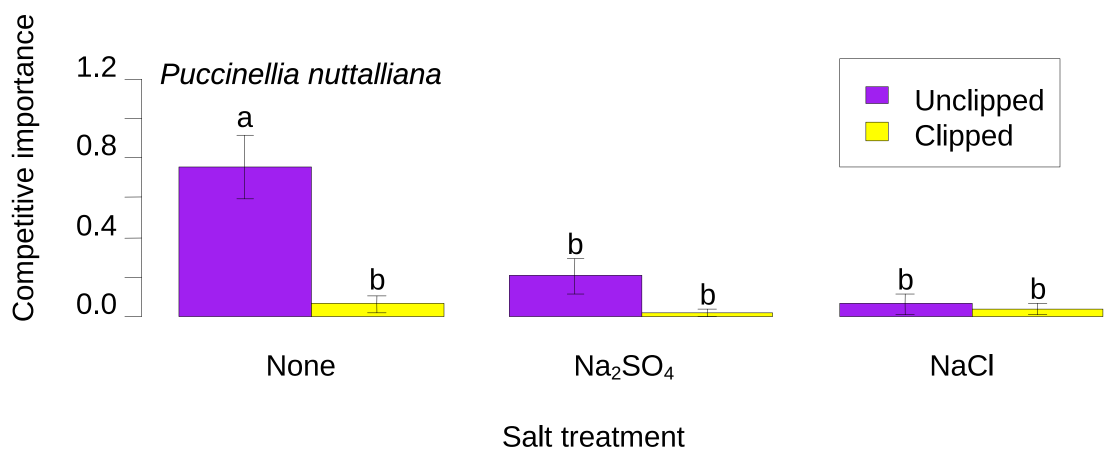

Figure 3.4. Competitive importance (± 1 SE) for (a) *Poa pratensis* and (b) *Puccinellia nuttalliana* clipped and unclipped at two salt treatment types and the control. Bars sharing the same letter are not significantly different using Tukey HSD (P>0.05).

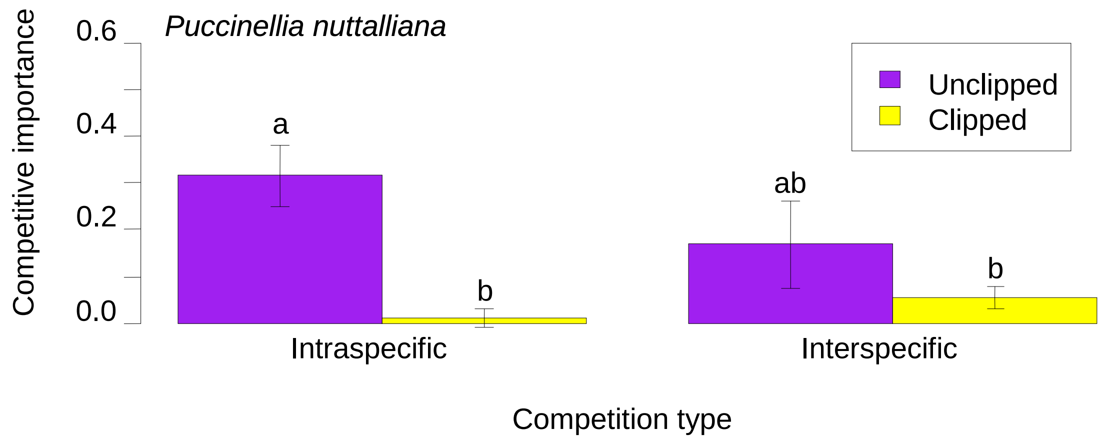

Figure 3.5. Competitive importance (± 1 SE) for *Puccinellia nuttalliana* clipped and unclipped at two competition treatments. Bars sharing the same letter are not significantly different using Tukey HSD (P>0.05).

Mortality

Species, salt type and presence of competition had the greatest impacts on mortality (Table 3.6). *Poa pratensis* had 59 of the 70 mortalities (84%). No mortalities were recorded for the control salt treatment (0 g/L), whereas the NaCl treatment represented 62 of the 70 mortalities (89%). The presence of competition was associated with 59 of the 70 mortalities (84%), with intraspecific competition accounting for 41 of the 59 competition present mortalities (69%) (Table 3.6). GLM results showed no significance differences between treatments (Table 3.7).

Table 3.6. Mortalities reported by species, competition type, clipped or unclipped, salt type and concentration.

			No Salt	Na_2SO_4			NaCl			Total
			0 g/L	5 g/L	10 g/L	15 g/L	5 g/L	10 g/L	15 g/L	
Poa pratensis	**Alone**	**No Clip**	0	1	0	0	2	1	1	**5**
		Clip	0	0	0	0	1	2	2	**5**
	Inter	**No Clip**	0	0	0	0	1	4	2	**7**
		Clip	0	0	0	1	0	5	1	**7**
	Intra	**No Clip**	0	2	0	1	4	3	6	**16**
		Clip	0	1	0	1	5	5	7	**19**
Puccinellia nuttalliana	**Alone**	**No Clip**	0	0	0	0	0	0	0	**0**
		Clip	0	0	0	0	0	0	1	**1**
	Inter	**No Clip**	0	0	0	0	0	0	1	**1**
		Clip	0	0	0	0	0	2	1	**3**
	Intra	**No Clip**	0	1	0	0	0	0	3	**4**
		Clip	0	0	0	0	0	0	2	**2**
Total			**0**	**5**	**0**	**3**	**13**	**22**	**27**	**70**

Table 3.7. GLM of mortalities by species, salt concentration, clipping and competition type.

	Z value	Pr(>|z|)
Poa pratensis	0.003	*0.998*
Puccinellia nuttalliana	0	1.000
5 g/L NaCl	-0.003	0.998
10 g/L NaCl	0	1.000
15 g/L NaCl	0	1.000
5 g/L Na_2SO_4	-0.003	0.998
10 g/L Na_2SO_4	-0.003	0.998
15 g/L Na_2SO_4	-0.003	0.998
Clipping	0	1.000
Intraspecific Competition	0	1.000
Interspecific Competition	0	1.000

Discussion

I found that as the concentration of salt increased plant biomass decreased. As predicted, there was a greater reduction in the relative biomass of *Poa pratensis* compared to *Puccinellia nuttalliana* with an increase in salt concentration. The effect of salt type was unexpected, with NaCl causing a greater reduction in plant growth than Na_2SO_4. Because salt concentration caused a reduction in plant growth, I can assume salt concentration was a stress. I found support for Grime's hypothesis that there was an inverse relationship between C_{imp} and salt stress, with the declining role of C_{imp} for both species as salt concentration increased.

Total Biomass

Total biomass for both species was greatest at the control salt treatment (0 g/L salt) and declined as salt concentration increased along both salt gradients (Na_2SO_4 and NaCl). These findings support my first hypothesis: biomass will decrease with increasing concentration of salt, with *Poa pratensis* experiencing a greater reduction in relative biomass than *Puccinellia nuttalliana* when subjected to the salt treatments. Previous studies examining the impacts of salinity gradients on plant biomass showed a reduction in growth, especially of glycophytes (Egan and Ungar 2001), shift in R:S ratio and increased chlorosis (Parrondo et al. 1978), reduction in water content and Na^+ ion accumulation (Glenn 1987). Salt type and concentration decreased the growth rate and biomass of both species but had a greater effect on *P. pratensis*, the glycophytic species.

While both species showed a decline in biomass along both salinity gradients, a greater reduction in biomass occurred along the NaCl gradient. Several studies have investigated the effects of salt composition on seed germination and seedling growth (Younis and Hatata 1971; Bhivare and Nimbalkar 1984), but few have examined the effects as plants mature (Ungar 1970). Younis and Hatata (1971) concluded that it was the salt cation that caused the reduction in wheat seed germination and growth. The plant community composition in the marsh systems they studied was not significantly influenced by the dominant anions and thus not as important in shaping plant communities as previously proposed. Therefore the nature of anions present was not as important as once thought (Ungar 1970). However, I show that chloride (Cl^-) anion reduced biomass to a greater degree than the sulphate (SO_4^{2-}) anion, indicating that the nature of dominant anion must also be considered an important factor in retarding and inhibiting plant growth.

Root to Shoot Ratio

The R:S ratio of glycophytes have been shown to decline with salt concentration whereas the R:S ratio of halophytes typically remain constant (Barbour 1970: Kenkel et al. 1991). My results support these studies and hypothesis 3, with *P. pratensis* showing a decrease in R:S ratio and *P. nuttalliana* exhibiting no significant change when exposed to both salt treatments. *Poa pratensis* experienced a significant increase in R:S ratio when clipped with the 10 NaCl treatments; contradicting the idea that R:S ratio should decrease with clipping due to a reallocation of energy, for re-growth, from the root to shoot (Barbour 1978) but supporting hypothesis 3. This may be attributed to the salt-intolerant plant's response to the stress of the NaCl treatment (Grime 2001). Stressed plants commonly grow slower and are more vulnerable to damage (clipping) and will likely take longer to recover (Grime 2001). The plant may be unable to allocate energy for shoot re-growth because the salt stress reduced available energy. The removal of the aboveground biomass may cause an imbalance in the R:S ratio resulting in a positive trend.

Competitive Importance

The results supported my final fourth hypothesis that C_{imp} would have an inverse relationship with increasing stress (salt presence or salt type) (Grime 1979; Kenkel et al. 1991); the addition of a salt treatment or salt type decreased competitive importance. A further reduction in C_{imp} occurred with clipping. Clipping acting as another stress agent reduced the degree of C_{imp} alone and in combination with salt treatment or salt type. The degree to which C_{imp} was reduced along the salinity gradient for *P. nuttalliana* was inconsistent with my hypothesis that C_{imp} of *P. nuttalliana* will be less affected by salt concentration than *P. pratensis*. Moreover, the decline in C_{imp} for *P. nuttalliana* from the control to 5 g/L Na_2SO_4 was much greater than expected considering the biomass results.

There was no apparent difference in competitive importance between interspecific and intraspecific competition (competition type). However, intraspecific competition and clipping showed a greater reduction in the degree of competitive importance for *P. nuttalliana* than interspecific competition and clipping. These results may be attributed to the low density of this study, the morphology of *P. nuttalliana* or general competitive ability of both species. Competitive importance for *P. pratensis* and *P. nuttalliana* at the unclipped control was comparable, supporting Tarasoff et al. (2009) results, from a 2 year greenhouse pair-wise competition study that of *P. pratensis, P. nuttalliana* and *Puccinellia distans*, that *P. nuttalliana* is a stronger competitor and *P. pratensis* is a weaker competitor for the first year. Also the cultivar or origin of the *P. pratensis* seed may play a role in its competitive ability, with some cultivars producing more competitive forms of the species (Eggens 1982; Tarasoff et al. 2009). Therefore, my study suggests that the presence of stress (salt) and disturbance (clipping) has a stronger influence on the species level responses of *P. pratensis* and *P. nuttalliana* than competition.

Competition can be affected by abiotic factors in non resource stress environments. Fraser and Miletti (2008) found that competition (competitive intensity) was reduced with increased water level stress. A reduction in biomass and competitive effect was observed for all plants at the highest stress level that could be attributed to inhibited plant growth (Fraser and Miletti 2008). Similar results were found in my study, with the addition of a salt treatment or type of salt (abiotic stress) the role of competition decreased. Wilson and Keddy (1985) concluded that diffuse competition was greater at undisturbed, nutrient rich sites and lesser at disturbed, nutrient poor sites, highlighting the relationship between abiotic stress and resource stress.

Numerous indices have been devised to assess the effects of competition on plants (Weigelt and Jolliffe 2003). Absolute competition, relative competition and competitive intensity indices and analysis were conducted on the data, but competitive importance was selected as the best representation of the data due to the presence of significant values and its applicability to gradient analysis (Brooker et al. 2005; Brooker and Kikividze 2008; Carlyle et al. 2010).

Mortality

Mortality trends were as predicted, with the salt intolerant species having the majority of mortalities. The mortality discrepancy between the two species supports the evidence that *P. nuttalliana* is a better salt stress tolerator than *P. pratensis* (Kenkel at al. 1991; Tarasoff et al. 2007a; Tarasoff et al. 2007b). My results showed no mortalities at the control salt level for either species indicating that 0 g/L is optimal for the survival of the glycophyte as well as the halophyte thus supporting the theory that most salt tolerant grasses tend to be facultative not obligate halophytes (Barbour 1970; Glenn 1987; Kenkel et al.1991). Both species experienced greater mortalities when exposed to NaCl than to Na_2SO_4 indicating that Cl is more detrimental to the survival of *P. pratensis* and *P. nuttalliana*. However the greater intolerance of both species to NaCl was surprising, suggesting that ionic composition also plays an important role in effecting plant fitness and survivorship. Competition represented by the presence of another plant caused a likely increase in stress leading to greater mortalities. The high number of intraspecific competition deaths may be because both plants require the same resources leading to a more stressful environment or because they were over-represented due to experimental design.

Conclusions

The concept that there is an inverse relationship between competition and stress that is the result of physiological trade-offs (Grime 1979; Kenkel et al. 1991) is supported by the findings in my study. Under optimal conditions *P. pratensis* is a larger, more palatable grass than *P. nuttalliana*; however, the addition of a stress (salt) gradient dramatically reduced the biomass and vigor of *P. pratensis* and to a lesser extent *P. nuttalliana. Puccinellia nuttalliana*, often limited in abundance in nature by its low competitive ability, was less affected by the stress of salt and the disturbance of clipping. This idea was further supported by the significant changes in the R:S ratio of *P. pratensis* when subjected to salt and clipping. Salt type was shown to significantly affect biomass, R:S ratio and C_{imp} in almost all experiments. Competition was found to be the greatest component influencing overall fitness of both species under optimal conditions. As expected, the importance of competition declined drastically for both species with the addition of stress. Competitive importance remained somewhat higher for the halophytic *P. nuttalliana* as salt stress (salt type) increased.

The controlled nature and size of my experiment presented some limitations to the scope of our study. Plant density was not manipulated or addressed in our study due to the increased complexity, size and space limitations. Study species were limited to only two grasses for functionality and presence in local grassland/ wetlands. Although a wide range of salts are found throughout British Columbia's lakes, ponds and wetlands, NaCl and Na_2SO_4 were chosen based on their common cation and presence in water bodies of Lac du Bois, Kamloops. A salt concentration gradient was used to simulate increasing salinity associate with climate change. While laboratory experiments can be criticized for being too narrow, they provide an opportunity to focus on specific interactions that can be manipulated and studied in greater detail than possible in the field. Laboratory experiments also provide the opportunity to conduct research that would not be possible in the field, such as the controlled salt concentrations. *Puccinellia nuttalliana* went to seed through the course of the experiment while *P. pratensis* displayed no signs of even flowering. This discrepancy in life histories may have contributed to unexpected similarities in competitive importance at the control. Tarasoff (2007) found that *P. pratensis* grew slower than *P. nuttalliana* and *Puccinellia distans* in the first year of the study but had surpassed both *Puccinellia* species in biomass by the second year. Thus the temporal scale of the study may have been too short to examine the full effects of inter-specific competition between the two species.

Blocking became a larger issue than expected. Blocking was included when developing the orientation of pots within the greenhouse rooms and used in all analyses when applicable.

This study provided a stepping stone towards more research in the field of stress gradients and competition. Density could be addressed by conducting the experiment in a field or large monoculture pots containing different numbers of plants. Additional species could be substituted in or added to future experiments to develop a greater understanding of the plant community's dynamics. The range of mineral salts found within Lac du Bois lends to the idea of examining the effect of other salt on wetland species.

Climate change may impact intermountain wetland systems in a variety of ways; increased salinity is only one potential scenario. Experimental manipulations investigating the effects of temperature shifts, water level changes and the introduction of invasive species may enable us to test potential future environments. An understanding of potential plant communities and their abiotic characteristic may improve planning and management now and for the future.

Management Implications

Management recommendations deduced from this study are directed toward the cattle and agricultural industries. *Puccinellia nuttalliana* and other salt-tolerant species should be considered and incorporated in the seeding of saline fields and rangeland. While they may not be as palatable as salt-intolerant species, such as *P. pratensis,* they may provide significantly more biomass in the event of climate change induced soil salinization. I recommend grazing of saline areas early in the season while soil and water salinity is lowest due to spring melt-out and precipitation. *Puccinellia nuttalliana* matured faster than *P. pratensis,* which may be an adaptation to avoid the increasing salinity of the dry late summer, resulting in higher quality *P. nuttalliana* for forage earlier in the growing season. As salt concentration increased, both species' ability to re-grow following the clipping treatment was suppressed, and in the case of *P. pratensis* ceased altogether, supporting the suggestion that earlier grazing increases the potential of plants to re-grow. Warming due to global climate change is inevitable, but with new research we should be able to better understand intermountain ecosystems and how best to manage them.

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Chapter 4- Summary and Management Implications

Environmental science is a multidisciplinary area of research that includes, but is not limited to, biology, chemistry, physics, geology and geography. Environmental science is a study of the relationship between living and non-living components of an ecosystem, with an emphasis on the impact of humans. How have the actions of humans changed our environment and what does a changing environment mean to humans? What have we as humans learned about our environment and how can we protect and manage it better? Environmental science can address these questions and highlight the effects humans have on the Earth. This can lead to controversy and backlash because some people do not want to take responsibility for poor stewardship and exploitation, or deny many environmental problems, such as global climate change, are human caused. However, many sustainable solutions to environmental issues are being developed because scientists are gaining an understanding of human actions. Environmental science enables us to better understand our world, and that understanding needs to be transferred into our environmental policies, sustainable management and conservation efforts.

General Overview of Research

My research investigated how plants compete and how increasing salinity and disturbance, such as clipping, affects that relationship. I used Kentucky bluegrass (*Poa pratensis*) and Nuttall's alkaligrass (*Puccinellia nuttalliana*) as my study plants. One experiment was done in Lac du Bois Provincial Park and the other was done in the research greenhouse at Thompson Rivers University, both located in Kamloops, British Columbia, Canada.

Kentucky bluegrass is found throughout the world and is often use as a lawn and pasture grass because of its ability to grow in most climates and tolerance of mowing and grazing. While it is believed to be introduced from Eurasia there are subspecies native to North America (Parish et al.1996). Kentucky bluegrass is not tolerant of saline (salty) soils. High levels of salt can be toxic to Kentucky bluegrass causing poor growth and plant death (Kenkel et al.1991). Nuttall's alkaligrass is a native species and can be found throughout much of the north and west coast of North America, can be used as forage for livestock or planted to prevent soil erosion (Parish et al.1996). Usually found in wetlands and areas with saline or alkali (basic, pH>7) soils, Nuttall's alkaligrass is a salt-tolerant species minimally affected by high levels of salt (Kenkel et al. 1991). Kentucky bluegrass and Nuttall's alkaligrass can be found in and around the Kamloops area and both have been identified within Lac du Bois Provincial Park.

Saline soil and saline wetlands are found throughout British Columbia's southern interior. Different types of bedrock and soil have created a patchwork of different types of salts in the region. Too much salt can be damaging to plants by affecting their water balance, which can lead to stunted growth, reduced reproduction, poor health and even death. Saline areas are often inhabited by specialized plants that can process high levels of salt. Some salt tolerant plants produce less forage, which is often less palatable and less nutritious for livestock and wildlife (El Shaer 2010).

Climate change is predicted to increase temperatures and decrease summer rain in the southern interior of British Columbia. Warmer, drier summers will lead to more evaporation from wetlands, ponds and lakes leaving less surface water. A lower volume of water but same amount of salts in these systems will cause an increase in salt concentration or higher salinity. Therefore, the plants in these systems will be subjected to higher salt levels likely causing more damage to the salt-intolerant species and a shift towards the salt-tolerant species. Livestock and wildlife relying on riparian forage may have less food to eat. Furthermore, grazing animals use the water bodies as a source of water and if the salinity gets too high it becomes toxic to the animals.

Grazing animals can be considered a form of disturbance impacting plants. Some plants are more tolerant of grazing than others. Grazing can reduce a plant's vigor, competitive ability, and relative abundance. The combination of high salinity and grazing can have a strong affect on the biomass of plant species and the composition of the ecosystem as a whole.

My field experiment investigated the effects of salinity and competition from other plants on transplanted Kentucky bluegrass and Nuttall's alkaligrass seedlings in Lac du Bois Provincial Park. I selected 6 ponds based on their water conductivity (salinity) readings: two 'fresh', two 'mid or moderately saline' and two 'saline'. Seeds of Kentucky bluegrass and Nuttall's alkaligrass were sown on 'peat pellets' in the greenhouse. The seedlings were transplanted into plots at the selected 6 sites (24 seedlings per site, 12 Kentucky bluegrass and 12 Nuttall's alkaligrass). At half of the plots (12 per site) the aboveground biomass (competition) was cut away. Seedlings were planted and monitored for 3 months. After 3 months, seedlings were harvested along with existing plots aboveground biomass. Plants from 'with competition' plots were separated to species dried and weighed. I collected additional physical and biological data from each plot to be analyzed as well.

The transplanted seedlings did poorly, with just over half surviving the 3 months and only 19 establishing and growing. All but one of the 19 plants that did well were from one site, mid 2. Mid 2 was a moderately saline site with naturally growing salt-tolerant species. At mid 2, the salt-tolerant Nuttall's alkaligrass grew better than the salt-intolerant Kentucky bluegrass and both species grew better in plots where the other plants were removed. Soil analysis showed all the sites to be alkaline with high levels of calcium and magnesium. The poor outcome of the transplanted seedling may be attributed to summer 2009 being hotter and much drier than average, logistical timing errors, herbivory and animal disturbance.

My greenhouse experiment investigated the effects of plant-plant competition along two salinity gradients with and without clipping. I used Kentucky bluegrass and Nuttall's alkaligrass as my plants, selected sodium chloride (NaCl) and sodium sulphate (Na_2SO_4) as my two salts, choose a concentration gradient ranging from 0 g/L to 15 g/L, and used clipping as a proxy for grazing. Seedlings were germinated in Petri dishes and then transferred to pots filled with sand. Each pot contained 1 or 2 seedlings. Pots were flushed weekly with a nutrient solution mixed with a predetermined concentration of salt.

Salt concentrations were gradually increased until optimal concentration was reached. I clipped 75% of the aboveground biomass from half of the pots twice. The final harvest occurred after 90 days. Plants were separated to root and shoot and dried and weighed.

Kentucky bluegrass was affected by salt type and salt concentration more than the Nuttall's alkaligrass. The total biomass of Kentucky bluegrass when given the salt treatment was much lower than the total biomass of Nuttall's alkaligrass. Plants given the sodium chloride treatment grew less than the plants given the sodium sulphate treatment. Clipping reduced the biomass of both species while the combination of a salt treatment and clipping further reduced the biomass of both species. Salt type and salt concentration caused Kentucky bluegrass to grow more roots than shoots but did not change Nuttall's alkaligrass' root:shoot ratio. The presence of another plant in the pot (competition) had the strongest effect on plants grown without salt. Competition became less important in impacting plant growth with the presence of salt especially sodium chloride. Clipping also reduced the role competition played in determining plant growth for both species. I found plant mortalities to be greatest for Kentucky bluegrass, when grown with sodium chloride or grown with competition.

Climate change

Global climate change is something humans cannot afford to ignore; the effects are now measurable and we can predict the future impact it will have on our planet (IPCC 2007). Human activity has caused climate change through greenhouse gas emissions, destruction of the ozone layer and exploitation of ecosystems (IPCC 2007). In addition, natural processes including volcanic activity and fluxes in solar radiation have also contributed to global climate change (IPCC 2007). Some evidence of climate change include: rising global mean temperature, altered precipitation trends, rising sea levels, reduction in glacier and sea ice thickness, ocean acidification and increased severity of extreme weather events (IPCC 2007). These changes can cause habitat degradation and loss, loss of species, shift in animal migration patterns, alter distribution as well as substantial effects on humans and our quality of life (McCarty 2001; IPCC 2002).

Recognition that climate change is occurring and that we as humans are a strong contributing factor, is essential to the future of the Earth. We must consider climate change predictions and model outputs when developing policy and conservation efforts in order to best manage our changing environment.

Key Management Points

The results of my research indicate that the interactions between plant species, salinity and disturbance (clipping) can affect the potential quality and quantity of forage material for livestock and wildlife. To optimize forage potential and protect the southern interiors' essential and sensitive ponds and wetlands, I have formulated some possible management suggestions.

If possible, grazing livestock should utilize areas of low or moderate soil salinity. These areas should provide greater amounts of biomass and more palatable species. Highly saline areas should be avoided or grazed early in the season while salinity is generally at its lowest and the vegetation has time to recover from grazing disturbance. Water sources can be too saline and thus toxic to livestock so alternative water sources should be utilized in areas of high salinity. If seeding is to be done in a saline pasture that will be used for livestock, native salt-tolerant forage species such as Nuttall's alkaligrass should be considered and used in the seeding mixture. Consultation of climate change scenarios is essential for us to predict possible adaptation pathways and shifts in our grassland and wetland ecosystems. Management and policy will be more effective if we attempt to understand what our environment may hold in the future.

We need to be aware of our environment, its needs and limitations. Scientific research can be an excellent supplement to the prior knowledge of our ranchers, managers and landowners. The more we understand the complex workings of our environment, the better we can manage and protect it. Sustainable practices that incorporate our knowledge of current ecosystem functions and an acknowledgement of possible future changes will allow us to continue to enjoy our world.

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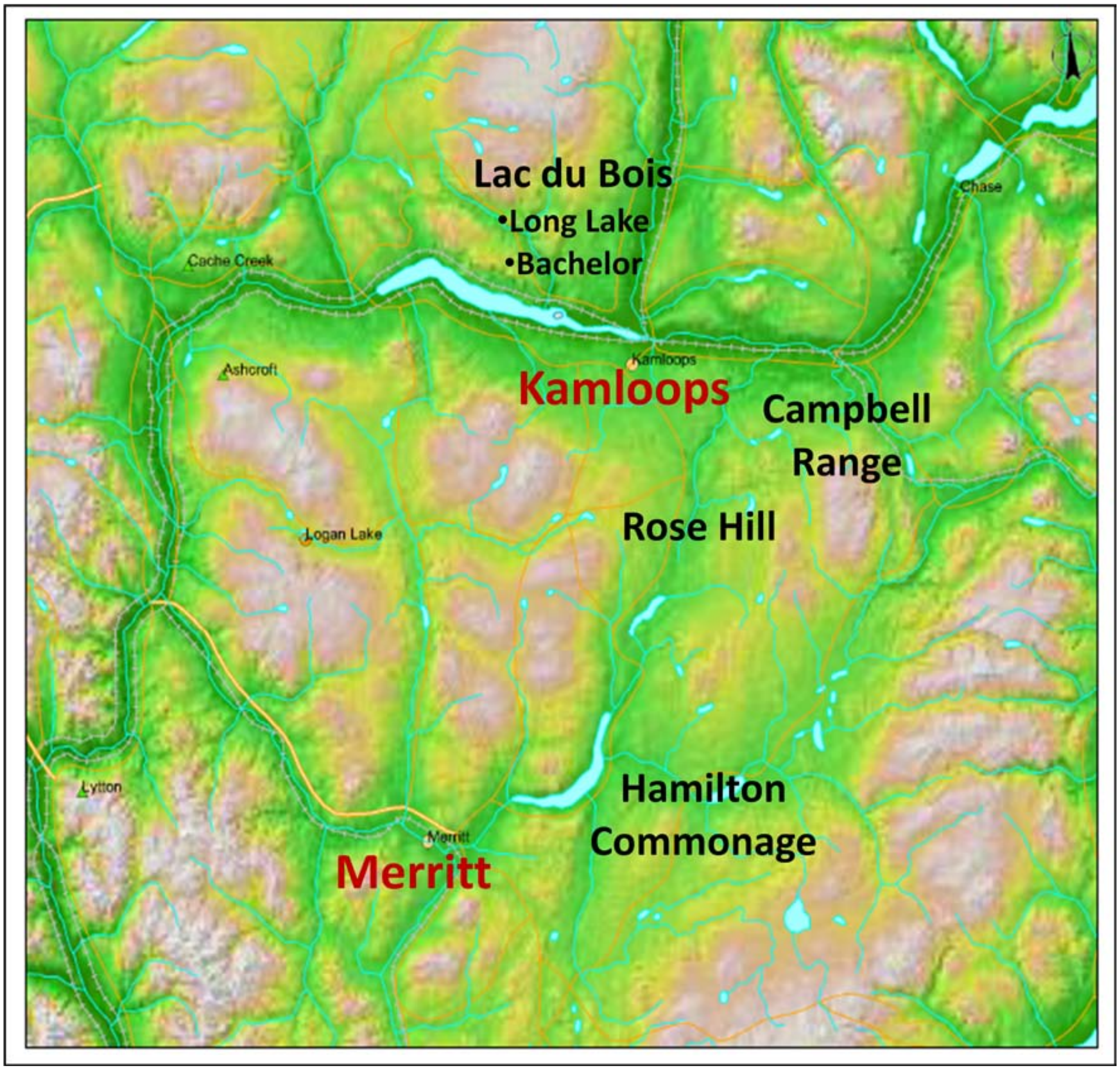
APPENDICES



Appendix A: Map of Kamloops/ Merritt, British Columbia, Canada. General locations of each group of ponds (Bachelor, Long Lake, Campbell Range, Rose Hill and Hamilton Commonage) used for water level and water depth collection. Map scale 1: 590 862 (iMap BC).

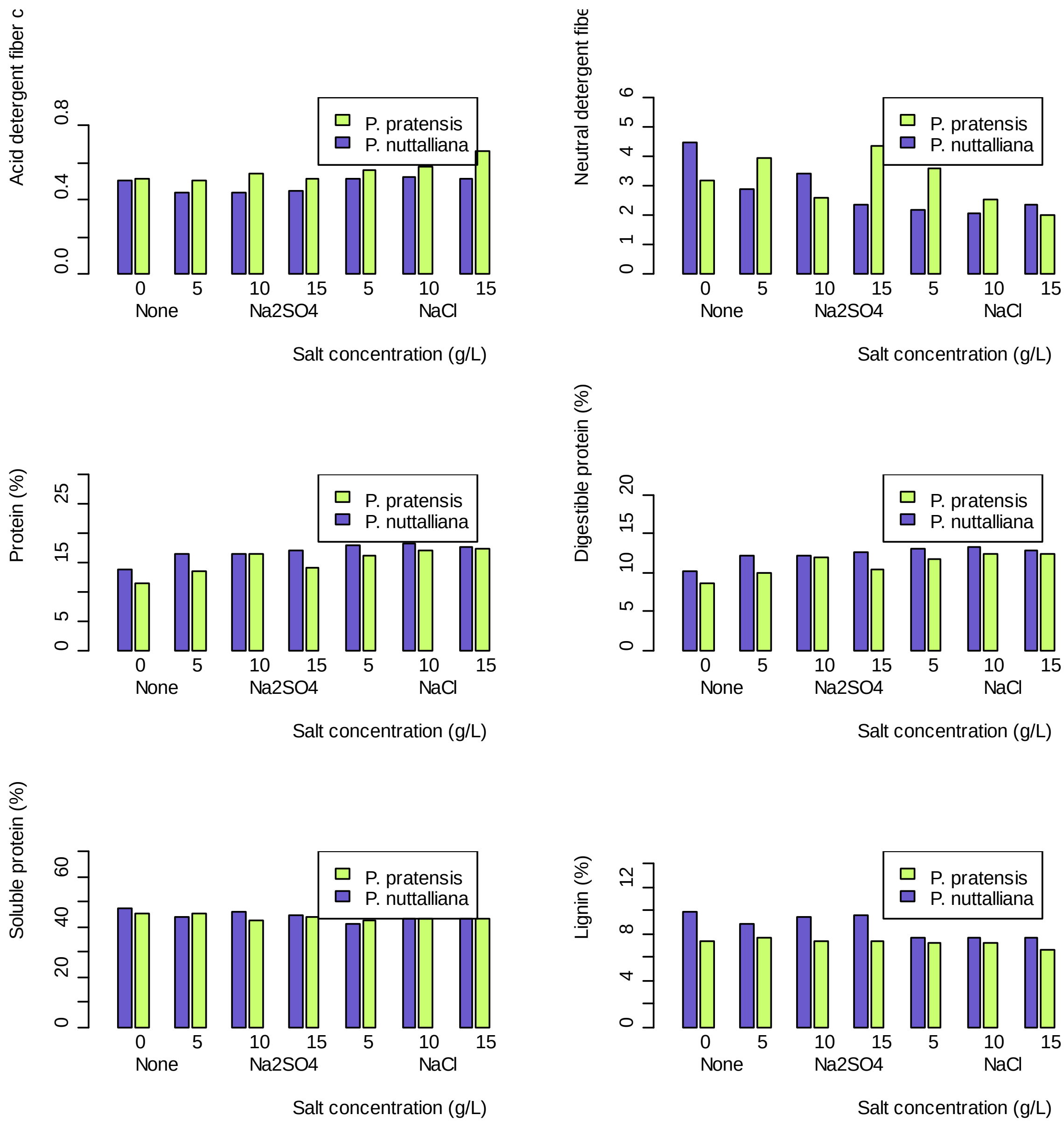
Appendix B: Pond water level measurements. Water levels collect from water meters during summer 2008 and 2009. NA indicates insufficient data or well not installed, WR indicates well was replaced, * indicates probe encountered mud in pipe.

	May 13/ 08	Jun 4/ 08	Jun 26/ 08	Jul 28/ 08	Jun 11/ 09	Jun 24/ 09	Jul 8/ 09	Jul 20/ 09
Bachelor								
B3	-19.4	-26	-35.3	-47.3*	D	D	D	D
B4	-29.9	-29.2	-35.5	-48.9*	D	D	D	D
B4.1	-9.6	-21.7	-30.8	D	D	D	D	D
B5	-27.8	-30.1	-40.8	D	D	D	D	D
B6	-13.7	-15.2	-23.4	-42.6*	D	D	D	D
B6.1	-24.1	-16.4	-25.3	-46.5	D	D	D	D
B9	0.4	-1.7	-4.4	-22.3	-17.1*	-20.7*	-20*	D
B9.1	1.8	-2.7	-4.8	-20.2	-25.2*	-32.2*	D	D
B10	-20.8	-19.2	-25.8	-43.9*	D	D	D	D
Campbell Range								
C6	NA	5.3	7	-5.6	-9.6*	-16.9*	-20.4*	D
C7	NA	-5.3	-25.2	D	D	D	D	D
C8	NA	-9	-19.1	D	D	D	D	D
Hamilton Commonage								
H4.2	-39.4	-40.7	-54.5	D	D	D	D	D
H4.3	-4.9	-19.1	-51.3	D	D	D	D	D
H5	-2.1	-10.1	-36.5	D	D	D	D	D
H5.1	10.9	WR	-22.5	D	D	D	D	D
H6	-7.5	-14.8	-33.7	D	D	D	D	D
H7.1	1	-6.6	D	D	D	D	D	D
H9	16.8	WR	-9.8	-34.7	-46.2*	D	D	D
Long Lake								
L2	NA	-0.4	-12	-23.2*	D	D	D	D
L3	NA	-0.1	-2.7	-3	-10.6*	-13.6*	-19.8*	D
L4	-6.5	-6.8	-4.9	-3.3	-7.9	-15.1	-20.2	D
L4.1	-17.9	-15.8	-22.5	D	-21.4*	-21.8*	-18.8*	-33.2*
L5	-0.2	-0.6	-5.4	-25.1*	D	-21.7	D	D
L6.3	0	-5.9	-8.5	-31.7	D	D	D	D
L7	-9.9	-5.7	-13.2	D	D	D	D	D
L8	-21.5	-16.6	-45.6	D	D	D	D	D
Rose Hill								
R5.2	NA	-40.4	D	D	D	D	D	D
R13	NA	-57.3	-59.5*	D	D	D	D	D
R14	NA	-11.1	-53.2	D	D	D	D	D
R15	NA	-25.2	-42.4*	D	D	D	D	D
R17	NA	-5	-18.7	D	D	D	D	D
R19	NA	7.7	-19*	D	8*	-0.4*	-8.7*	D

Appendix C-Pond depth measurements. Depth measurements collected from approximately deepest part of ponds during summer 2009. UTM indicates where location where measurements were taken.

Site	Coordinates	June 2009 Depth	July 2009 Depth	August 2009 Depth	Difference
Bachelor					
B3	10U 0681432-UTM 5627282	180	172	161	**-19**
B4	10U 0681244-UTM 5628832	15.5	0	0	**-15.5**
B4.1	10U 0680528-UTM 5628832	17	0	0	**-17**
B5	No standing water	0	0	0	**0**
B6	10U 0680396-UTM 5629395	470	429	420	**-50**
B6.1	10U 0680528-UTM 5628831	9	0	0	**-9**
B9	10U 0679798-UTM 5631529	140	109	104	**-36**
B9.1	10U 0679891-UTM 5631975	250	105	97	**-153**
B10	10U 0679901-UTM 5632198	40	0	0	**-40**
Campbell Range					
C6	10U 0708101-UTM 5605148	197.5	191	182	**-15.5**
C7	No standing water	0	0	0	**0**
C8	10U 0707518-UTM 5606553	9.5	0	0	**-9.5**
Hamilton Commonage					
H2	10U 0683312-UTM 5551429	8	0	0	**-8**
H4.2	10U 0683579-UTM 5553441	95.5	88	64	**-31.5**
H4.3	10U 0683752	13	0	0	**-13**
H5	10U 0685083-UTM 5552877	32	0	0	**-32**
H5.1	No standing water	0	0	0	**0**
H6	10U 0686046-UTM 5552599	272	277	253	**-19**
H7.1	No standing water	0	0	0	**0**
H9	10U 0683631-UTM 554978	20	5	0	**-20**
Long Lake					
L2	10U 0682470-UTM 5627967	134.5	113	98	**-36.5**
L3	10U 0682397-	574	564	552	**-22**

	UTM 5630350				
L4	10U 0682661- UTM 5630788	312.5	299	287	**-25.5**
L4.1	10U 0682850- UTM 5631217	73.5	63	69	**-4.5**
L5	10U 0683326- UTM 5631711	67	45	35	**-32**
L6.3	10U 0683197- UTM 5630007	226.5	209	207	**-19.5**
L7	10U 0683825- UTM 560655	30	17	0	**-30**
L8	No standing water	0	0	0	**0**
Rose Hill					
R5.2	No standing water	0	0	0	**0**
R13	10U 0692563- UTM 5611149	256	201	145	**-120**
R14	10U 0694207- UTM 5611472	105	49	11	**-94**
R15	10U 0693951- UTM 5610087	110	90	88	**-22**
R17	10U 0691493- UTM 5606337	112	99	82	**-30**
R19	10U 0692437- UTM 5605110	68.5	37	0	**-68.5**



Appendix D- Grass forage analysis. Pooled treatment NIR (near-infrared reflectance) results for both grasses (*Poa pratensis* and *Puccinellia nuttalliana*) grown in the greenhouse experiment. These results are just for curiosity due to small sample size, limited amount material available for testing, lack of replication and high potential error values.