

Effects of salinity and clipping on biomass and competition between a halophyte and a glycophyte

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Abstract Global climate change will likely result in the reduction of water levels in intermountain wetlands and ponds, and the vegetation communities associated with these wetlands are an important forage source for livestock. Lowered water levels will not only constrict wetland plant communities, it will potentially change aquatic and soil salt concentrations. Such an increase in salinity can reduce plant growth and potentially affect competitive interactions between plants. A greenhouse experiment examined the effects of salinity and competition on the growth of two wet meadow grass species, *Poa pratensis* (a glycophyte) and *Puccinellia nuttalliana* (a halophyte). The following hypotheses based on published data were tested: (1) Biomass of both species will decrease with increasing concentration of salt; (2) root:shoot (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; (3) competitive importance will decrease for *P. pratensis* and *P. nuttalliana* with increasing salt concentration because salt induces a stress response and competitive importance is reduced in stressed environments. A factorial design included 3 plant treatments (*P. nuttalliana* alone, *P. pratensis* alone, *P. nuttalliana* + *P. pratensis*) × 4 salinity rates (control;

5, 10, 15 g/L NaCl) × 2 clipping intensities (plants clipped or not clipped) for a total of 24 combinations replicated 6 times over a period of 90 days. We found a reduction in dry biomass as salinity increased, and this effect was greatest for *P. pratensis*. (1.94 g (SE 0.13) at 0 g/L NaCl to 0.22 g (SE 0.11) at 15 g/L NaCl). The R:S ratio of *P. pratensis* was reduced by salinity, but not for *P. nuttalliana*. Competitive importance of both species was reduced by clipping and by salinity, but the effect was greater and more consistent for *P. pratensis*. We conclude that salt concentration reduces plant growth and the effect of competition.

Keywords *Poa pratensis* · *Puccinellia nuttalliana* · Climate change · Competitive importance · Cattle grazing

Introduction

Hydrology, changes in the depth and duration of water levels, can explain over 50 % of the variation in the structure and composition of wetland plant communities (Keddy 2001; Mitsch and Gosselink 2007), but one aspect of hydrology that is rarely considered in wetland plant studies is the indirect effect 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

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(Topping and Scudder 1977; Wilson et al. 1994; Waizer 2006), which may affect wetland plant growth. 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 are an important source of riparian forage for livestock, due to high levels of productivity and diversity (Belsky et al. 1999). There is evidence that cattle grazing can increase salinity in soils by reducing aboveground plant and litter cover, which lead to higher soil temperatures and evaporation rates (Lavado and Taboada 1987; Chaneton and Lavado 1996; Amiaud et al. 1998). Thus, it is critical to gain an understanding of how riparian plant species might be affected by an increase in salinity.

Highly saline soils can reduce plant performance, vigor, biomass, nutritional value, and palatability (Younis and Hatata 1971; Parrondo et al. 1978; Cheeseman 1988; Kenkel et al. 1991; Covich et al. 1997). Increasing salt stress has been shown to cause a shift in biomass from below-ground to above-ground, especially in salt-intolerant species (Barbour 1978; Kenkel et al. 1991). Few species are found in highly saline areas and the species are dominated by salt-tolerant halophytes that possess mechanisms to maintain osmotic potential and maintain metabolic processes (Glenn 1987; Cheeseman 1988; Tarasoff et al. 2007b).

Competition has been shown to interact with hydrology to affect plant growth (Grosshans and Kenkel 1997; Fraser and Miletti 2008). There is also evidence that competition can interact with salinity to affect plant performance (Kenkel et al. 1991). The importance of competition 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 theory states that competition is greater in less stressful, more productive environments and as stress increases, the impact of competition decreases (Grime 1973, 2001; Keddy 2002). Another view is that competition remains constant along an environmental stress or productivity gradient, with a shift from below-ground competition for mineral nutrients and water resources in low productivity environments to above-ground for sunlight in high productivity environments (Tilman 1982, 1988). Disturbance, especially herbivory, has also been shown to influence

plant–plant interactions (Huston 1979; Campbell and Grime 1992; Turkington et al. 1993; Gough and Grace 1998). Herbivores are often selective, feeding preferentially on fast-growing plants adapted to high-resource environments (Fraser and Grime 1999). The removal of aboveground biomass by herbivores can cause a shift in root:shoot (R:S) ratio; plants that invest more energy in leaf production after herbivore disturbance may experience a reduction in their R:S ratio (Kuijper et al. 2005). Our study investigated the interactions between stress (salinity) and disturbance (clipping) on plant growth and competition, considering a glycophyte and a halophyte.

We studied the main and interacting effects of salt concentration and clipping on competition between two grass species, *Poa pratensis* L. and *Puccinellia nuttalliana* (Schult.) Hitchc. in a greenhouse environment. The species were selected based on salt-tolerance and the fact that they grow together in the intermountain freshwater ponds and wetlands of the southern interior of British Columbia, Canada (Jones et al. 2011). Although a wide range of ions and salt complexes are found throughout British Columbia's lakes, ponds, and wetlands, NaCl was the most common in BC (Topping and Scudder 1977), and is widespread in lakes around the world (Hart et al. 1991; Amiaud et al. 1998). A salt concentration gradient was used to simulate the natural lower range found in alkali ponds in the local area (1–130 mequiv/L; Topping and Scudder 1977) and in similar ecosystems (Kenkel et al. 1991). Clipping was chosen to simulate grazing, a prevalent land-use practice in the southern interior of BC. The competition treatment included one plant 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 focused 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 while considering the impact of other environmental factors (Brooker et al. 2005; Carlyle et al. 2010). 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.

We also investigated how competitive importance may be affected by the incorporation of a disturbance. Our study tested the following hypotheses: (1) Biomass will decrease with increasing concentration of salt, with *P. pratensis*, the glycophyte experiencing a greater reduction in relative biomass than *P. nuttalliana*, the halophyte; (2) 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; (3) competitive importance will decrease for *P. pratensis* and *P. nuttalliana* with increasing salt concentration.

Materials and methods

The factorial combination included three plant treatments (*P. nuttalliana* alone, *P. pratensis* alone, and the two species in a pair wise interaction) at four salt concentrations (control, 5, 10, and 15 g/L NaCl) \times 2 clipping intensities (clipped or not). The experiment was replicated six times for a total of 144 pots. *P. 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). *P. nuttalliana*, a perennial halophyte associated with saline and alkaline wetlands (Tarasoff et al. 2007a), represents a salt-tolerant forage grass.

Greenhouse conditions

The greenhouse climate was controlled at a 16:8 h day:night cycle with light supplemented by three 1,000 W halogen sulfide lamps. Temperature was maintained at 22:15 °C and relative humidity at 65:80 day:night cycle for 90 days. Pots were divided into six blocks and randomly arranged within each block.

Germination

Approximately 400 seeds of *P. nuttalliana* and *P. pratensis* were placed in separate plastic Petri dishes filled with a sand medium (fine-textured Home Depot© Play Sand) saturated in distilled water as recommend by Kenkel et al. (1991) and received 16 h of light in the greenhouse. *P. nuttalliana* seeds were sown 4 days before *P. pratensis* seeds to ensure germination of both species occurred within days of each other.

Treatments

Seedlings were transplanted from Petri dishes into 900 mL plastic pots (12.5 cm tall, 7.5 \times 7.5 cm base, and 11 \times 11 cm top) containing a sand medium on September 30 and October 1, 2009. Pots were placed in 350 mL styrofoam dishes (4.5 cm tall, 9 \times 9 cm base, and 13 \times 13 cm top). Each pot received one or two transplants: *P. nuttalliana* alone, *P. pratensis* alone, *P. nuttalliana* with *P. pratensis*.

The sand medium was saturated with 270 mL of Rorison's nutrient solution (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 to remove old salt-nutrient medium from the pots (Kenkel et al. 1991). During Week 2, 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 increased 2.5 g/L per week until the desired final concentrations were achieved (5, 10, 15 g/L NaCl). These concentrations reflected the natural range found in the south central intermountain region of British Columbia, Canada (Topping and Scudder 1977) and was similar to the concentration used by Kenkel et al. (1991). Flushing of the pots with distilled water occurred once a week. The control (0 g/L) 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. Plants that died within 2 weeks were replaced, after which no replacement occurred. If only one plant had died within a pot of two plants, a single mortality was recorded and the surviving plant was removed from all analyses except survivorship. Half of all treatment combinations were clipped on Day 44 and on Day 63. Clipping removed 75 % of the plants' photosynthetic material.

Harvesting

Harvesting occurred on Day 90. Individuals were separated by species and then by above-ground and below-ground biomass. Biomass was oven dried at 65 °C for 10 days and weighed ($d = 0.01/0.1$ mg).

Statistical analysis

To analyze mean potential biomass we used only the plants grown alone data. All biomass data were log

transformed to meet the assumptions of normality. An ANOVA (SYSTAT 13 SYSTAT 13 2009) was conducted to test the effects of species, salinity, and clipping on the total plant biomass and R:S ratio ($\alpha = 0.05$). Competitive importance was calculated using the equation:

$$C_{\text{imp}} = \frac{P_{-N} - P_{+N}}{MP_{\pm N} - \min(P_{-N}, P_{+N})}$$

where P_{-N} is plant grown without neighbors (alone) and P_{+N} is plant grown with neighbors, and $MP_{\pm N}$ is the maximum value of plant performance in the studied system, regardless of neighbors (Seifan et al. 2010—modified after Brooker et al. 2005). In this equation, the index has a limited range of -1 to 1 ; where negative values represent competitive interactions and positive values represent facilitation.

Results

Total biomass

The mean total dry biomass of plants when grown alone (without competition) was significantly affected by all three main effects (Table 1). *P. pratensis* had a greater mean biomass ($1.727 \text{ g} \pm 0.376 \text{ SE}$) than *P. nuttalliana* ($1.439 \text{ g} \pm 0.197 \text{ SE}$). Increased salinity reduced mean plant biomass: $3.570 \text{ g} \pm 0.458 \text{ SE}$ at 0 g/L NaCl; $1.170 \text{ g} \pm 0.232 \text{ SE}$ at 5 g/L NaCl; $0.540 \text{ g} \pm 0.130 \text{ SE}$ at 10 g/L NaCl; and $0.670 \text{ g} \pm 0.181 \text{ SE}$ at 15 g/L NaCl. Clipping reduced plant

biomass from $2.269 \text{ g} \pm 0.332 \text{ SE}$ unclipped to $0.837 \text{ g} \pm 0.157 \text{ SE}$ clipped.

An interaction between species and salinity was shown to be significant (Table 1) indicating that the two species were affected by salinity differently. Results showed that *P. pratensis* and *P. nuttalliana* had the greatest biomass at 0 g/L NaCl, and that *P. pratensis* had a greater biomass than *P. nuttalliana* at 0 g/L NaCl. Biomass of *P. nuttalliana* was equally reduced at 5, 10, and 15 g/L NaCl compared to *P. nuttalliana* at 0 g/L NaCl. Whereas *P. pratensis*' biomass was lower at 10 g/L NaCl compared to 5 g/L NaCl (Fig. 1a).

The two-way interaction between species and clipping was significant (Table 1), and showed that both species responded to clipping with a reduction in biomass (Fig. 1b).

The interaction between salinity and clipping was significant (Table 1); the effect of clipping was only apparent at 0 and 5 g/L NaCl, with clipping showing a reduction of biomass (Fig. 1c). At 10 and 15 g/L NaCl clipping had no effect on biomass of plants (Fig. 1c).

Root to shoot ratio

The dry root:shoot (R:S) ratio of plants grown without competition was significantly affected by two of the three main effects, species and salinity (Table 2). *P. pratensis* had a higher mean R:S ratio ($0.467 \pm 0.056 \text{ SE}$) than *P. nuttalliana* ($0.172 \pm 0.012 \text{ SE}$). An increase in salinity reduced R:S ratio: $0.496 \pm 0.090 \text{ SE}$ at 0 g/L NaCl; $0.253 \pm 0.031 \text{ SE}$ at 5 g/L NaCl; $0.227 \pm 0.036 \text{ SE}$ at 10 g/L NaCl; and $0.217 \text{ g} \pm 0.020 \text{ SE}$ at 15 g/L NaCl.

Table 1 Results of three-way ANOVA with blocking factor examining the effects of species, salinity, and clipping on the mean total biomass of *Poa pratensis* and *Puccinellia nuttalliana*

Source	Mean squares	Degrees of freedom	F ratio	P value
Block	0.078	5	0.583	0.391
Species	0.353	1	6.818	0.011
Salinity	5.585	3	107.927	<0.001
Clip	5.306	1	102.54	<0.001
Species \times salinity	0.875	3	16.919	<0.001
Species \times clip	0.333	1	6.432	0.014
Salinity \times clip	0.683	3	4.399	0.007
Species \times salinity \times clip	0.081	3	0.522	0.668
Error	3.363	65		

Significant ($\alpha < 0.05$) values in bold

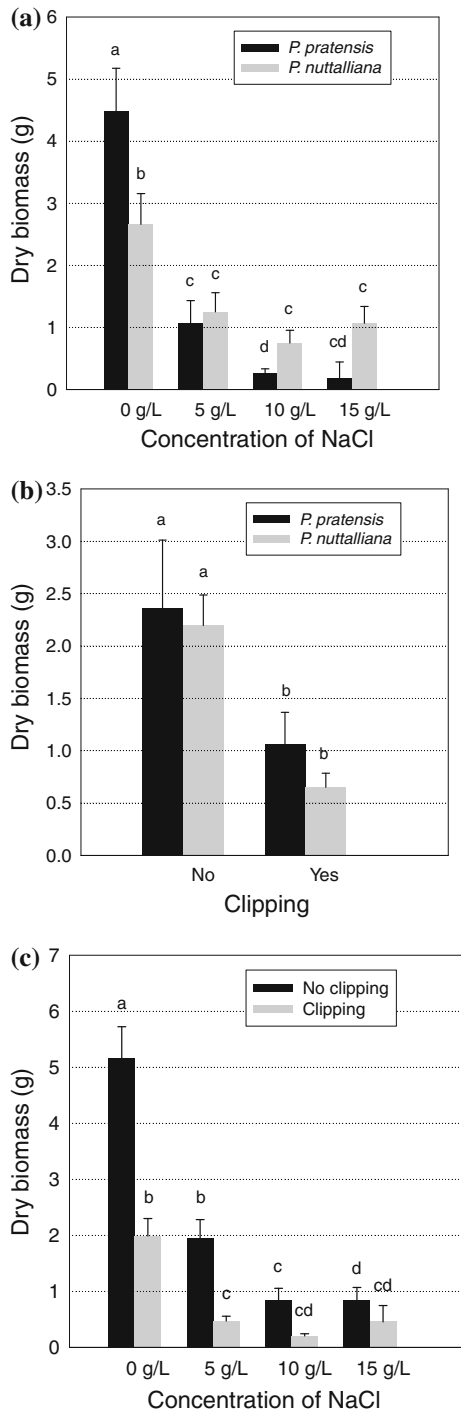


Fig. 1 Mean total dry biomass (± 1 SE) of **a** *Poa pratensis* and *Puccinellia nuttalliana* grown alone at four salinities; **b** *Poa pratensis* and *Puccinellia nuttalliana*: grown alone clipped and unclipped; and **c** clipped and unclipped plants grown at four salinities. Bars sharing the same letter are not significantly different using Tukey HSD ($P < 0.05$)

The two-way interaction between species and salinity was significant (Table 2). Post hoc Tukey analysis showed that the R:S ratio of *P. pratensis* was highest at 0 g/L NaCl and lowest at 15 g/L NaCl (Fig. 2a). Whereas the R:S ratio of *P. nuttalliana* remained consistently equal across all salinity levels (Fig. 2a), but lower than the R:S ratio of *P. pratensis* at 0 and 5 g/L NaCl.

The two-way interaction between salinity and clipping was significant (Table 2). Plants that were not clipped showed a reduction in R:S ratio with an increase in salinity from 0 g/L NaCl (Fig. 2b). Plants that were clipped showed no response in R:S ratio to salinity (Fig. 2b).

Competitive importance

Competitive importance (C_{imp}) was significantly affected by salinity and clipping (Table 3). An increase in salinity reduced competition (increased the value of C_{imp}): -0.259 ± 0.029 SE at 0 g/L NaCl; -0.024 ± 0.015 SE at 5 g/L NaCl; 0.025 ± 0.011 SE at 10 g/L NaCl; and, -0.051 ± 0.012 SE at 15 g/L NaCl. Clipping reduced competition from -0.160 ± 0.025 SE unclipped to -0.049 ± 0.009 SE clipped.

There was a two-way interaction effect on C_{imp} between species and salinity (Table 3) which shows that competition of *P. pratensis* was greater than *P. nuttalliana* at 0 g/L NaCl, but that competition of *P. nuttalliana* was greater than *P. pratensis* at 15 g/L NaCl (Fig. 3a). At 10 g/L NaCl there is evidence of facilitation for *P. pratensis* (Fig. 3a).

The significant two-way interaction between salinity and clipping (Table 3) shows that clipping reduced competition at 0 and 15 g/L NaCl, but not at 5 and 10 g/L NaCl (Fig. 3). At 10 g/L NaCl plants not clipped showed facilitation.

Discussion

We found that the concentration of salt increased plant biomass of *P. pratensis* and *P. nuttalliana* decreased, but, as predicted, there was a greater reduction in the relative biomass of *P. pratensis* compared to *P. nuttalliana*. We found partial support for Grime’s hypothesis as there was a general decline in competition with an increase in salinity for both *P. pratensis* and *P. nuttalliana*. However, competitive performance

Table 2 Results of three-way ANOVA with blocking factor examining the effects of species, salinity, and clipping on root to shoot ratio

Source	Mean squares	Degrees of freedom	F ratio	P value
Block	0.024	5	0.694	0.630
Species	1.493	1	42.356	<0.001
Salinity	0.364	3	10.339	<0.001
Clip	<0.000	1	0.003	0.957
Species × salinity	0.282	3	8.013	<0.001
Species × clip	0.004	1	0.100	0.753
Salinity × clip	0.123	3	3.484	0.021
Species × salinity × clip	0.063	3	1.782	0.159
Error	0.035	65		

Significant ($\alpha < 0.05$) values in bold

of *P. nuttalliana* increased from 10 to 15 g/L NaCl which was unexpected. Clipping of plants also generally reduced competition, but only at 0 and 15 g/L NaCl.

Total biomass

Total biomass for both species when grown alone was greatest at 0 g/L NaCl and declined as salt concentration increased. These findings support our first hypothesis with *P. pratensis* experiencing a greater reduction in relative biomass than *P. nuttalliana* when subjected to the salt treatment. Previous studies also recorded similar plant biomass reduction with increasing concentration of salt, especially of glycophytes (Egan and Ungar 2001), in part due to increased chlorosis (Parrondo et al. 1978), and reduction in water content and Na⁺ ion accumulation (Glenn 1987). Salt concentration decreased the growth rate and biomass of both species but had a greater effect on *P. pratensis*, the glycophytic species. However, there was no difference in *P. nuttalliana* performance between 5, 10, and 15 g/L NaCl which suggests that *P. nuttalliana*, unlike *P. pratensis*, will grow in and tolerate salinity up to 15 g/L NaCl,

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; Parrondo et al. 1978; Kenkel et al. 1991). Our

results support these findings. *P. pratensis* showed a decrease in R:S ratio and *P. nuttalliana* exhibited no significant change when exposed to the salt treatments. Clipping reduced the R:S ratio as shown by Barbour (1978). This may be attributed to plant response to the stress of the NaCl treatment (Grime 2001). Stressed plants grow slower and are generally more vulnerable to damage (clipping) and will likely take longer to recover (Grime 2001). Plants may be unable to allocate energy for shoot re-growth because the salt stress reduced available energy.

Competitive importance

The importance of competition is a relative measure of the effect of competition at a point along the gradient relative to other processes; the intensity of competition is a relative measure of competition at a single point along the gradient (Brooker et al. 2005; Brooker and Kikvidze 2008; Carlyle et al. 2010; Seifan et al. 2010). Only importance of competition can incorporate the role of other processes in describing the impact of competition. Our results support our final third hypothesis that the addition of a salt treatment decreased competitive importance (Grime 1979; Kenkel et al. 1991). A further reduction in C_{imp} occurred with clipping. A similar result was found in a test of the effect of clipping and stress on 11 freshwater wetland species (Fraser and Keddy 2005), with nutrient limitation as the stress agent. It should be noted that respective C_{imp} of the two species differed with salinity. At 0 g/L NaCl, *P. pratensis* had a greater

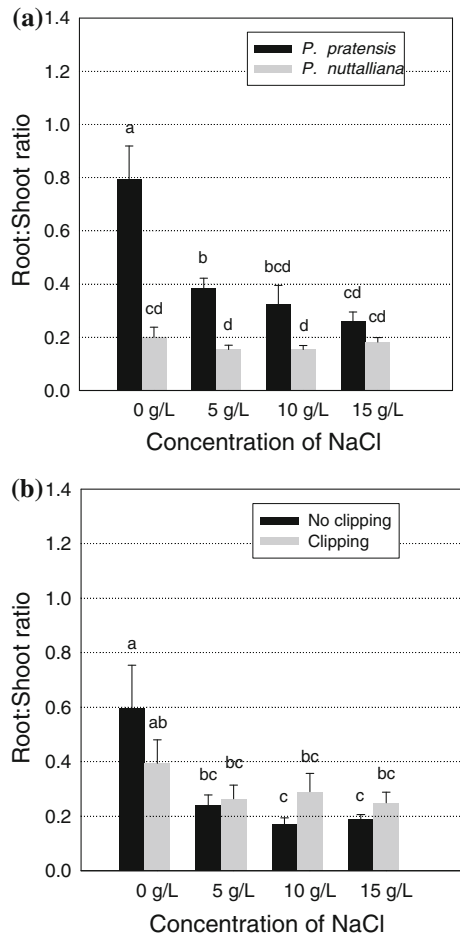


Fig. 2 Root to shoot ratio (± 1 SE) of **a** *Poa pratensis* and *Puccinellia nuttalliana* grown alone at four salinities; and **b** clipped and unclipped plants grown at four salinities. Bars sharing the same letter are not significantly different using Tukey HSD ($P < 0.05$)

competitive importance than *P. nuttalliana*; whereas at 15 g/L NaCl the opposite response occurred. Therefore, at high salinities, not only is *P. pratensis* under severe growth limitations due to salinity, it is being outcompeted by *P. nuttalliana*. Here, we see partial support for Tilman's theory that competitive interactions can also be potentially important in stressful environments (Tilman 1982, 1988). There is also evidence of facilitation, but facilitation only occurs at the 10 g/L NaCl treatment and only for *P. pratensis*. We suggest that facilitation in high saline environments may be an indirect effect of plant growth; such that plants that uptake salts will potentially reduce osmotic potential of the soil solution.

Clipping reduced C_{imp} at 0 and 15 g/L NaCl, but not at 5 and 10 g/L NaCl. Other studies have shown that clipping can reduce the importance of competition (see Carlyle et al. 2010). It is clear that clipping had no response to C_{imp} at 5 and 10 g/L NaCl because competition was not a factor at these salinity levels. In fact, there is an indication that facilitation is operating at 10 g/L NaCl but that clipping reduced facilitation.

A field study by Tarasoff et al. (2009) found that under agricultural, low salinity conditions after 1 year *P. nuttalliana* was more competitive than *P. pratensis*. However, by the end of the second year there had been a switch in competitive performance such that *P. pratensis* was more competitive than *P. nuttalliana* (Tarasoff et al. 2009). Our study suggests that under controlled greenhouse conditions, 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. While C_{imp} of *P. pratensis* seems to be greater than *P. nuttalliana* at 0 g/L NaCl, it is unclear how species interaction might change with as little as a 1 or 2 g/L increase in NaCl.

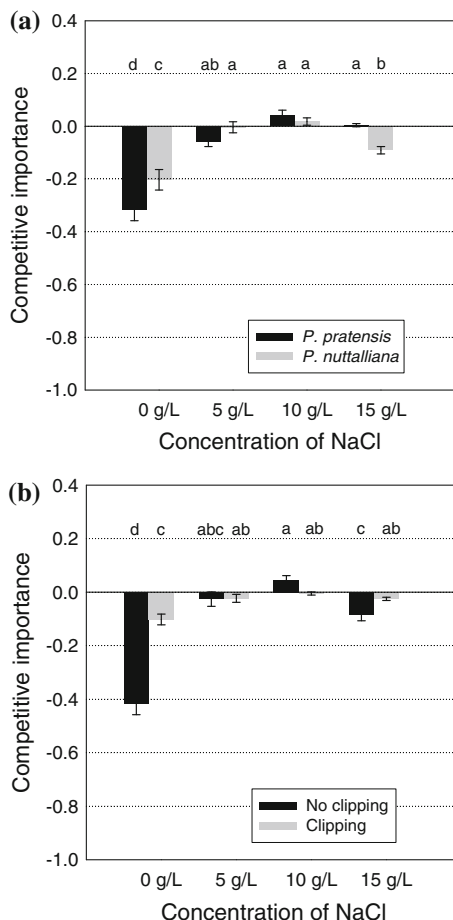
Wilson and Keddy (1988) concluded that diffuse competition was greater at undisturbed, nutrient rich sites and lesser at disturbed, nutrient poor sites, highlighting the relationship between abiotic stress and resource stress. Competition can also be affected by abiotic factors in non-resource stress environments. Fraser and Miletto (2008) found that competition (measured as 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 (Fraser and Miletto 2008). Similar results were found in our study, with the increase in salinity (abiotic stress) the role of competition decreased. In other words, it would seem to be more important for *P. nuttalliana* growing in high salinity to tolerate such abiotic stresses than to resist or respond to plant competition from neighboring species.

Management implications

Cattle on rangelands are dependent on the availability of fresh water, which can often be limiting, especially in semi-arid grassland environments. Not only do cattle require fresh water, abundant forage is often associated with ponds and riparian areas in rangeland

Table 3 Results of three-way ANOVA with blocking factor examining the effects of species, salinity, and clipping on competitive importance

Source	Mean squares	Degrees of freedom	F ratio	P value
Block	0.010	5	12.641	0.215
Species	0.007	1	0.417	0.519
Salinity	0.832	3	48.498	<0.001
Clip	0.271	1	15.819	<0.001
Species × salinity	0.098	3	5.728	0.001
Species × clip	0.013	1	0.735	0.392
Salinity × clip	0.352	3	20.492	<0.001
Species × salinity × clip	0.011	3	0.662	0.576
Error	0.017	109		

Significant ($\alpha < 0.05$) values in bold**Fig. 3** Competitive importance (C_{imp}) (± 1 SE) for **a** *Poa pratensis* and *Puccinellia nuttalliana* at four salinities; and **b** clipped and unclipped plants grown at four salinities. Bars sharing the same letter are not significantly different using Tukey HSD ($P < 0.05$)

(Powell et al. 2000; Jones et al. 2011). Global warming and alterations in precipitation patterns will likely cause a decline in water levels in intermountain wetlands, thus affecting availability of water and potentially increasing salinity of wetland soils. In order to provide forage for cattle around saline ponds, range managers should consider seeding of halophytic species, such as *P. nuttalliana*, that can tolerate saline soils, can out-compete glycophytes under saline conditions, and can be used by cattle for forage.

Conclusions

The concept of an inverse relationship between competition and stress resulting from physiological trade-offs (Grime 1979; Kenkel et al. 1991) was supported by the findings in our study. Under optimal conditions *P. pratensis* had greater biomass 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*. *P. 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 in combination with salt. This idea was further supported by the significant changes in the R:S ratio of *P. pratensis* when subjected to salt and clipping. Clipping was found to be the greatest component influencing overall growth of both species at 0 g/L NaCl. The importance of competition declined for *P. pratensis* at 5, 10, and 15 g/L compared to 0 g/L NaCl. C_{imp} of *P. nuttalliana* was not affected by salinity in a consistent way,

indicating that *P. nuttalliana*'s stress tolerance is a more important plant trait than competition.

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 plant species' growth response to their environment, combined with species by species interactions, will improve planning and management now and for the future.

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