

Final Technical Report

FIA-FSP Project Number: Y091081

Title: How will climate change effect the distribution and competitive performance of *Centaurea maculosa* and *Linaria vulgaris* in south interior grasslands?

Project start date: April 1, 2008

Length of project: 1 year

Abstract

Climate change can affect the range and distribution of species. Due to the very nature of invasive plants (e.g., fast growth and competitively dominant), it is possible that future changes in climate may have a disproportionately larger affect on non-native invasive plants. The purpose of this study was to test the effects of climate change on two invasive grassland plants (spotted knapweed and yellow toadflax) in a field experiment and a greenhouse study. This Final Technical Report comprises two sections: 1. The field experiment ‘A comparative analysis of biotic and abiotic parameters between a native bunchgrass community and two non-native invasive dominated patches, spotted knapweed and yellow toadflax’, and 2. The greenhouse experiment ‘The effects of warming and drought on competitive performance of two non-native invasive and two native grassland plants’.

A comparative analysis of biotic and abiotic parameters between a native bunchgrass community and two non-native invasive dominated patches, spotted knapweed and yellow toadflax

Amber Greenall and Lauchlan H. Fraser

Introduction

Non-native invasive plants are present on millions of acres of grassland in North America causing significant ecological and economic damage (Myers and Bazeley 2003). Grasslands are a particularly threatened and invaded ecosystem. One of the major concerns is a change in the native plant community structure as invasive forbs and annual grasses are replacing the dominant perennial grasses. Meiners *et al.* (2001) found that the impacts of invasive species was linked to their dominance, not simply their presence. Therefore, as we see these invasives become more prevalent the ecological effects should become more significant.

What exactly the effects on the environment will be depends on the species. The effects of spotted knapweed on its abiotic and biotic environment have received the most research of any of the grassland invaders. Despite the striking visual effects of its ability to replace the dominant graminoids very few other changes have been documented. Spotted knapweed invasions have been documented to slightly alter the soil surface which may result in an increase in erosion (Sperber *et al.* 2003), but did not alter the carbon or nitrogen pools (Hook *et al.* 2004). Invaded sites have shown a marked decrease in the arbuscular mycorrhizal fungi diversity and abundance (Mummey and Rillig 2006). This lack of change to the physical environment may be due to the length of time the invasive plants have been on the site, the regional climatic conditions, or land use practices. It is difficult to believe that such a huge shift in the plant community has had no effect on the abiotic environment.

Much work in invasive ecology has focused on which sites get invaded at the global, regional and site level (Myers and Bazeley 2003). What makes a site “invade-able”? In part this has been difficult, especially at the site level, because it is not possible to determine which site is at risk until it has been invaded. Once a site has been invaded the logic is that any variable we measure might in turn have been altered by the invader. As has been demonstrated with knapweed there seems to be little to no effects, and there are no comparative studies on yellow toadflax. Therefore, surveying invaded sites in comparison to native sites may still be an effective technique. These types of surveys also need to be completed for other invasive species as any changes may need to be mitigated as part of a successful restoration plan.

The study presented in this paper looked at spotted knapweed to determine if the have any effects can be detected in its northern range and to determine if grazing has altered or enhanced the effects of knapweed. Yellow toadflax was also included due to the striking lack of research into this species and because of its proximity to and site similarity to spotted knapweed invasions. We compared biotic and abiotic features from inside invaded patches to that of nearby native grassland.

The objectives of this study was to determine if biotic and abiotic parameters differ between sites dominated by invasive species and those dominated by native grassland.

Methods

Site Description:

Sites were located between 100 Mile House and Lac La Hache, British Columbia, Canada. All sites occurred within the Interior-Douglas-fir biogeoclimatic zone (Meidinger and Pojar 1991). Existing spotted knapweed and yellow toadflax patches were located within grazed grasslands. Grassland sites were either dominated by bluebunch wheatgrass or Canada bluegrass

Sampling:

At each site, the GPS location, elevation, slope and aspect were recorded. The length and width of the invasive patch was recorded. In the center of each invasive patch, a 50 cm² plot was established. Within each plot, biomass was clipped by species at ground level, and litter was collected in a separate bag. Four measures of light intensity were taken both above and below the canopy with a photon flux interception at the soil level (measured with a LiCor instrument). Average soil moisture from four locations was taken with a Fieldscout TDR 300 soil moisture probe (Spectrum Technologies Inc.). Three handfuls of topsoil (upper 5 cm) was removed, sealed in an air tight bag, and stored at approximately -4 C until processing for soil moisture and bulk density. Additional soil was removed and processed for carbon (C), nitrogen (N) and hydrogen (H). Three leaves of the present invasive species and three leaves of Canada bluegrass were removed and leaf area was measured using a LI-300A portable area meter (LI-COR).

The same measurements were taken in the native grasslands in a 50 cm² plot located 5 m north of the edge of the invasive patch, excluding those measurements of the invasive species.

Biomass and soil samples were dried in a constant temperature oven DKN812 (Yamato Inc.) for 48 hr at 65 C, they were then weighted on an analytical balance accu-225D (Fisher Scientific). Elemental analyzer samples were dried for 48 hr at 65 C, ground and processed using a CE-440 elemental analyzer (Exeter Analytical Inc.). Differences in variables were tested using one-way ANOVAs in terms of invaded or native status and based on the specific invasive species and the native patches associated with them.

Results

Variables measured in the field were compared considering the site they were collected, a spotted knapweed patch, a yellow toadflax patch or in native grassland. There were no significant differences based on these designations (Table 1). The variables were then compared more generally as invasive, regardless of the species, or native sites and it was found that invasive patches had greater biomass than native patches (Table 1).

Table 1. The variables measured in the field are compared according to the site and status of the area whether invasive (in) or native (out).

Variables	Site			In or Out		
	P-value	F- Stat	Df	P-value	F-stat	Df
Soil Carbon	0.9516	0.1135	3	0.8999	0.0161	1
Soil Hydrogen	0.8503	0.2648	3	0.9911	1.00E-04	1
Soil Nitrogen	0.4011	1.0073	3	0.935	0.0067	1
Elevation	0.9453	0.1233	3	1	5.85E-32	1
Slope	1.8712	0.1519	3	1	1.64E-31	1
Percent Soil Moisture	0.8094	0.322	3	0.8409	0.0409	1
Light Above the Canopy	0.3289	1.155	3	0.4803	0.5004	1
Light Below the Canopy	0.1777	1.6608	3	0.9366	0.0063	1
Difference in Shading	0.1578	1.7566	3	0.2402	1.39	1
Leaf area of Canada Bluegrass 1	0.3927	1.0258	3	0.3949	0.7405	1
Leaf area of Canada Bluegrass 2	0.779	0.3646	3	0.8499	0.0363	1
Leaf area of Canada Bluegrass 3	0.5484	0.7169	3	0.2451	1.3938	1
Total Biomass	0.1219	2.0666	3	0.01688	6.247	1
Species Richness	0.5876	0.6509	3	0.4658	0.5429	1

Discussion

None of the measured biotic and abiotic parameters differed between invaded and native sites, except for a significant change in biomass. The change in biomass was to be expected as these were all grazed sites and both of the invasives species were not palatable to cattle. Spotted knapweed and yellow toadflax, at its northern range and when interacting with commercial grazing, did not seem to have any measurable effect on soil nutrient levels, however their presence reduced the potential for forage grass growth. Either the effects to soil carbon and nitrogen are beyond the time scale of invasion in this area or these species do not seem to alter these soil parameters. Future investigations should investigate below ground interactions; for example, the differing rooting structures of the dominant grasses compared to spotted knapweed and yellow toadflax, and relate rooting structure to potential changes in soil moisture retention. Perhaps it was because there was no significant reduction in species richness that the other members of the community may have mitigated any differences? This study falls in line with other studies of spotted knapweed that have failed to find any significant changes (Sperber *et al.* 2003, Hook *et al.* 2004). Our study also extends these findings to yellow toadflax. Yellow toadflax has a different rooting structure and morphology compared to spotted knapweed and bluebunch wheatgrass but long term invasions do not seem to result in any significant changes in the biotic or abiotic environment. There are no published studies of yellow toadflax with which to compare our results.

In terms of informing management, an important result of this study is that there was no measured environmental difference between yellow toadflax sites and spotted knapweed sites. This suggests that spotted knapweed and yellow toadflax have similar growth requirements. What is unknown is whether they can coexist or if one will be the dominant competitor. In addition, these results show that when engaging in restoration of these sites the soil moisture and

soil carbon and nitrogen does not appear to be altered by these two invasives. It would still be important to measure the pH of the soil as that was one potentially important variable that was not considered in this study.

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The effects of warming and drought on competitive performance of two non-native invasive and two native grassland plants

Amber Greenall and Lauchlan H. Fraser

Introduction

Global climate change has serious implications for the state and function of ecosystems (IPCC 2007). Average seasonal temperatures in the southern interior of British Columbia (BC), Canada are expected to increase by 2 to 3 C within the next fifty years (PCIC 2008). The predicted changes in precipitation are less reliable but, in general, southwestern BC is predicted to have a slight increase in winter precipitation and a significant decrease (10-20%) in summer precipitation (Barrow and Maxwell 2004). These changes in climate will likely influence ecosystem structure and function. Already there has been measured plant species range shifts attributed to climate change, with movement to greater northern latitude and higher elevation (Parmesan and Yohe 2003). Therefore, it will be important to understand how relationships between species might change as a result of climate change in order to enable mitigation for the protection of threatened species and preempt the possible advancement of undesirable species.

Competition is a major factor that controls plant communities, and yet there is still debate and lack of clarity on the relative role of competition across environmental gradients (Grime 1977, Tilman 1980, Keddy *et. al.* 2001). There are two dominant plant competition theories: the CSR theory (Grime 1977) and the R* theory (Tilman 1980). CSR theory suggests that the intensity of competition increases with an increase in the productivity of the environment (Grime 1977) whereas R* theory poses no change in overall competition but rather a shift from below ground root competition for mineral nutrients at low productivity to above ground shoot competition for light at high productivity (Tilman 1980). More recently Goldberg (1990) has suggested that the dispute is a result of differing definitions of competition and that the R* theory is based on the intensity of competition and the CSR theory is based on the importance of competition. Understanding the role of competition is particularly important as we attempt to predict how climate change may influence biological interactions.

One of the characteristics of non native invasive species is that they can be competitively dominant. With the globalization of the world economy there has been a mass movement of both plant and animal species. While many remain localized, have not spread, and do not appear to pose any threats to native environments, a few have proliferated in their new environments causing serious economic and environmental damage (Myers and Bazeley 2003). In order to effectively manage these invasive species we need to understand the effects of increased temperature and altered precipitation on their growth response and their competitive performance. It has been speculated that some species will not be able to advance their geographic range at the same rate as climate change. It is also predicted that invasive species will have an advantage because they are typically good dispersers (Dukes and Mooney 1999, Simberloff 2000). In which case, it will be important to identify those non native invasive species that respond positively to climate change and will thus cause the most economic and environmental damage and focus our efforts on controlling them.

Controlled plant experiments involving pair-wise species combinations have been used extensively in the study of the role of competition (Keddy 2001; Weigelt and Jolliffe 2003). The

study presented in this paper compared two dominant native grasses with two invasive grassland forbs under two temperature and two water regimes in a greenhouse pair-wise competition trial. The results are discussed in terms of the intensity and importance of competition to test the differing assumptions of Tilman and Grime's competition theories.

The objectives of this study were to determine:

1. Whether alterations in water and temperature affect competitive relationships.
2. Whether the two selected invasive forbs were better competitors than the two native grasses.
3. Whether the two selected invasive forbs have a greater growth response and are better competitors than the two native grasses as a result of the alternations in water and temperature.

Methods

Experimental Design

Four species were tested. Two were invasive forbs (spotted knapweed [*Centaurea stoebe*] and yellow toadflax [*Linaria vulgaris*] and two native grasses (bluebunch wheatgrass [*Pseudoroegneria spicata*] and Canada bluegrass [*Poa compressa*]). Seeds of each species were collected in fall 2008. Seeds were taken from multiple individuals at multiple sites and mixed to ensure a wide genetic range. Seeds were stored at ~ 2 C for approximately three months. The seeds were germinated on a medium of sand and distilled water. Individuals with 5 – 15 mm of root and fully elongated cotyledons were potted. Individuals in the same pot were transplanted on the same day. The size of the pots were 12 cm high and 8 cm diameter.

The experiment ran for twelve weeks in the controlled environment of the Research Greenhouse at Thompson Rivers University, Kamloops, British Columbia, Canada. Plants received 8 hr of darkness and 16 hr of light with 65% day humidity and 80% night humidity. All pots received a weekly dose of 250 ml of Rorison's solution (Hendry and Grime 1993).

The experimental design included a pair wise competition trial and a two temperature by two water environmental treatment. All four species were grown alone (4) and grown in pair wise combination (4 x 4, without replacement) for a total of fourteen plant combinations. Each plant combination was grown at the four different environmental treatment combinations for a total of 80 individual treatment pots. Ten replicates were done for a total of 560 pots. The greenhouse contained four independent compartments – two were at normal temperature (25 C – 22 C day-night) and two were at high temperature (27 C – 25 C day-night). The 'normal' treatment reflects current average growing temperatures for the southern interior of BC, and the high temperature was used to simulate the predicted increase in summer temperatures due to climate change. Five replicates were put in each compartment and the pots were randomly placed within a configuration of 7 rows and 20 columns on a bench.

Each pot received either a high water or low water treatment. The low water treatment consisted solely of the 250 ml weekly addition of Rorison's solution. The high water treatment received the weekly full Rorison's solution and an additional 100 ml of distilled water half way through the week.

Data Collection

Soil moisture probes ECH2O – 10 Dielectric Aquameter (Decagon Devices Inc.) were installed in 42 of the pots in both the high and control temperature pots for selected species combinations. The number of probes available was too low to provide statistically testable measurements. Percent soil moisture was recorded every thirty minutes for ten weeks using U12 Outdoor/Industrial data loggers (HOBO). The measurements were recorded for the following species combinations: knapweed and toadflax, knapweed and bluebunch, knapweed and Canada bluegrass, and toadflax and Canada bluegrass.

All individuals were harvested, separated to roots and shoots, oven-dried at 65 C for a minimum of 48 hr using a constant temperature oven (Yamato DKN812) and weighed using an analytical balance (Fisher-Scientific accu-225D).

Analysis

Statistical analyses were conducted in R (R development core team 2008). A 3-way ANOVA (species by temperature by soil moisture) was applied to test the main and interacting effects on plant biomass and root:shoot ratios. Competitive response, competitive effect, competitive importance and competitive intensity was calculated for all combination of interacting species under the different temperature and water treatments. ANOVA's will test for any significant differences within these indices as a result of the temperature and water treatments. The formulas for each of these indices is listed in Table 1.

Table 1. The formulas and terms for the competitive indices calculated (Weigelt and Jolliffe 2003).

Competition Indices	Formula	Variables
Competitive Effect	$C_{eff} = (P_{alone} - P_{comp}) / P_{comp}$	P_{alone} = Total biomass of the plant grown alone P_{comp} = Total biomass of the plant grown in competition
Competitive Response	$C_{res} = P_{comp} / P_{alone}$	Same terms as above
Competitive Importance	$C_{imp} = (P_{comp} - P_{alone}) / (Max P_{alone} - y)$	Same terms as above $Max P_{alone}$ = The largest total biomass of the species in the specified competitive interaction regardless of climatic treatment y = The smaller of either P_{alone} or P_{comp}
Competitive Intensity	$C_{int} = (P_{comp} / P_{alone}) / x$	Same terms as above x = The larger of either P_{alone} or P_{comp}

Results & Discussion

General Results

Mean total biomass for each species was tested with an ANOVA to determine the difference due to competition not considering the climatic treatments (Figure 1). Competition significantly reduced the mean total biomass for all species except yellow toadflax.

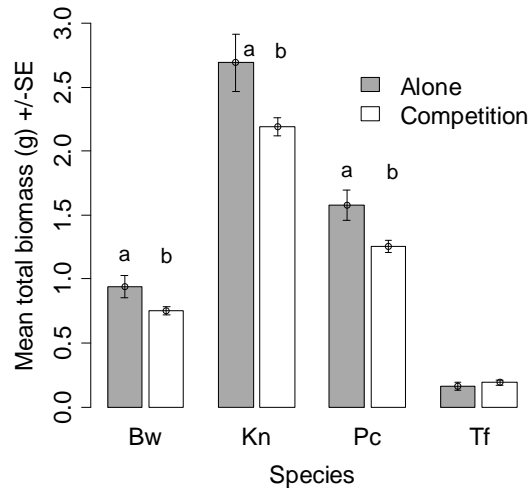


Figure 1. Mean total biomass (g) +/- SE by species in competition or grown alone. Letters designate differences at the $P=0.05$ level as determined by a Tukey test.

Mean total biomass of plants grown singly in pots was compared using an ANOVA across the climatic treatments. Bars are arranged from left to right in terms of a presumed increase in stress. All graphs displaying the climatic treatments are presented in the same order of low to high temperature and alternating high and low water treatments. Responses to the climatic treatments were species specific. Bluebunch wheatgrass was unaffected by the change in water but showed a significant reduction in biomass as a result of the increase in temperature. Alternatly, spotted knapweed responded significantly to the water treatments with an increase in biomass in the high water treatments. Similarly, Canada bluegrass increased in biomass when experiencing drought at the cool temperature but did not respond similarly at the high temperature.

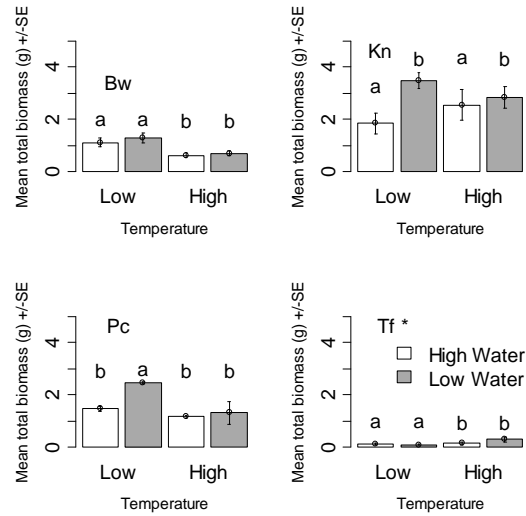


Figure 2. Mean total biomass (g) +/-SE for each species grown alone in each climatic treatment combination. Dark shading indicates low water treatments and white indicates high water treatment. Letters represent significant differences at the P=0.05 level as determined by a Tukey test.

The same comparison of mean total biomass across climatic treatments using an ANOVA was done for the individuals grown in competition (Figure 3). Similar trends between Figure 2 and Figure 3 can be seen for each species except either reduced or non significant level. Bluebunch wheatgrass still show significant reduction in biomass in the high temperature treatment but the difference is lessened. For spotted knapweed the trend shown in the alone biomass is still present but there is no longer a significant difference between the treatments. Canada bluegrass results changed slightly, when grown in competition at the high temperature is significantly lower in biomass then those grown at the low temperature, and the change in water had not effect. Yellow toadflax grown in competition was reduced to only achieving a significant increase in biomass in the high temperature, low water treatment.

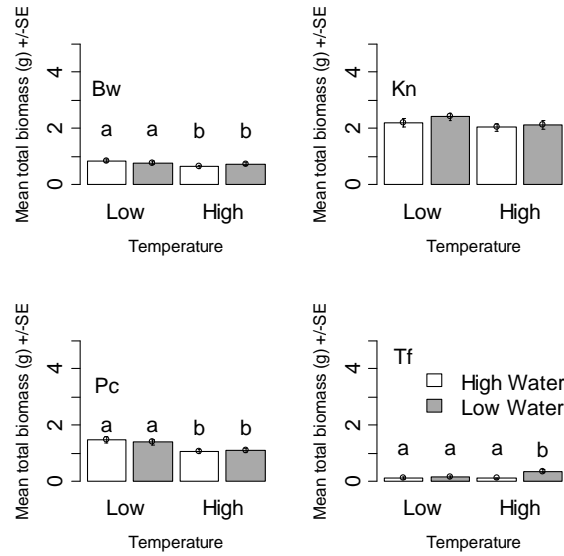


Figure 3. Mean total biomass (g) +/-SE for each species grown in competition for each climatic treatment combination. Dark shading indicates low water treatments and white indicates high water treatment. Letters represent significant differences at the P=0.05 level as determined by a Tukey test.

Mean root:shoot ratio was compared using an ANOVA (Figure 4). Only bluebunch wheatgrass showed a change in root:shoot ratio in response to competition. In competition bluebunch wheatgrass increased the biomass allocated to its roots. Spotted knapweed and Canada bluegrass showed a similar but non significant trend. Biomass allocation by yellow toadflax when grown alone was considerably more variable but not different from the biomass allocation when grown in competition.

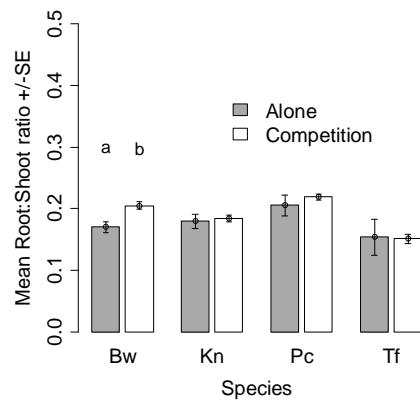


Figure 4. Mean root:shoot ratio (+/-SE) by species in competition or grown alone. One was added to all values and then the log was taken to produce positive normalized values. Letters designate differences at the P=0.05 level as determined by a Tukey test.

Mean root:shoot ratio of individuals in competition, using all species combinations, was compared across climatic treatments with an ANOVA (Figure 5). Bluebunch wheatgrass showed no response to the climatic treatments. Only spotted knapweed showed any significant changes in root:shoot ratios. There was a significant reduction in biomass allocated to roots as a result of the increase in temperature. Canada bluegrass showed a slight decrease in the root:shoot ratio with increasingly stressful environments. Yellow toadflax had more variable results but showed a slight decrease when at both low water treatments; as well the results were less variable at the low water treatments.

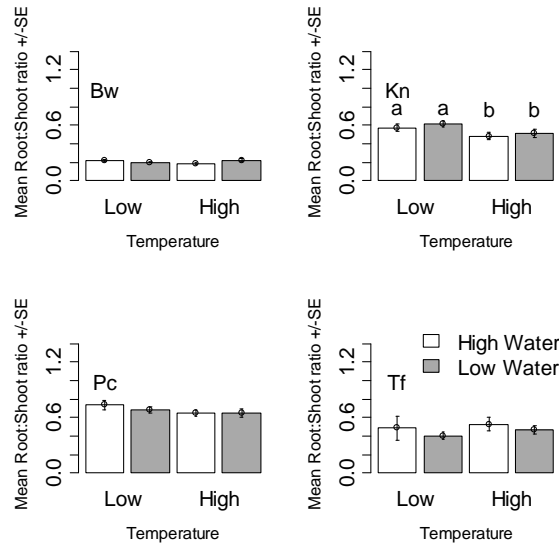


Figure 5. Mean root : shoot ratio +/-SE for each species grown in competition for each climatic treatment combination. One was added to each value and then the log was taken to produce positive normalized values. Dark shading indicates low water treatments and white indicates high water treatment. Letters represent significant differences at the P=0.05 level as determined by a Tukey test.

Competitive Intensity

Competitive intensity (Brooker 2005) was calculated as $C_{int} = (P_{comp} - P_{alone}) / x$. P_{comp} is the total biomass of target, P_{alone} is the average total biomass of that species grown without a neighbor, x is the greater of either P_{comp} or P_{alone} . Competitive intensity is defined as “The impact of competition irrespective of the impact of other environmental factors” (Brooker 2005). The following graphs are mean competitive intensity with each graph representing one species as the target paired with the other three species and in intra-specific competition. The treatments are presented as before with low temperature to high temperature and alternating high and low water treatments. The competitive intensity values were compared across climatic treatments with an ANOVA. The first comparison has bluebunch wheatgrass as the target species (Figure 6). While the results are neighbor specific, the intensity of competition decreases with increasing stress. The first two bars can be considered as current climatic conditions under a wet year (first white bar) and a dry year (first grey bar). Bluebunch wheatgrass in intra-specific competition shows a slight increase in intensity under drought conditions, but under the high temperature treatment competitive intensity become negligible and

under the most stressful condition the presence of a neighbor is actually an asset. When spotted knapweed was the neighbor there were no significant differences as a result of the climatic treatments. But it presents a similar trend, with an increase in intensity under ambient drought conditions and a lessening of intensity with increasing stress but never becomes positive. Canada bluegrass as a neighbor showed exactly the same pattern as spotted knapweed but with a significant difference as a result of the increase in temperature. Yellow toadflax produced variable non-significant results. There was the same increase in intensity with the low temperature drought conditions but the high temperature high water treatment had positive intensity values, which returned to slightly negative intensity values under high temperature, low water.

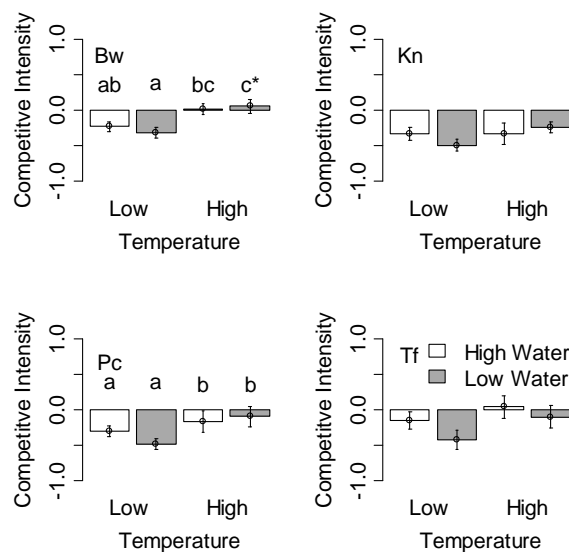


Figure 6. Mean competitive intensity \pm SE of Bw in competition with each species across the climatic treatments. Dark shading indicates low water treatments and white indicates high water treatment.

The second comparison is that with spotted knapweed as the target species (Figure 7). Under the low temperature, high water treatment all competitors, except intra-specific competition, produced a significantly positive intensity value. When bluebunch wheatgrass was the neighbor there was a negative intensity value under the low temperature drought condition, this significantly reduced when the temperature increased but was no significantly different from the high temperature low water treatment. With intra-specific competition the intensity values were always negative. Under ambient drought conditions the intensity values were significantly more negative than under ambient high water conditions. The high temperature treatments failed to produce significantly different values than those of the low temperature treatments. Canada bluegrass again had a negative intensity value under ambient temperature drought conditions. The low water treatments produced the most negative values regardless of the temperature treatment with the high temperature low water treatment producing the most negative value. The intensity of competition lessened under the two high water treatments. Spotted knapweed had

the largest positive intensity value when competing with yellow toadflax under the low temperature high water treatment. All other treatments produced a small negative intensity value.

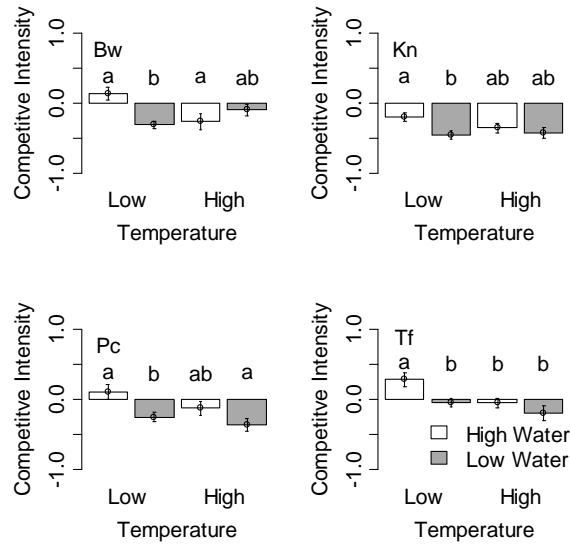


Figure 7. Mean competitive intensity +/-SE of Kn in competition with each species across the climatic treatments. Dark shading indicates low water treatments and white indicates high water treatment.

The third comparison is with Canada bluegrass as the target species (Figure 8). Canada bluegrass in competition with bluebunch wheatgrass did not significantly change intensity values across the climatic treatments, but had its largest negative values under the low temperature low water treatment. When spotted knapweed was the neighbor the trend was similar with a significantly more negative intensity value under the low temperature low water treatment. The two high water treatments were not significantly different, nor were the two low water treatments or the two high temperature treatments. In intra-specific competition Canada bluegrass showed the same trends as the spotted knapweed graph but with smaller intensity values. Yellow toadflax as a neighbor only produced competitive intensity values under the two drought conditions.

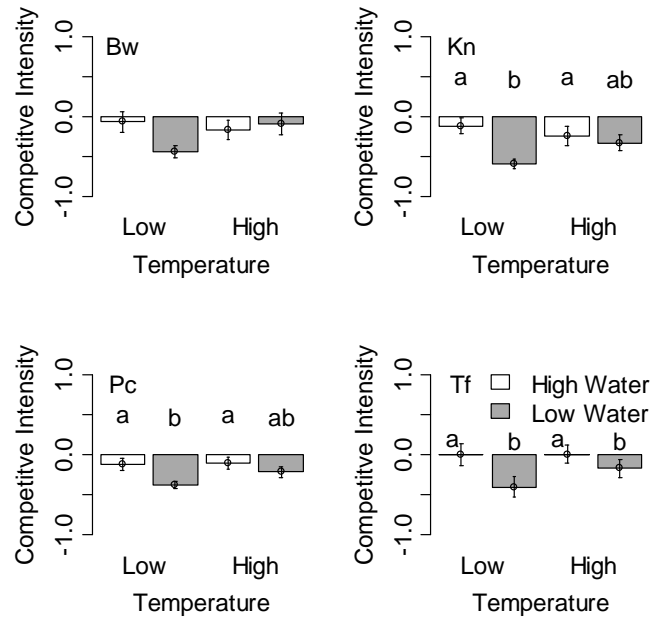


Figure 8. Mean competitive intensity +/-SE of Pc in competition with each species across the climatic treatments. Dark shading indicates low water treatments and white indicates high water treatment.

The final comparison of competitive intensity is that of yellow toadflax as the target species (Figure 9). Due to the highly variable nature of yellow toadflax growth, the competitive intensity values are also highly variable. With bluebunch wheatgrass as a neighbor none of the intensity values were significantly different across the climatic treatments, with the largest negative value in the low temperature high water treatment. When competing with spotted knapweed the intensity values became significantly more negative with the increase in temperature but did not vary with the water treatments. The same pattern is seen with Canada bluegrass; competitive intensity values differ significantly across the temperature treatments but do not differ with the water treatments. Under intra-specific competition insensitve values were more negative in the two high water treatments, and smaller in the two high water treatments. The high temperature low water treatment was significantly smaller then either of the high water treatments.

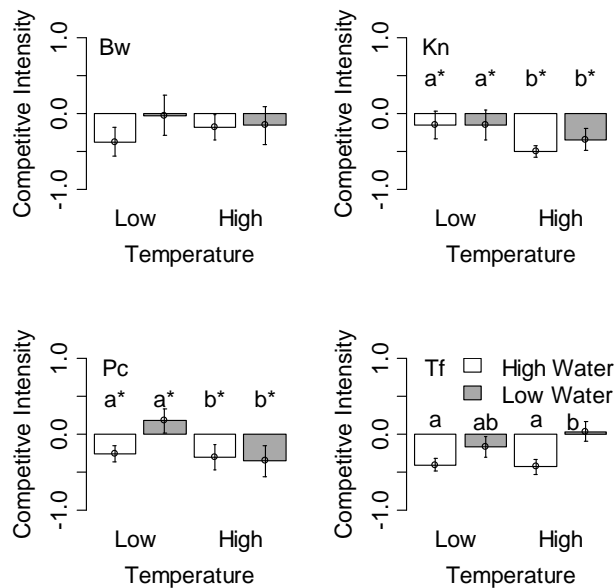


Figure 9. Mean competitive intensity +/-SE of Tf in competition with each species across the climatic treatments. Dark shading indicates low water treatments and white indicates high water treatment. *Signifies differences at 10%

Competitive Importance

Competitive importance is defined as “The impact of competition relative to the impact of all the other factors in the environment on plant success” (Brooker 2005). Here competitive importance is calculated as $C_{imp} = (P_{comp} - P_{alone}) / (MaxP_{alone} - y)$. Where P_{alone} is the mean total biomass of target species grown without a neighbor, P_{comp} is the total biomass of a target grown with a neighbor, $MaxP_{alone}$ is the largest value of P_{alone} across the climatic treatments, y is the smaller of either P_{alone} or P_{comp} . The graphs are presented in the same order that they were for the competitive intensity results section with each graph representing one target species and the bars presented as low then high temperature treatments with alternating high and low water treatments (Fig. 10). The first comparison of competitive importance is with bluebunch wheatgrass as the target species. Bluebunch wheatgrass in intra-specific competition showed a significant change as a result of the temperature increase at the low temperature treatments the importance was negative and at the high temperature treatments the importance values were positive. With spotted knapweed the same trend can be seen but with reduced significance and no positive importance values. Canada bluegrass also shows the trend of a change as a result of the temperature treatments, which smaller competitive importance values in the higher temperatures. Yellow toadflax as a neighbor reverses this trend and displays significant differences based on the water treatments.

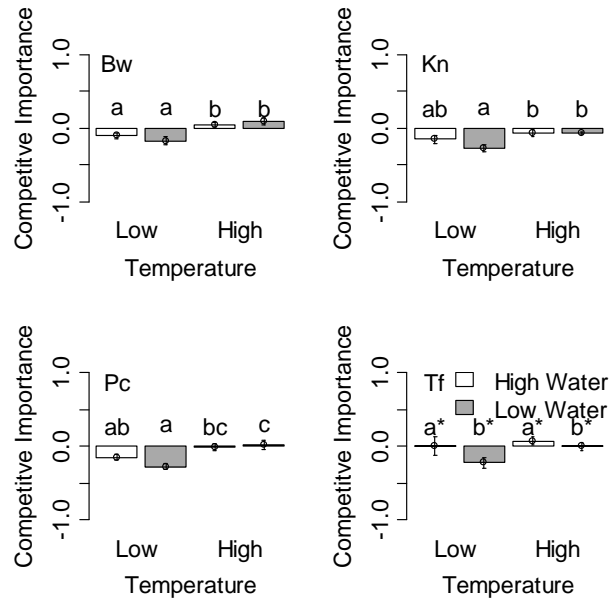


Figure 10. Mean competitive importance \pm SE of Bw in competition with each species across the climatic treatments. Dark shading indicates low water treatments and white indicates high water treatment. *Signifies differences at 10%.

The second set of graphs is that of spotted knapweed as the target (Figure 11). Overall, it appears that the changes in importance values are dominated by the water treatments. When competing with bluebunch wheatgrass positive importance values occur with high water treatments and negative values with low water treatments although not always significantly different. In intra-specific competition there is a similar pattern with low water treatments having more negative importance values, significantly so for the low temperature treatment. Again with Canada bluegrass as a neighbor the low temperature low water treatment is significantly more negative than the others with the high temperature low water treatment also slightly negative and the high water treatments being positive. With yellow toadflax as a competitor the pattern changes, showing a slow reduction across the climatic treatments but resulting in only the change in temperature being significantly different at the 10% level.

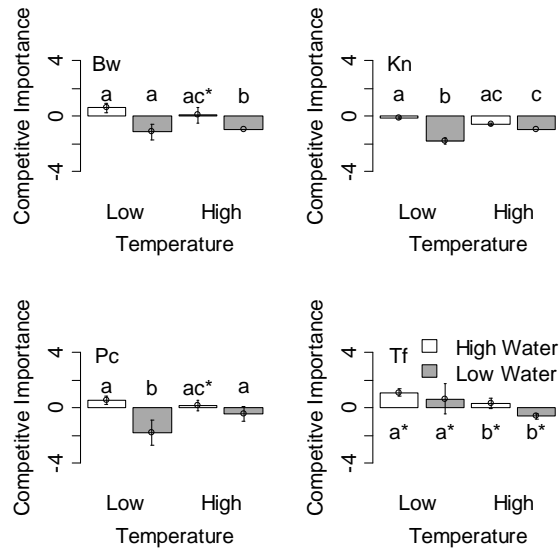


Figure 11. Mean competitive importance of Kn \pm SE in competition with each species across the climatic treatments. Dark shading indicates low water treatments and white indicates high water treatment. *Signifies differences at 10%.

The third comparison is with Canada bluegrass as the target species. When competing with bluebunch wheatgrass, spotted knapweed or itself the low water low temperature treatment produced a significant negative importance value, while all other treatments remained close to zero. Yellow toadflax as a neighbor produced similar but non significant results.

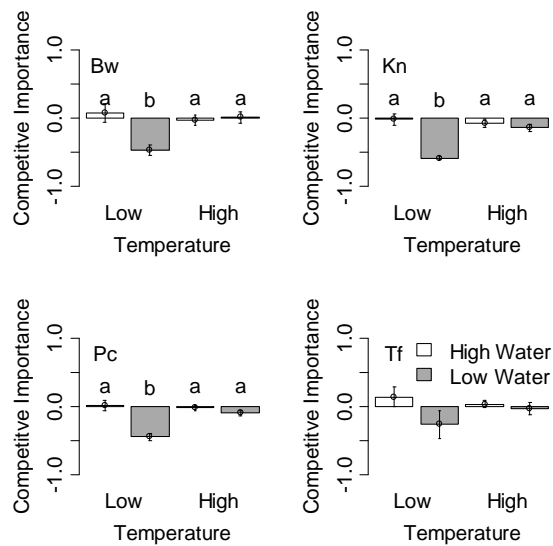


Figure 12. Mean competitive importance of Pc \pm SE in competition with each species across the climatic treatments. Dark shading indicates low water treatments and white indicates high water treatment.

The final comparison of competitive importance has yellow toadflax as the target species (Figure 13). With bluebunch wheatgrass as a neighbor there were no trends in the importance values. Spotted knapweed caused a decrease in importance values across the climatic treatments, resulting in a significant difference in temperature treatments. There were also no trends with the Canada bluegrass competition pairings. Yellow toadflax in intra-specific competition had a significant positive importance value at the high temperature low water treatment, while all others remained close to zero.

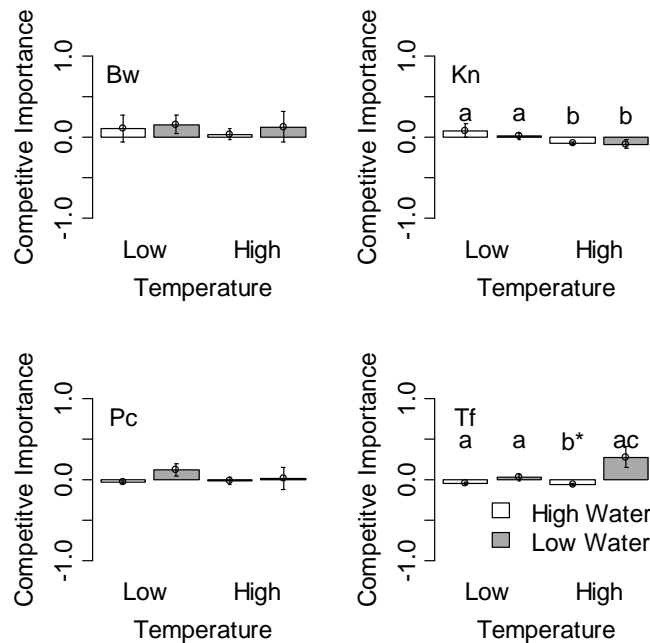


Figure 13. Competitive importance of Tf in competition with each species across the climatic treatments. Dark shading indicates low water treatments and white indicates high water treatment. *Signifies differences at 10%.

Management Implications

It is important to keep in mind that there are limitations to greenhouse trials. To apply these results for management we need to use them as a basis for developing more detailed hypotheses that can be tested in the field. There was a significant reduction in biomass of all four species as a result of the increase in temperature. While the growth response of invasive and natives were both reduced by the increase in temperature the invasives were better competitors than the natives. However, there was a decrease in the importance of competition with an increase in temperature, suggesting that competitive interactions may be affected by future climate change. If climate change creates stressful environments, this might lead to a reduction in the role of competition. Rather, species that are better able to tolerate these climate-induced stressful site conditions will be at an advantage. Field-based climate manipulations are needed to test these hypotheses.

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